

FLUCTUATION OF NON-STRUCTURAL CARBOHYDRATES IN THE  
STEM AND EARS OF MAIZE (ZEA MAYS (L.)) DURING GRAIN  
FILL AS INFLUENCED BY WATER STRESS

by

PAUL EDWARD SHANAHAN

(B.Sc. Agric.)

Submitted in partial fulfilment of the  
requirements for the degree of  
DOCTOR OF PHILOSOPHY IN AGRICULTURE  
in the  
Department of Agronomy  
Faculty of Agriculture  
University of Natal  
Pietermaritzburg

August 1991

## TABLE OF CONTENTS

CHAPTER	PAGE
<b>VOLUME I</b>	
TABLE OF CONTENTS	(i)
DECLARATION	(viii)
ACKNOWLEDGEMENTS	(ix)
LIST OF ABBREVIATIONS	(xii)
ABSTRACT	(xiii)
INTRODUCTION	(xvi)
1 LITERATURE REVIEW	1
1.1 Introduction	1
1.2 Occurrence and biochemistry of the predominant non-structural carbohydrates in maize	2
1.2.1 Monosaccharides - glucose and fructose	2
1.2.1.1 Hexose phosphates	4
1.2.1.2 Hexose nucleotides	10
1.2.2 Sucrose	12
1.2.2.1 Synthesis of sucrose	13
1.2.2.2 Sucrose utilization	17
1.2.3 Starch	19
1.2.3.1 Structure, occurrence and location	19
1.2.3.2 Starch synthesis and pattern of granule formation	23
1.2.3.3 Starch degradation	27
1.3 Carbohydrate partitioning as influenced by translocation and source-sink relations	30
1.3.1 Translocation	31
1.3.1.1 Phloem loading	31
1.3.1.2 Phloem transport or inter-organ	31

transport	37
1.3.1.3 Phloem unloading	38
1.3.2 Regulation of the partitioning of translocated photosynthate	40
1.3.2.1 Source strength and export of photosynthate	42
1.3.2.2 Regulation during translocation	47
1.3.2.3 Sink strength and import of photosynthate	48
1.3.2.4 Hormonal regulation of source sink interactions	54
1.3.2.5 Environmental effects on photosynthate partitioning	58
1.4 Non-structural carbohydrate partitioning in maize grown under favourable environmental conditions	63
1.4.1 Growth and development of maize	63
1.4.2 Carbohydrate partitioning during the vegetative phase	66
1.4.3 Carbohydrate partitioning during the reproductive phase	68
1.4.3.1 Leaves and sheaths	69
1.4.3.2 Stem	72
1.4.3.3 Carbohydrate partitioning in other organs	81
1.5 Manipulated source-sink relations	83
1.5.1 Leaf tissue removal	84
1.5.2 The effects of shade	87
1.5.3 Partial or complete prevention of fertilization	90
1.5.4 Ear tissue removal	92

1.6	Non-structural carbohydrate partitioning in maize grown under conditions of water deficits	95
1.6.1	Vegetative growth phase	95
1.6.2	Reproductive growth phase	97
1.6.2.1	The flowering period	97
1.6.2.2	The period of grain fill	101
1.6.3	Selection of genotypes tolerant to water deficits	105
2	1985/86 MAIZE HYBRID RAIN GROWN FIELD TRIAL	109
2.1	Introduction	109
2.2	Methods and materials	111
2.2.1	Field trial cultural and sampling procedures	111
2.2.2	Non-structural carbohydrate analysis	115
2.2.3	Statistical analysis and presentation of data	116
2.2.4	Climatic conditions during grain fill	121
2.3	Results and discussion	123
2.3.1	Non-structural carbohydrate analysis of stem segments	124
2.3.1.1	Reducing sugars composition	124
2.3.1.2	Reducing sugars content	128
2.3.1.3	Sucrose composition	137
2.3.1.4	Sucrose content	143
2.3.1.5	Starch composition	159
2.3.1.6	Starch content	162
2.3.1.7	Total non-structural carbohydrate composition	169
2.3.1.8	Total non-structural carbohydrate content, residual content and segment	

dry mass	176
2.3.2 Non-structural carbohydrate analysis of whole stem	201
2.3.2.1 Reducing sugars composition	201
2.3.2.2 Reducing sugars content	202
2.3.2.3 Sucrose composition	206
2.3.2.4 Sucrose content	208
2.3.2.5 Starch composition	211
2.3.2.6 Starch content	213
2.3.2.7 Total non-structural carbohydrate composition	215
2.3.2.8 Total non-structural carbohydrate content, residual content and whole stem dry mass	218
2.3.3 Non-structural carbohydrate analysis of the cob	227
2.3.3.1 Reducing sugars composition	227
2.3.3.2 Reducing sugars content	230
2.3.3.3 Sucrose composition	232
2.3.3.4 Sucrose content	233
2.3.3.5 Starch composition	238
2.3.3.6 Starch content	239
2.3.3.7 Total non-structural carbohydrate composition	242
2.3.3.8 Total non-structural carbohydrate content, residual content and cob dry mass	245
2.3.4 Non-structural carbohydrate analysis of the grain	249
2.3.4.1 Reducing sugars composition	249

2.3.4.2	Reducing sugars content	251
2.3.4.3	Sucrose composition	255
2.3.4.4	Sucrose content	256
2.3.4.5	Starch composition	261
2.3.4.6	Starch content	262
2.3.4.7	Total non-structural carbohydrate composition	264
2.3.4.8	Total non-structural carbohydrate content, residual content and grain dry mass	267
2.3.5	Leaf area index	272
2.3.6	Yield and yield components	274
3	1986/87 MAIZE SINGLE CROSS HYBRID RAIN-OUT SHELTER TRIAL	277
3.1	Introduction	277
3.2	Methods and materials	278
3.3	Results and discussion	284
3.3.1	Leaf water potential	284
3.3.2	Leaf area index	288
3.3.3	Non-structural carbohydrate analysis for stem segments A1 and B1	293
3.3.3.1	Reducing sugars composition	293
3.3.3.2	Reducing sugars content	301
3.3.3.3	Sucrose composition	309
3.3.3.4	Sucrose content	315
3.3.3.5	Starch composition	326
3.3.3.6	Starch content	333
3.3.3.7	Total non-structural carbohydrate composition and residual composition	341
3.3.3.8	Total non-structural carbohydrate	

	content, residual content and stem segment dry mass	348
3.3.4	Yield and yield components	373

## VOLUME II

4	1988/89 MAIZE SINGLE CROSS HYBRID <sup>14</sup> C-LABELLING STUDY	379
4.1	Introduction	379
4.2	Methods and materials	382
4.3	Results and discussion	402
4.3.1	Leaf water potential	402
4.3.2	Leaf area	408
4.3.3	Non-structural carbohydrate analysis	411
4.3.3.1	Reducing sugars composition	411
4.3.3.2	Reducing sugars content	415
4.3.3.3	Sucrose composition	421
4.3.3.4	Sucrose content	426
4.3.3.5	Starch composition	436
4.3.3.6	Starch content	440
4.3.3.7	Total non-structural carbohydrate composition	448
4.3.3.8	Total non-structural carbohydrate content, residual content and dry mass	452
4.3.4	Radioactivity analysis of plant segments	464
4.3.4.1	Specific radioactivity	464
4.3.4.2	Total radioactivity	499
4.3.4.3	Segment total radioactivity as a % of whole plant total radioactivity	538
4.3.4.4	Total radioactivity of the stem segments as a % of whole stem total radioactivity	558

4.3.5	Radioactivity analysis of whole stem	569
4.3.5.1	Specific radioactivity	569
4.3.5.2	Total radioactivity	582
4.3.5.3	Whole stem total radioactivity as a % of whole plant total radioactivity	594
4.3.6	Radioactivity analysis of whole shoot	600
4.3.6.1	Specific radioactivity	600
4.3.6.2	Total Radioactivity	614
4.3.6.3	Whole shoot total radioactivity as a % of whole plant total radioactivity	629
4.3.6.4	Ratio of total radioactivity in the grain to total radioactivity in the shoot	634
4.3.7	Radioactivity analysis of whole plant	638
4.3.7.1	Specific radioactivity	638
4.3.7.2	Total radioactivity	652
4.3.8	Radioactivity associated with total sugars and starch	668
4.3.9	Radioactivity associated with glucose, fructose and sucrose	706
4.3.10	Yield and yield components	711
5	REVIEW OF RESULTS AND FINAL CONCLUSIONS	715
	REFERENCES	754
	INDEX OF APPENDICES	769
	APPENDICES	778

## CHAPTER 4

### 1988/89 MAIZE SINGLE CROSS HYBRID $^{14}\text{C}$ -LABELLING STUDY

#### 4.1 Introduction

After synthesis in the leaves of the maize plant, photosynthate translocated out of the leaves may pass directly through the stem to the primary ear, or it may accumulate in the stem tissue for a period of anything from a few minutes or hours to a few days or weeks (Franceschi, 1986) before being utilized by the various sinks in the plant including the grain. Thus it is not entirely correct to term all non-structural carbohydrate in the stem as 'stored' photosynthate when there is continual addition to, and depletion of, the pools of non-structural carbohydrates in the stem. It is clear from the previous experiments discussed that non-structural carbohydrates do accumulate in the stem tissue of maize hybrids during grain fill and the levels of these non-structural carbohydrates fluctuate considerably during the course of grain fill. Under water stress conditions the depletion of non-structural carbohydrates in the stem is apparently enhanced to supplement the decline in the supply of current photosynthate to various sinks, particularly the grain. In order to determine the time course of the mobilization of labile photosynthate from the vegetative organs to the grain in maize under the influence of water stress a single cross maize hybrid was grown in pots and entire plants were exposed to  $^{14}\text{CO}_2$  at selected intervals during grain fill. The extent to which the assimilation of  $^{14}\text{CO}_2$  and the distribution and remobilization of  $^{14}\text{C}$ -labelled photosynthate

among the various plant parts is affected by water stress was determined by recovering and analyzing the  $^{14}\text{C}$ -radioactivity of 14 plant segments and that associated with the non-structural carbohydrate components, viz glucose, fructose, sucrose and starch in selected plant parts. An assessment could also be made of the length of time assimilated  $^{14}\text{C}$  occurred in the form of non-structural carbohydrates during grain fill.

The technique of labelling plants with  $^{14}\text{C}$  to study the partitioning pattern of assimilated  $^{14}\text{C}$  into various organic compounds among the organs has been variously used by research workers and it is perhaps useful to briefly describe the procedures used. Exposure of single leaves to  $^{14}\text{CO}_2$  is a method commonly employed by researchers to label photosynthate in maize plants with  $^{14}\text{C}$ . Palmer et al. (1973) labelled maize plants grown in the field at 15 to 18 d after flowering with  $^{14}\text{CO}_2$  to determine patterns of translocation within the plants, losses of  $^{14}\text{C}$  by respiration, and patterns of mobilization and redistribution of  $^{14}\text{C}$  among and within organs. These workers exposed the plants to  $^{14}\text{CO}_2$  at four single leaf positions. Hofstra and Nelson (1969) exposed single leaves of maize plants to  $^{14}\text{CO}_2$  to study the translocation of assimilated  $^{14}\text{C}$  in 3 to 6 week old maize plants in growth chambers. These workers also studied the distribution of  $^{14}\text{C}$  among the products of photosynthesis. Eastin (1970) exposed the third leaf from the top of field grown maize plants to  $^{14}\text{CO}_2$  on a single occasion 15 d after silk emergence. The velocity and time course of  $^{14}\text{C}$  labelled photosynthate export from the maize leaf labelled was then studied. Exposure of the entire plant to  $^{14}\text{CO}_2$  has been done on smaller plant species such as

timothy (Phleum pratense L.) plants grown in pots (Balasko and Smith, 1973) and wheat plants grown in the field (Austin, Edrich, Ford and Blackwell, 1977; Bidinger et al., 1977). However, exposure of entire maize plants to  $^{14}\text{CO}_2$  is not commonly practised probably due to the practical problems involved in labelling large plants. Simmons and Jones (1985) exposed entire maize plants grown in the field to  $^{14}\text{CO}_2$  several times during the pre- and post-silking periods in order to determine the contribution of pre-silking photosynthate to grain yield. On each labelling occasion a large plexiglass was placed over a pair of plants and they were exposed to  $1,85 \times 10^6$  Bq released from  $\text{Na}_2^{14}\text{CO}_3$ . To the knowledge of the author the procedure adopted in this thesis of repeatedly labelling water stressed and water non-stressed entire maize plants with  $^{14}\text{CO}_2$  during grain fill has not been conducted by other workers, therefore comparisons of data obtained from this study with that from other independent studies was not possible.

In this experiment the maize single cross hybrid, B254W x M162W was used. This hybrid is a cross of the two inbred lines used in the 1985/86 maize inbred rain-out shelter trial (data in press) with B254W a recovery of M37W. Both inbreds are purported to have drought tolerance characteristics with M37W commonly used throughout the world in breeding programmes to produce maize hybrids with a measure of drought tolerance (Gevers, 1986; personal communication). However, it was found in the 1985/86 rain-out shelter trial that responses to water stress were different for the two inbreds. In the 1985/86 rain-out shelter trial it was found that M37W is an early senescing inbred, and

under conditions of water stress it appeared to deplete stem non-structural carbohydrate pools for grain fill requirements from MGF to PM. On the other hand M162W is a late senescing inbred and photosynthesis was apparently less sensitive to water stress as non-structural carbohydrates continued to accumulate in the stem throughout grain fill. By selecting the single cross between these two inbred lines it was hoped that B254W x M162W would exhibit both the capacity to accumulate non-structural carbohydrates in the stem and the ability to deplete the non-structural carbohydrates in the stem for grain fill requirements, should water stress reduce the production of current photosynthate.

#### 4.2 Methods and materials

A site description for this trial conducted at the Faculty of Agriculture, University of Natal is provided in Appendix 3.

##### Cultural procedures

The soil used in this experiment was a commercially supplied Bainsvlei form Bainsvlei series which had all the horizons mixed together. The soil was sieved and mixed in batches of 100 kg with powdered fertilizer in a concrete mixer in order to achieve a uniform soil-fertilizer mix. In accordance with soil analysis conducted by Cedara, Fertilizer Advisory Service (Appendix 13), fertilizer was applied at the following rates: nitrogen applied as LAN (28) at 100 kg N ha<sup>-1</sup> at planting followed by a top dressing of 100 kg N ha<sup>-1</sup> at five weeks after planting.

Phosphorus was applied at  $100 \text{ kg P ha}^{-1}$  of single superphosphate (10,5) at planting. Potassium at  $60 \text{ kg K ha}^{-1}$  applied as KCl (50) before planting and a further  $60 \text{ kg K ha}^{-1}$  applied subsurface at 5 weeks. Soil 25 kg in mass was placed in 25 l tin drums lined with thick black plastic nursery bags. Each tin drum was 0,3 m in diameter and 0,6 m deep and had drainage holes punctured in the base. On 7 December 1988 two seeds were planted per drum at a depth of 50 mm and at three weeks after emergence treatments were thinned to one plant per drum. Plants were further supplied with macro- and micronutrients when they were watered with 2,5 l of a 0,1 % hydroponic nutrient powder solution (Chemicult<sup>(R)</sup> Products (Pty) Ltd) at five weeks after emergence, anthesis and four weeks after anthesis.

Plants were initially grown out-of-doors until approximately one week before tassel emergence (6 February 1989) whereupon they were placed in a growth tunnel constructed of polycarbonate. The trial was arranged as a randomized blocks design in three replications (Appendix 16). Half the plants continued to receive adequate domestic tap-water from anthesis onwards via a hand held hose pipe (non-stress treatment) while the remaining half were subjected to one week long periods without water (stress treatment). Each one week long period without water is referred to as one stress cycle for the remainder of this thesis. Temperature was controlled inside the growth tunnel through the evaporation of water sprayed on to the 'wet wall' at one end of the tunnel and the forced removal of the warm, humid air by large fan ducts at the other end of the tunnel. A system of thermostats placed around the tunnel were set to switch on the

fans and the pumps to spray water onto the wet wall when the temperature inside the tunnel reached 30°C. Night time temperatures seldom fell below 12°C during the period in which this study was conducted. Wet and dry bulb thermometer readings were taken inside and outside the growth tunnel on the 23 and 24 February 1989 at approximately 12h00, with the readings taken inside the tunnel approximately 5 min after the wet wall was last sprayed. Relative humidity (RH) was calculated from the wet and dry bulb readings and the RH inside the tunnel exceeded the RH outside the tunnel by 12 and 23 % respectively on the two consecutive days. Approximately one hour after sunset until approximately two to three hours after sunrise the RH inside the tunnel was 100 % as indicated by the condensation of water vapour on the roof of the growth tunnel. Thus it is apparent that the maize plants were grown under higher humidity conditions inside the tunnel relative to humidity conditions outside the tunnel. Photosynthetically active radiation (PAR) was measured inside the tunnel at 12h00 to be 1 982  $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$  using a LI-185 light meter fitted with a LI-190s quantum sensor. This translates to a 96 % transmission of PAR through the polycarbonate tunnel relative to the PAR measured outside the tunnel.

#### Pest and disease control

During early vegetative growth plants were protected from cutworm by using cutworm bait (a.i. sodium fluosilicate) and stalkborer by using Curaterr-71 granules (a.i. carbofuran). Weed control was maintained by hand weeding. After the plants were placed in

the growth tunnel they were attacked by aphids and control was exercised by spraying plants with Rogor CE (a.i. dimethoate). Sooty mould, growing on the honey-dew produced by the aphids, occurred on the leaves and control was exercised by spraying plants with Dithane M-45 (a.i. mancozeb).

#### <sup>14</sup>C-Labelling and sampling procedure

For studies of <sup>14</sup>C assimilation separate batches of plants were placed at anthesis (A), two weeks after anthesis (2 WAA), four weeks after anthesis (4 WAA) and six weeks after anthesis (6 WAA) (Table 4.1) in a 2 x 2 x 3 m labelling chamber at a population density of 65 746 ha<sup>-1</sup>. The chamber was of an aluminium angle bar frame covered with polycarbonate. All joints in the polycarbonate were sealed with silicone sealer. A temperature of 27°C was maintained inside the chamber by a 3,19 kW closed circulation air conditioning unit. The labelling chamber was positioned outside, but in close proximity to, the growth tunnel. Each labelling occasion commenced at 11h00 and batches of 12 plants were placed in the chamber. Excess 0,1 M lactic acid was released from a syringe pipette from the outside of the chamber down a glass tube into a petri dish within the chamber containing 12 x 10<sup>6</sup> Bq (720 x 10<sup>6</sup> dpm) Na<sub>2</sub><sup>14</sup>CO<sub>3</sub> in NaOH. Upon acidification of the Na<sub>2</sub><sup>14</sup>CO<sub>3</sub>, <sup>14</sup>CO<sub>2</sub> was evolved from the petri dish positioned in the air flow of the air conditioner to rapidly mix <sup>14</sup>CO<sub>2</sub> throughout the chamber. After 15 min the chamber was purged and the plants returned to their randomized positions within the growth tunnel.

Table 4.1 Fortnightly sampling from each water stress treatment plot of maize plants labelled with  $^{14}\text{C}$  at anthesis (A), 2, 4 and 6 weeks after anthesis (WAA)

Plants labelled at:	WAA									
	Anthesis					Physiological maturity				
	0	1	2	3	4	5	6	7	8	
A	2 <sup>48†</sup>		2		2		2			2
2 WAA			2 <sup>48</sup>		2		2			2
4 WAA					2 <sup>48</sup>		2			2
6 WAA							2 <sup>48</sup>			2

†2<sup>48</sup> = Two plants per plot sampled at 48 h after labelling

The distribution of  $^{14}\text{C}$  among the various plant organs after assimilation on each labelling occasion was determined by sampling plants at 48 h and consecutive fortnightly intervals after labelling until PM (Table 4.1). When the data for a particular labelling occasion are discussed, and no confusion may arise, the 48 h period after labelling at A, 2 WAA, 4 WAA and 6 WAA is respectively often simply referred to as A, 2 WAA, 4 WAA and 6 WAA i.e. with the 48 h specification dropped. Thus, for example, the phrase 'when plants were labelled at A and sampled 48 h after labelling at A' is synonymous with the phrase 'when plants were labelled at A and sampled at A'. Two plants were sampled per plot on each sampling occasion. Plants were separated into laminae, sheaths, tassels, entire secondary ear (2° ear) and stems were divided into paired internodes above and below the primary ear. Collectively the sheaths and laminae are referred to as leaves. The 2° ear included the shank, husks, grain, silks and cob. The primary ear was separated into the

shank, husks, grain and cob (Figure 2.1). In all, plants were divided up into a total of 14 segments. In the manner of the 1985/86 maize hybrid rain grown trial the shank is regarded as stem tissue; the grain is defined as the collective term for all the kernels of the primary ear, and the cob is defined as the rachis or cylindrical terminating branchlet to which the grain are attached. The roots were not studied in this experiment as Jurgens et al. (1978) found that less than 2 % of assimilated  $^{14}\text{C}$  was mobilized to the roots during grain fill.

Corresponding segments of the two plants sampled per plot were grouped together to form composite samples. Composite samples were dried at  $70^{\circ}\text{C}$  in a forced draught oven for 48 h, weighed and milled to pass through a 1 mm mesh. The milled material was placed in 30 ml plastic bottles, dried again at  $70^{\circ}\text{C}$ , stoppered and put into storage until radioactivity and non-structural carbohydrate analysis could be conducted.

#### Analysis of $^{14}\text{C}$ total radioactivity in each plant part

Total radioactivity in each plant part was determined from combusting a 200 mg subsample of each plant part in a Packard Tricarb sample oxidizer Model 306 (Packard, USA) and counting radioactivity on a Packard Model 1 500 liquid scintillation counter. All radioactivity data are expressed in decays per minute (dpm). Total radioactivity in the tissue of each plant part was calculated on a dry ( $70^{\circ}\text{C}$ ) mass basis as dpm per plant part. Specific radioactivity was determined as dpm per gram of dry tissue mass. All counts were corrected for background

radioactivity. It is emphasised that an increase or decrease in the specific radioactivity of a plant segment does not necessarily represent an absolute gain or loss in  $^{14}\text{C}$ . In order to determine whether real losses or gains in  $^{14}\text{C}$  have occurred, the total radioactivity for each plant segment must be studied.

#### Non-structural carbohydrate analysis

Total non-structural carbohydrates were determined in five plant parts namely the A1, B1, shank, cob and grain plant parts sampled from plants 48 h after labelling at A, 2 WAA, 4 WAA and 6 WAA; while composite samples were formed across labelling occasions of corresponding plant parts sampled at PM. In essence this provided data on the levels of non-structural carbohydrates in the selected plant parts at A, 2, 4 and 6 WAA, and at PM. In addition, composite samples were formed of the samples from the three replications for each of the water stress treatments. Total non-structural carbohydrates were determined using the modified Weinmann method (Weinmann, 1947) as discussed for the 1985/86 maize hybrid rain-grown trial (Section 2.2.2).

#### Thin layer chromatography determinations of radioactivity associated with glucose, fructose and sucrose

Thin layer chromatography determination of radioactivity associated with glucose, fructose and sucrose was conducted on five plant parts namely the A1, B1, shank, cob and grain plant parts sampled 48 h after labelling and at PM from stressed and non-stressed plants labelled at A, 2 WAA, 4 WAA and 6 WAA.

Composite samples were formed of samples from the three replications for each of the water stress treatments. Further detail of the development of the thin layer chromatography procedure adopted in this experiment is provided in Appendix 32.1.

#### Preparation of plates

The 200 x 200 mm glass plates were washed with a detergent, rinsed well with tap-water, followed by distilled water and finally ethanol. Initially the cellulose slurry was prepared according to Lewis and Smith (1969) with 100 g of the Whatman CC41 microcrystalline cellulose blended in a mixer for 15-45 s with 430 ml of distilled water. However, this resulted in an extremely watery mix. After trial and error it was found that 100 g of the cellulose powder mixed for 30 s in a blender with 250 ml followed by adding a further 35 ml of distilled water and blending for a further 15 s provided a mix of the correct consistency that 'peaked' slightly when a glass rod was drawn out of it. The cellulose slurry was degassed in a Buchner funnel flask under vacuum for a few minutes. The plates were spread using a Shandon Unoplan TLC spreader (Shandon, UK) to a thickness of 1,0 mm and dried overnight at room temperature. No activation of the plates before use was necessary. Plates 1,0 mm thick were prepared to increase the sugar-carrying capacity.

## Solvent

The solvent used was formic acid:butanone:tert-butanol:water (15:30:40:15) solvent highly recommended by Vomhof and Tucker (1965) which they had used with MN 300 cellulose powder.

## Visualization reagent

The visualizing reagent used, aniline oxalate, is prepared by adding to 100 ml of 0,1 N oxalic acid, 0,9 ml of aniline. The chromatogram is sprayed with the reagent and treated at 100-105°C for 10-20 min. The reducing sugars appear as brown spots. When the same chromatogram is sprayed with 1 %  $\text{KMNO}_4$  solution containing 3 %  $\text{H}_2\text{SO}_4$ , and heated to 100°C for a few minutes fructose and sucrose appear as grey black spots. This technique distinguishes between ketoses and aldoses (Block, Durrum and Zweig, 1955).

## Sample preparation

Glucose, fructose and sucrose were extracted from plant part samples by mechanically shaking the tissue sample for 12 h with 50 ml of 80 % (v/v) ethanol in a stoppered 125 ml Erlenmeyer flask. The residue was filtered off and the supernatant was made up to 100 ml. volume with 95 % (v/v) ethanol. Using the percentage of TS in each plant part sample data obtained from the Weinmann procedure conducted earlier, the necessary  $\mu\text{l}$  of TS in ethanol solution containing the necessary  $\mu\text{g}$  of TS (i.e. glucose plus fructose plus sucrose) could be calculated.

From these flasks 10 ml of solution was pipetted into scintillation vials and 10 ml of Insta-Gel<sup>1</sup> was added. This procedure achieved 50 % dilution of the colour in the solutions.

(iii) A range of 10 ml solutions was made up in scintillation vials each containing increasing amounts of the gold colour. Each solution was spiked with 3 000 dpm of radioactive sucrose (Amersham). To each vial was added 10 ml of Insta-Gel. Five standards were made up containing 10 ml of clear distilled water, 10 ml of Insta-Gel and spiked with 3 000 dpm of radioactive sucrose. The radioactivity of the solutions containing the range of gold colour was counted in the scintillation counter with the tSIE (internal quench correction factor) mode on. The dpm counts obtained from the coloured solutions were compared to the clear standard solutions. A coloured solution for which the dpm count fell to less than 3 % of the clear standards, i.e. < 2 910 dpm, was regarded as the threshold darkness of colour and the tSIE value outputted by the scintillation counter was noted, namely 78,1. Any solution that recorded a tSIE value of less than 78,1 was rejected and re-run through the procedure but diluted by more than 50 %.

Ion-exchange column separation of total sugars from amino acids and organic acids

Pyrex glass tubing (diameter 10 mm) with one end shaped to a narrow tip was used as column supports. The tip of each glass column was plugged with glass-fibre and the anion exchange beads

---

<sup>1</sup>Insta-Gel<sup>(R)</sup> (Packard, USA) can hold up to 50 % water and has a high capacity to hold solids and salts in suspension.

(IRA-400; Rohm and Haas, USA) in 80 % ethanol were poured gently into the glass columns and packed to a volume of 5 ml. The cation exchange beads (IR-120; Rohm and Haas, USA) in 80 % ethanol were then poured directly on top of the packed anion exchange beads to a volume of 5 ml making a combined total of 10 ml of cation and anion exchange beads. To maintain a constant head of ethanol above the 10 ml of beads, surgical rubber tubing was connected to the tip of the glass column and looped up the outside of the glass column with the open end of the surgical tubing approximately 15 mm above the top of the cation exchange beads. To facilitate collection of the sample solutions a small curved section of glass tubing was inserted into the open end of the surgical tubing thus directing the drops of solution into a beaker placed underneath. The column was washed to neutrality with vast quantities of 80 % ethanol. Neutrality of the columns was tested by comparing the electrical conductivity of distilled, demineralized and decarbonized water passed through the column with a standard amount of the same pure water. Further detail of the preparation of the ion-exchange column chromatography procedure, efficacy of the ion-exchange column in removing amino acids and organic acids, and efficiency of recovery of radioactivity is provided in Appendix 32.3.

After extraction and evaporating off the excess ethanol each 10 ml sample solution containing TS was poured directly onto the ion-exchange columns. The sugars were eluted slowly at one drop every 3 s with 80 ml of 80 % ethanol. The flow rate was controlled by pinching the surgical tubing of each column with miniature screw clamps. The solutions were collected in beakers

and the excess 80 % ethanol was once again carefully evaporated off leaving the TS in 2 ml of water. Each beaker was rinsed into a scintillation vial using 4 ml of water and 4 ml of 80 % ethanol. This was followed by 10 ml of Insta-Gel. Samples were then placed in the scintillation counter and counted for radioactivity.

Total and specific radioactivity associated with the TS in each plant part was then determined from the TS content (g (plant part)<sup>-1</sup>) data obtained from the Weinmann (1947) procedure detailed earlier.

After passing through the ion-exchange column it was occasionally found that some TS solutions had a yellow-green colour which caused quenching. It was attempted to remove the colouring compounds by passing the solution through: (i) activated charcoal, and (ii) Polyclar AT<sup>(R)</sup> (polyvinylpyrrolidone insoluble; BDH Chemicals, Ltd) without success. Initially extracting the milled sample in a methanol:chloroform:water (12:5:3) mix (Dickson, 1979) in order to separate out the pigments into the chloroform fraction also failed. As is discussed with the hydrolysed starch solutions, Cl<sub>2</sub> water proved to be a fairly satisfactory decolorizing or bleaching agent. Samples were decolorized with 2 ml of chlorine water after they were eluted through the ion-exchange columns and had been rinsed into the scintillation vials but before Insta-Gel was added.

### Leaf water potential determination

Pre-dawn leaf  $\Psi_w$  readings were taken from two plants per plot on a weekly basis on the mornings on which stressed plants were to be watered at the end of each stress cycle but prior to watering (Section 3.2).

### Leaf area determination

The method of cutting discs of known area from stacks of leaves (Section 3.2), was employed to determine leaf area from plants sampled at two weekly intervals for radioactivity analysis. Since plants were grown in pots leaf area was expressed as  $m^2 \text{ plant}^{-1}$ .

### Yield and yield component determination

Four plants per plot were left to dry out for three weeks after reaching physiological maturity. All primary and 2° ears were harvested. Mass of grain per plant for each plot (primary plus 2° ears) was then determined and corrected to 12,5 % moisture content. The following yield components - kernels  $\text{ear}^{-1}$ , kernels  $\text{row}^{-1}$ , rows  $\text{ear}^{-1}$  and mass  $\text{kernel}^{-1}$  were also determined from primary ears only.

### Statistical analysis and presentation of data

As with the two previous trials all data was analyzed on the GENSTAT Version 4.04 statistical package.

## Leaf water potential and leaf area data

As for the radioactivity data the highest order interaction is graphically presented and discussed whether it is significant or not since physiologically important trends may be shown by the data of non-significant highest order interactions. Least significant differences are, however, only presented on graphs of significant highest order interactions. Polynomial regression equations were fitted to the leaf  $\Psi_w$  and leaf area data. Third order polynomial equations were necessary to adequately describe these variates.

## Non-structural carbohydrate data

Composite samples were formed of the samples from the three replications for each of the water stress treatments. Analysis of variance on these data was therefore not conducted.

## Radioactivity of plant segments, whole stem, whole shoot and whole plant data

The data for each labelling occasion were in essence regarded as individual experiments and were separately analyzed. Thus the trial was analyzed as a split split plot with water stress treatments as whole-plot factor, sampling occasions (within a labelling occasion and denoted as WAA) as the sub-plot factor and the 14 plants segments as the subsub-plot factor. Thus there was a total of four split split plot analyses for each of the four labelling occasions with five sampling occasions as the sub-plot

factor for plants labelled at A, four sampling occasions as the sub-plot factor for plants labelled at 2 WAA, three sampling occasions as the sub-plot factor for plants labelled at 4 WAA and two sampling occasions as the sub-plot factor for plants labelled at 6 WAA. In the manner of the 1985/86 maize hybrid rain grown trial (Section 2.2.3), the Greenhouse-Geisser epsilon factor was derived and multiplied by the degrees of freedom (DF1 and DF2) for those F-tests involving the EMS for sampling occasions. The epsilon factor is always one when the number of time periods (sampling occasions) is two, therefore the epsilon factor for the F-tests involving the EMS for the two sampling occasions of plants labelled at 6 WAA is one and the F-test levels of significance are not adjusted. Additionally, since the EMS for plant segments (subsub-plot factor) is calculated over sampling occasions, the plant segments were treated as 14 time periods and the epsilon factor was derived to be multiplied by the degrees of freedom (DF1 and DF2) for those F-tests involving the EMS for plant segments. Occasionally the EMS for sampling occasions was larger than the EMS for water stress treatment. In these situations a weighted pooling of the two EMS's was conducted, i.e. the trial was analyzed as a split plot factorial with two water stress treatment x n sampling occasions as the whole-plot factors and stem segments now as the sub-plot factor. When pooling of the two EMS's was necessary the epsilon factor was multiplied by the degrees of freedom (DF1 and DF2 (pooled EMS)) of those F-tests that would have involved the EMS for sampling occasions before pooling was done.

The data for the 14 segments was also summed together in three different ways. Whole stem data was obtained by summing together the data for the top, A1, B1, B2, B3, B4 and shank stem segments. Whole shoot data, defined as all aboveground plant parts excluding the primary grain, was derived by summing together data for the tassel, top, A1, B1, B2, B3, B4, shank, sheaths, laminae, cob, husks and 2° ear. Whole plant data was obtained by summing together all the data for the 14 segments sampled. The whole stem, whole shoot and whole plant data for each labelling occasion was, as for the 14 segment data, analyzed separately. Thus the trial was analyzed as a split plot with water stress treatments as whole-plot factor and sampling occasions (within a labelling occasion) as the sub-plot factor. Thus four separate split plot analyses were conducted corresponding to the four labelling occasions. The Greenhouse-Geisser epsilon factor was derived and multiplied by the degrees of freedom (DF1 and DF2) for those F-tests involving the EMS for sampling occasions. Occasionally the EMS for sampling occasions was larger than the EMS for water stress treatment. In these situations a weighted pooling of the two EMS's was conducted, i.e. the trial was analyzed as a factorial of two stress treatments x n sampling occasions. When pooling of the EMS's was necessary, the epsilon factor was multiplied by the degrees of freedom (DF1 and DF2 (pooled EMS)) of those F-tests that would have involved the EMS for sampling occasions before pooling was done. As with data for the 14 plant segments, the epsilon factor for the F-tests involving the EMS for the two sampling occasions of plants labelled at 6 WAA is one and F-test levels of significance are not adjusted.

Except for the highest order interaction, significant interactions are presented in tabulated form along with LSD's and the interactions of the treatment factors are discussed. Data for the main effect of a treatment factor are not discussed per se unless the treatment factor was not involved in a significant interaction. Since the C.V.'s for the 14 segments, whole stem, whole shoot and whole plant total and specific radioactivity data was usually above 20 % the degree of interaction between the treatment factors water stress treatment, WAA (sampling occasion) and segment (the latter treatment factor is not relevant to the whole stem, shoot and plant data) would have to be substantial in order to provide a significant F-test for that interaction. Consequently the highest order interaction for each labelling occasion was non-significant. However, the data of the highest order interactions are graphically presented and discussed as they show important physiological trends in the changes in the specific and total radioactivity in the plant segments as affected by water stress during grain fill. Since none of the highest order interactions for the data of each labelling occasion was significant, LSD's are not presented on the graphs.

In the analysis of variance of the specific and total radioactivity data, and the leaf  $\Psi_w$  and leaf area data the sum of squares for sampling occasion was partitioned (depending on the degrees of freedom available) into linear, quadratic and cubic regression effects and deviations from regression providing a description of the changes in the specific and total radioactivity, leaf  $\Psi_w$  and LAI as a function of WAA.

Data expressed as a percentage of whole stem or whole plant total radioactivity

These data are graphically presented for descriptive purposes as an aid to the discussion. Analysis of variance tables on these data are therefore not presented.

Thin layer chromatography and ion-exchange column data

Composite samples were formed of the samples from the three replications for each of the water stress treatments. Analysis of variance tables on these data are therefore not presented.

#### 4.3 Results and discussion

##### 4.3.1 Leaf water potential

The main effects for stress treatment and WAA were significant (Appendix 33). However, since these factors were involved in a significant higher order interaction their main effects are of limited interest.

The first order interaction of stress treatment with WAA was non-significant. However, the stress treatment x WAA(linear) component of the interaction was significant (Figure 4.1). After 48 h without water the leaf  $\Psi_w$  of stressed plants was 291 kPa less than that of non-stressed plants. However, the difference was non-significant. From A to PM, leaf  $\Psi_w$  of both stressed and non-stressed plants declined but at a more rapid rate in the

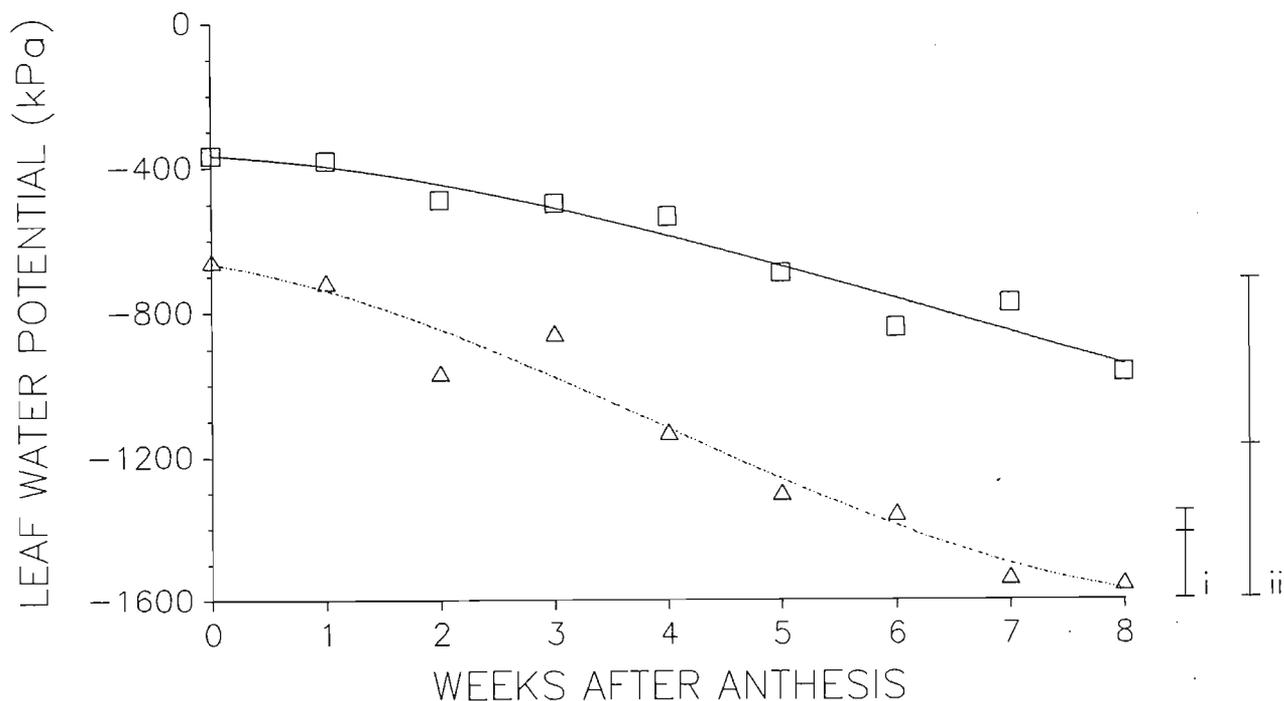


Figure 4.1 Effect of water stress (△----△) and lack of water stress (□—□) from anthesis to physiological maturity on leaf water potential of the maize hybrid B254W x M162W. NOTE: the readings at anthesis were taken 48 h after imposition of water stress which has resulted in the leaf water potential for stressed plants being lower than that for non-stressed plants.

Comparisons using LSD's of means at the same level of (i) stress; and (ii) weeks after anthesis or with neither factor in common.

Polynomial equations:

Stress	$-665,01 - 55,22x - 22,32x^2 + 1,89x^3$	$r^2=0,964$
Non-stress	$-366,42 - 21,79x - 11,11x^2 + 0,59x^3$	$r^2=0,950$

stressed plants than in the non-stressed plants. Leaf  $\Psi_w$  was non-significantly less in the stressed plants than the non-stressed plants at 1 and 3 WAA and significantly ( $p = 0,05$ ) less at 2 WAA and from 4 WAA to PM. At PM leaf  $\Psi_w$  in the stressed plants was 580 kPa less than that of the non-stressed plants and had reached -1 553 kPa. As mentioned earlier in this thesis (Section 3.3.1), it is often reported in the literature that photosynthesis is completely inhibited in maize leaves as leaf  $\Psi_w$  reaches -1 600 to -1 800 kPa (Westgate and Boyer, 1985a). If this range of leaf  $\Psi_w$  values is a universal threshold range for all maize genotypes which when reached or exceeded photosynthesis is completely inhibited, then it is clear that in this particular experiment photosynthesis was not completely inhibited. That photosynthesis was not completely inhibited in the stressed plants is clearly evident from the data of whole plant mass gain (Section 4.3.7.1, Table 4.58). Whole plant mass of the stressed plants continued to increase throughout grain fill. However, it is clear that photosynthesis was reduced in the stressed plants as whole plant dry mass and grain dry mass of the stressed plants at PM was 86,4 and 82,0 % respectively, of the non-stressed plants.

Despite stressed plants attaining a low leaf  $\Psi_w$ , the effects of water stress were apparently mild in this experiment. It should be borne in mind that the objective of this study was to induce enough stress in the plants to ascertain the effects of water stress on the partitioning patterns of the assimilated  $^{14}\text{C}$  and in particular the  $^{14}\text{C}$ -labelled total non-structural carbohydrates. All plants subjected to the water stress treatment were exposed

to weekly periods without water from anthesis onward. Before the water stress treatment was commenced at anthesis, four of the spare plants used in the border rows were not watered when the plants were approximately two weeks from tasselling. After three days without water the four test plants were showing severe signs of water stress, viz leaf curl and wrinkling of the sheaths, and the soil water content had declined to 1,0 %. However, in order to keep the period without water a simple multiple of the period between labelling occasions, it was decided to continue not watering the plants until a full week had elapsed to determine whether or not the plants would recover upon being rewatered at the end of the week. Two plants were rewatered at the end of the week and they recovered, apparently suffering minimal after effects of water stress. The remaining two plants were not watered and after 10 d without water these plants were so severely dehydrated that they did not recover when watered, and subsequently died. Thus it was decided that a one week long exposure to water deficits was sufficient to induce enough stress in the plants without killing them. Obviously in this experiment the objectives were somewhat conflicting in that it was desired to induce enough water stress to alter the partitioning patterns of assimilated  $^{14}\text{C}$  while, on the other hand, the level of stress could not be too severe, otherwise the fortnightly labelling of the plants would have been carried out on dead plants in the stress treatment. Also, severe water stress would have induced earlier death in the plants, thus preventing the assessment of the effects of stress over a long enough period of grain fill. Additionally, if severe water stress were induced thereby completely inhibiting photosynthesis, causing excessive leaf

senescence and disrupting metabolism with a resultant reduction in sink demand, then clearly the stressed plants would not assimilate enough  $^{14}\text{C}$  for recovery and analysis. Furthermore, any  $^{14}\text{C}$  assimilated may not have been partitioned to the primary ear as its ability to demand photosynthate may have been severely retarded by the effects of stress. A problem associated with water stress studies conducted on plants grown in pots is that stress induction is rapid and the general metabolism of the plants is quickly disrupted. In order to combat the rapid induction of stress, the plants were grown in a growth tunnel during grain fill where the relative humidity was higher than that outdoors. It was hoped that the higher relative humidity inside the growth tunnel would reduce the transpirational loss of water from the plants exposed to water stress thus enabling a slower rate of stress induction. However, it is likely that because the plants were grown outdoors throughout the vegetative period in air with lower relative humidity they had developed a degree of 'stress hardening' and were less sensitive to water stress. McPherson and Boyer (1977) subjected maize plants to two desiccation pretreatments during the entire vegetative stage. Half the plants were exposed to a low vapour pressure (VP) pretreatment (leaf-air vapour pressure difference of 2,6 kPa i.e. low humidity) and the other half were exposed to a high VP pretreatment (leaf-air vapour pressure difference of 0,5 kPa i.e. high humidity). The net result was that the two sets of plants were subjected to a different evaporative demand during the day, which caused leaf  $\Psi_w$  to average 100 kPa lower in the low VP plants than in the high VP plants. At tasselling, identical high VP conditions (0,5 kPa) were imposed on the all plants so that

pollination occurred under favourable moisture conditions. After pollination, the soil was desiccated in half the plants so that leaf  $\Psi_w$  declined to between -1 800 and -2 000 kPa. Thereafter the stressed plants received one-seventh the amount of water received by the controls for the remainder of grain fill. The plants that previously had been grown at low VP exhibited high leaf  $\Psi_w$  and high rates of photosynthesis for a longer time than their counterparts previously grown under high VP. Plants previously exposed to low VP had a grain yield of 7 970 kg ha<sup>-1</sup> which was 68 % of low VP control plants; while plants previously exposed to high VP had a grain yield of 4 930 kg ha<sup>-1</sup> which was 47 % of the high VP control plants. There was apparently little difference in the tolerance of photosynthesis to low leaf  $\Psi_w$  in the two sets of plants. For both, net photosynthesis was inhibited initially at leaf  $\Psi_w$  of -800 kPa and became zero at leaf  $\Psi_w$  of about -1 800 to -2 000 MPa. However, less water was used by low VP plants than high VP plants during grain fill. This resulted in the conservation of soil water, and consequently leaf  $\Psi_w$ , transpiration and photosynthesis were preserved in the low VP adapted plants for a longer time than in the high VP adapted plants. Through the evaporative cooling effect of transpiration plants maintain leaf temperatures within a range favourable to metabolic processes. However, in order to conserve water under conditions of water deficits stomatal closure occurs reducing the rate of transpiration (Hsiao, 1973; Schulze, 1986). This, unfortunately for plants, has the side effect of higher leaf temperatures which may severely disrupt metabolic processes. The high humidity in the growth tunnel may have resulted in heat energy being lost from the leaves as the water vapour surrounding

the leaves evaporated and was removed from the tunnel by the fan ducts. Thus leaf temperatures may have been kept favourable for metabolic processes to occur through the cooling effect of cool, humid air being drawn through the leaf canopy.

#### 4.3.2 Leaf area ( $m^2$ plant<sup>-1</sup>)

The main effect for stress treatment was significant (Table 4.2 and Appendix 34). Water stress resulted in a significant ( $p = 0,05$ ) reduction in leaf area per plant.

Table 4.2 Effect of water stress (S) and lack of water stress (NS) on leaf area ( $m^2$  plant<sup>-1</sup>) of a maize hybrid meaned over five growth periods during grain fill

Stress treatment	
S	NS
0,435	0,499
LSD (0,05)	0,057
LSD (0,01)	0,078

The main effect for WAA was significant (Table 4.3) in which there was a significant negative linear component superimposed with a significant negative quadratic component. This indicates that averaged over the stressed and non-stressed plants the leaf area of the plants declined from A to PM but more rapidly from 6 WAA to PM. Leaf area at PM was significantly ( $p = 0,01$ ) less than at A.

Table 4.3 Leaf area ( $\text{m}^2 \text{ plant}^{-1}$ ) of a maize hybrid meaned over water stress treatments from anthesis to eight weeks after anthesis (WAA)

		WAA				
		0	2	4	6	8
		0,708	0,500	0,576	0,375	0,178
LSD (0,05)			0,090			
LSD (0,01)			0,123			

The first order interaction of stress treatment with WAA was non-significant (Figure 4.2). There were no significant components of the interaction either. However, the apparent trends in these data are discussed. At A the leaf area for the stressed and non-stressed plants was 0,703 and 0,713  $\text{m}^2 \text{ plant}^{-1}$ , respectively (Figure 4.2). From A to 6 WAA leaf area declined more markedly in the stressed plants to 0,326  $\text{m}^2 \text{ plant}^{-1}$  compared to 0,424  $\text{m}^2 \text{ plant}^{-1}$  in the non-stressed plants. However, from 6 WAA to PM leaf area of the non-stressed plants declined more markedly to 0,209  $\text{m}^2 \text{ plant}^{-1}$  compared to 0,146  $\text{m}^2 \text{ plant}^{-1}$  in the stressed plants. At PM the leaf area of the stressed plants was 69,9 % of that of the non-stressed plants. The leaf area of the stressed plants at PM was 20,8 % of that at A, while the leaf area of the non-stressed plants at PM was 29,3 % of that at A.

That this maize hybrid at PM retained 29,3 % of the leaf area at A under non-stress conditions, is indicative of its inheritance of the stay green or late senescence characteristic from the one parent M162W. It is likely that this stay green characteristic would, under favourable environmental conditions, enable

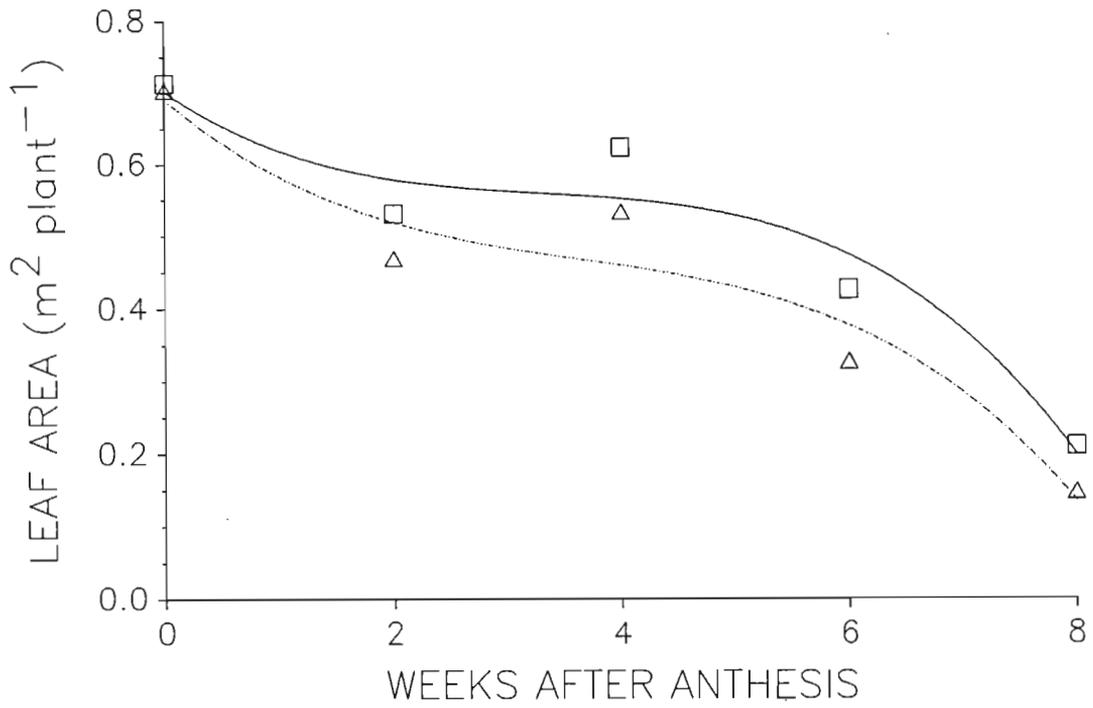


Figure 4.2 Effect of water stress (Δ----Δ) and lack of water stress (□—□) from anthesis to physiological maturity on leaf area of the maize hybrid B254W x M162W

Polynomial equations:

Stress	$0,691 - 0,137x + 0,031x^2 - 0,028x^3$	$r^2=0,941$
Non-stress	$0,701 - 0,110x + 0,030x^2 - 0,003x^3$	$r^2=0,935$

B254W x M162W to meet a greater proportion of the grain requirements with current photosynthate without having to extensively deplete TNC pools accumulated in the stem. It is possible that the stay green characteristic may be advantageous under conditions of water stress since the plant may be able to continue photosynthesizing later into the grain filling period. On the other hand, tolerance to water stress may not simply be afforded by delayed senescence as it is also dependent on the photosynthetic activity of the leaves under conditions of water stress. Additionally, maintenance of viable leaf area later into the grain filling period under stress conditions may result in greater transpiration and therefore greater depletion of soil water which would eventually result in lower leaf  $\Psi_w$ , lower turgor pressure and therefore possibly lower rates of photosynthesis.

#### 4.3.3 Non-structural carbohydrate analysis

##### 4.3.3.1 Reducing sugars composition

The RS composition in the stem segments of stressed plants ranged from 3,3 % in the A1 plant part at 2 WAA to 23,3 % in the shank at A; and in the stem segments of non-stressed plants it ranged from 3,2 % in the B1 plant part at 2 WAA to 26,4 % in the shank at A. The RS composition in the cob of stressed plants ranged from 0,8 % at 4 WAA to 8,8 % at A, and in the cob of non-stressed plants it ranged from 1,7 % at PM to 21,5 % at A. The RS composition in the grain of stressed plants ranged from 0,5 % at

PM to 11,8 % at A; and in the grain of non-stressed plants it ranged from 0,6 % at PM to 20,1 % at A (Figure 4.3).

At A the shank of non-stressed plants recorded the highest RS composition out of all the five plant parts, namely, 26,4 % (Figure 4.3). The RS composition in the stem segments of stressed and non-stressed plants declined sharply from A to 2 WAA with the decline being more marked in the stem segments of the stressed plants. As this decline in the RS composition of the stem segments from A to 2 WAA was accompanied by a decline in the RS content it appears that some utilization of the RS pool occurred during this period. In stressed plants RS composition of the stem segments then increased from 2 to 4 WAA and then declined from 4 WAA to PM. In non-stressed plants RS composition in the stem segments increased from 2 to 6 WAA and then declined sharply to PM. The RS composition in the shank of non-stressed plants was generally higher than that of stressed plants except at PM. On the other hand, the A1 and B1 segments of stressed plants had similar RS composition from A to 2 WAA but RS composition in these stem segments of stressed plants at 4 WAA was higher than that of the non-stressed plants. However, from 4 WAA to PM RS composition in the A1 and B1 stem segments of non-stressed plants was higher than that of stressed plants. On average over grain fill, non-stressed plants maintained higher RS composition levels in the stem segments than stressed plants. This may indicate that water stress resulted in a greater depletion of the RS pools in these stem segments. It appears that as a result of the reduced photosynthetic capacity of the stressed plants due to water stress, available photosynthate was

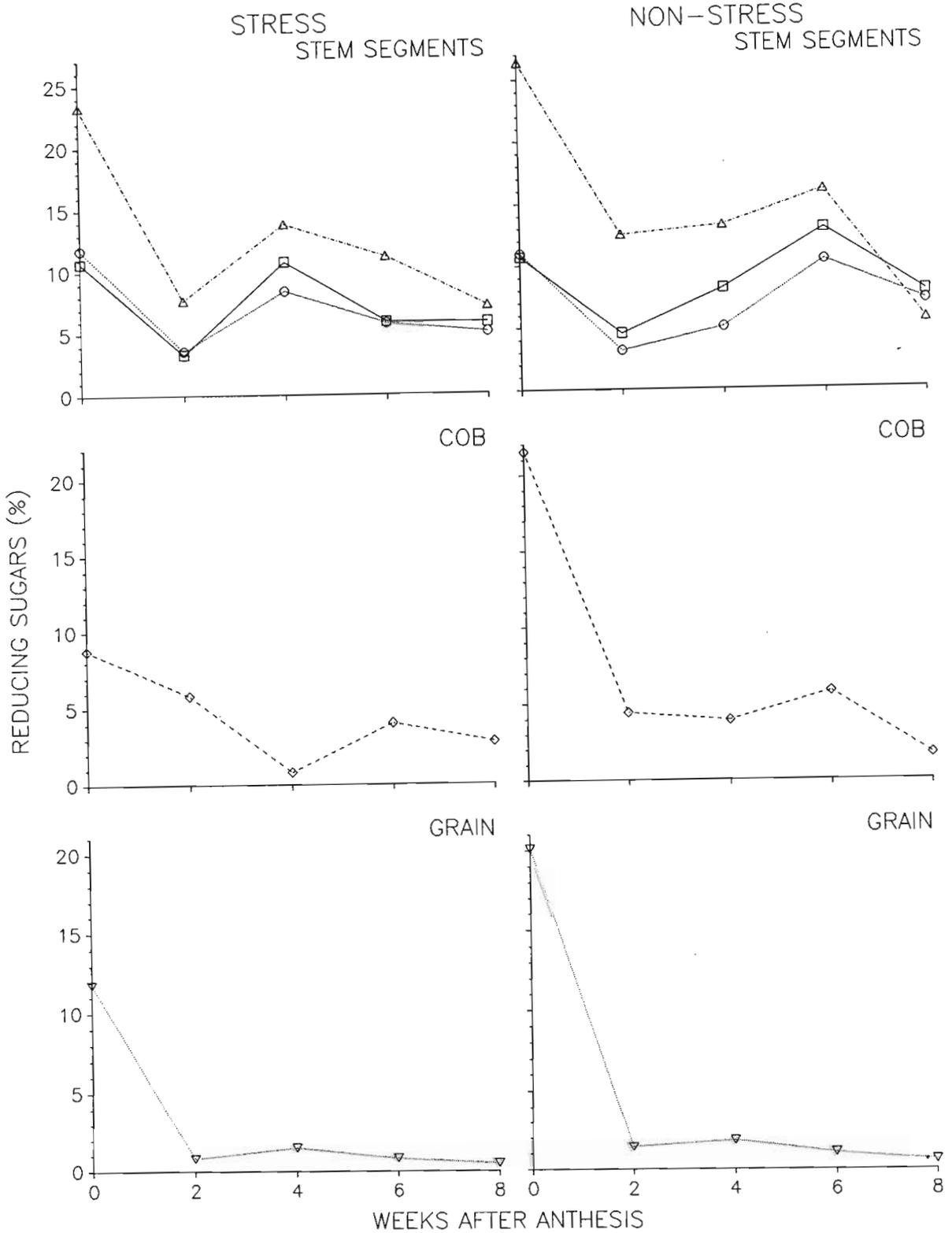


Figure 4.3 Effect of water stress from anthesis to physiological maturity on reducing sugars composition of selected plant parts from a maize hybrid

Key: A1 □—□, B1 ○—○, shank △---△

rapidly translocated to the grain with little fixed CO<sub>2</sub> accumulating as RS in the stem segments under stress conditions.

The pattern in the changes of RS composition levels in the cob of stressed plants was quite different to that of non-stressed plants (Figure 4.3). The RS composition in the cob of stressed plants at A was 12,7 % less than that of non-stressed plants. It appears that in the 48 h period that water was withheld from the stressed plants, RS composition levels had declined or remained low in stressed plants compared to non-stressed plants. It is not certain why water stress resulted in this marked suppression of the RS composition levels in the cob of stressed plants. Whereas RS composition declined in the cob of stressed plants from A to 4 WAA by 8,0 %, then increased to 6 WAA and then declined slightly at PM, in the non-stressed cob RS composition declined markedly by 17,6 % from A to 2 WAA, remained fairly constant to 4 WAA, increased to 6 WAA and then declined to its lowest level of 1,7 % at PM. In fact, RS composition in the cob of stressed plants at PM was 1,1 % higher than that of non-stressed plants. The sharp decline in RS composition of the cob of non-stressed plants from A to 2 WAA was not accompanied by a decline in the RS content and was therefore due to the large increase in the dry mass of the cob during this period i.e. the dilution effect. On the other hand, the decline in the RS composition in the cob of stressed plants from A to 4 WAA, was accompanied by an initial sharp increase in the RS content from A to 2 WAA, followed by a sharp decline in the RS content from 2 to 4 WAA. On average over grain fill, non-stressed plants

maintained the higher RS composition levels in the cob in comparison to stressed plants.

The patterns in the changes of RS composition in the grain of stressed and non-stressed plants were similar, except that at A the RS composition in the grain of non-stressed plants was 8,3 % higher than that of stressed plants (Figure 4.3). It appears that after 48 h without water the RS composition levels in the grain of stressed plants had declined, or remained lower, relative to non-stressed plants. From A to 2 WAA the RS composition in the grain of stressed and non-stressed plants declined substantially by 10,3 and 18,3 %, respectively. Since this decline in RS composition was not accompanied by a decline in RS content, it was due to the dilution effect of the rapid increase in the dry mass of the grain. From 2 to 4 WAA RS composition in the grain of stressed and non-stressed plants increased slightly and then declined to its lowest levels at PM. On average over grain fill, non-stressed plants maintained higher grain RS composition levels than the stressed plants.

#### 4.3.3.2 Reducing sugars content

The RS content in the stem segments of stressed plants ranged from 0,15 g (plant part)<sup>-1</sup> in the shank at 2 WAA to 1,04 g (plant part)<sup>-1</sup> in the B1 plant part at A; and in the stem segments of non-stressed plants it ranged from 0,21 g (plant part)<sup>-1</sup> in the A1 plant part at 2 WAA to 1,01 g (plant part)<sup>-1</sup> in the B1 plant part at A. The RS content in the cob of stressed plants ranged from 0,14 g (plant part)<sup>-1</sup>

at 4 WAA to 0,85 g (plant part)<sup>-1</sup> at 2 WAA; and in the cob of non-stressed plants it ranged from 0,48 g (plant part)<sup>-1</sup> at PM to 1,20 g (plant part)<sup>-1</sup> at 6 WAA. The RS content in the grain of stressed plants ranged from 0,31 g (plant part)<sup>-1</sup> at 2 WAA to 1,45 g (plant part)<sup>-1</sup> at 4 WAA; and in the grain of non-stressed plants it ranged from 0,48 g (plant part)<sup>-1</sup> at A to 1,95 g (plant part)<sup>-1</sup> at 4 WAA (Figure 4.4).

The B1 plant part, which was the largest stem segment, generally recorded the highest RS content of the three stem segments throughout grain fill in stressed and non-stressed plants (Figure 4.4). Except for the B1 plant part of non-stressed plants, RS content in the stem segments peaked at A and then declined sharply in all stem segments from A to 2 WAA. The physiological significance of the sharp decline in the RS content in the stem segments from A to 2 WAA is not certain. However, it may indicate that at A the grain was not yet established as the major sink for photosynthate and RS accumulated in the stem segments as a result of the high metabolic activity in these stem segments as final increases in structural growth occurred. However, at 2 WAA endosperm cell division had been completed and rapid dry mass gain by the grain occurred. Thus photosynthate was rapidly translocated to the grain with little accumulating in the stem segments. From 2 to 4 WAA RS content increased more markedly in the stem segments of stressed plants than non-stressed plants. In both stressed and non-stressed plants the RS content in the A1 and B1 plant parts was very similar. The physiological significance of the sharp increase in RS content in the stem segments of stressed plants is not certain. From 4 WAA to PM RS

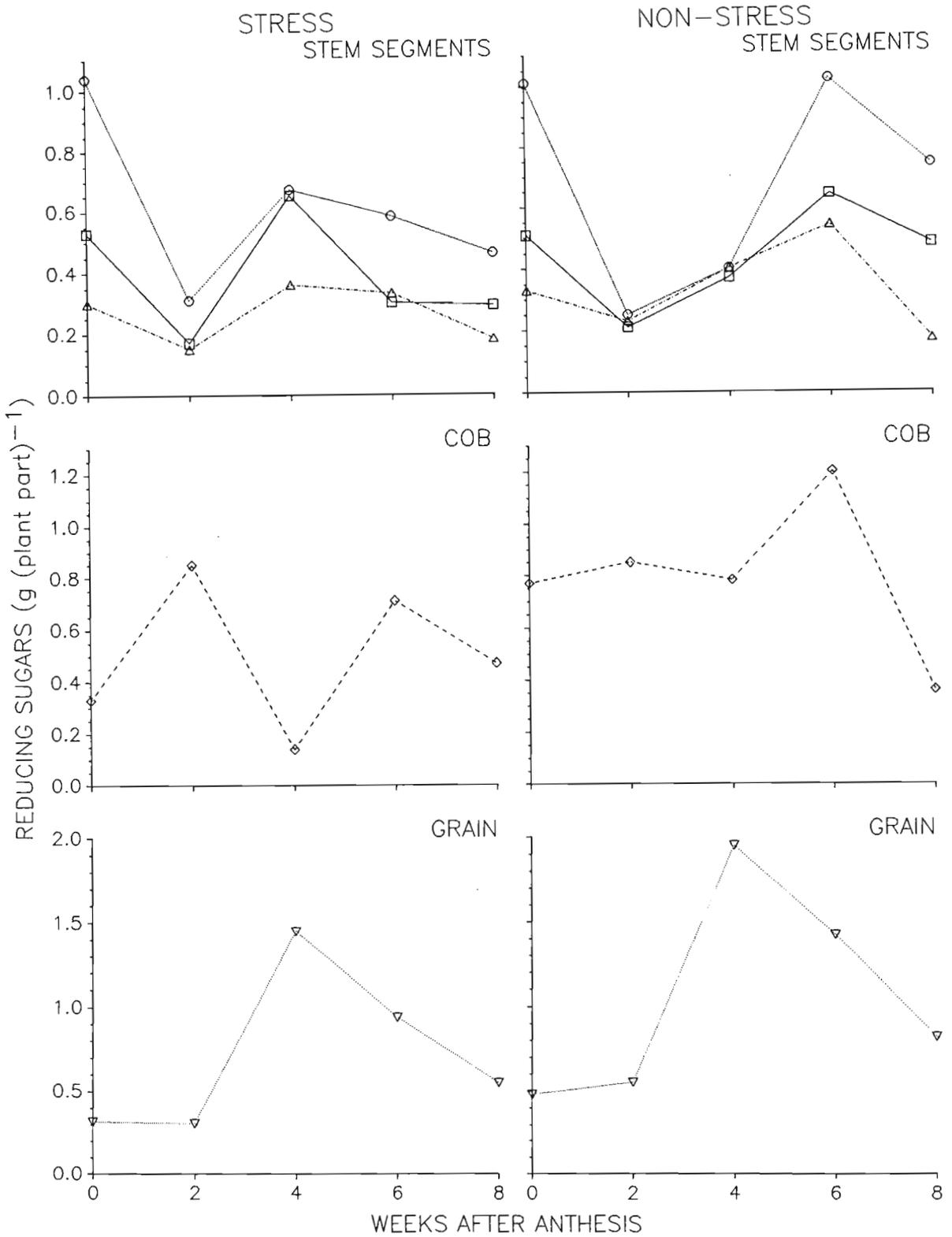


Figure 4.4 Effect of water stress from anthesis to physiological maturity on reducing sugars content of selected plant parts from a maize hybrid

Key: A1 □—□ , B1 ○—○ , shank △----△

content in the stem segments of stressed plants declined, whereas in non-stressed plants RS content increased to 6 WAA and then declined sharply at PM. The decline in RS content from 4 WAA to PM in the stem segments of stressed plants may indicate that water stress reduced the photosynthetic capacity of the plants so that current photosynthate could not maintain RS levels in the stem as they were utilized for grain fill, respiration and conversion to other non-structural carbohydrates or residual components. Of course, compounding the decline in RS content in the stem segments was the general senescence of the leaves as the plants approached maturity. The marked increase in the RS content in the stem segments of non-stressed plants from 4 to 6 WAA may indicate that as the rate of grain fill declined the leaves produced excess photosynthate that accumulated in the stem segments raising the levels of RS. The decline of the RS content in the stem segments of non-stressed plants from 6 WAA to PM may indicate that as the plants approached maturity the photosynthetic rate of the plants declined resulting in less photosynthate being available to maintain RS levels. On the other hand, it is important to point out that sucrose and starch content levels did not decline as markedly as the RS content levels from 6 WAA to PM and in fact increased slightly in some of the stem segments of non-stressed plants. It is therefore difficult to conclude that the decline in the RS content levels from 6 WAA to PM represents utilization of the RS pool for grain fill, as RS may have been converted to sucrose and starch within the stem segments. Averaged over grain fill, the stem segments of non-stressed plants maintained higher RS content levels than stressed plants. This indicates that as a result of the reduced

photosynthetic capacity of stressed plants, photosynthate was rapidly translocated to the grain with less photosynthate available to maintain RS content levels in the stem segments as high as that in non-stressed plants.

At A the RS content of the cob of stressed plants was  $0,44 \text{ g (plant part)}^{-1}$  less than that of non-stressed plants (Figure 4.4). This may indicate that after 48 h without water stressed plants were translocating most of the available photosynthate into the grain with less photosynthate accumulating in the cob in the form of RS. If it is assumed that RS are associated with high metabolic activity of tissue during periods of, for example, structural growth then it is possible that the stressed plants partitioned less photosynthate to the cob itself to be utilized for structural growth. During the first two weeks the cob of stressed and non-stressed plants underwent a large increase in dry mass (Figure 4.12). From A to 2 WAA RS content levels in the cob of stressed plants increased sharply and exactly matched that in the cob of non-stressed plants which had increased slightly from A to 2 WAA. The physiological significance of the sharp rise in RS content in the cob of the stressed plants from A to 2 WAA is uncertain. From 2 to 4 WAA the RS content in the cob of stressed plants declined sharply by  $0,71 \text{ g (plant part)}^{-1}$  to its lowest levels, whereas that in non-stressed plants declined slightly. This sharp decline in RS content in the cob of stressed plants was associated with high levels of sucrose content and a sharp increase in the starch content in the cob. From 4 to 6 WAA RS content in the cob of stressed and non-stressed plants increased sharply and then

declined from 6 WAA to PM with the decline being marked in non-stressed plants. In fact, the RS content in the cob of stressed plants at PM was 0,11 g (plant part)<sup>-1</sup> more than that of non-stressed plants. The increase in the RS content in the cob of stressed and non-stressed plants from 4 to 6 WAA may indicate that after mid-grain fill the rate of grain dry mass gain declined and more photosynthate became available to accumulate in the cob. However, from 6 WAA to PM RS content in the cob of stressed and non-stressed plants declined which may indicate that less photosynthate was partitioned to the primary ear as the grain approached physiological maturity and it also may indicate that leaf senescence decreased the photosynthetic capacity of the plants. It is not certain why the RS content in the cob of the stressed plants at PM was higher than that of the non-stressed plants. On average over grain fill, non-stressed plants maintained higher RS content levels in the cob than did stressed plants. This indicates that as a result of the reduced photosynthetic capacity of the stressed plants, less photosynthate was available to maintain RS content levels in the cob as high as that of the non-stressed plants.

As with RS composition the patterns in the changes of RS content in the grain of stressed and non-stressed plants were very similar (Figure 4.4). At A the RS content in the grain of stressed plants was 0,16 g (plant part)<sup>-1</sup> less than that of non-stressed plants. It would appear that after 48 h without water stressed plants accumulated less carbohydrate in the grain in the form of RS. The physiological significance of this is not certain, however, since at A TNC content levels in the grain of

stressed plants was 0,16 g (plant part)<sup>-1</sup> more than that of non-stressed plants (Section 4.3.3.8). From A to 2 WAA the RS content in the grain of stressed and non-stressed plants remained fairly constant and then increased sharply from 2 to 4 WAA, with RS content in the grain of stressed and non-stressed plants reaching 1,45 and 1,95 g (plant part)<sup>-1</sup>, respectively. The peak RS content levels at 4 WAA coincided with mid-grain fill which is the period of maximal increase in the dry mass of the grain on an absolute basis. The high RS content levels at 4 WAA are associated with the process of sucrose inversion and starch deposition in the endosperm cells discussed earlier (Section 2.3.4.2). The higher RS content levels at 4 WAA in the grain of non-stressed plants reflect the overall greater amount of photosynthate translocated to the grain under non-stress conditions. From 4 WAA to PM the RS content in the grain of stressed and non-stressed plants declined sharply, as the rate at which sucrose was translocated to the grain and converted to starch declined. At PM the RS content in the grain of stressed plants was 0,27 g (plant part)<sup>-1</sup> less than that in non-stressed plants. Averaged over grain fill, non-stressed plants maintained higher RS content levels in the grain than stressed plants. This is indicative of the greater assimilation of CO<sub>2</sub> under non-stress conditions with consequently more photosynthate available to be partitioned to the grain.

#### 4.3.3.3 Sucrose composition

Sucrose composition in the stem segments of stressed plants ranged from 4,3 % in the A1 plant part at A to 34,6 % in the

shank at 2 WAA; and in the stem segments of non-stressed plants it ranged from 3,3 % in the shank at A to 26,5 % in the shank at 4 WAA. Sucrose composition in the cob of stressed plants ranged from 4,0 % at PM to 11,5 % at 2 WAA; and in the cob of non-stressed plants it ranged from 3,7 % at 6 WAA to 11,0 % at 2 WAA. Sucrose composition in the grain of stressed plants ranged from 0,8 % at 4 WAA to 9,0 % at A; and in the grain of non-stressed plants it ranged from 0,9 % at 6 WAA to 3,8 % at A (Figure 4.5).

At A sucrose composition in the stem segments of stressed and non-stressed plants was at its lowest levels (Figure 4.5). Except in non-stressed plants at A, sucrose composition in the shank of stressed and non-stressed plants throughout grain fill was higher than that in the A1 and B1 plant parts. This is indicative of the rôle of the shank as a conduit for photosynthate translocated to the grain, with sucrose the main translocatory form of carbohydrate. Also the A1 plant part of stressed and non-stressed plants generally recorded higher sucrose composition levels throughout grain fill than the B1 plant part. Sucrose composition increased in the stem segments of stressed and non-stressed plants from A to 2 WAA with the increase being most marked in the shank, particularly that of stressed plants. In fact, at 2 WAA sucrose composition in the shank of stressed plants was 8,8 % higher than that of non-stressed plants. The sharp increase in sucrose composition in the shank was accompanied by an increase in the sucrose content and therefore appears to reflect the increase in the partitioning of photosynthate to the grain from A to 2 WAA. On a relative basis it would appear that stressed plants mobilized more sucrose

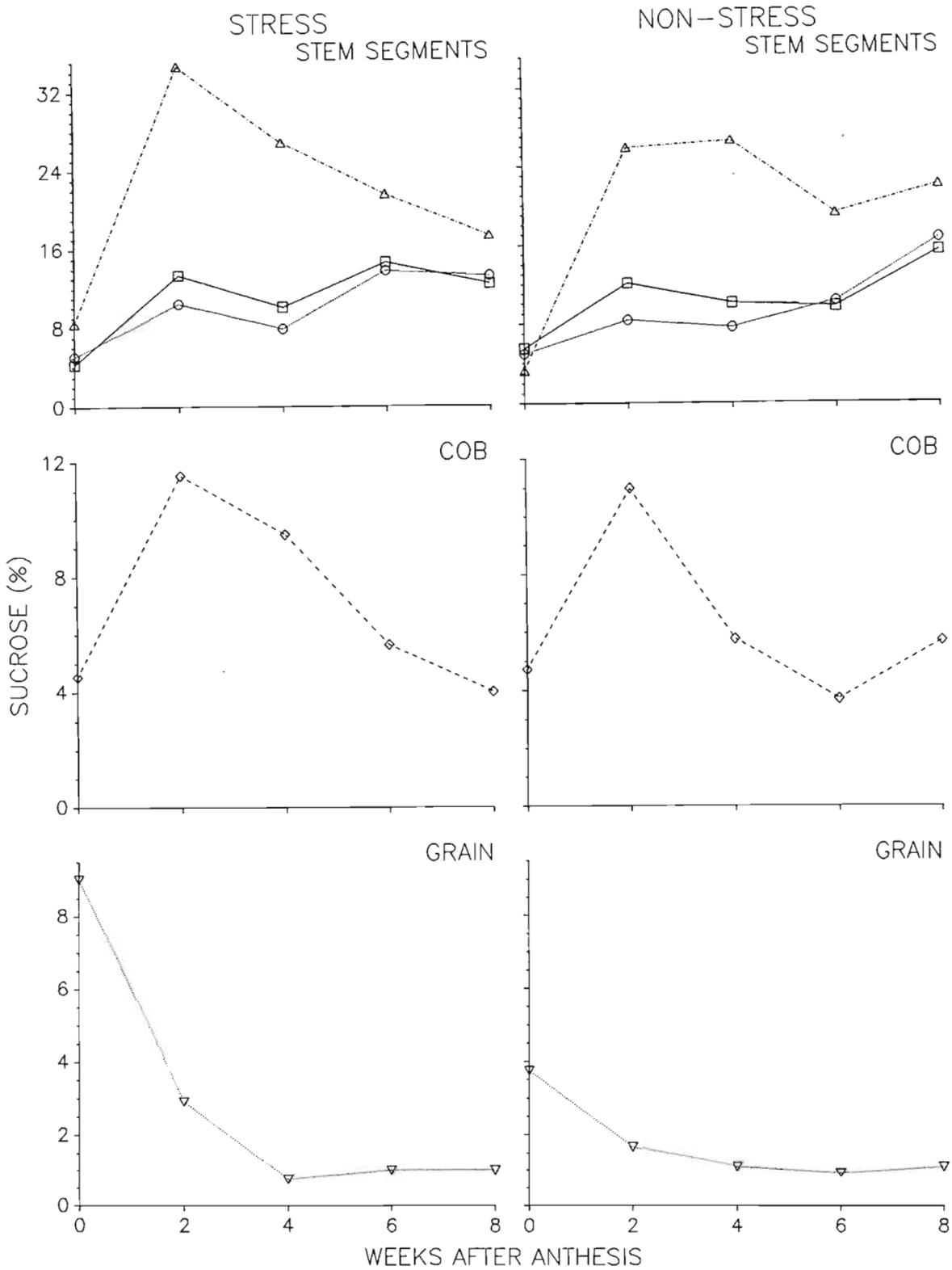


Figure 4.5 Effect of water stress from anthesis to physiological maturity on sucrose composition of selected plant parts from a maize hybrid

Key: A1 □—□ , B1 ○—○ , shank △—△

through the shank at 2 WAA than did non-stressed plants. This may indicate that stressed plants mobilized more of the available photosynthate directly to the grain. However, it is important to point out that the high concentration of sucrose in the shank of stressed plants may not necessarily translate into a higher amount of carbohydrate in the grain on an absolute basis. From 2 WAA to PM the sucrose composition in the shank of stressed plants declined. On the other hand, from 2 to 4 WAA sucrose composition in the shank of non-stressed plants increased slightly and then declined to 6 WAA before increasing to PM. It would appear that non-stressed plants maintained a higher concentration of sucrose in the shank in the latter half of grain fill than did stressed plants. This may indicate that stressed plants had less photosynthate available to mobilize to the grain from 4 WAA to PM, than did non-stressed plants. From 2 WAA to PM sucrose composition in the A1 and B1 plant parts of stressed plants fluctuated marginally, with levels declining at 4 WAA but with levels at PM similar to those at 2 WAA. In non-stressed plants sucrose composition in the A1 and B1 plant parts remained fairly constant from 2 to 6 WAA and then increased sharply to PM. This sharp increase in sucrose composition in the A1 and B1 plant parts of non-stressed plants was accompanied by a sharp increase in the sucrose content of these plant parts. This suggests that non-stressed plants produced photosynthate in excess to grain requirements during late grain fill which accumulated in the A1 and B1 plant parts as sucrose.

At A sucrose composition in the cob of stressed and non-stressed plants were similar, namely 4,5 and 4,7 %, respectively (Figure

4.5). Sucrose composition in the cob of stressed and non-stressed plants increased sharply to 11,5 and 11,0 % respectively, at 2 WAA. This sharp increase in sucrose composition was accompanied by a sharp increase in sucrose content and therefore probably reflects the increased translocation of sucrose through the cob to the grain. From 4 to 6 WAA sucrose composition declined sharply in both stressed and non-stressed plants. In fact, at 6 WAA sucrose composition in the cob of stressed plants was 1,9 % higher than that in non-stressed plants. The sharp decline in sucrose composition in the cob of non-stressed plants from 2 to 6 WAA was accompanied by a sharp decline in sucrose content. This may reflect the decline in sucrose mobilized to the grain, or it may indicate that the rate of grain fill was so rapid that little sucrose accumulated in the cells of the cob, with most of the sucrose occurring in the phloem of the cob as it was rapidly moved through the cob to the grain. From 6 WAA to PM sucrose composition in the cob of stressed plants declined, which was accompanied by a decline in sucrose content. However, from 6 WAA to PM sucrose composition in the cob of non-stressed plants increased, accompanied by an increase in the sucrose content. It would appear that as a result of their reduced photosynthetic capacity, stressed plants did not produce excess photosynthate during late grain fill which accumulated as sucrose in the cob, whereas non-stressed plants did.

At A sucrose composition in the grain of stressed plants was 5,2 % higher than that of non-stressed plants (Figure 4.5). It would appear that stressed plants concentrated more sucrose into

the grain than non-stressed plants, after 48 h without water. From A to 2 WAA sucrose composition declined markedly in the grain of stressed plants by 6,2 % and less markedly in the grain of non-stressed plants by 2,1 %. Since this decline in sucrose composition in the grain of stressed and non-stressed plants was accompanied by a sharp increase in sucrose content, it was due to the dilution effect of the substantial increase in dry mass of the grain that occurred during this period. From 2 to 4 WAA sucrose composition in the grain of stressed plants declined more markedly than that in the grain of non-stressed plants. From 4 WAA to PM sucrose composition increased slightly in the grain of stressed and non-stressed plants. Averaged over grain fill, the grain of stressed plants maintained higher sucrose composition levels than non-stressed plants, largely as a result of the higher concentration of sucrose that occurred in the grain of stressed plants from A to 2 WAA.

#### 4.3.3.4 Sucrose content

Sucrose content in the stem segments of stressed plants ranged from 0,11 g (plant part)<sup>-1</sup> in the shank at A to 1,38 g (plant part)<sup>-1</sup> in the B1 plant part at 6 WAA; and in the stem segments of non-stressed plants it ranged from 0,04 g (plant part)<sup>-1</sup> in the shank at A to 1,73 g (plant part)<sup>-1</sup> in the B1 plant part at PM. Sucrose content in the cob of stressed plants ranged from 0,17 g (plant part)<sup>-1</sup> at A to 1,69 g (plant part)<sup>-1</sup> at 2 WAA; and in the cob of non-stressed plants it ranged from 0,17 g (plant part)<sup>-1</sup> at A to 2,11 g (plant part)<sup>-1</sup> at 2 WAA. Sucrose content in the grain of

stressed plants ranged from 0,25 g (plant part)<sup>-1</sup> at A to 1,13 g (plant part)<sup>-1</sup> at 6 WAA; and in the grain of non-stressed plants it ranged from 0,09 g (plant part)<sup>-1</sup> at A to 1,54 g (plant part)<sup>-1</sup> at PM (Figure 4.6).

At A, and generally throughout grain fill, the B1 plant part, which was the largest stem segment, recorded the highest sucrose content of the three stem segments (Figure 4.6). It is of interest to note that at A the sucrose content in the shank of stressed plants was 0,16 g (plant part)<sup>-1</sup> more than that of the shank of non-stressed plants. It would appear that after 48 h without water stressed plants had mobilized more sucrose on an absolute basis into the shank, indicating perhaps a more rapid translocation of photosynthate to the grain under stress conditions. From A to 2 WAA the sucrose content in the stem segments of stressed and non-stressed plants increased. This may indicate that as final structural growth of the stem segments was completed excess photosynthate accumulated in the stem segments. It is noteworthy that sucrose content in the shank of stressed plants increased by 0,56 g (plant part)<sup>-1</sup> from A to 2 WAA compared to 0,45 g (plant part)<sup>-1</sup> for non-stressed plants. This may indicate that stressed plants mobilized more sucrose on an absolute basis through the shank during early grain fill than non-stressed plants. From 2 WAA to PM sucrose content in the A1 plant part and the shank of stressed plants declined slightly, whereas sucrose content in the B1 plant part of stressed plants declined sharply from 2 to 4 WAA, then increased sharply to 6 WAA and then declined to PM. In non-stressed plants sucrose content in the shank continued to increase from 2 to 4 WAA before

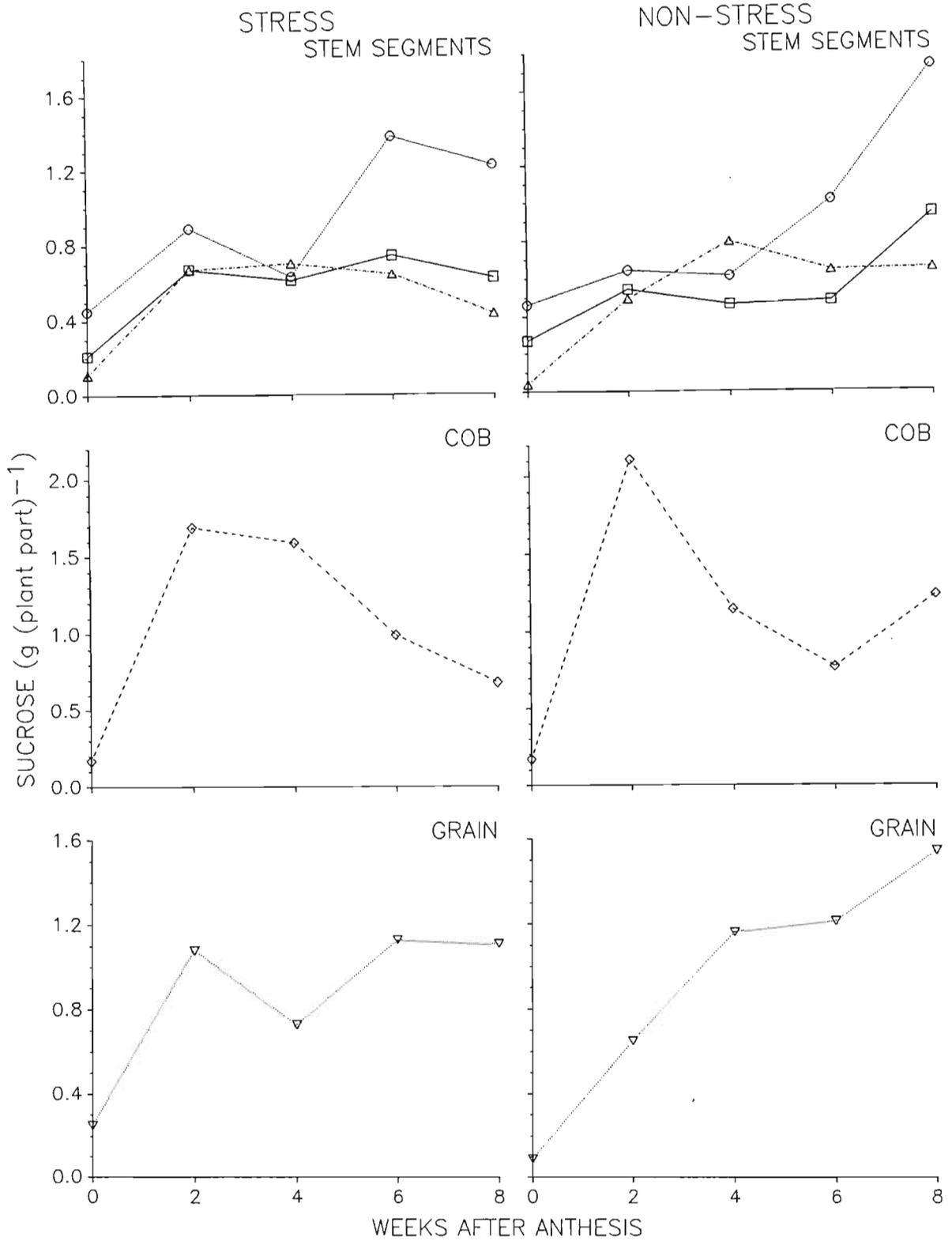


Figure 4.6 Effect of water stress from anthesis to physiological maturity on sucrose content of selected plant parts from a maize hybrid

Key: A1 □—□ , B1 ○—○ , shank △---△

declining slightly from 4 WAA to PM. Sucrose content in the A1 plant part of non-stressed plants declined slightly from 2 to 6 WAA and then increased sharply from 6 WAA to PM. Sucrose content in the B1 plant part of non-stressed plants declined slightly from 2 to 4 WAA and then increased most markedly from 4 WAA to PM by 1,12 g (plant part)<sup>-1</sup>. The greater increase in sucrose content in the shank of non-stressed plants from 2 to 4 WAA coinciding with peak grain fill compared to stressed plants, indicates that non-stressed plants were able to mobilize more photosynthate through the shank to the grain during peak grain fill, than were stressed plants. Also the marked increases in the sucrose content in the A1 and particularly the B1 plant parts from 4 WAA to PM in non-stressed plants, compared to the decline in sucrose content in these plant parts of stressed plants from 6 WAA to PM, indicates that stressed plants produced little excess photosynthate during late grain fill which accumulated in the stem segments as sucrose. In fact, it appears that stressed plants were forced to deplete the sucrose pool in the A1 and B1 plant parts to meet final grain and respiration requirements.

At A the sucrose content in the cob of stressed and non-stressed plants was the same (Figure 4.6). From A to 2 WAA sucrose content in the cob of stressed plants increased by 1,52 g (plant part)<sup>-1</sup>, whereas that in the cob of non-stressed plants increased more markedly by 1,94 g (plant part)<sup>-1</sup>. This sharp increase in sucrose content in the cob of stressed and non-stressed plants from A to 2 WAA is indicative of the increased translocation of photosynthate through the cob to the grain. It

would appear that non-stressed plants were able to mobilize more sucrose on an absolute basis through the cob than stressed plants. On the other hand, the lower sucrose content in the cob of stressed plants may indicate that sucrose occurred primarily in the phloem of the cob and was directly translocated to the grain with little sucrose accumulating in the cells of the cob. Once again, it is difficult to distinguish between sucrose in the translocation pathway and sucrose in temporary storage. From 2 to 4 WAA sucrose content declined slightly in the cob of stressed plants but declined sharply in the cob of non-stressed plants. From 4 WAA to PM sucrose content in the cob of stressed plants continued to decline, whereas sucrose content in the cob of non-stressed plants declined from 4 to 6 WAA and then increased sharply to PM. In fact, at PM sucrose content in the cob of non-stressed plants was  $0,55 \text{ g (plant part)}^{-1}$  more than that in the cob of stressed plants. The fact that non-stressed plants, on average over grain fill, maintained higher sucrose content levels in the cob than did stressed plants, together with the increase in sucrose content in the cob of non-stressed plants from 6 WAA to PM, is indicative of the greater capacity of non-stressed plants to synthesize and translocate photosynthate to the grain compared to stressed plants.

At A sucrose content in the grain of stressed plants was  $0,16 \text{ g (plant part)}^{-1}$  higher than that in the grain of non-stressed plants (Figure 4.6). From A to 2 WAA sucrose content in the grain of stressed plants increased markedly by  $0,83 \text{ g (plant part)}^{-1}$  compared to an increase of  $0,56 \text{ g (plant part)}^{-1}$  in non-stressed plants. Thus it would

appear that during the early part of grain fill stressed plants mobilized more sucrose into the grain on an absolute basis than did non-stressed plants. This may support the assertion made earlier that stressed plants had a smaller increase in the cob from A to 2 WAA than non-stressed plants as the sucrose mostly occurred in the phloem en route to the grain. However, from 2 to 4 WAA sucrose content in the grain of stressed plants declined by 0,35 g (plant part)<sup>-1</sup> whereas that in non-stressed plants increased by 0,51 g (plant part)<sup>-1</sup>. It would appear that at 4 WAA i.e. peak grain fill, the amount of photosynthate available to be mobilized to the grain as sucrose was limited in stressed plants and sucrose levels declined in the grain as it was converted to starch. On the other hand, non-stressed plants were able to mobilize enough sucrose to the grain, so much so that sucrose levels increased from 2 to 4 WAA. From 4 to 6 WAA sucrose content in the grain of stressed plants increased, whereas that in non-stressed plants remained constant. From 6 WAA to PM sucrose content in the grain of stressed plants declined marginally while that in the grain of non-stressed plants increased sharply. The fact that non-stressed plants on average over grain fill maintained higher sucrose content levels in the grain than did stressed plants, together with continual increases in sucrose content in the grain from A to PM, is indicative of the greater capacity of non-stressed plants to synthesize and translocate photosynthate to the grain compared to stressed plants.

The ratio of sucrose content to RS content was derived for each of the five plant parts in order to more readily assess the

amount of sucrose and RS in each plant part relative to one another (Table 4.4, Figure 4.7).

In the stem segments stressed plants on average maintained a higher sucrose content to RS content ratio in all three stem segments during grain fill than did non-stressed plants (Table 4.4, Figure 4.7). Generally stressed and non-stressed plants recorded the highest ratio of sucrose content to RS content in the three stem segments at 2 WAA, although the shank of non-stressed plants recorded its highest ratio at PM. The high sucrose content to RS content ratio recorded in the stem segments at 2 WAA is indicative of the decline in RS content from A to 2 WAA accompanied by the increase in sucrose content from A to 2 WAA. It appears that as structural growth of the stem segments ceased at 2 WAA and the grain became established as the major sink for photosynthate, sucrose became the more predominant sugar over RS in the stem segments. This probably reflects the occurrence of sucrose in these segments destined for the grain, with less carbohydrate in the form of RS being utilized for metabolic processes within the stem segments. At 2 WAA the ratio for the A1 and shank plant parts of stressed plants was markedly higher than that of non-stressed plants. This may indicate that stressed plants converted more assimilated CO<sub>2</sub> to sucrose for translocation to the grain in these plant parts and retained less carbohydrate in the form of RS for utilization within these plant parts.

As with the stem segments the ratio of sucrose content to RS content increased to greater than one from A to 2 WAA in the cob

Table 4.4 Ratio of sucrose content to reducing sugars (RS) content and ratio of starch content to sucrose content for selected plant parts of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from anthesis to eight weeks after anthesis (WAA)

Stress treatment	WAA	Plant part									
		A1		B1		Shank		Cob		Grain	
		Sucrose : RS	Starch: sucrose								
S	0	0,40	1,86	0,43	1,35	0,36	1,08	0,51	3,71	0,76	1,94
	2	4,01	0,59	2,89	0,65	4,53	0,21	1,98	0,84	3,52	20,98
	4	0,94	0,61	0,94	0,89	1,94	0,21	11,54	1,98	0,50	88,67
	6	2,47	0,51	2,37	0,53	1,94	0,34	1,39	2,13	1,20	68,75
	8	2,12	0,40	2,62	0,46	2,42	0,27	1,43	3,18	2,00	70,50
NS	0	0,52	1,46	0,46	1,46	0,13	2,52	0,22	4,19	0,19	4,64
	2	2,64	0,49	2,61	0,88	2,07	0,28	2,47	0,85	1,17	37,50
	4	1,23	0,48	1,52	0,48	2,01	0,26	1,47	1,91	0,60	62,39
	6	0,75	0,64	0,99	0,76	1,19	0,29	0,64	3,12	0,85	75,54
	8	1,96	0,33	2,33	0,45	3,95	0,31	3,41	2,39	1,88	66,74

Ratio of sucrose : RS SE ( $\bar{x}$ ) 1,02

Ratio of starch : sucrose SE ( $\bar{x}$ ) 13,72

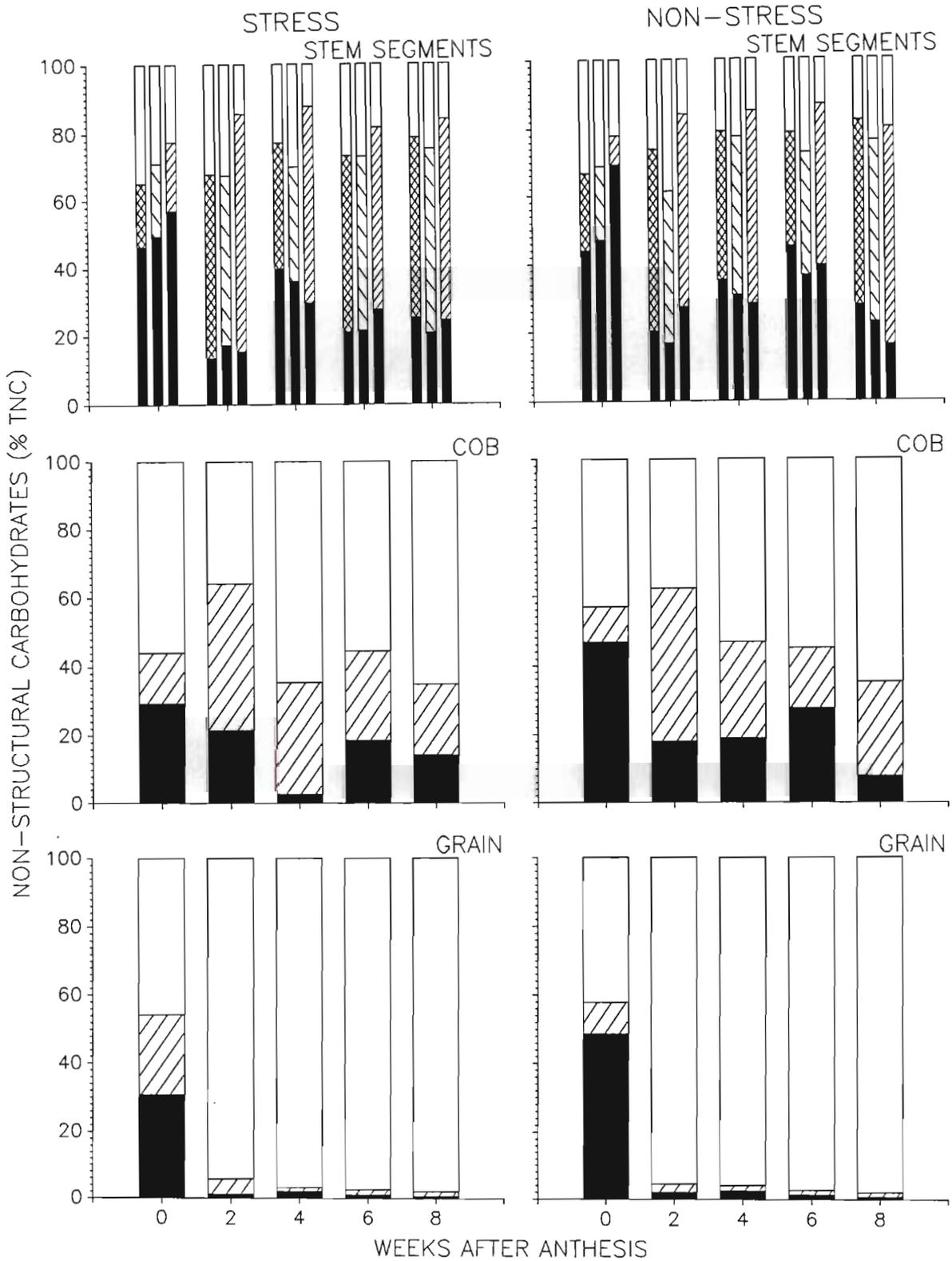


Figure 4.7 Effect of water stress from anthesis to physiological maturity on component non-structural carbohydrate content expressed as a percentage of total non-structural carbohydrate (TNC) content in selected plant parts from a maize hybrid

Key STEM SEGMENTS



COB & GRAIN



and, except for the cob of non-stressed plants at 6 WAA, remained above one for the rest of grain fill (Table 4.4, Figure 4.7). The increase in the ratio to greater than one at 2 WAA is indicative of sucrose becoming the predominant sugar in the cob as carbohydrate was mobilized to the grain in the form of sucrose. It is interesting to note that at 4 WAA the ratio of sucrose content to RS content in the cob of stressed plants was 11,54. This was the highest ratio recorded for the cob and is indicative of the marked depletion of RS in the cob of stressed plants at 4 WAA, probably as stressed plants converted all available carbohydrate to sucrose for translocation to the grain.

The patterns in the changes of the ratio of sucrose content to RS content in the grain are particularly interesting (Table 4.4, Figure 4.7). From 1 to 2 WAA the ratio increased to above one in the grain of stressed and non-stressed plants. This is indicative of the increased mobilization of sucrose to the grain, with the amount of sucrose in the grain exceeding the amount of RS. However, at 4 WAA i.e. peak grain fill, the rate at which sucrose was being inverted to RS for conversion to starch was apparently so rapid that the amount of RS in the grain exceeded the amount of sucrose arriving in the grain. The stressed plants at 2 WAA had a higher ratio of sucrose content to RS content indicating, perhaps, that they had translocated more sucrose to the grain, relative to the amount of RS in the grain, than had the non-stressed plants at this stage. At 4 WAA the non-stressed plants had a higher amount of sucrose relative to RS in the grain than did the stressed plants. This may indicate that stressed plants inverted more sucrose to RS in the grain at peak grain

fill than did non-stressed plants. From 6 WAA to PM, however, the stressed plants maintained a higher amount of sucrose relative to RS in the grain than did the non-stressed plants. This may indicate that in the latter phase of grain fill non-stressed plants inverted more sucrose to RS than stressed plants and therefore continued to form starch in the grain to a greater extent late into grain fill than stressed plants.

#### 4.3.3.5 Starch composition

Starch composition in the stem segments of stressed plants ranged from 4,7 % in the shank at PM to 9,2 % in the shank at A; and in non-stressed stem segments it ranged from 3,6 % in the B1 plant part at 4 WAA to 8,4 % in the shank at A. Starch composition in the cob of stressed plants ranged from 9,7 % at 2 WAA to 18,8 % at 4 WAA; and in the cob of non-stressed plants it ranged from 9,3 % at 2 WAA to 19,8 % at A. Starch composition in the grain of stressed plants ranged from 17,5 % at A to 70,5 % at PM; and in the grain of non-stressed plants it ranged from 17,4 % at A to 72,8 % at PM (Figure 4.8).

Starch composition in the stem segments of both stressed and non-stressed plants fluctuated considerably during grain fill (Figure 4.8). The shank of stressed and non-stressed plants recorded the highest starch composition of the stem segments at A. Starch composition in the A1 plant part of stressed plants remained constant from A to 2 WAA and then declined sharply to 4 WAA. Starch composition in the shank of stressed plants declined from A to 2 WAA with levels at 2 WAA similar to those in the A1 plant

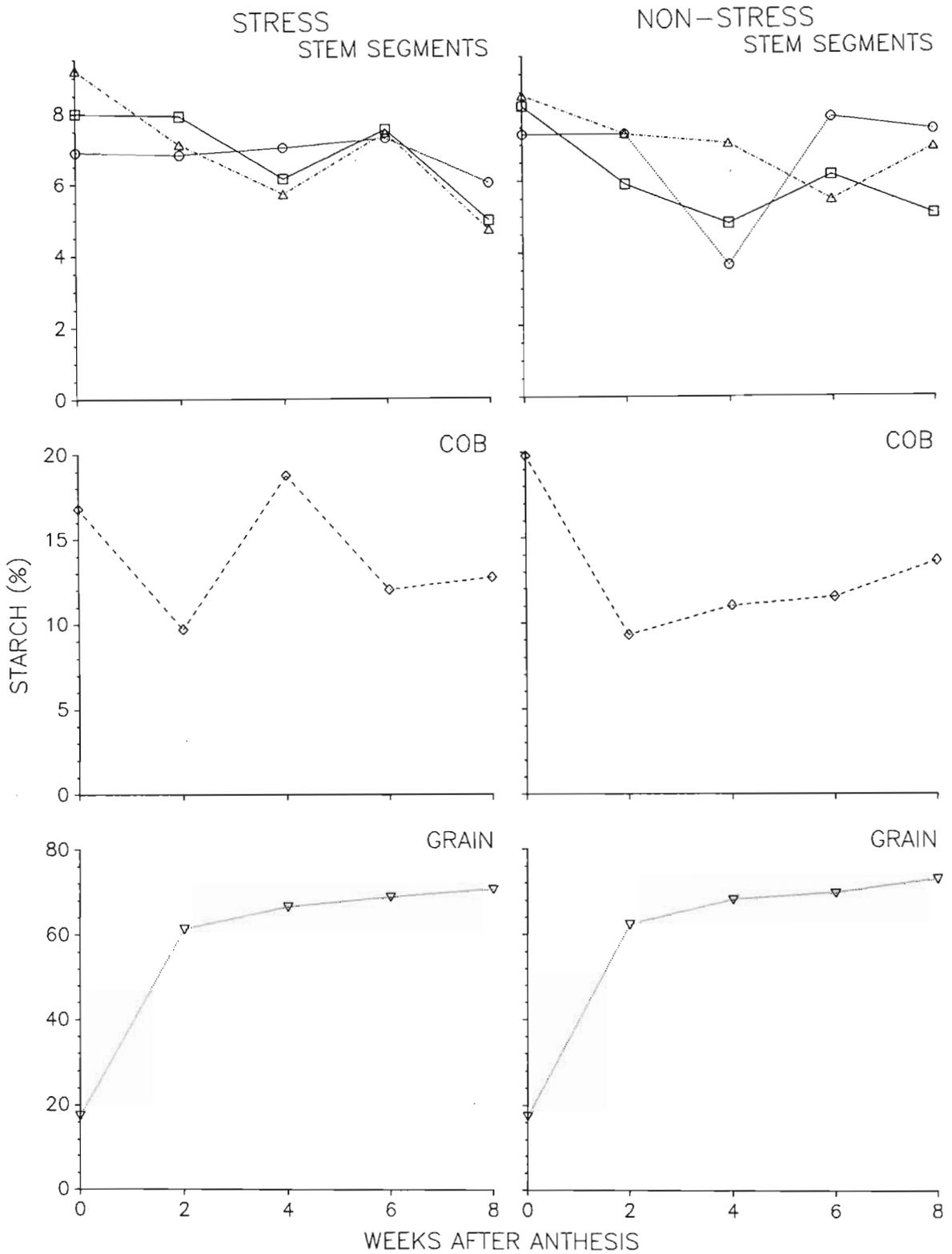


Figure 4.8 Effect of water stress from anthesis to physiological maturity on starch composition of selected plant parts from a maize hybrid

Key: A1  $\square-\square$  , B1  $\circ-\circ$  , shank  $\triangle-\triangle$

part. Since these changes in the starch composition of the A1 and shank plant parts of stressed plants were accompanied by fairly constant starch content levels from A to 2 WAA, they were due to changes in other components contributing to the dry mass of the plant parts. From 4 WAA to PM starch composition levels in the A1 and shank plant parts of stressed plants were very similar and initially increased from 4 to 6 WAA and then declined sharply to PM. Starch composition in the B1 plant part of stressed plants increased slightly from A to 6 WAA and then declined to PM. The decline in the starch composition of the three stem segments of stressed plants from 6 WAA to PM was accompanied by a decline in starch content and therefore indicates a depletion of the starch reserves in the last phase of grain fill. In the A1 and B1 plant parts of non-stressed plants starch composition declined from A to 4 WAA with the decline from 2 to 4 WAA, particularly marked in the B1 plant part. This decline in starch composition from A to 4 WAA in the A1 and B1 plant parts of non-stressed plants was accompanied by a decline in starch content and was therefore indicative of the depletion of starch reserves in these stem segments at peak grain fill. From 4 to 6 WAA starch composition in the A1 and B1 plant parts of non-stressed plants increased and then declined from 6 WAA to PM. Starch composition in the shank of non-stressed plants declined slightly from A to 4 WAA and then sharply to 6 WAA before increasing to PM. However, these changes in starch composition in the shank were accompanied by starch content levels increasing from A to 4 WAA and then remaining fairly constant to PM and are therefore due to changes in the amounts of other components contributing to dry mass of the shank.

Starch composition peaked at A in the cob of non-stressed plants and was 3,0 % higher than that in the cob of stressed plants (Figure 4.8). From A to 2 WAA starch composition declined sharply in the cob of stressed and non-stressed plants. However, since this was accompanied by an increase in the starch content in the cob of stressed and non-stressed plants it was due to the dilution effect of the substantial increase in dry mass the cob underwent from A to 2 WAA (Figure 4.12). From 2 to 4 WAA starch composition in the cob of stressed plants increased sharply and was due to a sharp increase in starch content in the cob. It appears that at peak grain fill stressed plants tended to convert a greater amount of the sucrose translocated to the cob, en route to the grain, to starch within the cob. The physiological significance of this is uncertain however, as it would perhaps have been expected that stressed plants would translocate the available sucrose directly into the grain with little available for accumulation in the cob in any labile form. From 4 to 6 WAA starch composition in the cob of stressed plants declined sharply and then increased slightly from 6 WAA to PM. These changes were mirrored by the changes in sucrose content and therefore it appears that stressed plants depleted the starch reserves in the cob from 4 to 6 WAA with a marginal reaccumulation occurring from 6 WAA to PM. In contrast to stressed plants starch composition in the cob of non-stressed plants increased gradually from 2 WAA to PM. As this increase in starch composition was accompanied by an increase in the starch content in the cob from 2 WAA to PM, it appears that non-stressed plants were able to increase the starch levels in the cob throughout grain fill. This is indicative of the greater assimilation of CO<sub>2</sub> and synthesis of

photosynthate that occurred under non-stress conditions, with photosynthate in excess to grain requirements accumulating as starch in the cob throughout grain fill.

The most outstanding feature of the data for starch composition in the grain is that the patterns of changes, and the absolute amount by which starch composition increased in the grain during grain fill, were remarkably similar for stressed and non-stressed plants (Figure 4.8). At A starch composition in the grain of stressed and non-stressed plants was 17,5 and 17,4 %, respectively. This increased sharply to 61,3 and 62,3 % at 2 WAA in stressed and non-stressed plants, respectively. From 2 WAA to PM starch composition increased less markedly to 70,5 and 72,8 % in stressed and non-stressed plants, respectively. Thus the stressed plants at PM had deposited 0,023 g of starch per gram of grain dry mass less than did the non-stressed plants.

#### 4.3.3.6 Starch content

Starch content in the stem segments of stressed plants ranged from 0,12 g (plant part)<sup>-1</sup> in the shank at A and at PM to 0,73 g (plant part)<sup>-1</sup> in the B1 plant part at 6 WAA; and in the stem segments of non-stressed plants it ranged from 0,11 g (plant part)<sup>-1</sup> in the shank at A to 0,77 g (plant part)<sup>-1</sup> in the B1 plant part at 6 WAA and at PM. Starch content in the cob of stressed plants ranged from 0,64 g (plant part)<sup>-1</sup> at A to 3,15 g (plant part)<sup>-1</sup> at 4 WAA; and in the cob of non-stressed plants it ranged from 0,71 g (plant part)<sup>-1</sup> at A to 2,94 g (plant part)<sup>-1</sup> at PM. Starch content in the grain of

stressed plants ranged from 0,40 g (plant part)<sup>-1</sup> at A to 78,04 g (plant part)<sup>-1</sup> at PM; and in the grain of non-stressed plants it ranged from 0,39 g (plant part)<sup>-1</sup> at A to 102,85 g (plant part)<sup>-1</sup> at PM (Figure 4.9).

The amount of starch in the stem segments was in accordance with the size of the segment, with the B1 plant part recording the highest starch content throughout grain fill and the shank the lowest starch content throughout grain fill (Figure 4.9). In stressed plants starch content in the A1 and B1 plant parts declined marginally from A to 4 WAA. From 4 to 6 WAA starch content increased marginally in the A1 plant part, while it increased sharply in the B1 plant part. From 6 WAA to PM starch content in the A1, and particularly the B1 plant part, of the stressed plants declined sharply. Starch content in the A1 and B1 stem segments at PM was lower than at A. Starch content in the shank of stressed plants increased gradually from A to 4 WAA and then increased more sharply from 4 to 6 WAA before declining to levels at PM which were the same as those at A. The physiological significance of the increase in starch content in the three stem segments of stressed plants from 4 to 6 WAA is not certain, however it may indicate that as the rate of grain dry mass gain slowed after peak grain fill more photosynthate became available to accumulate in these stem segments in the form of starch. However, as a result of the reduction in photosynthetic capacity through water stress and enhanced leaf senescence, the stressed plants depleted the starch reserves from 6 WAA to PM, so that at PM levels in the A1 and B1 plant parts were less than, and those in the shank equal to, the levels at A. In non-

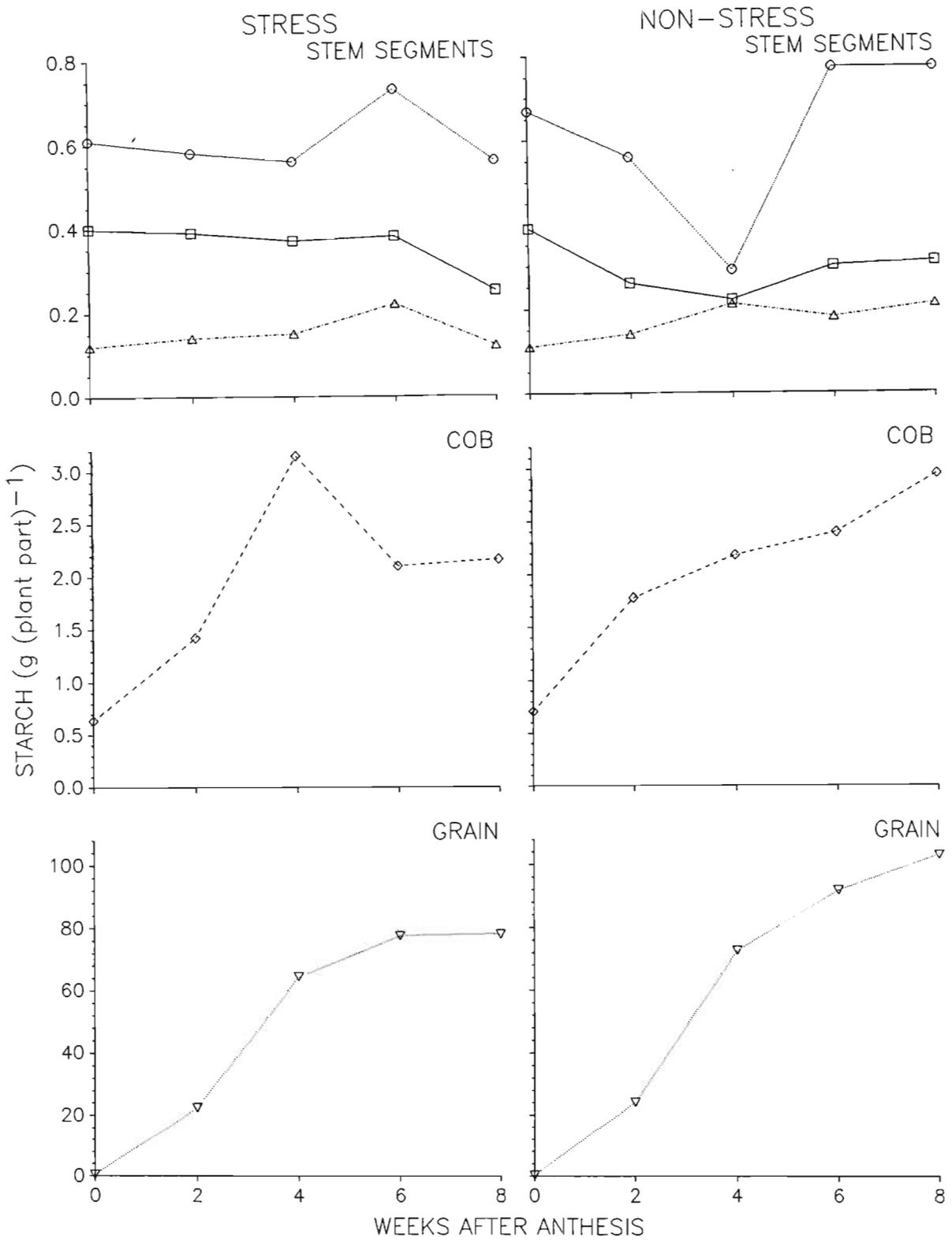


Figure 4.9 Effect of water stress from anthesis to physiological maturity on starch content of selected plant parts from a maize hybrid

Key: A1 □—□ , B1 ○—○ , shank △-△

stressed plants starch content in the A1 and B1 plant parts declined from A to 4 WAA with the decline being particularly marked in the B1 plant part from 2 to 4 WAA. Surprisingly, therefore, non-stressed plants appeared to deplete starch reserves in the A1 and B1 plant parts at peak grain fill to a much greater extent than did stressed plants. The physiological significance of this is uncertain. However, it may indicate the greater demand for carbohydrate by the grain under non-stress conditions. From 4 to 6 WAA starch content increased in the A1 and B1 plant parts. The increase of 0,48 g (plant part)<sup>-1</sup> during this period in the B1 plant part was particularly marked. From 6 WAA to PM starch content increased marginally in the A1 plant part and remained constant in the B1 plant part. It would appear that after peak grain fill, photosynthate in excess to grain requirements was available to accumulate in the A1 and B1 plant parts as starch. In the shank of non-stressed plants starch content increased from A to 4 WAA, decreasing slightly at 6 WAA and then increasing to levels at PM the same as at 4 WAA. The higher starch content in the shank at peak grain fill may be indicative of the rapid mobilization of photosynthate to the grain, with excess photosynthate to grain requirements accumulating in the shank. It is also possible that the starch in the shank serves as an emergency buffer to enable linear grain fill to continue should environmental conditions inhibit the production of current photosynthate. The increase in starch content from 4 to 6 WAA in the A1 and B1 plant parts of non-stressed plants, plus the higher starch content in all three stem segments at PM compared to stressed plants, was once again indicative of the greater capacity of non-stressed plants to

produce photosynthate in excess to grain requirements during late grain fill, which accumulated in the stem segments as starch. The stressed plants, on the other hand, did not deplete starch reserves in the stem segments at peak grain fill but did show a depletion of starch reserves in the stem segments from 6 WAA to PM. It would appear, therefore, that the reduced photosynthetic capacity of stressed plants as a result of water stress forced the depletion of available starch reserves to meet grain and respiration requirements.

At A starch content in the cob of stressed plants was 0,07 g (plant part)<sup>-1</sup> less than that in the cob of non-stressed plants (Figure 4.9). From A to 2 WAA starch content in the cob of stressed plants increased to 1,42 g (plant part)<sup>-1</sup> at 2 WAA and then increased sharply to 3,15 g (plant part)<sup>-1</sup> at 4 WAA. The high starch content in the cob of stressed plants at 4 WAA may explain the low RS content recorded in the cob at 4 WAA. It would appear that stressed plants converted some of the available RS in the cob to starch reserves. It is not certain what rôle the high levels of starch play in the cob under stress conditions since at 4 WAA non-stressed plants had not accumulated the same high levels of starch. In fact, it would have been expected that stressed plants would have had a reduced capacity to accumulate any starch in the cob with most available photosynthate being converted to starch in the grain itself. From 4 to 6 WAA starch content in the cob of stressed plants declined and then increased marginally to PM. It appears that after peak grain fill starch reserves were depleted in the cob as they were possibly utilized for grain and respiration requirements. In contrast to stressed

plants, starch content in the cob of non-stressed plants increased from A to PM reaching 2,94 g (plant part)<sup>-1</sup> at PM. This is indicative of the greater capacity of non-stressed plants to produce photosynthate in excess to grain requirements which continued to accumulate in the cob in the form of starch.

At A starch content in the grain of stressed plants was 0,48 g (plant part)<sup>-1</sup> while that in non-stressed plants was 0,42 g (plant part)<sup>-1</sup> (Figure 4.9). The fortnightly increase in starch content of the grain in stressed plants from A to PM was 22,14, 41,88, 13,11 and 0,43 g (plant part)<sup>-1</sup>, representing a daily starch accumulation of 1,58, 2,99, 0,94 and 0,03 g day<sup>-1</sup> for the same periods. In non-stressed plants the corresponding fortnightly increase in starch content was 23,80, 48,40, 19,07 and 11,16 g (plant part)<sup>-1</sup>, representing a daily starch accumulation of 1,70, 3,46, 1,36 and 0,80 g day<sup>-1</sup> for the same periods. It is clear that water stress reduced the rate at which starch was deposited in the grain of stressed plants and at PM starch content was 24,81 g (plant part)<sup>-1</sup> less in the grain of stressed plants than non-stressed plants. By 4 WAA or mid-grain fill stressed plants had attained 82,6 % of their final starch content and non-stressed plants had attained 70,6 % of their final starch content. This is once again indicative of the fact that non-stressed plants were able to produce more photosynthate than stressed plants to be mobilized to the grain, particularly in the last half of grain fill.

The ratio of starch content to sucrose content was derived for each of the five plant parts in order to more readily assess the

amount of starch and sucrose in each plant part relative to one another (Table 4.4, Figure 4.7).

On average over grain fill, stressed plants maintained a higher starch content to sucrose content ratio in the A1 plant part than non-stressed plants but a lower ratio in the B1 and shank plant parts (Table 4.4, Figure 4.7). As sucrose became the predominant form of non-structural carbohydrate from 2 WAA to PM, the ratio of starch content to sucrose content declined to less than one in all stem segments. It is of interest to note that at 4 WAA or peak grain fill stressed plants had a higher starch content to sucrose content ratio in the A1 and B1 plant parts than non-stressed plants but a lower ratio than non-stressed plants in the shank. The physiological significance of the higher starch content to sucrose content ratio at 4 WAA in the A1 and B1 plant parts under stress conditions is uncertain. However, the lower starch content to sucrose content ratio in the shank of stressed plants at 4 WAA compared to non-stressed plants, implies that there was less photosynthate to accumulate as starch in the shank under stress conditions.

Averaged over grain fill, non-stressed plants maintained a higher starch content to sucrose content ratio in the cob than did stressed plants (Table 4.4, Figure 4.7). It is of interest to note that at A the starch content to sucrose content ratio in the cob of stressed and non-stressed plants was greater than one, but at 2 WAA the starch content to sucrose content ratio declined to less than one. However, from 4 WAA to PM the starch content to sucrose content ratio was once again greater than one. It

appears that at 2 WAA there was a sharp increase in the amount of sucrose mobilized through the cob to the grain relative to the amount of starch in the cob. However, from 4 WAA to PM both stressed and non-stressed plants maintained a higher starch content to sucrose content ratio. It is possible that the starch in the cob serves as a temporary storage form of any excess sucrose mobilized to the grain that cannot be immediately converted into starch in the grain. The stressed plants had a higher starch content to sucrose content ratio for the cob at PM than did the non-stressed plants. It is not certain why the stressed plants had accumulated more starch relative to sucrose in the cob than did the non-stressed plants. However, it will be recalled that starch deposition in the grain of stressed plants declined markedly from 6 WAA to PM and it is therefore possible that any photosynthate that was available to be mobilized to the grain accumulated as starch in the cob during this period.

As is expected the starch content to sucrose content ratio in the grain of stressed and non-stressed plants was greater than one throughout grain fill (Table 4.4, Figure 4.7). The starch content to sucrose content ratio increased sharply from A to 2 WAA and again from 2 to 4 WAA in both stressed and non-stressed plants. The lower starch content to sucrose content ratio for the grain of stressed plants at A reflects the higher sucrose content recorded in the grain of stressed plants at A than non-stressed plants. The high starch content to sucrose content ratio for the grain of stressed plants at 4 WAA reflects the lower sucrose content recorded in the grain compared to non-

stressed plants. This implies that the amount of sucrose translocated to the grain under stress conditions was less than that under non-stress conditions, and therefore did not accumulate in the grain before being converted to starch to the same extent as was the case under non-stress conditions.

#### 4.3.3.7 Total non-structural carbohydrate composition

The TNC composition in the stem segments of stressed plants ranged from 20,8 % in the B1 plant part at 2 WAA to 49,3 % in the shank at 2 WAA; and in the stem segments of non-stressed plants it ranged from 16,2 % in the B1 plant part at 4 WAA to 46,7 % in the shank at 4 WAA. The TNC composition in the cob of stressed plants ranged from 19,5 % at PM to 30,1 % at A; and in the cob of non-stressed plants it ranged from 21,0 % at 6 WAA and at PM to 46,1 % at A. The TNC composition in the grain of stressed plants ranged from 38,3 % at A to 72,0 % at PM; and in the grain of non-stressed plants it ranged from 41,3 % at A to 74,4 % at PM (Figure 4.10).

The TNC composition in the shank of stressed and non-stressed plants was higher than that in the A1 and B1 plant parts throughout grain fill (Figure 4.10). This reflects its rôle as a conduit for photosynthate being translocated through it from the rest of the plant to the grain. The TNC composition in the shank of stressed plants increased from 41,0 % at A to 49,3 % at 2 WAA and then declined steadily to 29,0 % at PM. The TNC composition in the A1 and B1 plant parts of stressed plants generally increased from A to 6 WAA and then declined to PM. The

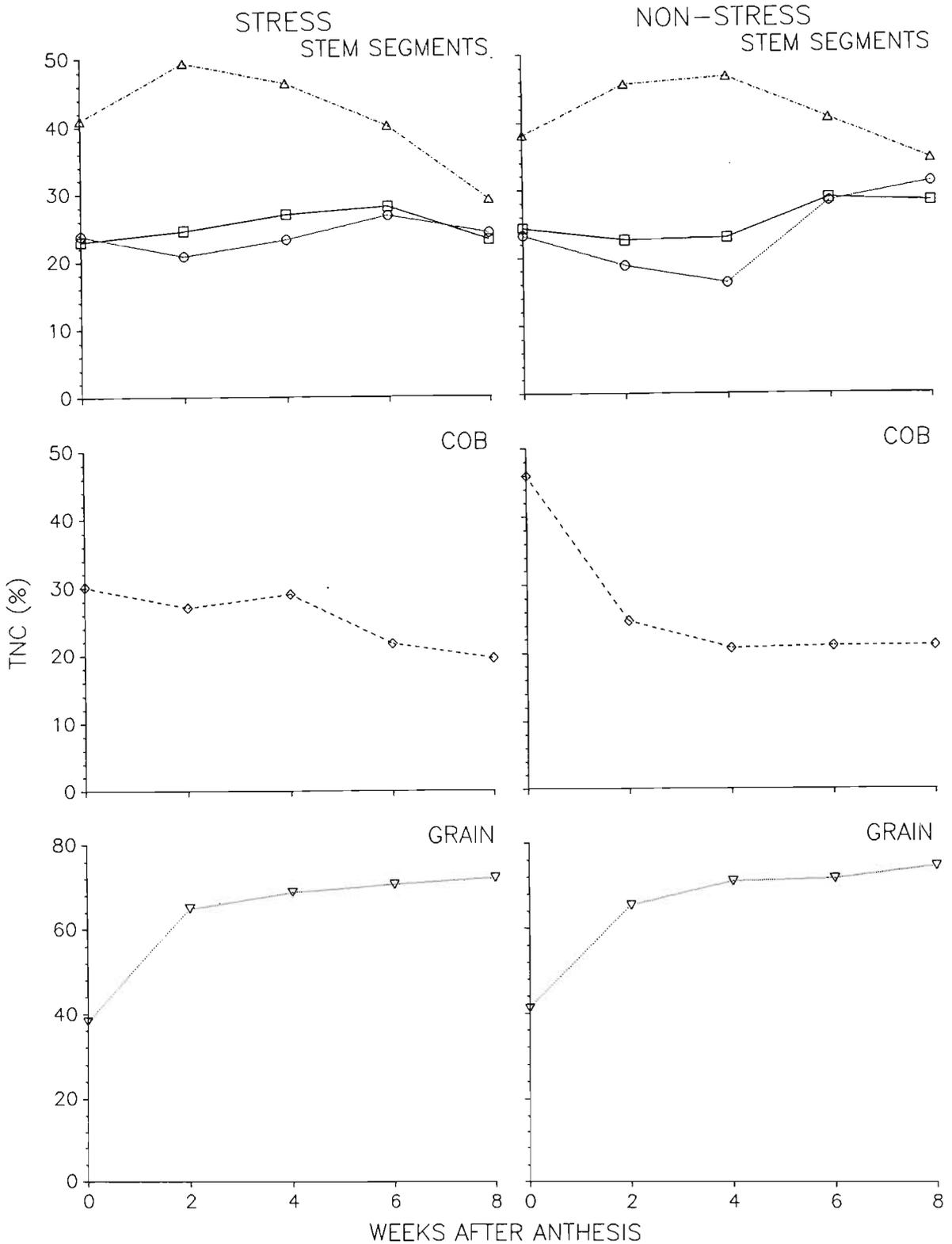


Figure 4.10 Effect of water stress from anthesis to physiological maturity on total non-structural carbohydrate (TNC) composition of selected plant parts from a maize hybrid  
 Key: A1  $\square$ — $\square$  , B1  $\circ$ — $\circ$  , shank  $\triangle$ — $\triangle$

decline in TNC composition from 6 WAA to PM in the three stem segments of stressed plants was accompanied by a decline in the TNC content during this period and is therefore indicative of a depletion of the TNC pool within these stem segments under stress conditions. In non-stressed plants TNC composition in the shank increased from 38,1 % at A to 45,6 % at 2 WAA, remained fairly constant from 2 to 4 WAA and then declined steadily to 34,4 % at PM. The TNC composition in the A1 plant part of non-stressed plants decreased from 24,4 % at A to 22,9 % at 4 WAA, then increased to 28,7 % at 6 WAA and then declined marginally to 28,2 % at PM. The TNC composition in the B1 plant part of non-stressed plants declined from 23,3 % at A to 16,2 % at 4 WAA and then increased to 31,0 % at PM. The initial increase in TNC composition from A to 4 WAA in the shank of non-stressed plants was accompanied by an increase in TNC content, and was therefore indicative of an increase in the amount of photosynthate, largely in the form of sucrose, being mobilized through it to the grain. The decline in TNC composition in the shank of non-stressed plants was accompanied by a decline in TNC content and was therefore indicative of a decline in the amount of photosynthate mobilized to the grain in the last half of grain fill. The decline in TNC composition in the A1 and B1 plant parts of non-stressed plants from A to 4 WAA was accompanied by a decline in TNC content, particularly in the B1 plant part, and was therefore indicative of a depletion of TNC in these stem segments as photosynthate was rapidly mobilized to the grain. The subsequent increase in the TNC composition from 4 WAA to PM in the A1 and B1 plant parts, accompanied by an increase in TNC content, was therefore indicative of the replenishment of TNC pools in these

stem segments as the rate of grain dry mass gain declined in the last half of grain fill.

The TNC composition in the cob of stressed plants declined slightly from 30,1 % at A to 29,0 % at 4 WAA and then declined more sharply to 19,5 % at PM (Figure 4.10). However, the initial decline in TNC composition in the cob from A to 4 WAA was accompanied by a sharp increase in TNC content and was therefore due to an increase in the amount of residual components which contribute to dry mass. The subsequent decline in TNC composition from 4 WAA to PM was accompanied by a decline in TNC content and was therefore indicative of the depletion of TNC pools in the cob in the last half of grain fill. The TNC composition in the cob of non-stressed plants declined sharply from 46,1 % at A to 24,7 % at 2 WAA. This was, however, accompanied by an increase in TNC content in the cob and is therefore indicative of the dilution effect, as the amount of residual components which contribute to dry mass increased during this period. From 2 WAA TNC composition in the cob declined to 21,0 % at PM. This was accompanied by a decline in TNC content at 4 WAA followed by an increase in TNC content to levels at PM lower than at 2 WAA. Overall then, the decline in TNC composition in the cob of non-stressed plants was due to lower levels of TNC being maintained in the cob during this period.

The changes in TNC composition in the grain of stressed and non-stressed plants were very similar to the changes in starch composition in the grain (Figure 4.10). The TNC composition in the grain of stressed plants increased from 38,3 % at A to 65,0 %

at 2 WAA and then increased marginally to 72,0 % at PM. The TNC composition in the grain of non-stressed plants increased from 41,3 % at A to 65,3 % at 2 WAA and increased marginally to 74,4 % at PM. Thus at PM the stressed plants had deposited 0,024 g of TNC per gram of grain dry mass less than did the non-stressed plants.

#### 4.3.3.8 Total non-structural carbohydrate content, residual content and dry mass

The TNC content in the stem segments of stressed plants ranged from 0,52 g (plant part)<sup>-1</sup> in the shank at A to 2,69 g (plant part)<sup>-1</sup> in the B1 plant part at 6 WAA; and in the stem segments of non-stressed plants it ranged from 0,48 g (plant part)<sup>-1</sup> in the shank at A to 3,24 g (plant part)<sup>-1</sup> in the B1 plant part at PM. Residual content in the stem segments of stressed plants ranged from 0,75 g (plant part)<sup>-1</sup> in the shank at A to 7,37 g (plant part)<sup>-1</sup> in the B1 plant part at 6 WAA; and in the stem segments of non-stressed plants it ranged from 0,78 g (plant part)<sup>-1</sup> in the shank at A to 7,21 g (plant part)<sup>-1</sup> in the B1 plant part at PM. Dry mass of the stem segments of stressed plants ranged from 1,27 g (plant part)<sup>-1</sup> for the shank at A to 10,06 g (plant part)<sup>-1</sup> for the B1 plant part at 6 WAA; and in the stem segments of non-stressed plants it ranged from 4,80 g (plant part)<sup>-1</sup> for the shank at A to 10,45 g (plant part)<sup>-1</sup> for the B1 plant part at PM (Figures 4.11 and 4.12).

The TNC content in the cob of stressed plants ranged from 1,14 g (plant part)<sup>-1</sup> at A to 4,88 g (plant part)<sup>-1</sup> at 4 WAA; and

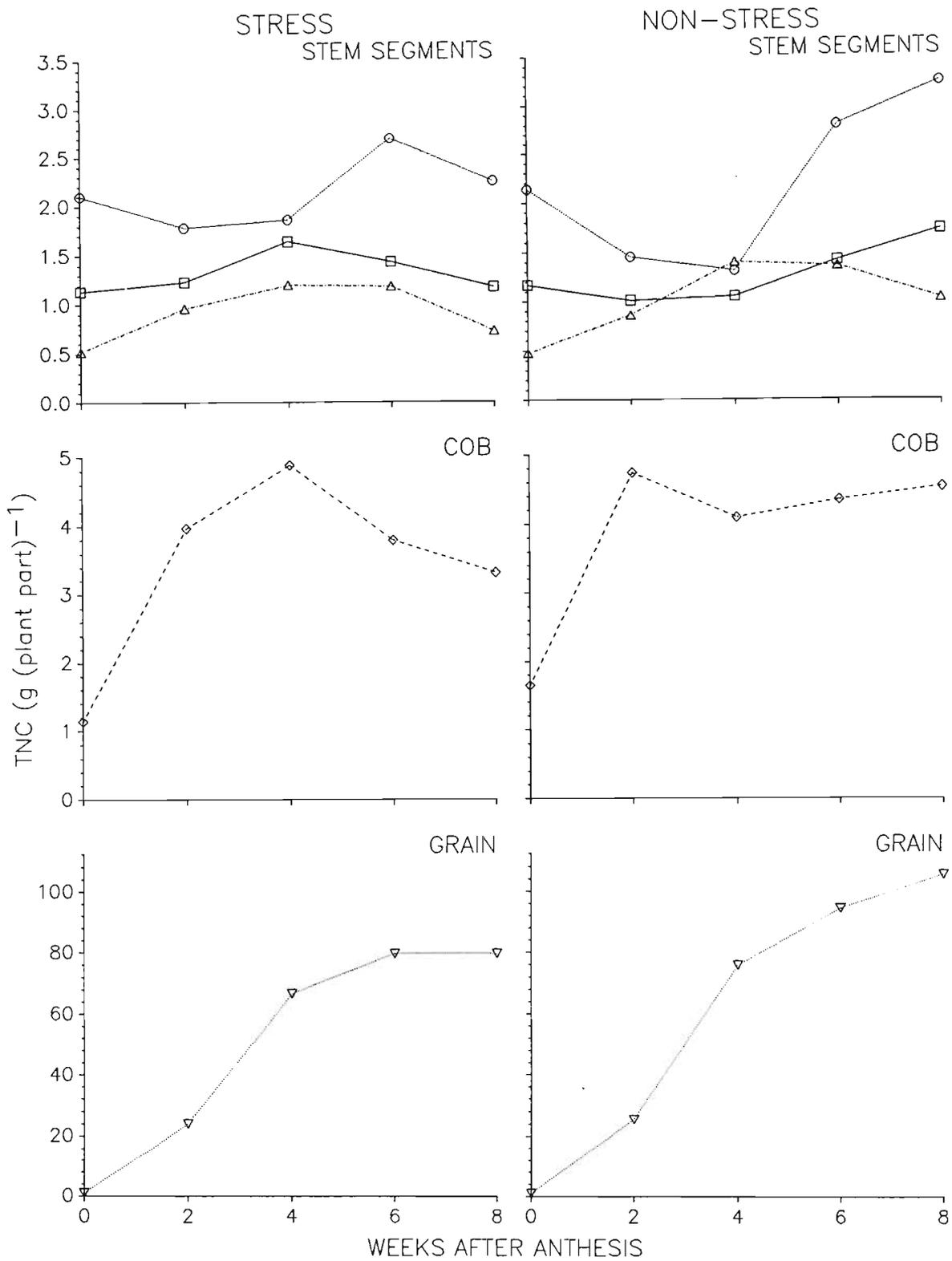


Figure 4.11 Effect of water stress from anthesis to physiological maturity on total non-structural carbohydrate (TNC) content of selected plant parts from a maize hybrid

Key: A1  $\square$ — $\square$  , B1  $\circ$ — $\circ$  , shank  $\triangle$ — $\triangle$

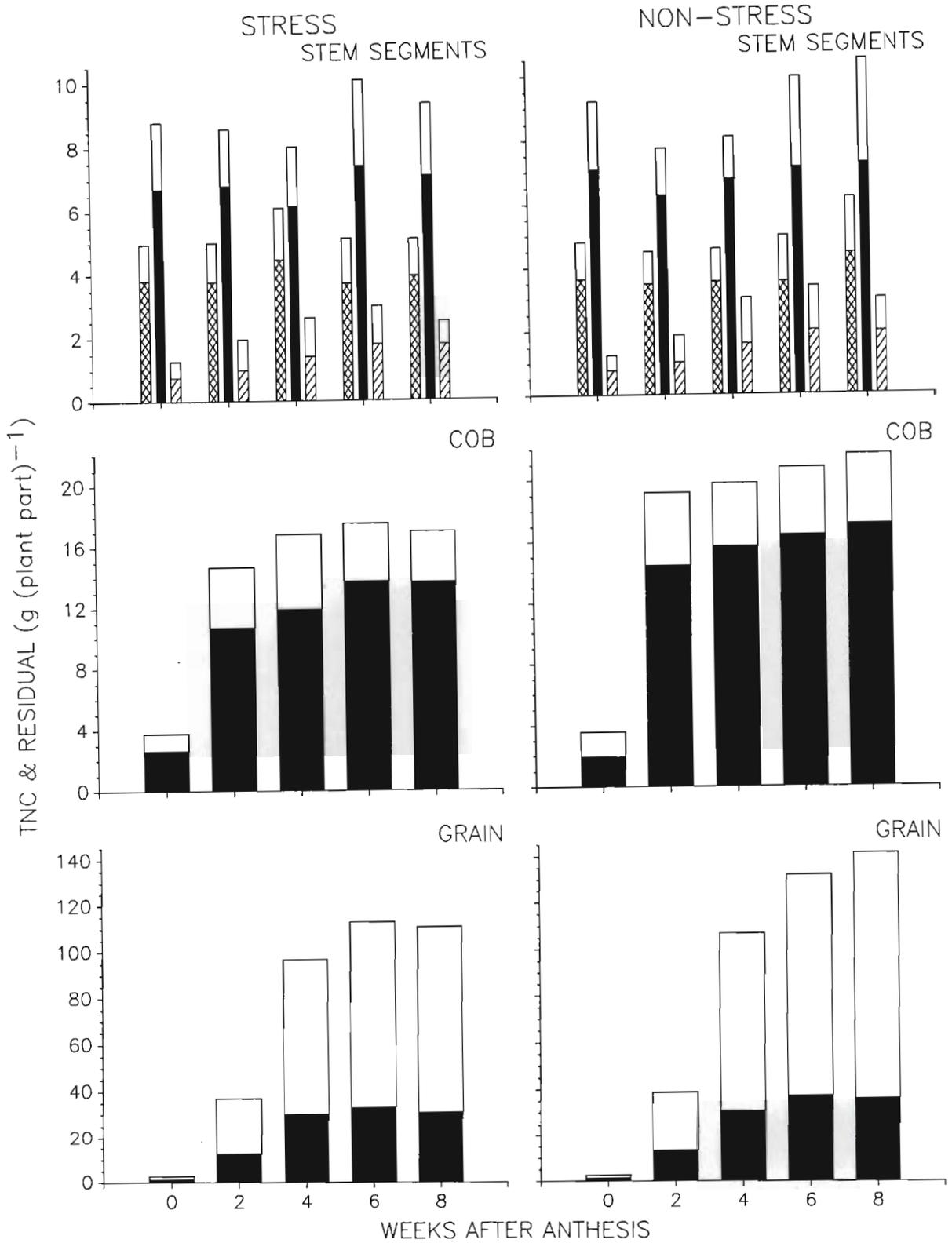


Figure 4.12 Effect of water stress from anthesis to physiological maturity on total non-structural carbohydrate (TNC) and residual content, and dry mass of selected plant parts from a maize hybrid

Key

STEM SEGMENTS

- TNC Residual A1
- TNC Residual B1
- TNC Residual Shank

COB & GRAIN

- TNC
- Residual

in the cob of non-stressed plants it ranged from 1,65 g (plant part)<sup>-1</sup> at A to 4,74 g (plant part)<sup>-1</sup> at 2 WAA. Residual content in the cob of stressed plants ranged from 2,66 g (plant part)<sup>-1</sup> at A to 13,71 g (plant part)<sup>-1</sup> at 6 WAA; and in the cob of non-stressed plants it ranged from 1,94 g (plant part)<sup>-1</sup> at A to 17,07 g (plant part)<sup>-1</sup> at PM. Dry mass of the cob of stressed plants ranged from 3,80 g (plant part)<sup>-1</sup> at A to 17,50 g (plant part)<sup>-1</sup> at 6 WAA; and in the cob of non-stressed plants it ranged from 3,59 g (plant part)<sup>-1</sup> at A to 21,60 g (plant part)<sup>-1</sup> at PM (Figures 4.11 and 4.12).

The TNC content in the grain of stressed plants ranged from 1,05 g (plant part)<sup>-1</sup> at A to 79,07 g (plant part)<sup>-1</sup> at PM; and in the grain of non-stressed plants it ranged from 0,99 g (plant part)<sup>-1</sup> at A to 105,21 g (plant part)<sup>-1</sup> at PM. Residual content in the grain of stressed plants ranged from 1,70 g (plant part)<sup>-1</sup> at A to 33,21 g (plant part)<sup>-1</sup> at 6 WAA; and in the grain of non-stressed plants it ranged from 1,41 g (plant part)<sup>-1</sup> at A to 37,60 g (plant part)<sup>-1</sup> at 6 WAA. Dry mass of the grain of stressed plants ranged from 2,75 g (plant part)<sup>-1</sup> at A to 112,89 g (plant part)<sup>-1</sup> at 6 WAA; and in the grain of non-stressed plants it ranged from 2,40 g (plant part)<sup>-1</sup> at A to 141,38 g (plant part)<sup>-1</sup> at PM (Figures 4.11 and 4.12).

The amount of TNC in the stem segments was in accordance with the size of the plant part, with the B1 plant part recording the highest TNC content throughout grain fill and the shank the

lowest TNC content throughout grain fill (Figures 4.11 and 4.12). However, TNC content in the shank of non-stressed plants at 4 WAA was higher than that in the A1 plant part at 4 WAA. The TNC content in the A1 plant part of stressed plants increased from 1,14 g (plant part)<sup>-1</sup> at A to 1,64 g (plant part)<sup>-1</sup> at 4 WAA and then declined to 1,17 g (plant part)<sup>-1</sup> at PM. The dry mass and residual content of the A1 plant part of stressed plants also increased from A to 4 WAA and, in fact, peaked at 4 WAA before declining to PM. It appears that in the first half of grain fill the stressed plants accumulated TNC and residual components in the A1 plant part, before depleting TNC and residual components in the A1 plant part during the last half of grain fill. The TNC content in the B1 plant part of stressed plants declined from 2,10 g (plant part)<sup>-1</sup> at A to 1,78 g (plant part)<sup>-1</sup> at 2 WAA, then increased slightly to 1,86 g (plant part)<sup>-1</sup> at 4 WAA and then increased sharply to 2,69 g (plant part)<sup>-1</sup> at 6 WAA, before declining to 2,24 g (plant part)<sup>-1</sup> at PM. Residual content in the B1 plant part generally reflected these changes in TNC content. It appears that from A to 4 WAA there was an overall depletion of TNC and residual components in the B1 plant part of stressed plants, followed by a reaccumulation from 4 to 6 WAA and then a depletion from 6 WAA to PM in TNC and residual components. The TNC content in the shank of stressed plants increased from 0,52 g (plant part)<sup>-1</sup> at A to 1,20 g (plant part)<sup>-1</sup> at 4 WAA, then decreased to 1,18 g (plant part)<sup>-1</sup> at 6 WAA and then declined sharply to 0,72 g (plant part)<sup>-1</sup> at PM. Residual content in the shank of stressed plants increased from 0,75 g (plant part)<sup>-1</sup> at A to 1,78 g (plant part)<sup>-1</sup> at 6 WAA before declining marginally to 1,76 g (plant part)<sup>-1</sup> at PM. The increase in TNC content in

the shank from A to 4 WAA reflects the increase in the amount of photosynthate mobilized through the shank to the grain from the rest of the plant, with the highest amount of TNC in the shank occurring at 4 WAA i.e. peak grain fill. The decline in TNC content in the shank of stressed plants from 4 WAA to PM reflects the decline in the amount of photosynthate mobilized to the grain with TNC levels in the shank being depleted. On the other hand, it is surprising to note that the amount of residual components in the shank of stressed plants increased steadily from A to 6 WAA and only declined marginally at PM. Why the stressed plants could afford to convert available photosynthate into residual components in the shank is not certain. The TNC content in the A1 plant part of non-stressed plants declined from 1,17 g (plant part)<sup>-1</sup> at A to 1,05 g (plant part)<sup>-1</sup> at 4 WAA and then increased sharply to 1,73 g (plant part)<sup>-1</sup> at PM. Residual content in the A1 plant part at A was 3,63 g (plant part)<sup>-1</sup> at A and remained fairly constant at this level until 6 WAA whereupon it increased to 4,41 g (plant part)<sup>-1</sup> at PM. It appears that non-stressed plants depleted TNC levels in the A1 plant part slightly during the first half of grain fill and then as the rate of grain dry mass gain declined in the last half of grain fill, excess photosynthate became available which accumulated and increased TNC levels in the A1 plant part. Residual components were not depleted in the A1 plant part from A to 6 WAA, in fact as excess photosynthate became available it was also accumulated as residual components in the A1 plant part from 6 WAA to PM. The TNC content in the B1 plant part declined from 2,14 g (plant part)<sup>-1</sup> at A to 1,31 g (plant part)<sup>-1</sup> at 4 WAA and then increased sharply to 3,24 g (plant part)<sup>-1</sup> at PM. Residual

content in the B1 plant part of non-stressed plants declined from 7,07 g (plant part)<sup>-1</sup> at A to 6,27 g (plant part)<sup>-1</sup> at 2 WAA before increasing to 7,21 g (plant part)<sup>-1</sup> at PM. Thus it appears that non-stressed plants depleted TNC in the B1 plant part during the first half of grain fill and in fact, rather surprisingly, to a greater extent than did stressed plants. The non-stressed plants also apparently depleted residual components from A to 2 WAA. However, in the last half of grain fill, as the rate of grain dry mass gain declined, photosynthate in excess to grain requirements accumulated and increased TNC levels in the B1 plant part. The TNC content in the shank of non-stressed plants increased from 0,48 g (plant part)<sup>-1</sup> at A to 1,40 g (plant part)<sup>-1</sup> at 4 WAA. In fact, at 4 WAA the TNC content in the shank of non-stressed plants was 0,20 g (plant part)<sup>-1</sup> more than that in the shank of stressed plants. This probably reflects the greater capacity of non-stressed plants to translocate more photosynthate through the shank to the grain than stressed plants. However, as the rate of grain dry mass gain declined from 4 WAA to PM, TNC content declined in the shank of non-stressed plants to 1,03 g (plant part)<sup>-1</sup> at PM. At PM the TNC content in the A1, B1 and shank plant parts of stressed plants was 67,6, 69,1 and 69,9 % of that in respective plant parts of non-stressed plants. This reflects the lower photosynthetic capacity of stressed plants to maintain TNC levels in the stem segments at the same levels as non-stressed plants. While TNC content increased in the A1 and B1 plant parts of non-stressed plants during the final phase of grain fill, TNC content declined in the A1 and B1 plant parts of stressed plants.

The TNC content in the cob of stressed plants increased markedly from 1,14 g (plant part)<sup>-1</sup> at A to 3,97 g (plant part)<sup>-1</sup> at 2 WAA and then increased less markedly to 4,88 g (plant part)<sup>-1</sup> at 4 WAA before declining to 3,31 g (plant part)<sup>-1</sup> at PM (Figures 4.11 and 4.12). Residual content in the cob of stressed plants increased from 2,66 g (plant part)<sup>-1</sup> at A to 13,71 g (plant part)<sup>-1</sup> at 6 WAA before declining marginally to 13,64 g (plant part)<sup>-1</sup> at PM. The substantial increase in residual content in the cob from A to 2 WAA of 8,03 g (plant part)<sup>-1</sup> reflects the large increase in volume and mass that the cob underwent during early grain fill. The substantial increase in TNC content in the cob from A to 4 WAA reflects the mobilization of photosynthate through the cob to the grain. However, it is not certain why at 4 WAA TNC content in the cob of stressed plants was 0,79 g (plant part)<sup>-1</sup> higher than that in the cob of non-stressed plants. It will be recalled that stressed plants had accumulated a higher amount of starch in the cob at 4 WAA than did non-stressed plants. In fact, the greater proportion of the TNC in the cob of stressed plants was made up by starch. The decline in the TNC content in the cob of stressed plants from 4 WAA to PM reflects the decline in the production of photosynthate resulting in a depletion in TNC levels in the cob. On the other hand, residual content in the cob increased by 1,79 g (plant part)<sup>-1</sup> from 4 to 6 WAA before declining slightly to PM. It appears that part of the TNC in the cob of stressed plants may have been converted to residual components. The physiological significance of this is, however, uncertain. The TNC content in the cob of non-stressed plants increased from 1,65 g (plant part)<sup>-1</sup> at A to 4,74 g (plant part)<sup>-1</sup> at 2 WAA and then declined to 4,09 g (plant part)<sup>-1</sup> at 4 WAA

before increasing to 4,53 g (plant part)<sup>-1</sup> at PM. Residual content in the cob of non-stressed plants increased from 1,94 g (plant part)<sup>-1</sup> at A to 17,07 g (plant part)<sup>-1</sup> at PM. The substantial increase in residual content of 12,50 g (plant part)<sup>-1</sup> from A to 2 WAA reflects the large increase in volume and mass that the cob underwent during early grain fill. The substantial increase in TNC content in the cob of non-stressed plants from A to 2 WAA reflects the mobilization of photosynthate through the cob to the grain. However, in contrast to stressed plants, non-stressed plants depleted the TNC in the cob at 4 WAA and then in the last half of grain fill photosynthate in excess to grain requirements accumulated and increased the levels in the cob. The non-stressed plants did, however, manage to increase the residual content in the cob throughout grain fill. At PM TNC content in the cob of stressed plants was 73,1 % of that in the cob of non-stressed plants. At PM the dry mass of the cob of stressed plants was 78,5 % of that of non-stressed plants. Thus the lower TNC content in the cob of stressed plants at PM, plus the lower dry mass of the cob of stressed plants is indicative of the reduced photosynthetic capacity of stressed plants with less photosynthate partitioned to the cob under stress conditions.

The TNC content in the grain of stressed plants increased from 1,05 g (plant part)<sup>-1</sup> at A to 79,70 g (plant part)<sup>-1</sup> at PM (Figures 4.11 and 4.12). Residual content in the grain of stressed plants increased from 1,70 g (plant part)<sup>-1</sup> at A to 33,21 g (plant part)<sup>-1</sup> at 6 WAA before declining to 30,99 g (plant part)<sup>-1</sup> at PM. The TNC content in the grain of non-stressed plants increased from

0,99 g (plant part)<sup>-1</sup> at A to 105,21 g (plant part)<sup>-1</sup> at PM. Residual content in the grain of non-stressed plants increased from 1,70 g (plant part)<sup>-1</sup> at A to 37,60 g (plant part)<sup>-1</sup> at 6 WAA and then declined to 36,17 g (plant part)<sup>-1</sup> at PM. The fortnightly increase in grain dry mass of stressed plants from A to 6 WAA was 34,18, 60,07 and 15,89 g (plant part)<sup>-1</sup>, representing a daily increase in the grain dry mass of 2,44, 4,29 and 1,14 g day<sup>-1</sup> during the same periods. From 6 WAA to PM grain dry mass in stressed plants declined by 2,20 g (plant part)<sup>-1</sup>, representing a daily decrease in grain dry mass of 0,16 g day<sup>-1</sup> during the same period. In non-stressed plants the fortnightly increase in grain dry mass from A to PM was 36,51, 67,88, 25,14 and 9,45 g (plant part)<sup>-1</sup>, representing a daily increase in grain dry mass of 2,61, 4,85, 1,80 and 0,68 g day<sup>-1</sup> for the same periods. It is apparent from these calculations that the peak rate of grain dry mass gain for stressed and non-stressed plants was from 2 to 4 WAA. Throughout grain fill the rate of dry mass gain by the grain of non-stressed plants exceeded that of stressed plants. At PM the TNC content in the grain of stressed plants was 75,8 % of that in the grain of non-stressed plants; and the dry mass of the grain of stressed plants at PM was 78,3 % of that of non-stressed plants. By 4 WAA or mid-grain fill stressed plants had attained 87,6 % of their final grain dry mass, whereas non-stressed plants had attained 75,5 % of their final grain dry mass. Thus it is clear that non-stressed plants were able to produce more current photosynthate than stressed plants, to be mobilized to the grain. In fact, non-stressed plants produced photosynthate in excess to grain requirements in the last half of grain fill, which accumulated as TNC and

residual components in the stem segments and cob. This indicates that sink size limited yield production in B254W x M162W under the non-stress conditions that prevailed in this experiment. On the other hand, current photosynthate production in stressed plants was particularly limited in the last half of grain fill as TNC and residual components in the stem segments and cob were depleted to meet grain fill and respiration requirements.

The ratio of TNC content to residual content was derived to more readily assess the amounts of these fractions relative to one another (Table 4.5). It is of interest to note that averaged over grain fill stressed and non-stressed plants had the same ratio of TNC content to residual content in the A1 and B1 plant parts. However, averaged over grain fill the ratio of TNC content to residual content was slightly higher in the shank of stressed plants than non-stressed plants. This may indicate that stressed plants mobilized less residual components through the shank, or accumulated less residual components in the shank, than did non-stressed plants during grain fill. On the other hand, averaged over grain fill non-stressed plants maintained a higher TNC content to residual content ratio in the cob and grain. This is indicative of the capacity of non-stressed plants to accumulate more TNC in the cob and grain relative to the residual components in these plant parts compared to stressed plants.

Table 4.5 Ratio of total non-structural carbohydrate (TNC) content to residual content for selected plant parts of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from anthesis to eight weeks after anthesis (WAA)

Stress treatment	WAA	Plant part				
		A1	B1	Shank	Cob	Grain
		TNC : residual				
S	0	0,30	0,31	0,70	0,43	0,62
	2	0,33	0,26	0,97	0,37	1,86
	4	0,37	0,30	0,86	0,41	2,20
	6	0,39	0,36	0,67	0,28	2,40
	8	0,30	0,32	0,41	0,24	2,57
NS	0	0,32	0,30	0,62	0,85	0,70
	2	0,29	0,23	0,84	0,33	1,88
	4	0,30	0,19	0,88	0,26	2,44
	6	0,40	0,39	0,68	0,27	2,51
	8	0,39	0,45	0,52	0,27	2,91

Ratio of TNC : residual                      SE ( $\bar{x}$ )                      0,43

#### 4.3.4 Radioactivity analysis of plant segments

##### 4.3.4.1 Specific radioactivity

###### Labelling at A

The main effect for stress treatment was non-significant (Table 4.6 and Appendix 35.1). Stressed plants had marginally higher specific radioactivity (SR) than non-stressed plants.

The main effects for weeks after anthesis (WAA) and segment were significant. However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interaction of stress treatment with WAA was non-significant. There were no significant components of the interaction either.

The interaction of stress treatment with segment was just non-significant. Since the response to stress was not entirely the same for each segment the interaction has been presented in Table 4.6. Whereas SR was lower in the tassel, top, A1, B1, B2, sheaths, laminae and 2° ear under stress conditions than under non-stress conditions, it was higher in the B3, B4, shank, grain, cob and husks under stress conditions than under non-stress conditions. The tendency for SR to be higher in the shank, grain and cob under stress conditions than non-stress conditions is not unexpected for a number of reasons. These segments, in particular the grain, are organs that are receivers of

Table 4.6 Effect of water stress (S) and lack of water stress (NS) on specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over five growth periods during grain fill from a maize hybrid labelled at anthesis

Stress treatment	Segment														Stress treatment marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
S	13,06	68,19	72,05	64,92	72,26	95,57	92,56	243,35	34,39	28,42	135,62	203,32	225,12	90,38	102,80
NS	14,61	78,63	75,71	72,47	76,94	79,58	78,91	211,63	34,74	34,59	110,36	176,49	204,02	144,74	99,53
Segment marginal means	13,84	73,41	73,88	68,69	74,60	87,57	85,74	227,49	34,57	31,51	122,99	189,90	214,57	117,56	

Body of table

	LSD	
Comparison of means at the same level of stress treatment	0,05	0,01
Comparison of means at the same level of segment or with neither factor in common	NS	NS

Marginal means

Comparison of stress treatment means	NS	NS
Comparison of segment means	18,53	24,36

photosynthate. Under stress conditions the  $^{14}\text{CO}_2$  assimilated at A appears to be utilized to a greater extent for grain filling requirements. The concentration of  $^{14}\text{C}$  in the shank, grain and cob would also tend to remain high under stress conditions as less more recently assimilated  $\text{CO}_2$  diluted the  $^{14}\text{C}$  in these organs. Also stressed plants would tend to respire less than non-stressed plants (Boyer, 1970a; Boyer and McPherson, 1975). Finally, it would be expected that these organs would be smaller in terms of total dry mass under stress conditions and so the  $^{14}\text{C}$  would be concentrated to a greater extent in the tissue of these organs.

The interaction of WAA with segment was significant (Table 4.7). The WAA(linear, quadratic and cubic) x segments components of the interaction were also significant. The cob, grain and, to a lesser extent, the husks were the only segments that showed substantial increases in dry mass during grain fill (Table 4.8 and Appendix 46). The cob dry mass in fact peaked at 6 WAA under stress and non-stress conditions, while the other shoot segments generally peaked in dry mass at 2 WAA (Table 4.8 and Appendix 46). Thus the dry mass of the grain and cob was lowest at A, but SR of these segments was highest. The SR of all the other segments except the B3 and B4 stem segments was also highest at A. The high SR of all the non-leaf segments within 48 h of labelling at A provides an indication of the rapid rate at which  $^{14}\text{C}$ -labelled photosynthate moved out of the leaves into the rest of the plant. The SR of the shank, grain and cob at A was significantly ( $p = 0,01$ ) higher than that of any of the other segments at A. With the cob this is an indication of

Table 4.7 Specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over water stress treatments from anthesis to eight weeks after anthesis (WAA) for a maize hybrid labelled at anthesis

WAA	Segment														WAA marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
0	19,90	91,34	119,06	107,88	107,98	103,48	114,34	432,50	52,71	59,92	408,77	443,30	292,68	235,25	184,94
2	15,86	78,33	78,87	90,23	100,71	145,24	157,86	257,07	42,46	30,99	96,07	171,08	194,90	104,48	111,73
4	11,88	69,14	63,78	53,18	54,42	63,74	48,77	178,54	29,95	25,49	44,61	126,91	201,45	50,84	73,05
6	12,09	63,42	53,81	47,57	62,83	68,10	59,95	131,69	25,88	21,64	37,33	96,15	189,75	96,48	69,05
8	9,45	64,81	53,89	44,60	47,07	57,30	47,76	137,65	21,83	19,50	28,17	112,08	194,06	100,75	67,07
Segment marginal means	13,84	73,41	73,88	68,69	74,60	87,57	85,74	227,49	34,57	31,51	122,99	189,90	214,57	117,56	

Body of table

LSD

Comparison of means at the same level of WAA

0,05                      0,01

Comparison of means at the same level of segment or with neither factor in common

41,44                      54,46

45,21                      59,94

Marginal means

Comparison of WAA means

21,23                      29,08

Comparison of segment means

18,53                      24,36

Table 4.8 Dry mass of segments (g segment<sup>-1</sup>), meaned over corresponding sampling occasions from each labelling occasion, from a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill

Stress treatment	WAA	Segment													
		Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear
S	0	5,1	6,2	5,0	8,8	10,4	11,9	15,2	1,3	16,6	38,5	2,8	3,2	11,4	4,7
	2	5,6	5,2	5,0	8,9	10,3	11,0	13,2	1,9	19,7	35,2	26,0	13,1	15,4	2,0
	4	5,3	4,9	5,1	8,2	9,7	10,3	10,5	2,4	17,1	36,6	79,6	16,1	11,7	1,1
	6	3,7	5,7	5,3	10,0	12,1	12,6	12,3	2,8	18,9	28,0	109,8	17,8	10,5	0,8
	8	4,2	4,9	5,0	9,3	11,1	12,5	12,5	2,4	18,8	27,0	116,8	15,7	9,7	1,0
NS	0	5,9	6,2	4,8	9,2	11,2	11,6	12,7	1,3	21,5	39,3	2,4	3,6	10,9	5,6
	2	5,6	5,7	6,0	9,0	10,9	10,7	13,0	2,1	18,4	39,6	26,3	18,4	19,5	2,7
	4	5,4	5,2	5,8	8,2	9,6	10,2	10,3	2,8	17,7	39,6	85,9	19,2	15,4	1,7
	6	4,8	6,1	5,6	10,4	13,0	13,4	14,1	3,2	19,1	32,7	120,6	20,3	12,4	1,0
	8	4,1	5,7	5,6	9,9	11,6	13,5	13,8	2,7	18,7	30,5	142,4	18,5	12,0	1,1

photosynthate being partitioned to it to be utilized for the extensive increase in size it must undergo, and it is also an indication of photosynthate being translocated through it for grain fill. The high SR of the shank is an indication of its translocatory function in serving as a conduit for photosynthate destined for the cob and, particularly, the grain. From A to 2 WAA the shank almost doubled in dry mass so the high concentration of  $^{14}\text{C}$  at A is also an indication of photosynthate being partitioned to the shank, to be specifically utilized for structural growth. From A to PM the SR of the shank, grain and cob declined significantly ( $p = 0,01$ ) by 294 850, 380 599 and 331 223 dpm  $\text{g}^{-1}$ , respectively. These declines in SR were the most marked of all the segments. It is noteworthy that the decline in the SR of the shank, grain, cob, husks and 2° ear was most marked from A to 2 WAA. With the shank, grain, cob and husks this reflects the substantial increases in dry mass that occurred during this period (Table 4.8 and Appendix 4.3.4). With the 2° ear the marked decline in SR from A to 2 WAA reflects the marked decline in total radioactivity as  $^{14}\text{C}$  was mobilized out of the 2° ear into the rest of the plant (Section 4.3.4.2). As mentioned, the SR of the B3 and B4 segments did not peak at A but in fact increased from A to 2 WAA before declining through to PM. The increase in SR from A to 2 WAA in these segments reflects the increase in their total radioactivity during the same period (Section 4.3.4.2). It is possible that this may indicate substantial mobilization of  $^{14}\text{C}$  out of the leaves that originate from these stem segments. It is also possible that the plant partitioned  $^{14}\text{C}$  to these segments for final structural growth. Of the main stem segments (i.e. excluding the shank), the A1

segment recorded the highest SR at A. Since this segment consists of the pair of stem internodes above the primary ear, the high SR at A may be indicative of extensive mobilization of  $^{14}\text{C}$  out of the leaves attached to these internodes, for deposition into the grain.

The general decline in SR for all the segments during grain fill was due to a number of effects, namely: (i) the dilution effect - as the segments increase in dry mass the concentration of  $^{14}\text{C}$  per unit mass declines. This was particularly marked in the cob and especially the grain; (ii) mobilization of labile organic compounds out of the vegetative organs to the grain; and (iii) losses due to respiration. Also, for the receiver organs i.e. the shank, cob, and particularly the grain, the decline in SR was due to a decline in the amount of  $^{14}\text{C}$  available in vegetative organs for mobilization to the grain. This of course, in terms of the grain, includes  $^{14}\text{C}$  available in the shank and cob themselves.

#### Labelling at 2 WAA

The main effect for stress treatment was non-significant, while the main effects for WAA and segment were significant (Appendix 35.2). However, since these factors were involved in higher order interactions their main effects are of limited interest.

The interaction of stress treatment with WAA was non-significant. There were no significant components of the interaction either.

The interaction of stress treatment with segment was significant (Table 4.9). Whereas SR was lower in the tassel, top, A1, B1, B2, B3, shank, sheaths, laminae and 2° ear under stress conditions, it was higher in the B4, grain, cob and husks under stress conditions than under non-stress conditions. A number of 'concentrating effects' may be hypothesised to explain the basis for the significantly ( $p = 0,01$ ) higher SR in the grain and cob under stress conditions. When the plants were labelled at 2 WAA the stressed plants had already undergone two consecutive one week long exposures to water deficits. It is likely that the stressed plants were assimilating less  $\text{CO}_2$  than the non-stressed plants towards the end of each stress cycle. It is hypothesised that the stressed plants 'switched' over to a survival condition with most of the currently assimilated C being immediately translocated to the primary ear with very little initially becoming part of existing pools of labile organic compounds in the vegetative organs. Thus assimilated  $^{14}\text{C}$  in stressed plants would be immediately translocated to the ear. On the other hand, in the non-stressed plants there would be a greater tendency for assimilated C to initially be incorporated with pools of labile organic compounds in vegetative organs before being translocated to the ear. Thus although the demand for carbohydrate by the grain of non-stressed plants was as high or higher than that of the stressed plants, the supply of C to the grain was derived from current plus previously assimilated pools of C. Therefore, when the non-stressed plants were labelled with  $^{14}\text{C}$  the C translocated to the ear would consist of a greater proportion of non-radioactive C from assimilation prior to labelling. Additionally it may be hypothesised that as stress developed

Table 4.9 Effect of water stress (S) and lack of water stress (NS) on specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over four growth periods during grain fill from a maize hybrid labelled at two weeks after anthesis

Stress treatment	Segment														Stress treatment marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
S	8,94	17,49	25,13	18,78	16,78	18,23	8,00	62,68	12,75	17,23	153,56	68,27	23,95	3,59	32,53
NS	10,10	21,27	26,73	21,60	18,94	19,29	7,32	66,80	13,93	19,58	127,39	47,87	16,35	4,59	30,13
Segment marginal means	9,52	19,38	25,93	20,19	17,86	18,76	7,66	64,74	13,34	18,40	140,47	58,07	20,15	4,09	

Body of table

	LSD	
Comparison of means at the same level of stress treatment	0,05	0,01
Comparison of means at the same level of segment or with neither factor in common	8,26	10,85
	10,18	13,66

Marginal means

Comparison of stress treatment means	NS	NS
Comparison of segment means	5,84	7,67

towards the end of each stress cycle the rate at which stressed plants assimilated 'new' non-radioactive C declined. Thus less non-radioactive photosynthate would dilute the pools of  $^{14}\text{C}$ -labelled photosynthate to a lesser extent in the stressed plants compared to the non-stressed plants. This would mean that the receiving organs, in particular the grain, would retain a higher concentration of  $^{14}\text{C}$ . It is also generally accepted that stressed plants respire less, and so it is hypothesised that the turnover rate of photosynthate pools would initially be slower in stressed plants. Stressed plants would also deplete the available pools of labile organic compounds in vegetative organs to a greater extent for grain fill requirements. This would result in a decline in any  $^{14}\text{C}$  available in the form of labile organic compounds in the vegetative organs and an increase in  $^{14}\text{C}$  in the primary ear. The non-significantly higher SR under stress conditions in the husks is not easy to explain. Palmer *et al.* (1973) found that the husks and cob obtained a substantial proportion of  $^{14}\text{C}$  supplied to maize plants within 24 h of labelling and that the  $^{14}\text{C}$  assimilated by these organs was subsequently remobilized and translocated to the grain. Since the husks may also serve as a temporary reservoir for photosynthate, the direct translocation of current photosynthate to the primary ear under stress conditions would perhaps result in a higher concentration of  $^{14}\text{C}$  in the husks. The B4 segment which represents the internodes of the stem base serves as a conduit for photosynthate destined for the roots (Palmer *et al.*, 1973). As the internodes of this segment had largely lost their leaves through senescence at the beginning of the reproductive phase, most of the photosynthate was probably translocated from

other photosynthesising organs. Balasko and Smith (1973) observed high specific activity of  $^{14}\text{C}$  in the stem bases of timothy grass plants between 8 h and 168 h following exposure to  $^{14}\text{CO}_2$ . This is indicative of the perennial nature of timothy grass, with the stem bases serving as storage organs for reserve carbohydrates utilized for the following seasons growth. If there are vestiges of a perennial growth habit left in modern maize genotypes then it is possible that the stem base serves as a storage organ for labile organic compounds. Thus the concentrating effects described earlier would result in a higher SR in the B4 segment under stress conditions.

The interaction of WAA with segment was significant (Table 4.10). The WAA(linear, quadratic and cubic) x segments components of the interaction were also significant. All segments declined substantially in SR from 2 WAA to PM with the initial decline in SR from 2 to 4 WAA being most marked. The significant ( $p = 0,01$ ) decline in SR from 2 to 4 WAA of 128 081, 61 869 and 48 413 dpm  $\text{g}^{-1}$  for the shank, grain and cob respectively, were particularly marked. The overall decline in SR from 2 WAA to PM of 146 853 and 125 625 dpm  $\text{g}^{-1}$  in the shank and grain respectively, were the most marked of the segments. As with plants labelled at A, the overall decline in SR for all segments during grain fill was due to a number of effects, namely: (i) the dilution effect - as the segments increased in dry mass the concentration of  $^{14}\text{C}$  per unit mass declined (this was particularly the case for the grain); (ii) mobilization of labile organic compounds out of the vegetative organs to the grain; and (iii) losses due to respiration. Also for the receiver organs

Table 4.10 Specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over water stress treatments from two weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at two weeks after anthesis

WAA	Segment														WAA marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
2	21,54	50,40	60,48	47,60	39,12	42,87	15,63	169,42	31,24	37,92	215,59	92,93	34,37	7,25	61,88
4	7,46	13,08	22,51	17,77	15,86	17,31	6,06	41,34	11,04	17,20	153,72	44,52	17,29	4,09	27,80
6	5,35	7,81	11,89	8,20	9,14	8,99	5,85	25,62	6,83	8,84	102,63	41,74	10,60	2,37	18,28
8	3,73	6,22	8,85	7,18	7,33	5,87	3,10	22,57	4,25	9,64	89,96	53,09	18,35	2,64	17,34
Segment marginal means	9,52	19,38	25,93	20,19	17,86	18,76	7,66	64,74	13,34	18,40	140,47	58,07	20,15	4,09	

Body of table

LSD

Comparison of means at the same level of WAA

0,05  
11,68  
15,35

Comparison of means at the same level of segment or with neither factor in common

14,40  
19,32

Marginal means

Comparison of WAA means

9,00  
12,49

Comparison of segment means

5,84  
7,67

i.e. the shank, cob and particularly the grain, the decline in SR was due to a decline in the amount of  $^{14}\text{C}$  available in vegetative organs for mobilization to the grain. This of course includes the  $^{14}\text{C}$  available in the shank and cob themselves.

#### Labelling at 4 WAA

The main effect for stress treatment was significant (Table 4.11 and Appendix 35.3). Specific radioactivity was significantly ( $p = 0,01$ ) reduced as a result of stress. When this batch of plants was labelled at 4 WAA the stressed plants had already undergone four consecutive stress cycles. Stressed and non-stressed plants were watered as usual in the morning of the day on which labelling took place. At 4 WAA, however, the stressed plants had a lower leaf  $\Psi_w$  and stress resulted in greater leaf senescence (Sections 4.3.1 and 4.3.2). Both these factors would reduce the rate at which the stressed plants assimilated  $^{14}\text{C}$ .

Table 4.11 Effect of water stress (S) and lack of water stress (NS) on mean segment specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over three growth periods during grain fill for a maize hybrid labelled at four weeks after anthesis

	Stress treatment	
	S	NS
	16,75	21,81
LSD (0,05)	3,25	
LSD (0,01)	4,63	

This was confirmed by the fact that whole plant <sup>14</sup>C total radioactivity was significantly lower under stress conditions (Section 4.3.7.2). Thus the lower total radioactivity for the stressed plants meant that the stressed plants could not even establish a higher average SR than the non-stressed plants.

The main effects for WAA and segment were significant. However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interactions of stress treatment with WAA, and stress treatment with segment were non-significant. There were no significant components of the former interaction either.

The interaction of WAA with segment was significant (Table 4.12). The WAA(linear and quadratic) x segments components of the interaction were also significant. Possibly as a result of sampling error, SR initially declined from 4 to 6 WAA and then increased from 6 WAA to PM in the tassel, top, A1, shank, leaves, cob, husks and 2° ear. The SR of the A1, B1 and shank segments declined significantly ( $p = 0,01$ ) and most markedly of all the segments, from 4 WAA to PM. The grain SR increased non-significantly from 4 WAA to PM, although this trend may have been due to the high SR recorded for the grain from plants sampled from stress and non-stress treatments of replication one.

Table 4.12 Specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over water stress treatments from four weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at four weeks after anthesis

WAA	Segment														WAA Marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
4	5,40	29,18	35,96	35,84	34,83	30,22	21,91	83,78	13,58	17,64	41,61	33,53	11,04	3,40	28,42
6	2,25	8,54	12,16	15,60	19,44	20,09	14,78	31,25	8,23	6,96	38,74	15,92	4,95	2,25	14,37
8	4,14	11,58	12,63	15,55	17,85	14,87	11,10	32,51	4,84	7,88	46,63	18,69	8,42	4,03	15,05
Segment marginal means	3,93	16,43	20,25	22,33	24,04	21,72	15,93	49,18	8,88	10,83	42,33	22,72	8,13	3,23	

Body of table

	LSD	
Comparison of means at the same level of WAA	0,05	0,01
Comparison of means at the same level of segment or with neither factor in common	6,64	8,73
	7,53	10,10

Marginal means

Comparison of WAA means	3,98	5,66
Comparison of segment means	3,84	5,04

## Labelling at 6 WAA

The main effect for stress treatment was non-significant (Table 4.13 and Appendix 35.4). Specific radioactivity was non-significantly less under stress conditions than under non-stress conditions. Whole plant  $^{14}\text{C}$  total radioactivity was non-significantly less in stressed plants than in non-stressed plants 48 h after labelling at 6 WAA (Section 4.3.7.2). Thus the lower total radioactivity for the stressed plants meant that the stressed plants could not even establish a higher average SR than the non-stressed plants. That the SR of non-stressed plants was only non-significantly higher than that of stressed plants was possibly due to the declining photosynthetic activity of non-stressed plants as PM approached.

Table 4.13 Effect of water stress (S) and lack of water stress (NS) on mean segment specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over two growth periods during grain fill for a maize hybrid labelled at six weeks after anthesis

Stress treatment	
S	NS
6,84	7,98
LSD (0,05)	NS
LSD (0,01)	NS

The main effects for WAA and segment were significant. However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interactions of stress treatment with WAA, and stress treatment with segment were non-significant. There were no significant components of the former interaction either.

The interaction of WAA with segment was significant (Table 4.14). Both the grain and husks had non-significantly higher SR at PM than at 6 WAA. This may be due to the fact that the gain in dry mass had declined in the husks, and particularly the grain, from 6 WAA to PM (Table 4.8 and Appendix 46). Thus the dilution effect as a result of large gains in dry mass was not as pronounced as it had been during the earlier phase of grain fill. Therefore the assimilation of  $^{14}\text{C}$  photosynthate by the grain and husks from 6 WAA to PM 'kept up' with and in fact marginally exceeded the rate of dry mass gain and any losses due to respiration. On the other hand, SR significantly ( $p = 0,01$ ) declined in the other segment of the primary ear, the cob, from 6 WAA to PM. Since the cob had completed dry mass gain by 6 WAA this would seem to indicate that most photosynthate arriving in the cob was moved into the grain (Table 4.8 and Appendix 46). The significant ( $p = 0,01$ ) decline in SR in the stem segments, viz the A1, B1, B2, B3, B4 and shank, from 6 WAA to PM is also indicative of mobilization of photosynthate to the primary ear as dry mass of these segments remained fairly constant during the final phase of grain fill (Table 4.8 and Appendix 46).

Table 4.14 Specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over water stress treatments from six weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at six weeks after anthesis

WAA	Segment														WAA marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
6	0,72	10,49	15,73	14,62	14,62	14,21	12,29	21,47	3,04	6,96	8,38	10,86	1,65	1,01	9,72
8	0,61	3,85	5,82	7,05	7,59	7,87	7,20	9,71	1,02	2,44	10,25	5,25	1,92	0,89	5,10
Segment marginal means	0,67	7,17	10,78	10,83	11,11	11,04	9,74	15,59	2,03	4,70	9,31	8,06	1,78	0,95	

Body of table

	LSD	
Comparison of means at the same level of WAA	0,05	0,01
Comparison of means at the same level of segment or with neither factor in common	1,76	2,33
	2,51	3,72
<u>Marginal means</u>		
Comparison of WAA means	1,90	3,15
Comparison of segment means	1,25	1,65

Second order interactions for labelling at A, 2 WAA, 4 WAA and 6 WAA

Each second order interaction of stress treatment, WAA and segment for labelling at A, 2 WAA, 4 WAA and 6 WAA, was non-significant (Figure 4.13a,b,c,d). There were no significant components of each interaction either. However, the apparent trends shown in the data of the second order interactions are discussed.

When the plants were labelled at A, 69,0 and 73,2 % of the  $^{14}\text{C}$  recovered in the whole plant at PM in the stressed and non-stressed plants respectively, occurred in the whole shoot (Section 4.3.6.3). Thus it is clear that much of the  $^{14}\text{C}$  assimilated by the plants at A remained in the shoot and was not translocated to the grain. This indicates that much of the  $^{14}\text{C}$  assimilated at A was 'irreversibly' utilized for the final structural growth of the whole shoot including the cob of the primary ear. This explains why the segments of the whole shoot (all aboveground plant parts excluding the primary grain) for stressed and non-stressed plants labelled at A generally had a higher SR on all sampling occasions than did the segments of the whole shoot when plants were labelled at 2, 4 and 6 WAA (Figure 4.13a,b,c,d). When stressed and non-stressed plants were sampled at 48 h after labelling at A, the shank, leaves (sheaths and laminae), grain, cob, husks and 2° ear recorded the highest SR. Of these segments the shank of the stressed plants recorded the highest SR of 513 175 dpm g<sup>-1</sup> at 48 h after labelling at A. Not only does this indicate the direct translocation of assimilated

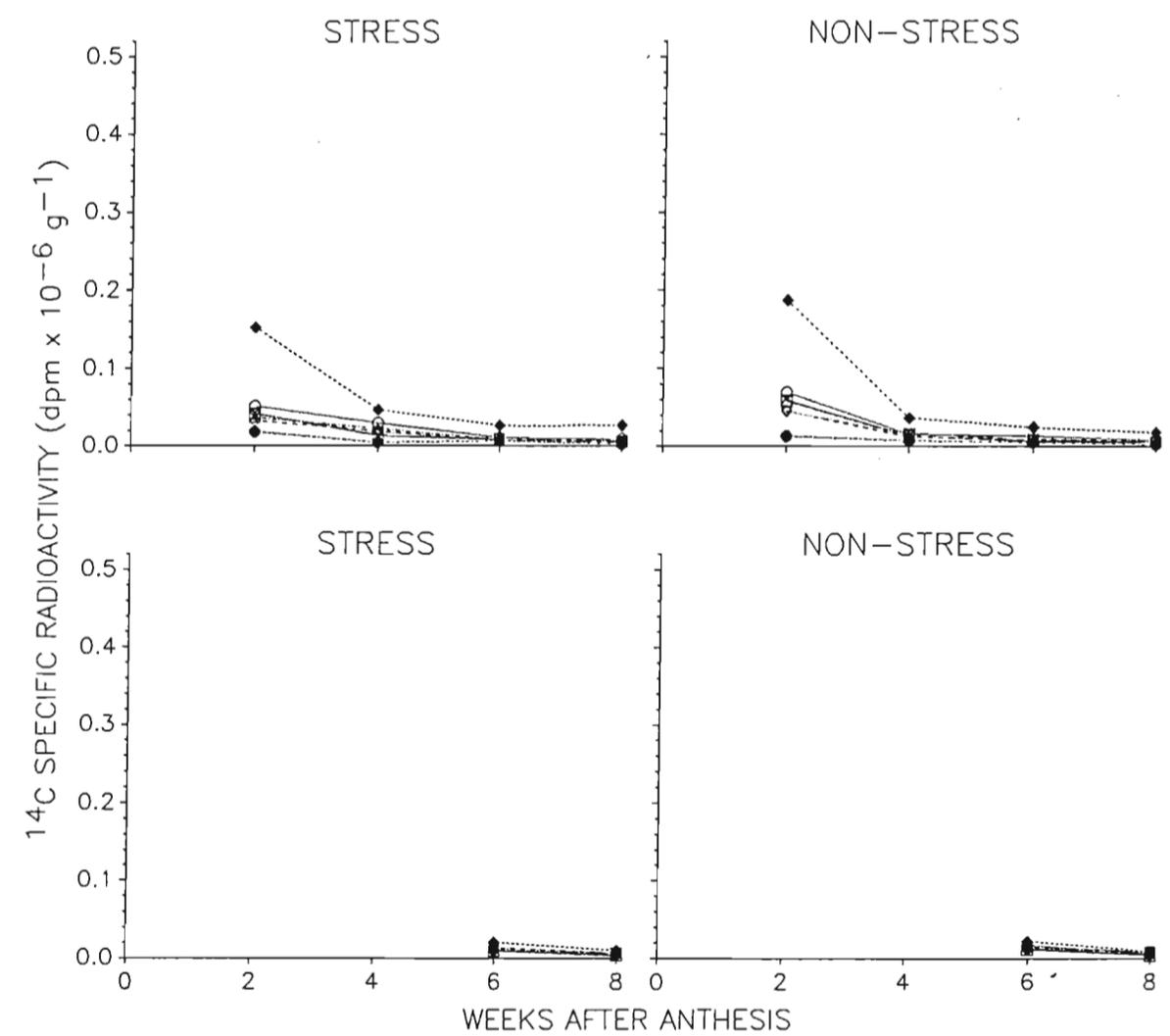
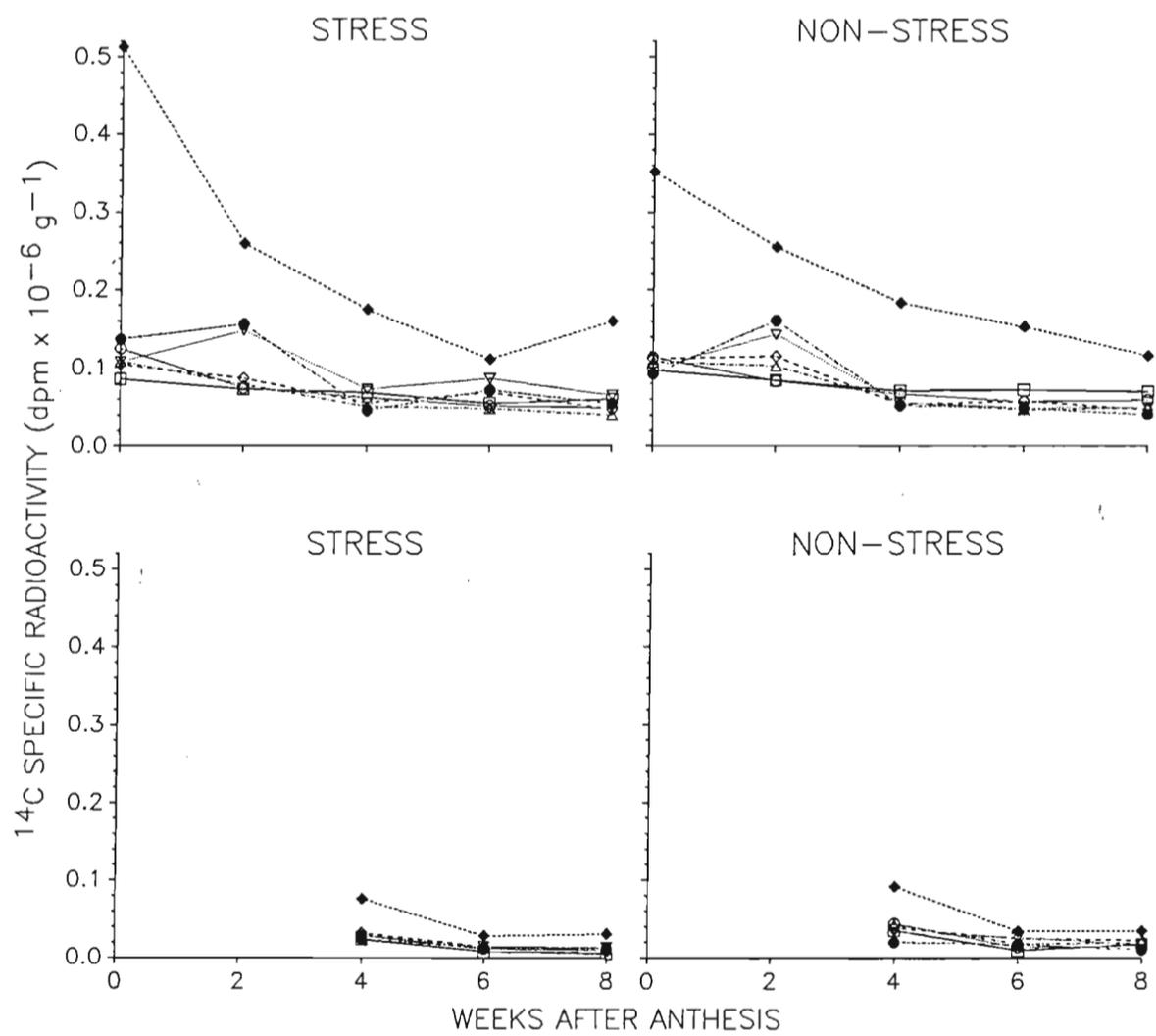


Figure 4.13a Effect of water stress during grain fill on specific radioactivity of stem segments sampled at fortnightly intervals from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis

Key: top  $\square-\square$ , A1  $\circ-\circ$ , B1  $\triangle-\triangle$ , B2  $\diamond-\diamond$ , B3  $\nabla-\nabla$ , B4  $\bullet-\bullet$ , shank  $\blacklozenge-\blacklozenge$

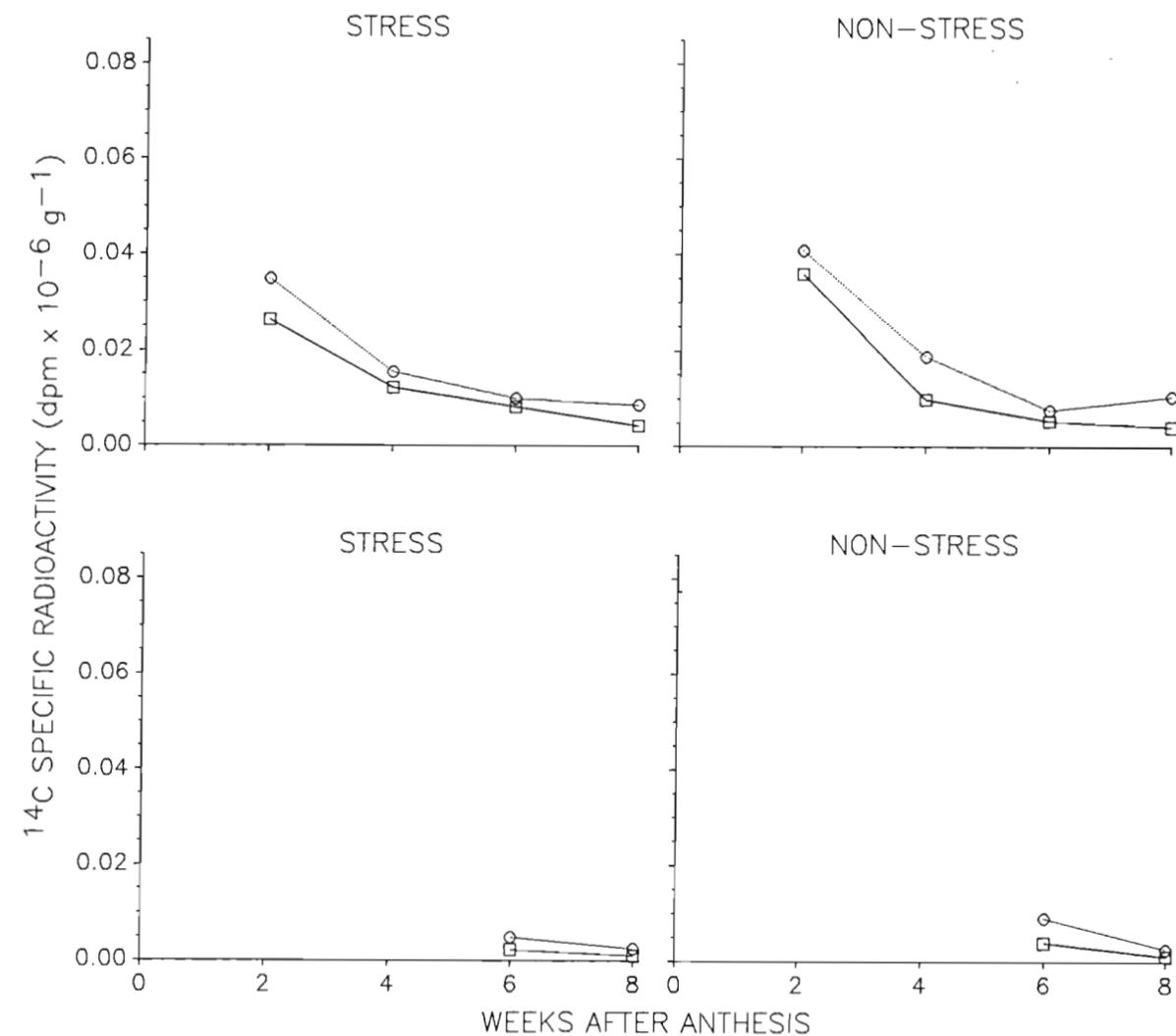
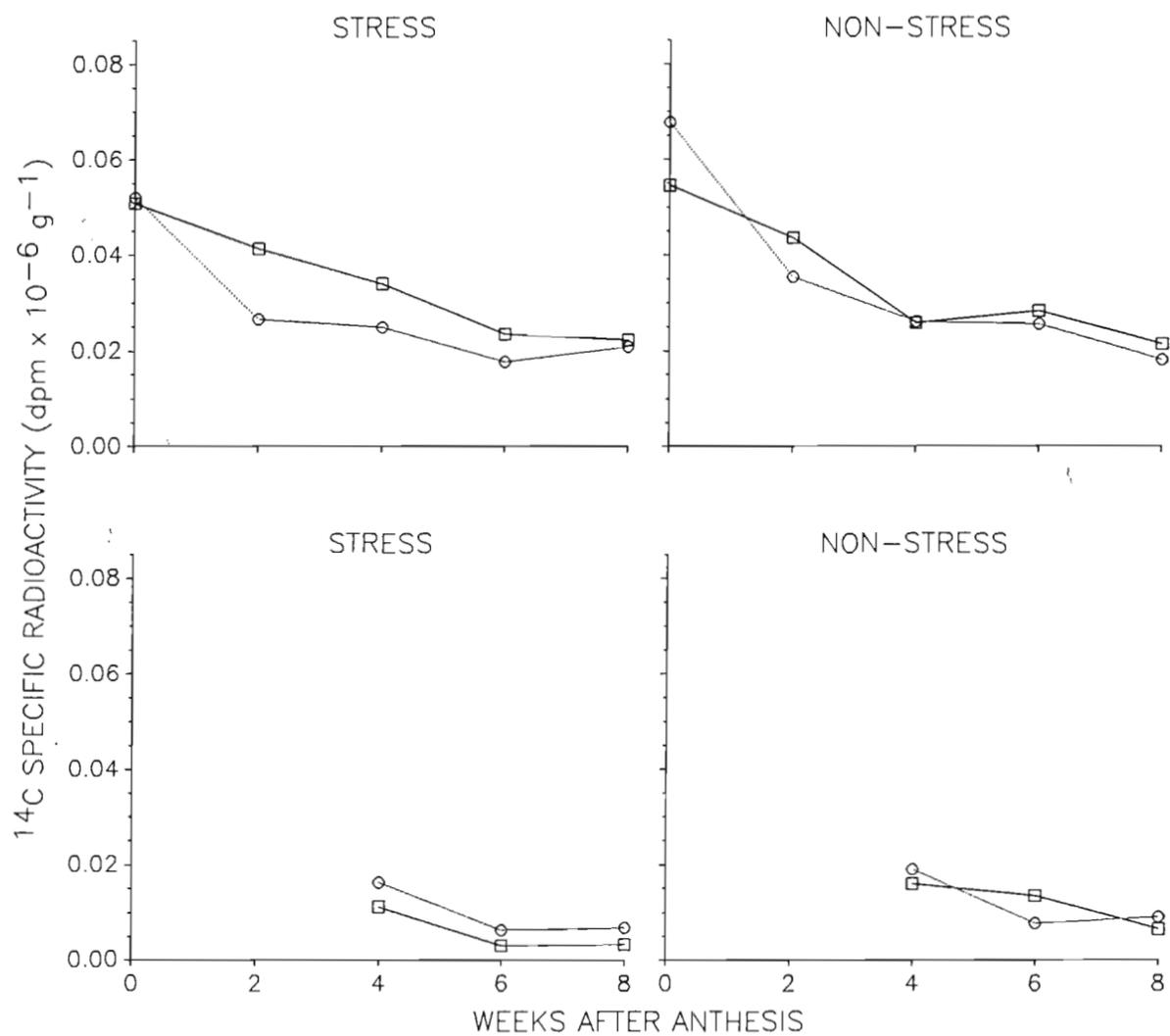


Figure 4.13b Effect of water stress during grain fill on specific radioactivity of leaves sampled at fortnightly intervals from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis

Key: sheaths  $\square-\square$ , laminae  $\circ-\circ$

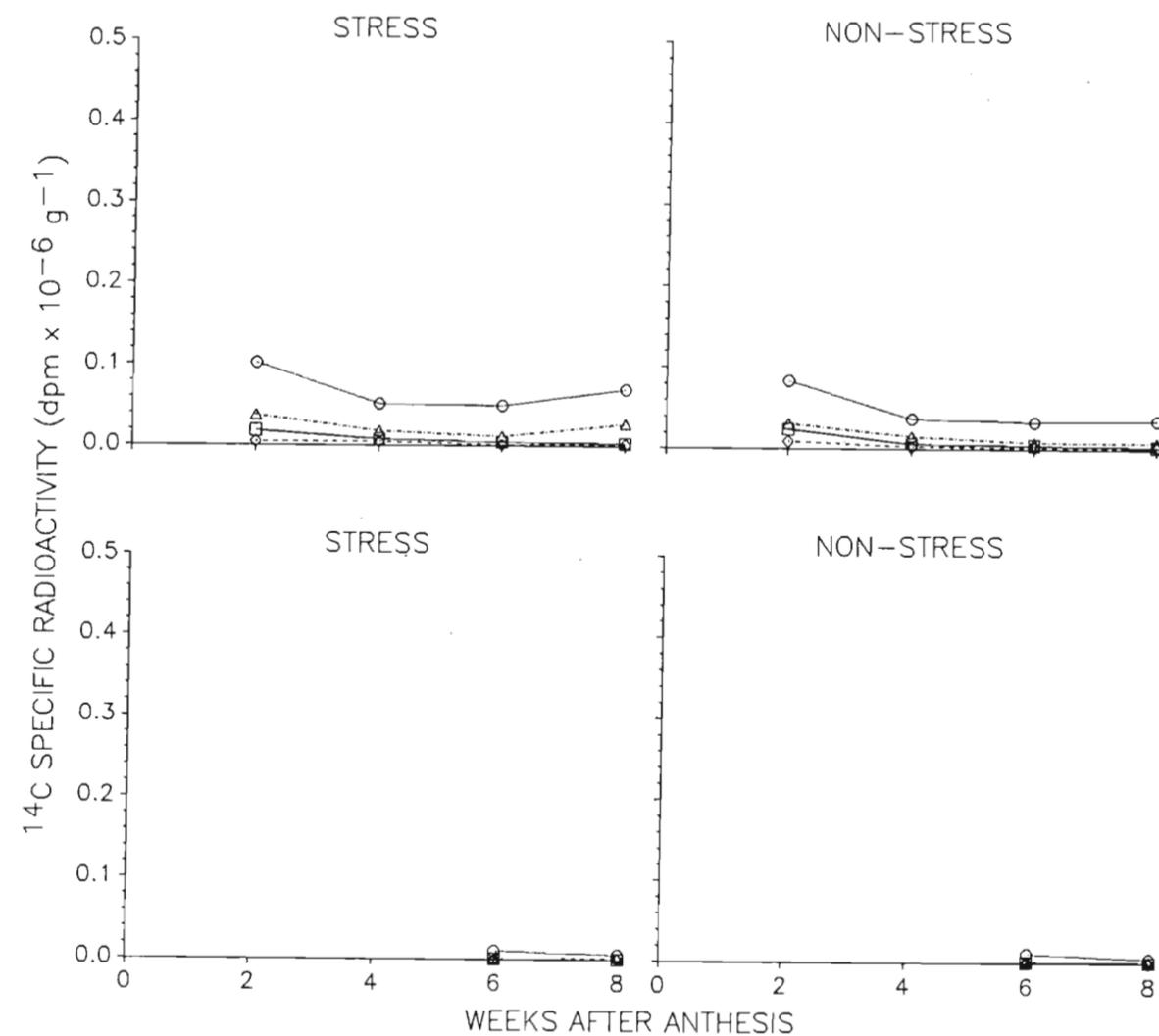
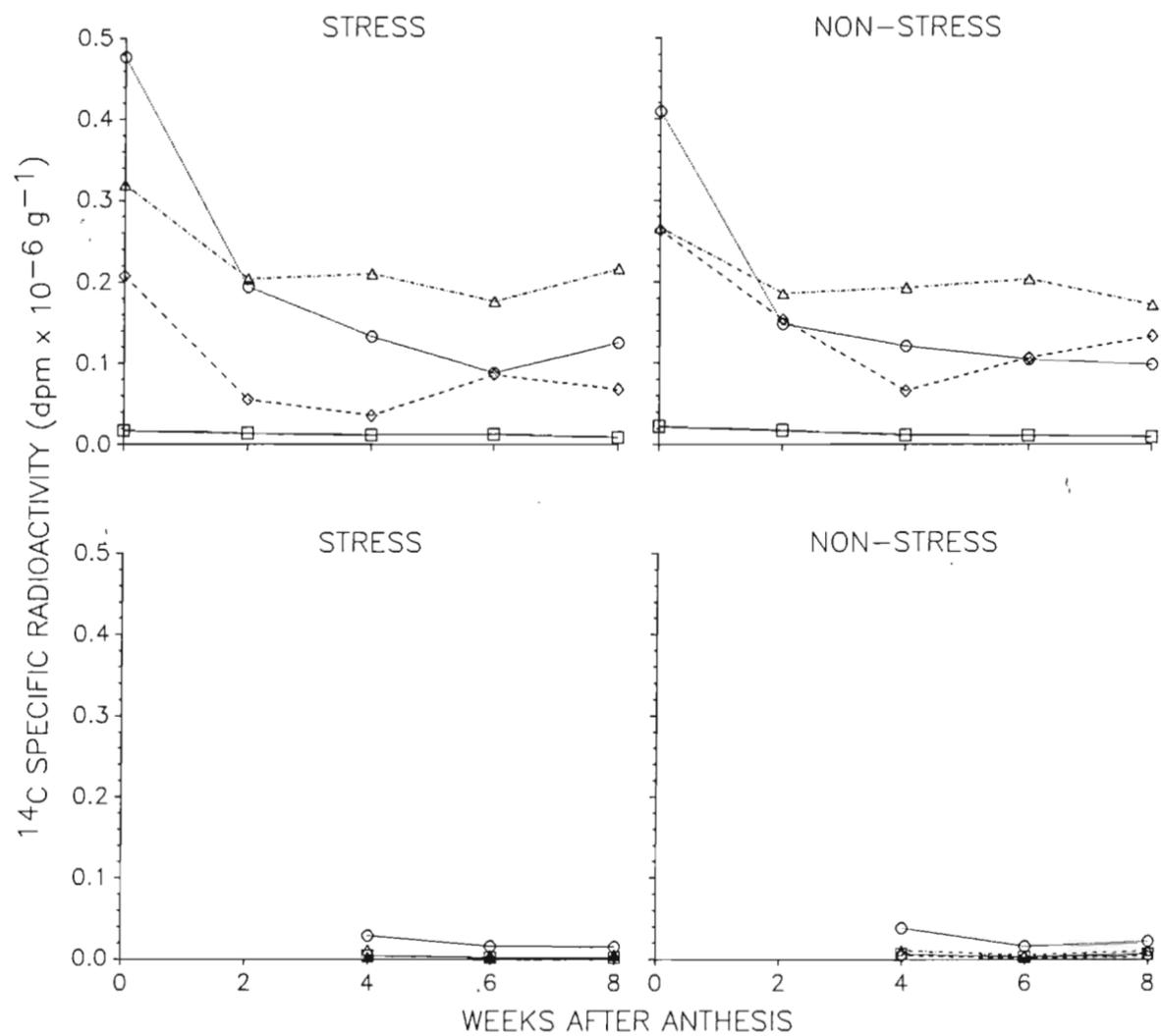


Figure 4.13c Effect of water stress during grain fill on specific radioactivity of segments sampled at fortnightly intervals from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis

Key: tassel  $\square-\square$ , cob  $\circ-\circ$ , husks  $\triangle-\triangle$ , 2° ear  $\diamond-\diamond$

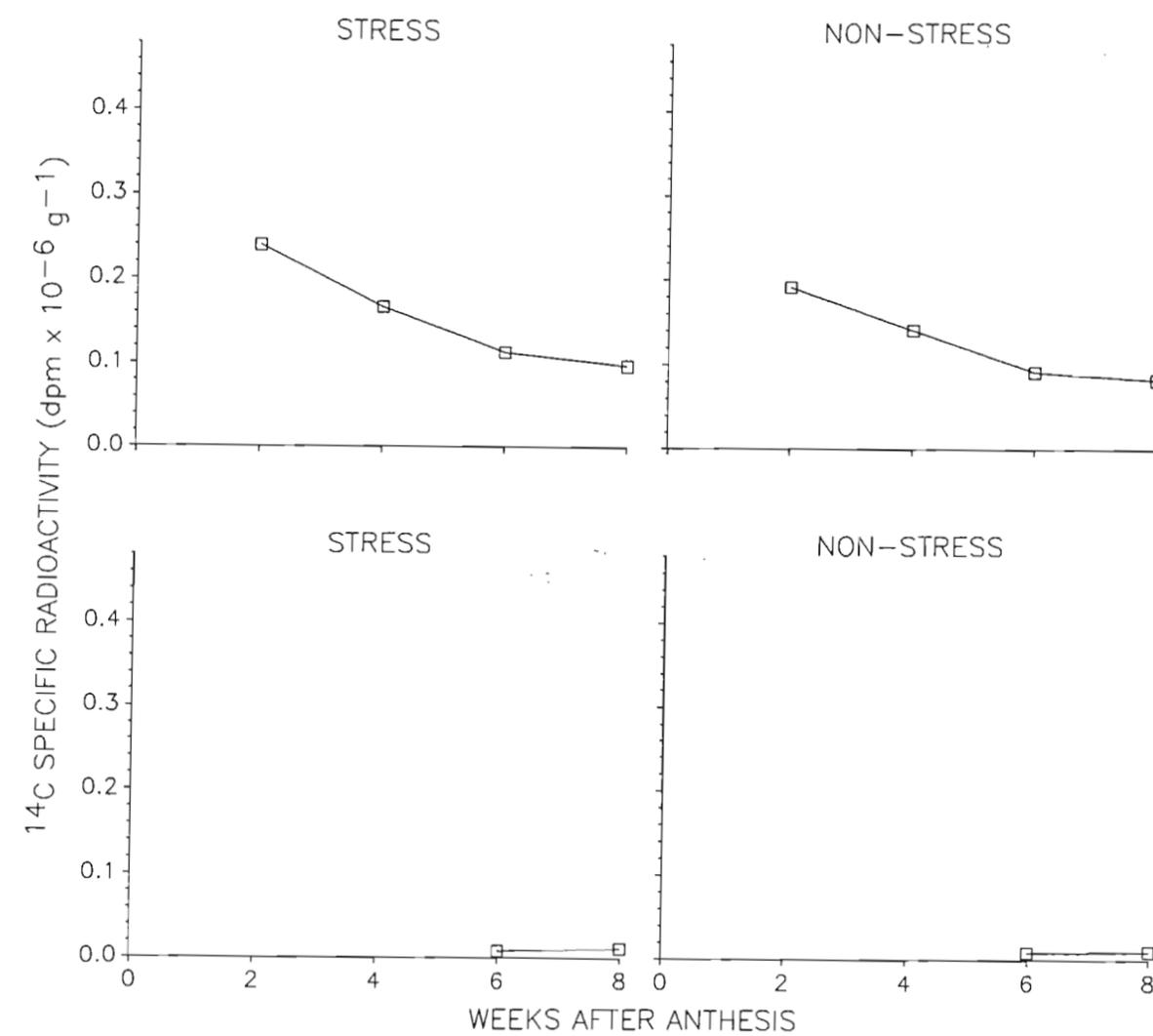
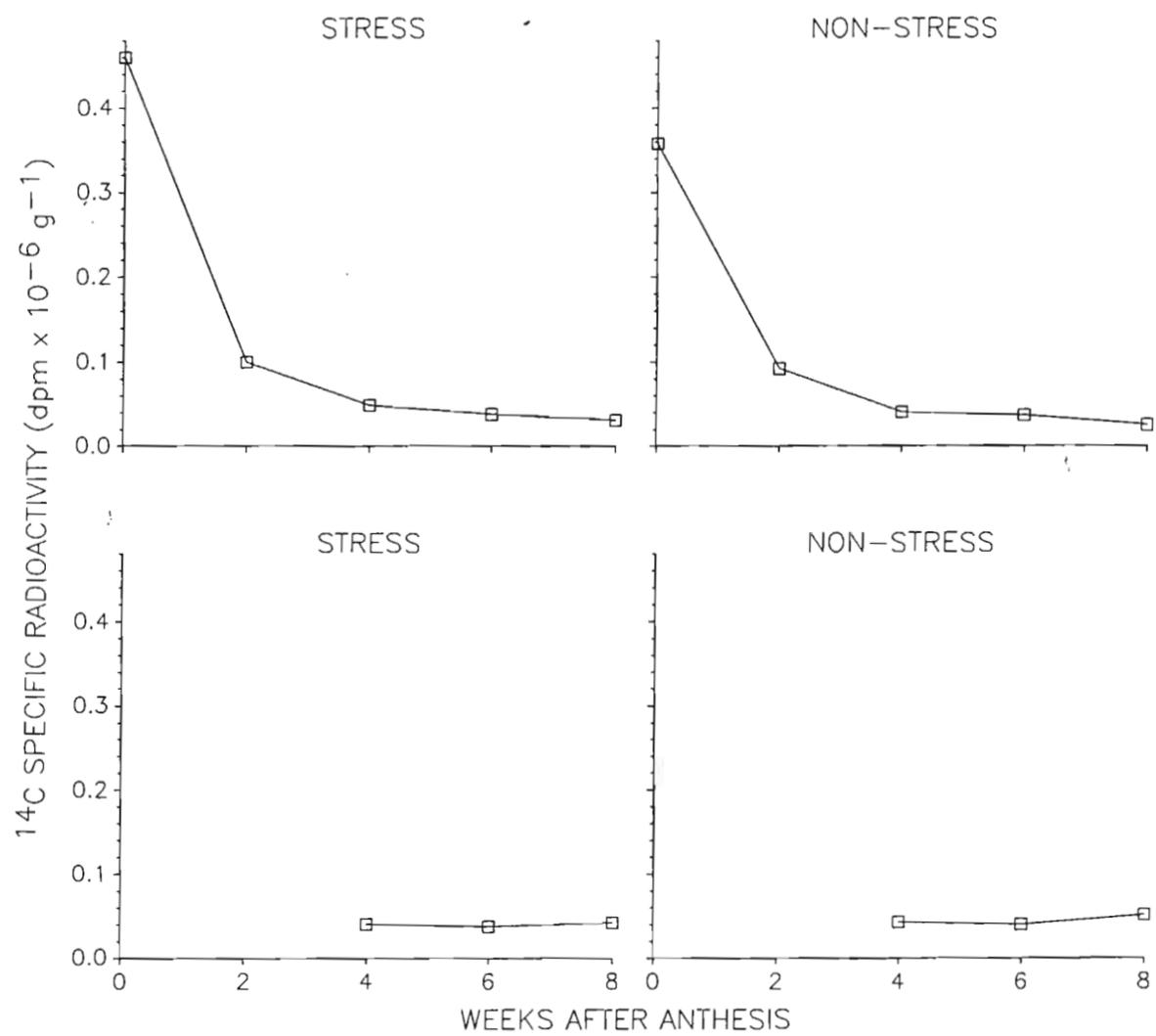


Figure 4.13d Effect of water stress during grain fill on specific radioactivity of grain sampled at fortnightly intervals from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis

$^{14}\text{C}$  through the shank to the primary ear under stress conditions, but it also indicates the translocation of  $^{14}\text{C}$  to the shank for structural growth. The cob recorded the next highest SR at A, with the SR of the cob under stress conditions higher than that under non-stress conditions. It appears that in the 10 to 14 d period following fertilization, the so called lag phase of grain fill during which the endosperm cells of the kernels undergo rapid division, the cob is a major sink for photosynthate. The cob underwent a rapid increase in dry mass from A to 2 WAA (Table 4.8 and Appendix 46). The higher SR of the cob under stress conditions was probably due to the concentrating effects of stress hypothesised earlier. At PM the cob of the stressed plants still had a higher SR than that of non-stressed plants. This would appear to indicate that the stressed plants utilized less  $^{12}\text{C}$  photosynthate for the structural growth and maintenance requirements of the cob. It also possibly indicates that labile  $^{14}\text{C}$  compounds continue to be mobilized from the rest of the plant to the primary ear up to PM particularly under stress conditions. The grain had the next highest SR at A, with the SR of the grain under stress conditions higher than that under non-stress conditions. The higher SR of the grain under stress conditions was probably due to the concentrating effects hypothesised earlier. The SR of the grain declined markedly from A to 2 WAA as  $^{12}\text{C}$  photosynthate was incorporated into the dry mass of the grain. From 2 to 6 WAA the total radioactivity of the grain of both stressed and non-stressed plants increased substantially which resulted in the SR of the grain declining less rapidly during this period as the  $^{14}\text{C}$  in the grain was diluted less rapidly by the incorporation of  $^{12}\text{C}$  photosynthate into the dry

mass of the grain. As with the cob the SR of the grain at PM of stressed plants was higher than that of non-stressed plants. The reasons for this are as for the cob. It is interesting to note that the husks were also a major sink for  $^{14}\text{C}$  assimilated at A as indicated by the high SR at A. The stressed plants recorded a higher SR in the husks at A than did the non-stressed plants. The SR of the husks for both stressed and non-stressed plants declined from A to 2 WAA which is indicative of the increase in husk dry mass that occurred during this period (Table 4.8 and Appendix 46). However, from 2 WAA to PM the SR of the husks remained fairly constant although the total radioactivity of the husks declined slightly during this period. That the SR of the husks remained fairly constant from 2 WAA to PM while the dry mass of the husks declined (Table 4.8 and Appendix 46) indicates that the decline in total radioactivity of the husks matched the decline in dry mass. The SR of the 2° ear of the non-stressed plants was higher than that of stressed plants from A to PM. This is indicative of the higher total radioactivity of the 2° ear of non-stressed plants than stressed plants recorded from A to PM. Thus it appears that the non-stressed plants were able to partition a greater amount of the  $^{14}\text{C}$  assimilated at A to the 2° ear throughout grain fill than the stressed plants. It is noteworthy that the SR of the 2° ear was highest at A and then declined from A to 4 WAA in both the stressed and non-stressed plants. The decline in SR from A to 4 WAA was more marked in the 2° ear of the stressed plants. From 4 WAA to PM the SR of the 2° ear of the non-stressed plants increased which is indicative of the increased total radioactivity of the 2° ear during this period. The SR of the 2° ear of the stressed plants initially

increased from 4 to 6 WAA and then declined again from 6 WAA to PM. Thus it appears that during the first half of grain fill  $^{14}\text{C}$  was mobilized out of the 2° ear and probably translocated to the primary ear. The mobilization of  $^{14}\text{C}$  out of the 2° ear occurred to a greater extent in stressed than non-stressed plants. In the latter half of grain fill, as the rate of dry mass gain by the primary grain slowed, it appears that available  $^{14}\text{C}$  which still occurred as labile compounds in the vegetative segments was translocated to the 2° ear. This mobilization of  $^{14}\text{C}$  to the 2° ear in the latter phase of grain fill occurred to a greater extent in non-stressed plants than stressed plants. The sheaths and laminae of the non-stressed plants recorded higher SR at 48 h after labelling at A than those of the stressed plants. This is probably indicative of the more direct and rapid translocation of assimilated  $^{14}\text{C}$  to the primary ear that occurred in the stressed plants. The stressed plants, however, recorded a higher SR of the sheaths and laminae at PM than did the non-stressed plants. This is possibly due to the reduced incorporation of  $^{12}\text{C}$  after labelling into the dry mass of the leaves under stress conditions, as well as reduced respiration losses under stress conditions. Of the stem segments the A1 segment recorded the highest SR at 48 h after labelling at A. The high SR of the A1 segment is indicative of the rapid translocation of  $^{14}\text{C}$  from the leaves immediately above the primary ear into the stem internodes to which they are attached. The SR of the A1 segment was higher in stressed plants than non-stressed plants and is again probably due to the concentrating effects of stress. Out of all the segments the tassel recorded the lowest SR throughout grain fill in both stressed and non-stressed plants. The SR of the tassel

was highest at 48 h after labelling at A, with the SR of the tassel of non-stressed plants higher than that of stressed plants. The SR of the tassel declined from A to PM in both stressed and non-stressed plants which is indicative of the decline in total radioactivity of the tassel (Section 4.3.4.2). It would appear that the tassel still had a requirement for C in the period after fertilization. However, in comparison to the other segments of the plant this requirement was small. From A to PM  $^{14}\text{C}$  was mobilized out of the tassel for utilization elsewhere in the plant. The stressed plants partitioned less of the  $^{14}\text{C}$  assimilated at A to the tassel during grain fill compared to non-stressed plants.

When plants were labelled at 2 WAA, 15,8 and 12,1 % of the  $^{14}\text{C}$  recovered in the whole plant at PM in stressed and non-stressed plants respectively, occurred in the whole shoot (Section 4.3.6.3). This was the lowest proportion of  $^{14}\text{C}$  assimilated, that remained in the shoot at PM for all the labelling occasions. Thus it is clear that much of the  $^{14}\text{C}$  assimilated by the plants at 2 WAA was translocated to the grain. The primary ear at 2 WAA was established as the major sink for photosynthate, thus much of the  $^{14}\text{C}$  assimilated by plants at 2 WAA was translocated to the grain. Averaged over the stressed and non-stressed plants the total radioactivity of the whole plant 48 h after labelling at 2 WAA was 2 526 851 dpm plant<sup>-1</sup> less than the total radioactivity of the whole plant 48 h after labelling at A (Section 4.3.7.2). Thus the lower amount of  $^{14}\text{C}$  assimilated by the whole plant at 2 WAA coupled with the tendency to translocate much of the assimilated  $^{14}\text{C}$  to the grain resulted in the SR of the segments

of the whole shoot for plants labelled at 2 WAA being generally less on all sampling occasions in comparison to the SR of the segments of the whole shoot of plants labelled at A. The SR of the grain at 48 h after labelling at A was also higher than the SR of the grain 48 h after labelling at 2 WAA. This was due to the lower dry mass of the grain at A in comparison to that at 2 WAA. As the grain increased rapidly in dry mass from A to PM the SR of the grain declined to much lower levels for plants labelled at A in comparison to plants labelled at 2 WAA. The grain recorded the highest SR at 48 h after labelling at 2 WAA. The SR of the grain of stressed plants was higher than that of non-stressed plants from 2 WAA to PM due to the concentrating effects of stress. As indicated by the increase in total radioactivity of the grain (Section 4.3.4.2) most of the translocation of  $^{14}\text{C}$  assimilated at 2 WAA to the grain occurred from 2 to 4 WAA. Thus the decline in the SR of the grain from 2 WAA to PM indicates the dilution effect of  $^{12}\text{C}$  photosynthate being incorporated into the dry mass of the grain after labelling. The grain of stressed plants had a higher SR at PM than that of non-stressed plants. This was probably due to the concentrating effects of stress. The shank recorded the next highest SR at 48 h after labelling at 2 WAA. The non-stressed plants unexpectedly recorded the highest SR of the shank at 2 WAA although the stressed plants recorded the highest SR of the shank at 4 and 6 WAA and at PM. The shank in fact recorded a higher SR from 2 WAA to PM than did the other stem segments. The high SR of the shank at 48 h after labelling at 2 WAA is indicative of its rôle as a conduit for photosynthate destined for the primary ear. The cob recorded the next highest SR at 48 h after

labelling at 2 WAA. The SR of the cob of stressed plants was higher than that of the non-stressed plants at 2 WAA and at PM. This was probably due to the concentrating effects of stress. The SR of the cob declined from 2 to 6 WAA and then increased slightly from 6 WAA to PM. This reflects the decline in total radioactivity of the cob from 2 to 6 WAA, followed by an increase in total radioactivity from 6 WAA to PM (Section 4.3.4.2). It appears that  $^{14}\text{C}$  arriving in the cob was translocated to the grain from 2 to 6 WAA. However, as the rate of grain fill declined from 6 WAA and ceased at PM (Section 4.3.3.8),  $^{14}\text{C}$  actually accumulated in the cob from 6 WAA to PM. The SR of the husks peaked at 48 h after labelling at 2 WAA, with SR of the husks of stressed plants higher than that of the non-stressed plants. The SR of the husks declined from 2 WAA to PM, more so in the non-stressed plants than the stressed plants. Since the total radioactivity of the husks of both stressed and non-stressed plants declined from 2 WAA to PM, the less rapid decline in the SR of the husks of the stressed plants indicates that the total radioactivity of the husks of the stressed plants declined by a smaller proportion than did the dry mass of the husks (Table 4.8 and Appendix 46). The SR of the 2° ear of non-stressed plants was higher than that of stressed plants from 2 WAA to PM. This is indicative of the higher total radioactivity of the 2° ear generally recorded for non-stressed plants compared to stressed plants from 2 WAA to PM (Section 4.3.4.2). Thus it appears that the non-stressed plants were able to partition a greater amount of the  $^{14}\text{C}$  assimilated at 2 WAA, to the 2° ear from 2 WAA to PM in comparison to the stressed plants. It is noteworthy that the SR of the 2° ear was highest at 2 WAA and then declined from

2 to 6 WAA and then increased from 6 WAA to PM. This reflects the trend in total radioactivity and dry mass of the 2° ear from 2 WAA to PM (Section 4.3.4.2 and Table 4.8). It appears that <sup>14</sup>C was mobilized out of the 2° ear from 2 to 6 WAA during peak translocation of photosynthate to the grain of the primary ear. In the final two weeks of grain fill i.e. from 6 WAA to PM the rate of dry mass gain by the primary grain was slower than during the earlier phase of grain fill and ceased at PM (Section 4.3.3.8). It appears that some of the <sup>14</sup>C which occurred in the vegetative segments as labile organic compounds once again became available for translocation to the 2° ear from 6 WAA to PM. As with plants labelled at A, the SR of the sheaths and laminae of plants labelled at 2 WAA peaked at 48 h after labelling and then declined from 2 WAA to PM. The sheaths and laminae of non-stressed plants recorded higher SR at 48 h after labelling at 2 WAA compared to stressed plants. This is again probably indicative of the more direct and rapid translocation of assimilated <sup>14</sup>C to the primary ear that occurred in the stressed plants. Of the stem segments the A1 segment recorded the highest SR at 48 h after labelling at 2 WAA. The SR of the A1 segment was higher in the non-stressed plants than the stressed plants at 2 WAA, but lower in the non-stressed plants than the stressed plants at PM. This somewhat inconsistent trend in the SR of the A1 segment under stress and non-stress conditions makes it difficult to ascertain the effects of water stress on the SR of this segment. The SR of the tassel peaked at 48 h after labelling at 2 WAA with SR of the tassel higher in non-stressed plants than stressed plants. The SR of the tassel declined from 2 WAA to PM which reflects the decline in total radioactivity of

the tassel (Section 4.3.4.2). It appears that  $^{14}\text{C}$  was mobilized out of the tassel for utilization in the rest of the plant. At PM the SR of the tassel of non-stressed plants was marginally higher than that of stressed plants.

When plants were labelled at 4 WAA, 20,3 and 19,7 % of the  $^{14}\text{C}$  recovered in the whole plant at PM in stressed and non-stressed plants, respectively, occurred in the whole shoot (Section 4.3.6.3). This was a greater proportion of  $^{14}\text{C}$  assimilated that remained in the shoot at PM compared to plants labelled at 2 WAA. It was, however, a smaller proportion in comparison to plants labelled at A. It is clear that the primary ear was still established as the major sink for photosynthate at 4 WAA, however, to a lesser extent than was the case at 2 WAA. Averaged over the stressed and non-stressed plants, the total radioactivity of the whole plant 48 h after labelling at 4 WAA was 6 914 836 dpm plant<sup>-1</sup> less than the total radioactivity of the whole plant 48 h after labelling at 2 WAA, and 9 441 687 dpm plant<sup>-1</sup> less than the total radioactivity of the whole plant 48 h after labelling at A. Thus the lower amount of  $^{14}\text{C}$  assimilated by the whole plant at 4 WAA coupled with the tendency to translocate much of the assimilated  $^{14}\text{C}$  to the grain resulted in the SR of the segments of the whole shoot being less on all sampling occasions in comparison to segments of the whole shoot of plants labelled at A and 2 WAA. The SR of the grain of plants labelled at 2 WAA was higher on all sampling occasions than the SR of the grain of plants labelled at 4 WAA on all sampling occasions. The grain of non-stressed plants labelled at 4 WAA had a higher SR at 4 and 6 WAA and at PM than the grain

of non-stressed plants labelled at A and sampled at 4 and 6 WAA and at PM. The grain of the stressed plants labelled at 4 WAA had a higher SR only at PM than the grain of the stressed plants labelled at A and sampled at PM. It will be recalled, however, that the grain of the stressed and particularly the non-stressed plants labelled at 4 WAA and sampled at PM from replication one recorded higher SR than plants sampled from the other two replications. This resulted in the total radioactivity of the whole plant increasing from 6 WAA to PM. This may therefore have exaggerated the trend in the SR of the grain from 6 WAA to PM. It is noteworthy that apart from the B4 segment and the husks, all the segments of the non-stressed plants recorded a higher SR than the respective segments of the stressed plants from 4 WAA to PM. As mentioned earlier the stressed plants at 4 WAA had a lower leaf  $\Psi_w$  and stress resulted in greater leaf senescence (Sections 4.3.1 and 4.3.2). Both these factors would reduce the rate at which the stressed plants assimilated  $^{14}\text{C}$ . This was confirmed by the fact that the whole plant total radioactivity of the stressed plants 48 h after labelling at 4 WAA was 6 870 564 dpm plant<sup>-1</sup> in comparison to 8 410 327 dpm plant<sup>-1</sup> for non-stressed plants (Section 4.3.7.2). Thus the lower total radioactivity for the stressed plants meant that they could not even establish higher SR of the segments than the non-stressed plants. The shank recorded the highest SR at 48 h after labelling at 4 WAA. The dry mass of the grain at 4 WAA was obviously much greater than at A or 2 WAA and this, coupled with the lower amount of  $^{14}\text{C}$  assimilated by the whole plant, meant that the smaller (by dry mass) shank recorded the highest SR at 48 h after labelling at 4 WAA. The high SR of the

shank at 48 h after labelling at 4 WAA is indicative of its rôle as a conduit for  $^{14}\text{C}$  being translocated to the primary ear. The fact that the SR of the shank peaked at 48 h after labelling at 4 WAA also indicates that the bulk of the translocation of  $^{14}\text{C}$  to the ear occurred shortly after assimilation at labelling. The A1 segment of the non-stressed plants recorded the next highest SR at 48 h after labelling at 4 WAA. This was also the highest SR recorded for the stem segments of the non-stressed plants at 4 WAA. However, at 4 WAA the stressed plants recorded the highest SR for the stem segments in the B2 segment. This inconsistent trend in the SR of the stem segments under stress and non-stress conditions makes it difficult to hypothesize on the physiological rôles played by the stem segments during grain fill. The SR of the sheaths and laminae peaked at 48 h after labelling at 4 WAA and then declined from 4 WAA to PM as  $^{14}\text{C}$  was translocated out of the leaves, primarily to the grain. The SR of the cob peaked at 48 h after labelling at 4 WAA and then declined from 4 WAA to PM in stressed plants but initially decreased from 4 to 6 WAA in non-stressed plants and then increased from 6 WAA to PM. This increase in the SR of the cob of non-stressed plants from 6 WAA to PM was largely due to the decline in dry mass recorded for the cob during the same period. Generally, however, the rapid decline in the SR of the cob from 4 to 6 WAA in stressed and non-stressed plants reflects the rapid decline in total radioactivity of the cob during the same period as  $^{14}\text{C}$  was translocated to the grain. The SR of the tassel, husks and 2° ear peaked at 48 h after labelling at 4 WAA, with the husks recording the highest SR. The SR of the tassel and the husks decreased from 4 to 6 WAA and then increased from 6 WAA to

PM under stress and non-stress conditions. This generally reflected the changes in total radioactivity of these segments during the same period. This may indicate that  $^{14}\text{C}$  became available for translocation to these segments in the latter phase of grain fill. While the SR of the 2° ear of non-stressed plants decreased from 4 to 6 WAA and then increased from 6 WAA to PM, the SR of the 2° ear of stressed plants increased from 4 WAA to PM.

When plants were labelled at 6 WAA, 32,4 and 33,0 % of the  $^{14}\text{C}$  recovered in the whole plant at PM in stressed and non-stressed plants, respectively, occurred in the whole shoot (Section 4.3.6.3). This was a greater proportion of  $^{14}\text{C}$  assimilated that remained in the shoot at PM compared to plants labelled at 2 and 4 WAA. It was, however, a smaller proportion in comparison to plants labelled at A. It is therefore apparent that the grain was still established as the major sink for photosynthate synthesized at 6 WAA, however, to a lesser extent than was the case at 2 and 4 WAA. Averaged over the stressed and non-stressed plants the total radioactivity of the whole plant 48 h after labelling at 6 WAA was 5 238 623, 12 153 459 and 14 680 310 dpm plant<sup>-1</sup> less than the total radioactivity of the whole plant 48 h after labelling at 4 WAA, 2 WAA and A, respectively. Thus the lower amount of  $^{14}\text{C}$  assimilated by the whole plant at 6 WAA coupled with the tendency to translocate a large proportion of the assimilated  $^{14}\text{C}$  to the grain, resulted in the SR of the whole shoot segments being less on all sampling occasions in comparison to segments of the whole shoot of plants labelled at A, 2 WAA and 4 WAA and sampled on all occasions. The

grain too, as a result of the low amount of  $^{14}\text{C}$  assimilated at 6 WAA, had a lower SR on all sampling occasions compared to the grain sampled on all occasions from plants labelled at A, 2 WAA and 4 WAA. The stressed plants had a non-significantly lower total radioactivity of the whole plant 48 h after labelling at 6 WAA than the non-stressed plants (Section 4.3.6.3). Nonetheless, the marginally higher total radioactivity of the whole plant of the non-stressed plants enabled them to establish a higher SR of all segments, apart from the tassel, than the stressed plants 48 h after labelling at 6 WAA. The shank recorded the highest SR 48 h after labelling at 6 WAA and the SR of the shank declined from 6 WAA to PM. However, the SR of the shank of non-stressed plants at PM was less than that of stressed plants. This may be indicative of continued mobilization of  $^{14}\text{C}$  from the segments of the whole shoot to the primary ear under stress conditions. The A1 segment of the non-stressed plants recorded the next highest SR at 6 WAA. However, in the stressed plants, after the shank, the next highest SR was recorded in the B2 segment at 6 WAA. In fact the A1, B1, B2, B3 and B4 segments recorded higher SR than any of the other segments at 6 WAA except, of course, for the shank. This is indicative of the increased proportion of  $^{14}\text{C}$  assimilated at 6 WAA that remained in the shoot. The SR of the stem segments of both stressed and non-stressed plants declined from 6 WAA to PM. This reflects the decline in total radioactivity of these stem segments during the same period as  $^{14}\text{C}$  was mobilized from the stem to the grain (Section 4.3.4.2). The SR of the tassel, sheaths, laminae and cob of both stressed and non-stressed plants declined from 6 WAA to PM which reflects the decline in total radioactivity as  $^{14}\text{C}$  was

mobilized from these segments to the grain. The SR of the cob of stressed plants at PM was higher than that of non-stressed plants which may indicate the continued mobilization of  $^{14}\text{C}$  to the primary ear under stress conditions. The SR of the grain increased from 6 WAA to PM with the SR of the grain of stressed plants higher at PM than that of non-stressed plants. The increase in the SR of the grain indicates that the total radioactivity of the grain increased by a greater proportion than the dry mass did from 6 WAA to PM, more so in the stressed plants than the non-stressed plants. This indicates that the stressed plants mobilized more  $^{14}\text{C}$  to the grain than the non-stressed plants as they were forced to utilize previously assimilated C to meet the requirements of the grain.

#### 4.3.4.2 Total radioactivity

##### Labelling at A

The main effect for stress treatment was non-significant (Table 4.15 and Appendix 36.1). Non-stressed plants had marginally higher total radioactivity (TR) than stressed plants.

The main effects for WAA and segment were significant. However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

Table 4.15 Effect of water stress (S) and lack of water stress (NS) on total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over five growth periods during grain fill from a maize hybrid labelled at anthesis

Stress treatment	Segment														Stress treatment marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
S	61	363	358	581	790	1 137	1 292	443	583	969	2 659	1 915	2 878	259	1 021
NS	79	493	442	721	925	987	1 054	468	682	1 308	2 496	2 157	3 180	543	1 110
Segment marginal means	70	428	400	651	857	1 062	1 173	456	633	1 138	2 578	2 036	3 029	401	

Body of table

LSD

0,05

0,01

Comparison of means at the same level of stress treatment

NS

NS

Comparison of means at the same level of segment or with neither factor in common

NS

NS

Marginal means

Comparison of stress treatment means

NS

NS

Comparison of segment means

233

306

The interaction of stress treatment with WAA was non-significant. There were no significant components of the interaction either.

The interaction of stress treatment with segment was non-significant. This indicates that the response to stress was generally similar for all segments. However, there were apparent exceptions (Table 4.15). The B3 and B4 stem segments, as well as the grain, had higher TR under stress conditions than non-stress conditions. With the grain this may indicate direct translocation of current photosynthate to the primary ear under stress conditions. The higher TR in the B3 and B4 stem segments under stress conditions is not easy to explain. It may be due to direct translocation of photosynthate to these stem internodes for root carbohydrate requirements and final increases in the structural growth of the stem base (Section 4.3.4.1).

The interaction of WAA with segment was significant (Table 4.16). The WAA(linear and cubic) x segments components of the interaction were also significant. Although TR fluctuated considerably during grain fill it was generally lower in all segments except the grain and cob at PM than at A. The most noteworthy feature of the data of this interaction is that the husks recorded significantly ( $p = 0,01$ ) the highest TR of all the segments at A. The husks also recorded the highest TR of all the segments at 2 and 4 WAA. Only at 6 WAA and at PM did the TR of the grain significantly ( $p = 0,01$ ) exceed the TR of the husks. That the TR of the husks at A was significantly ( $p = 0,01$ ) higher than the TR of the laminae indicates that the husks were a major sink for  $^{14}\text{C}$  at A. The extent to which the  $^{14}\text{C}$  in the husks at A

Table 4.16 Total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over water stress treatments from anthesis to eight weeks after anthesis (WAA) for a maize hybrid labelled at anthesis

WAA	Segment														WAA marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
0	110	537	579	965	1 158	1 195	1 623	548	996	2 343	1 083	1 447	3 255	1 245	1 220
2	94	479	487	878	1 171	1 805	2 254	533	708	1 108	1 376	2 434	3 829	303	1 247
4	62	372	312	453	545	661	511	453	540	964	2 832	2 177	3 271	78	945
6	56	421	316	510	827	897	755	368	495	703	3 870	1 990	2 448	156	987
8	29	333	305	450	586	752	724	376	424	574	3 729	2 130	2 342	222	927
Segment marginal means	70	428	400	651	857	1 062	1 173	456	633	1 138	2 578	2 036	3 029	401	

Body of table

	LSD	
Comparison of means at the same level of WAA	0,05	0,01
Comparison of means at the same level of segment or with neither factor in common	520	683
	520	686

Marginal means

Comparison of WAA means	141	195
Comparison of segment means	233	306

was assimilated through own photosynthesis is, however, not known in this study. The dry mass of the husks did decline from 2 WAA to PM possibly as a result of labile organic compounds being translocated to the grain. However, since TR of the husks at PM was 72,0 % of that at A, it appears that much of the  $^{14}\text{C}$  assimilated by the husks at A was utilized irreversibly for structural growth. The significantly ( $p = 0,01$ ) higher TR of the grain at PM than at A was due to the translocation of  $^{14}\text{C}$  from the rest of the plant to the grain during grain fill. The fact that the grain continued to increase in TR in the weeks following labelling at A, provides evidence that not all  $^{14}\text{C}$  was immediately upon assimilation by the leaves translocated to the grain, but that  $^{14}\text{C}$  which was assimilated as early as at A and partitioned to other parts of the plant, could be remobilized and translocated to the grain long after it was originally assimilated by the leaves. It is noteworthy that the TR of the grain increased non-significantly from A to 2 WAA by 293 228 dpm segment<sup>-1</sup>, but increased significantly ( $p = 0,01$ ) from 2 to 4 WAA by 1 453 313 dpm segment<sup>-1</sup>. In fact from 2 to 4 WAA the TR of the grain increased by 205,7 %. The increase in the grain TR of 1 037 523 dpm segment<sup>-1</sup> from 4 to 6 WAA was also significant ( $p = 0,01$ ) and represented a 136,6 % increase in TR. It appears that the primary ear was established as the major sink for photosynthate from 2 WAA onwards and that the most substantial mobilization of  $^{14}\text{C}$ , assimilated at A, to the grain occurred from 2 to 6 WAA. It is also noteworthy that the TR in the grain peaked at 6 WAA and declined non-significantly to PM. This may indicate that in the last two weeks of grain fill the  $^{14}\text{C}$  assimilated at A that was part of labile, and therefore

remobilizable, organic components in vegetative organs had been depleted. Thus the rate at which radioactive photosynthate was deposited in the grain was marginally exceeded by the rate of respiration losses in the grain. The cob continued to increase in dry mass until approximately 6 WAA (Table 4.8 and Appendix 46). Thus the significantly ( $p = 0,05$ ) higher TR in the cob at PM than at A is indicative of  $^{14}\text{C}$  incorporated into the structural organic compounds of the cob, plus  $^{14}\text{C}$  in the form of labile organic compounds translocated to the cob, primarily for deposition in the grain. It is also possible that as the rate of grain fill declined in the final phase of grain fill the cob served as an alternative sink for photosynthate. The general decline in TR in all the other vegetative organs is indicative of the continual turnover of  $^{14}\text{C}$  in the form of labile organic compounds. Part of the  $^{14}\text{C}$  lost from the vegetative organs may have been remobilized and translocated to the primary ear while another part may have been utilized for respiratory requirements (Section 4.3.7.2). It is noteworthy that the 2° ear initially received non-significantly more  $^{14}\text{C}$  than the primary ear during the 48 h after labelling. However, as the primary ear was established as the major sink for photosynthate the availability of carbohydrate for the 2° ear became limited. In fact, TR of the 2° ear declined significantly ( $p = 0,01$ ) from A to 4 WAA which may indicate losses due to respiration and it may also indicate remobilization of  $^{14}\text{C}$  to the primary ear. However, as the rate at which the primary ear utilized available photosynthate declined the 2° ear began to receive  $^{14}\text{C}$  again as reflected by the non-significant increase in  $^{14}\text{C}$  from 4 WAA to PM. At A the TR of the main stem segments increased basipetally, with

the B4 segment recording the highest TR of the main stem segments at A. The TR of the B4 segment at A was significantly ( $p = 0,01$ ) higher than that of the top and A1 segments, and significantly ( $p = 0,05$ ) higher than that of the B1 segment. Many of the leaves attached to the B4 segment at A were in the process of senescing. It is likely, therefore, that much of the  $^{14}\text{C}$  in the B4 segment was translocated to it from upper photosynthesising leaves. The B4 segment on average is the largest main stem segment by dry mass (Table 4.8 and Appendix 46), thus it is likely that its C requirements for cell maintenance and respiration were also high. The B4 segment probably serves as a conduit for photosynthate translocated to the roots (seminal and adventitious). It is likely that besides the roots requiring C for respiration and cell maintenance requirements, some C may be utilized for final increases in structural growth of the root system just after anthesis. Whereas the TR of the top, A1 and B1 segments declined non-significantly from A to PM, the TR of the B2, B3 and B4 segments initially increased from A to 2 WAA before declining from 2 WAA to PM. However, the initial increase was only significant ( $p = 0,05$ ) in the B3 and B4 segments while the decline in TR was significant ( $p = 0,05$ ) in the B2 segment and significant ( $p = 0,01$ ) in the B3 and B4 segments. The physiological significance for the initial increase in TR in the B2, B3 and B4 segments from A to 2 WAA is uncertain. However, the sheaths and laminae underwent a substantial decline in TR from A to 2 WAA and it is likely that the increase in the TR of the B2, B3 and B4 segments during this period was due to the mobilization of  $^{14}\text{C}$  out of the leaves into these stem segments.

## Labelling at 2 WAA

The main effect for stress treatment was non-significant (Table 4.17 and Appendix 36.2). Stressed plants had non-significantly higher TR than non-stressed plants.

The main effect for WAA was non-significant, while the main effect for segment was significant. However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interaction of stress treatment with WAA was non-significant. There were no significant components of the interaction either.

The interaction of stress treatment with segment was non-significant. This indicates that the response to stress was generally similar for all segments. However, there were apparent exceptions (Table 4.17). The A1, B4, sheaths, grain, cob and husks had higher TR while the tassel, top, B1, B2, B3, shank, leaves and 2° ear had lower TR under stress than non-stress conditions. The concentrating effects hypothesised earlier may again be responsible for the high TR in the receiving organs, viz the cob, grain and husks, under stress conditions. The higher TR in the B4 segment under stress conditions may be due to photosynthate being translocated to it (perennial tendency - Section 4.3.4.1) for storage, or translocated through it for root requirements and the concentrating effects of stress resulted in the higher TR of the B4 segment. It is possible that the A1 segment served as the conduit for a large proportion of

Table 4.17 Effect of water stress (S) and lack of water stress (NS) on total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over four growth periods during grain fill from a maize hybrid labelled at two weeks after anthesis

Stress treatment	Segment														Stress treatment marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
S	44	88	124	163	169	201	94	136	272	604	11 551	1 049	285	5	1 056
NS	49	103	119	172	187	205	92	143	255	749	10 336	934	239	8	970
Segment marginal means	46	96	121	167	178	203	93	140	263	677	10 943	992	262	6	

Body of table

LSD

0,05

0,01

Comparison of means at the same level of stress treatment

NS

NS

Comparison of means at the same level of segment or with neither factor in common

NS

NS

Marginal means

Comparison of stress treatment means

NS

NS

Comparison of segment means

290

382

photosynthate destined for the primary ear. Palmer et al. (1973) for instance found that the upper and middle leaves relative to the ear of the maize plant were the major contributors of  $^{14}\text{C}$  to the developing grain. The concentrating effects of stress possibly resulted in more  $^{14}\text{C}$  moving through the A1 segment to the grain under stress conditions. The sheaths of the leaves, as well as photosynthesising, serve as conduits for photosynthate passing from the leaves into the stem tissue. The concentrating effects of stress possibly resulted in more  $^{14}\text{C}$  directly moving from the leaves through the sheaths to the stem tissue and on to the grain. It would possibly have been expected that the shank too would have had a higher TR under stress conditions. It is not, however, clear why this was not the case. The lower TR in the other segments under stress conditions is indicative of less current photosynthate being initially incorporated into pools of labile organic compounds in vegetative organs. It is also indicative of the greater depletion of these pools of organic compounds during grain fill under stress conditions.

The interaction of WAA with segment was significant (Table 4.18). The WAA(linear and quadratic) x segment components of the interaction were also significant. The most noteworthy feature of these data is that 48 h after labelling at 2 WAA the grain had accumulated 8 036 492 dpm segment<sup>-1</sup> which was significantly ( $p = 0,01$ ) higher than that occurring in any other segment at 48 h. In the next two weeks the grain accumulated a further 4 602 048 dpm segment<sup>-1</sup>. Forty-eight hours after labelling at 2 WAA the grain had accumulated 55,4 % of the  $^{14}\text{C}$  assimilated by the whole plant at labelling. At 4 WAA the TR in the grain

Table 4.18 Total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over water stress treatments from two weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at two weeks after anthesis

WAA	Segment														WAA marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
2	112	246	282	377	367	428	194	319	650	1 488	8 036	1 528	511	15	1 040
4	39	58	100	142	148	189	62	103	198	699	12 639	760	213	5	1 097
6	19	47	59	84	116	125	79	80	129	272	11 596	764	116	2	963
8	17	32	44	66	80	70	38	57	75	248	11 501	914	207	3	954
Segment marginal means	47	96	121	167	178	203	93	140	263	677	10 943	992	262	6	

Body of table

Comparison of means at the same level of WAA

Comparison of means at the same level of segment or with neither factor in common

Marginal means

Comparison of WAA means

Comparison of segment means

LSD

0,05

0,01

581

763

592

782

NS

NS

290

382

represented 82,4 % of that recovered in the whole plant at 4 WAA. Thus it is clear that at 2 WAA the grain was established as the major sink for photosynthate. The cob, followed by the sheaths and laminae had also accumulated substantial amounts of  $^{14}\text{C}$  48 h after labelling at 2 WAA. These segments also declined more markedly in TR from 2 WAA to PM than did any of the other segments, with the laminae undergoing the most substantial decline in TR. Of the main stem segments the B3 segment recorded the highest TR at 2 WAA. The physiological significance of this is not certain. However, the B3 segment at 2 WAA had the largest leaves attached to it and except for the B4 segment it had greater dry mass than any of the other stem segments. The B4 segment recorded the lowest TR at 2 WAA even though it was the largest stem segment on a dry mass basis. The leaves attached to the B4 segment at 2 WAA were largely senesced and so most of the  $^{14}\text{C}$  in this segment must have been translocated to it from the upper leaves. As mentioned the B4 segment probably serves as a conduit for  $^{14}\text{C}$  translocated to the roots (seminal and adventitious) to be utilized for the respiratory and cell maintenance requirements of the roots. Judging by the low TR recorded in the B4 segment it appears that the relative requirements for photosynthate by the B4 segment itself and the roots are low at 2 WAA. All the stem segments declined in TR from 2 WAA to PM with a considerable proportion of the  $^{14}\text{C}$  being translocated to the grain.

### Labelling at 4 WAA

The main effect for stress treatment was significant (Table 4.19 and Appendix 36.3). Stressed plants had significantly ( $p = 0,01$ ) less TR than non-stressed plants.

The main effect for WAA was non-significant, while the main effect for segment was significant. However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interaction of stress treatment with WAA was non-significant. There were no significant components of the interaction either.

The interaction of stress treatment with stem segment was just non-significant. This indicates that the response to stress was generally similar for all segments. However, there were apparent exceptions (Table 4.19). All segments recorded lower TR under stress conditions than non-stress conditions. Whole plant TR was lower under stress than non-stress conditions (Section 4.3.7.2). At 4 WAA the stressed plants had already undergone four consecutive stress cycles which resulted in less  $^{14}\text{C}$  being assimilated in comparison to the non-stressed plants. The grain had markedly less TR ( $1\ 339\ 774\ \text{dpm segment}^{-1}$ ) under stress conditions than under non-stress conditions in comparison to the other segments.

The interaction of WAA with segment was just non-significant. However, the WAA(linear) x segment component of the interaction

Table 4.19 Effect of water stress (S) and lack of water stress (NS) on total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over three growth periods during grain fill from a maize hybrid labelled at four weeks after anthesis

Stress treatment	Segment														Stress treatment marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
S	13	63	90	159	207	206	184	116	97	326	4 392	327	74	3	447
NS	27	108	119	232	300	302	189	145	212	435	5 732	441	86	3	595
Segment marginal means	20	86	104	196	254	254	186	131	154	381	5 062	384	80	3	

Body of table

LSD

0,05

0,01

Comparison of means at the same level of stress treatment

NS

NS

Comparison of means at the same level of segment or with neither factor in common

NS

NS

Marginal means

Comparison of stress treatment means

97

138

Comparison of segment means

273

359

was significant (Table 4.20). Total radioactivity declined the most in the laminae from 4 WAA to PM followed by the cob, shank and sheaths. As with labelling at 2 WAA, the grain was the major sink for photosynthate and 48 h after labelling at 4 WAA the TR of the grain was 4 246 676 dpm segment<sup>-1</sup> which represented 55,6 % of the <sup>14</sup>C assimilated by the whole plant at labelling. The whole plant TR for plants labelled at 4 WAA was not as high as that for plants labelled at 2 WAA which indicates that whole plant photosynthetic rate had declined from 2 to 4 WAA. However, plants at 4 WAA allocated similar percentages of <sup>14</sup>C to the grain 48 h after labelling as did plants labelled at 2 WAA. The TR of the grain increased markedly and significantly (p = 0,01) from 4 WAA to PM, and although this trend may be real the high TR of the grain at PM was probably exaggerated by sampling error.

#### Labelling at 6 WAA

The main effect for stress treatment was non-significant (Table 4.21 and Appendix 36.4). Stressed plants had non-significantly less TR than non-stressed plants.

The main effect for WAA was non-significant, while the main effect for segment was significant. However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interactions of stress treatment with WAA, and stress treatment with segment were non-significant.

Table 4.20 Total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over water stress treatments from four weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at four weeks after anthesis

WAA	Segment														WAA marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
4	30	155	182	284	325	299	225	232	225	684	4 247	616	130	5	546
6	11	49	67	153	243	262	199	90	150	214	4 787	296	53	2	470
8	19	54	65	150	192	200	135	70	87	244	6 154	240	57	2	548
Segment marginal means	20	86	104	196	254	254	186	131	154	381	5 062	384	80	3	

Body of table

	LSD	
Comparison of means at the same level of WAA	0,05	0,05
Comparison of means at the same level of segment or with neither factor in common	473	622
	471	622

Marginal means

Comparison of WAA means	NS	NS
Comparison of segment means	273	359

Table 4.21 Effect of water stress (S) and lack of water stress (NS) on mean segment total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) meaned over two growth periods during grain fill for a maize hybrid labelled at six weeks after anthesis

Stress treatment	
S	NS
137	171
LSD (0,05)	NS
LSD (0,01)	NS

The interaction of WAA with segment was significant (Table 4.22). Total radioactivity declined the most in the cob and, particularly, the laminae from 6 WAA to PM. The grain was the major sink for photosynthate at 6 WAA and 48 h after labelling at 6 WAA the TR of the grain was 1 029 990 dpm segment<sup>-1</sup> which represented 43,2 % of the <sup>14</sup>C assimilated by the whole plant at labelling. Whole plant photosynthetic capacity was lower at 6 WAA in comparison to that at A, 2 WAA and 4 WAA as reflected by the lower whole plant TR at 6 WAA (Section 4.3.7.2). However, the plants still allocated a large proportion of the assimilated <sup>14</sup>C for direct translocation to the grain.

Table 4.22 Total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of segments meaned over water stress treatments from six weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at six weeks after anthesis

WAA	Segment														WAA marginal means
	Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear	
6	3	56	79	146	176	177	164	68	58	218	1 030	208	19	1	172
8	3	22	31	66	85	110	88	26	20	67	1 283	89	20	1	136
Segment marginal means	3	39	55	106	130	144	126	47	39	142	1 157	149	20	1	

Body of table

	LSD	
Comparison of means at the same level of WAA	0,05	0,01
Comparison of means at the same level of segment or with neither factor in common	61	81
	72	101

Marginal means

Comparison of WAA means	NS	NS
Comparison of segment means	43	57

Second order interactions for labelling at A, 2 WAA, 4 WAA and 6 WAA

Each second order interaction of stress treatment, WAA and segment for labelling at A, 2 WAA, 4 WAA and 6 WAA was non-significant. There were no significant components of each interaction either. However, the apparent trends shown in the data of the second order interactions are discussed (Figure 4.14a,b,c,d).

When plants were labelled at A the imposition of water deficits commenced after labelling. Thus there was, theoretically, no difference in the photosynthetic capacity of the plants when they were labelled at A. In fact at A, the whole plant TR of plants to be stressed of 17 347 474 dpm plant<sup>-1</sup> was marginally higher than the whole plant TR of 16 816 792 dpm plant<sup>-1</sup> for the non-stressed plants. When plants were labelled at A, 69,0 and 73,2 % of the <sup>14</sup>C recovered in the whole plant at PM in the stressed and non-stressed plants, respectively, occurred in the whole shoot (Section 4.3.6.3). Thus it is clear that much of the <sup>14</sup>C assimilated by the plants at A remained in the shoot and was not translocated to the grain. This indicates that much of the <sup>14</sup>C assimilated at A was irreversibly utilized for the final structural growth of the whole shoot including the cob of the primary ear. This explains why the segments of the whole shoot for stressed and non-stressed plants generally had higher TR on all sampling occasions than did the segments of the whole shoot when plants were labelled at 2, 4 and 6 WAA. The husks recorded the highest TR 48 h after labelling at A, with the TR of the

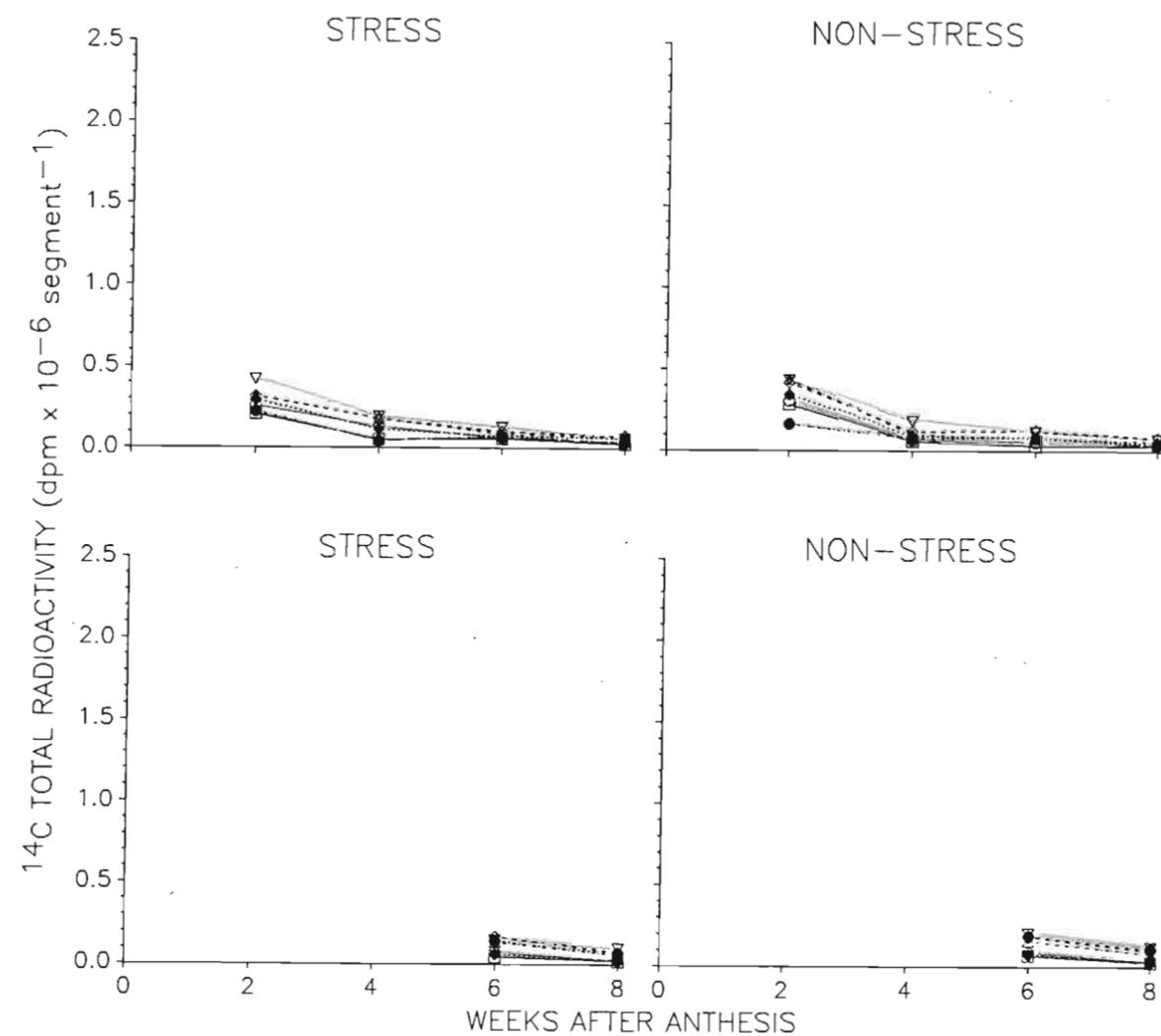
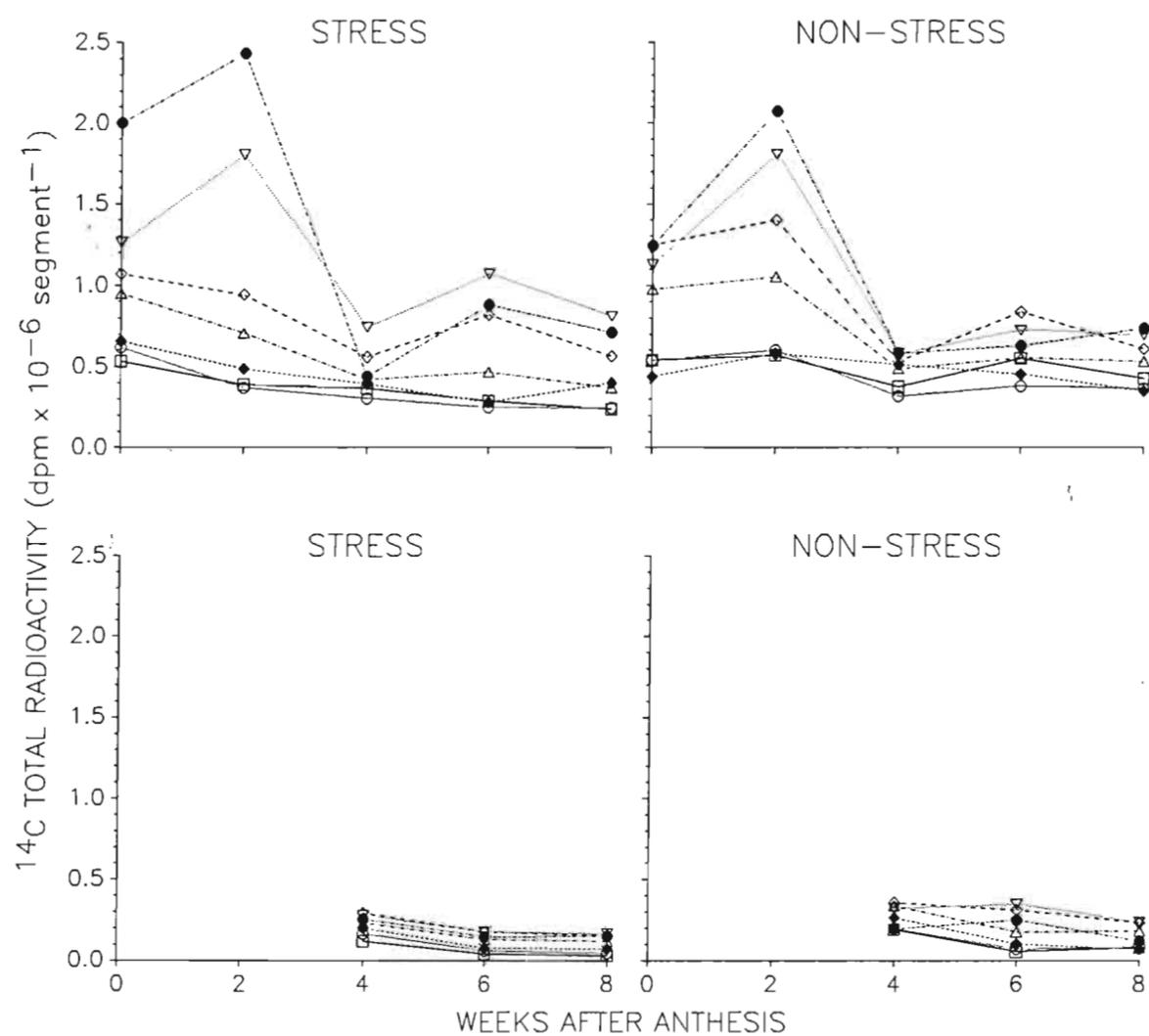


Figure 4.14a Effect of water stress during grain fill on total radioactivity of stem segments sampled at fortnightly intervals from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis

Key: top  $\square$ — $\square$  , A1  $\circ$ — $\circ$  , B1  $\triangle$ — $\triangle$  , B2  $\diamond$ — $\diamond$  , B3  $\nabla$ — $\nabla$  , B4  $\bullet$ — $\bullet$  , shank  $\blacklozenge$ — $\blacklozenge$

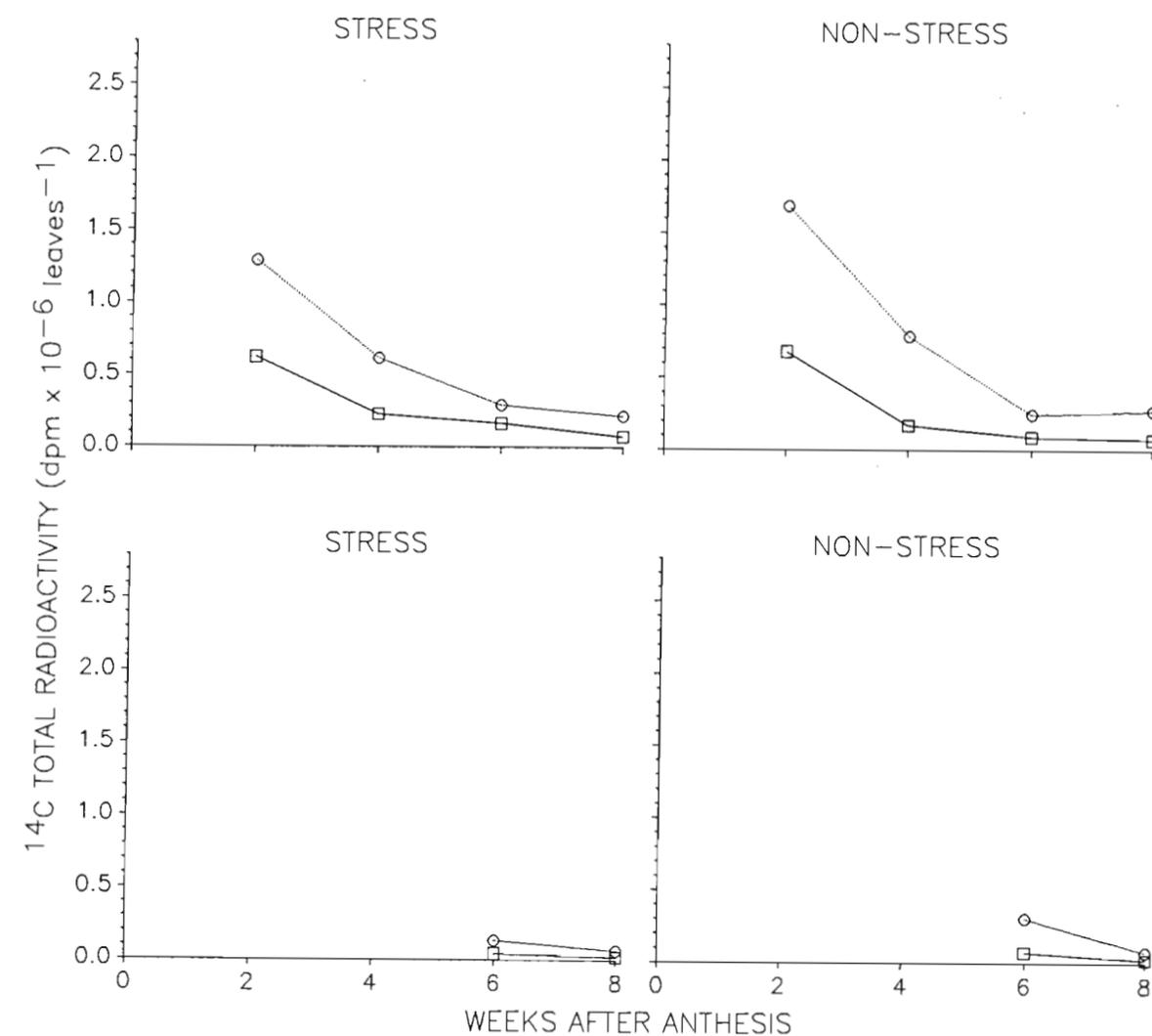
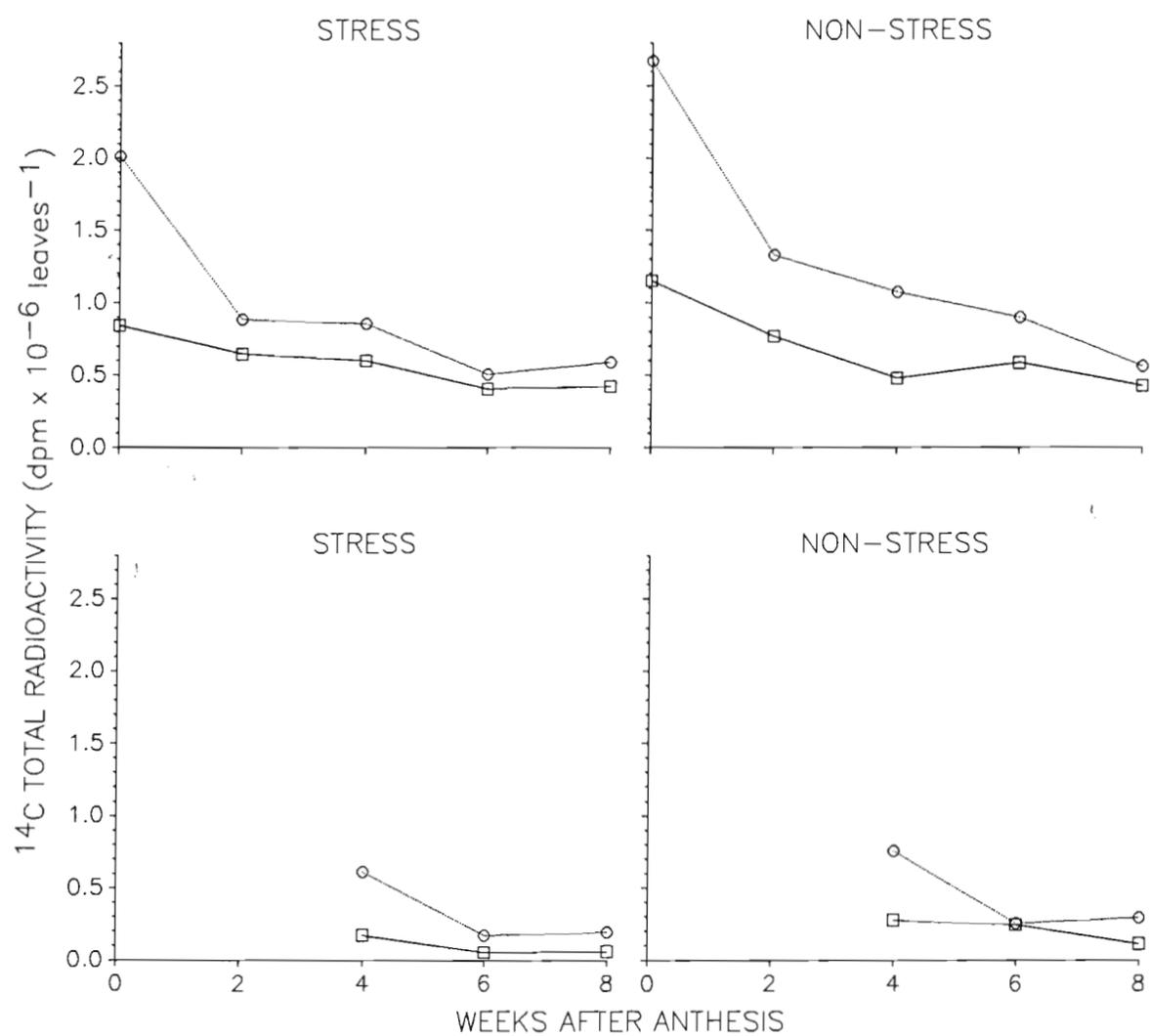


Figure 4.14b Effect of water stress during grain fill on total radioactivity of leaves sampled at fortnightly intervals from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis

Key: sheaths  $\square-\square$ , laminae  $\circ-\circ$

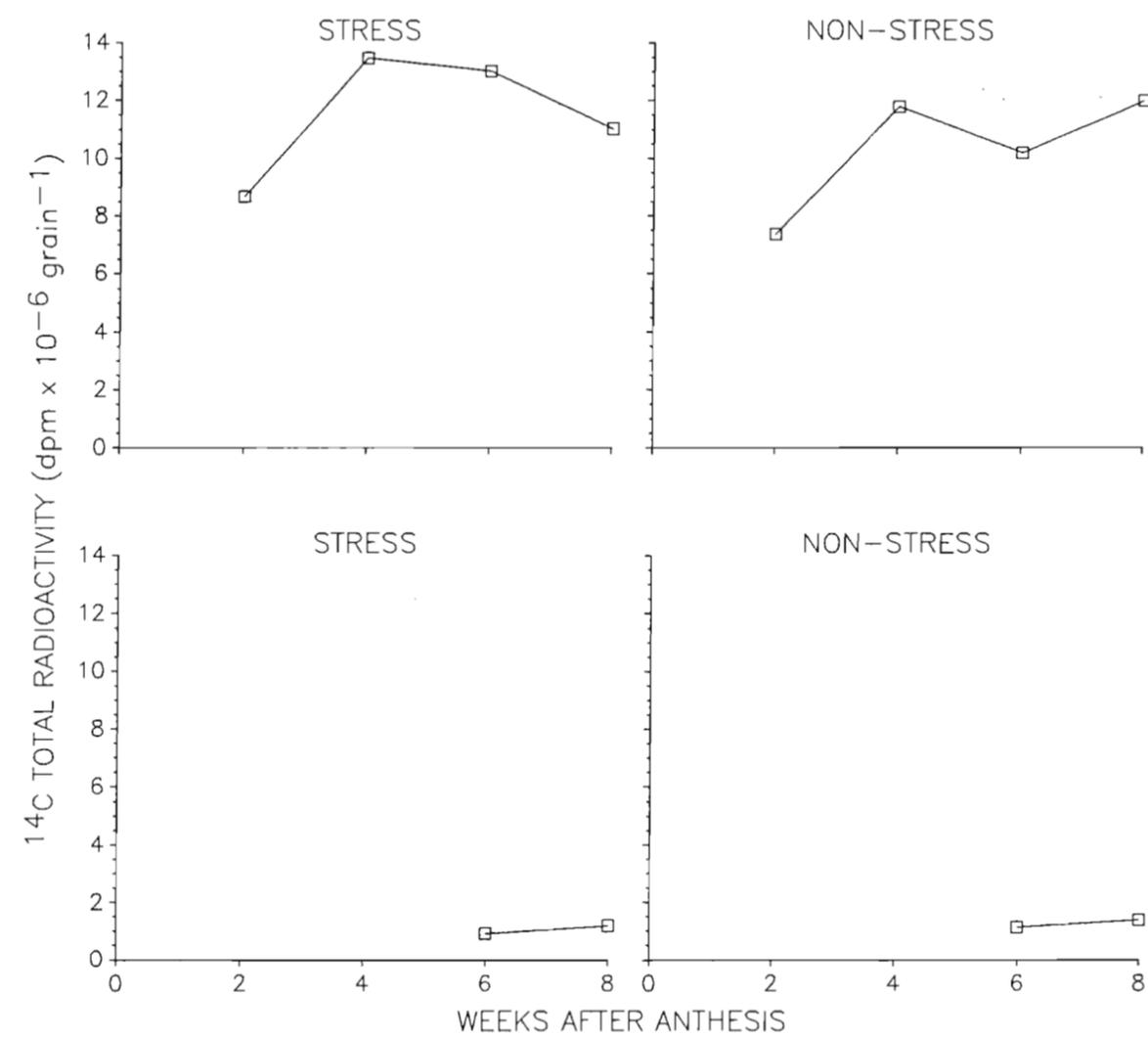
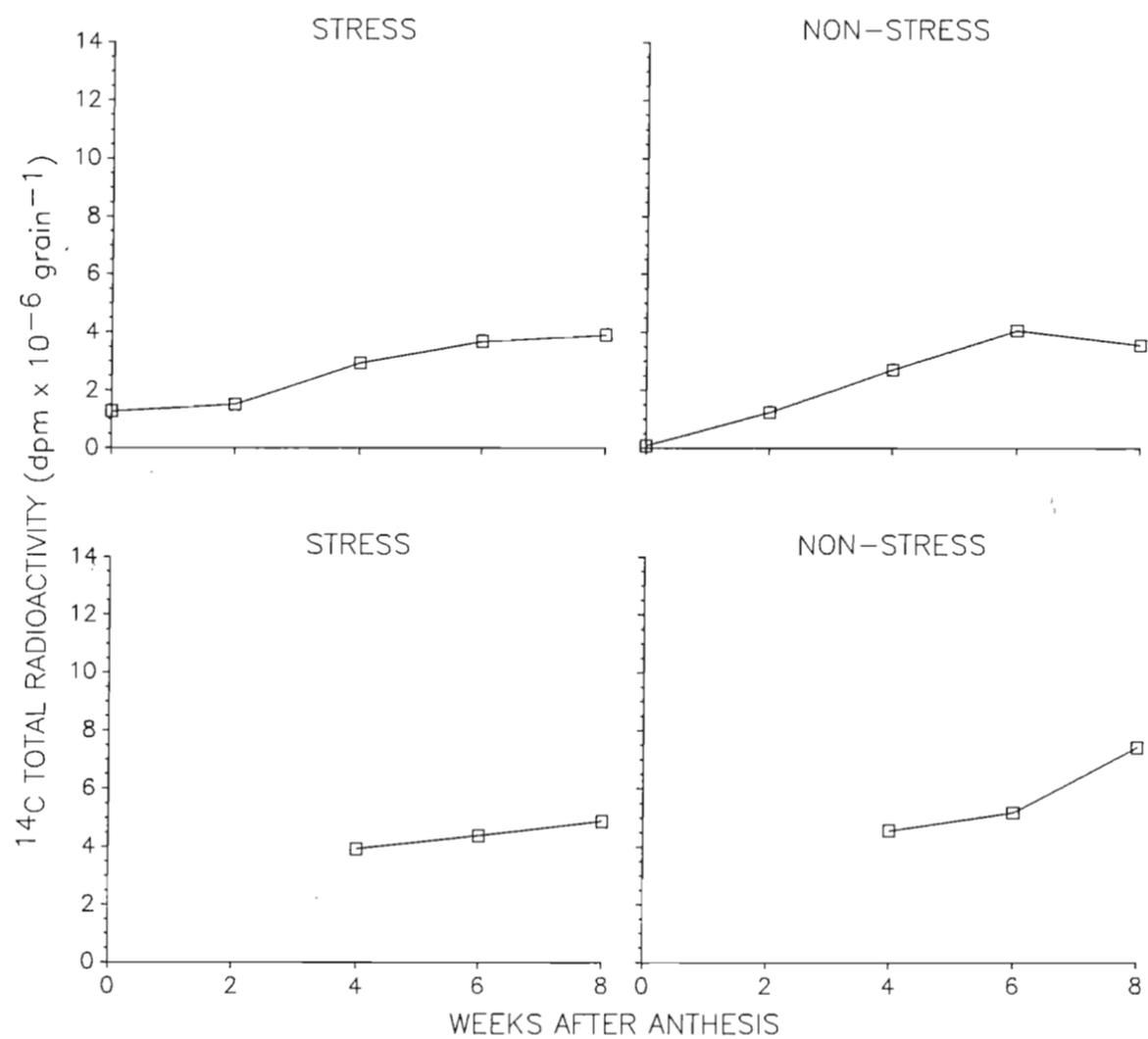


Figure 4.14d Effect of water stress during grain fill on total radioactivity of grain sampled at fortnightly intervals from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis

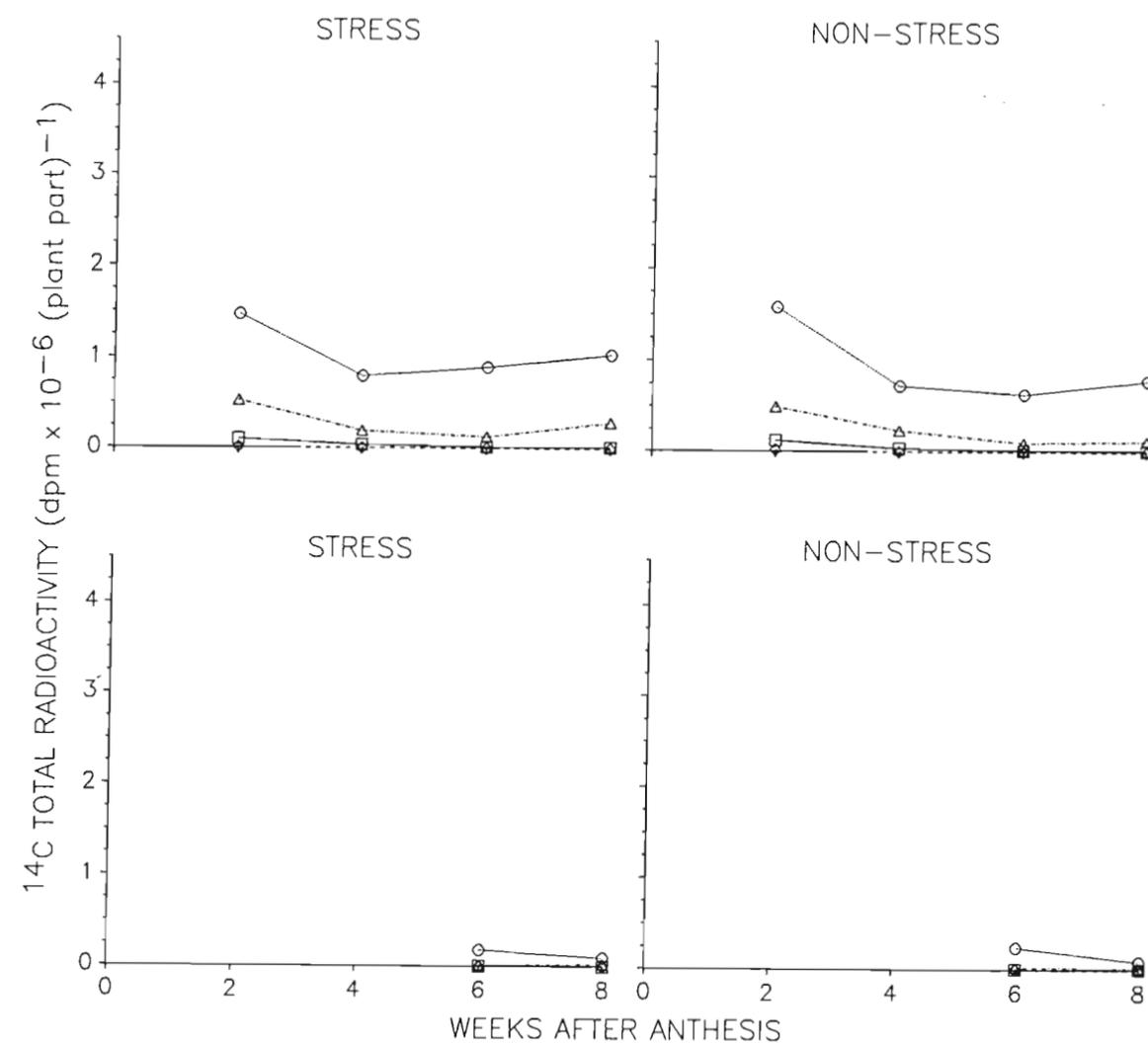
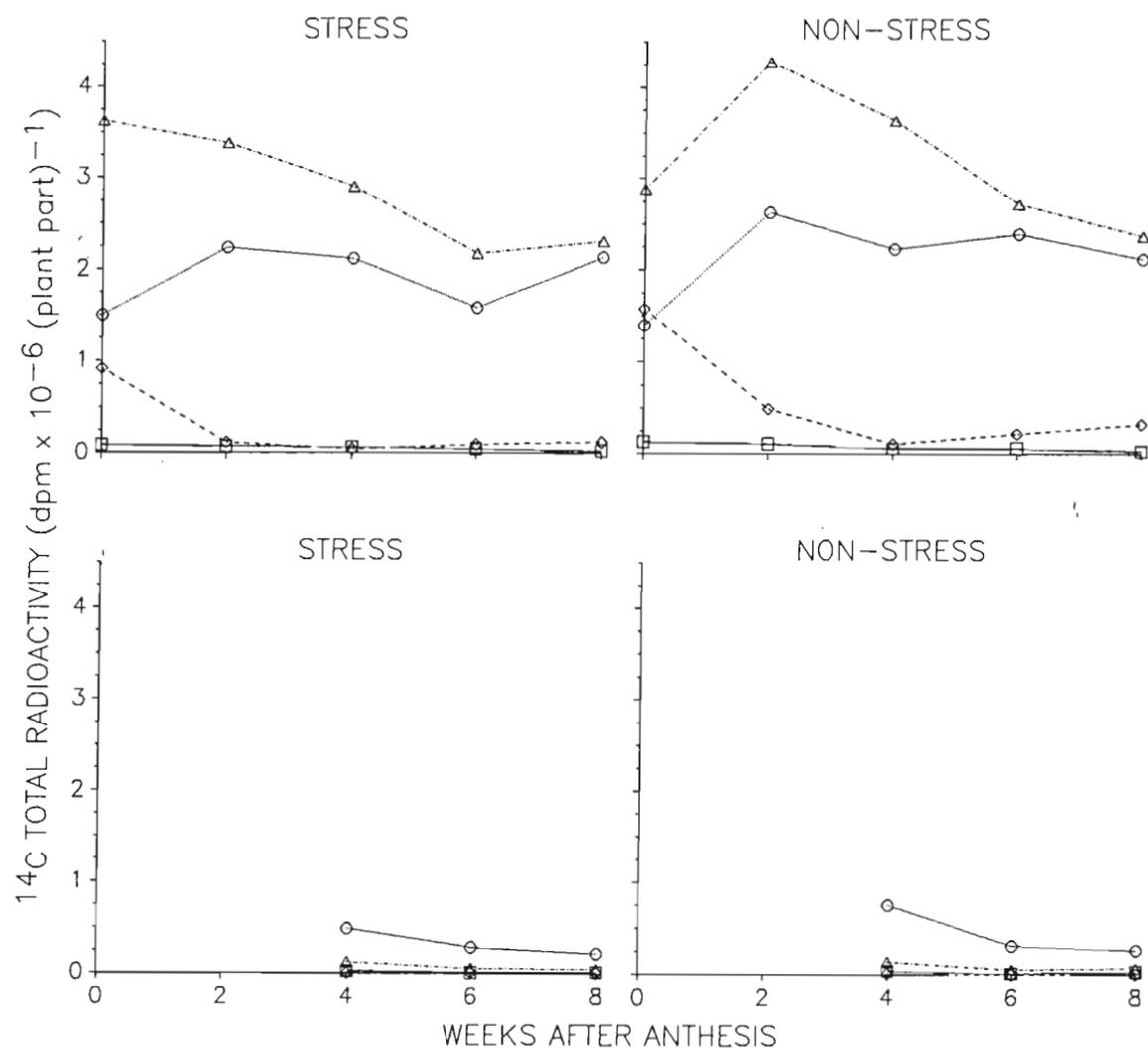


Figure 4.14c Effect of water stress during grain fill on total radioactivity of segments sampled at fortnightly intervals from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis

Key: tassel  $\square$ — $\square$ , cob  $\circ$ — $\circ$ , husks  $\triangle$ — $\triangle$ , 2° ear  $\diamond$ — $\diamond$

husks of the stressed plants higher than that of the non-stressed plants. It is not certain how much of the  $^{14}\text{C}$  in the husks was assimilated through own photosynthesis and how much was translocate from the rest of the plant. The physiological significance of the husks serving as the major sink for  $^{14}\text{C}$  assimilated at A is not certain. It may be theorised that the  $^{14}\text{C}$  was assimilated by the husks to be utilized for the increase in size that they undergo as the primary ear increases in dry mass (Table 4.8 and Appendix 46). It may also be theorised that the husks serve as a temporary reservoir for C which is later translocated into the grain. However, the husks did not decline substantially in TR from A to PM indicating that much of the  $^{14}\text{C}$  assimilated at A was irreversibly utilized for structural growth. It is not certain why the stressed plants had a higher TR of the husks at A than did the non-stressed plants. It is possible that after 48 h without water the stressed plants translocated more of the  $^{14}\text{C}$  assimilated at A directly to the ear which includes the husks. After the husks the laminae of both the stressed and non-stressed plants recorded the highest TR 48 h after labelling at A. This is in direct contrast to when plants were labelled at 2, 4 and 6 WAA where the grain recorded the highest TR 48 h after labelling. It is clear that  $^{14}\text{C}$  was not as rapidly translocated out of the leaves within 48 h after labelling at A, as was the case when plants were labelled at 2, 4 and 6 WAA. The laminae of non-stressed plants recorded a higher TR at A than the laminae of stressed plants which probably indicates that the stressed plants had mobilized  $^{14}\text{C}$  out of the leaves more rapidly than the non-stressed plants. The TR of the sheaths and laminae declined from A to PM as  $^{14}\text{C}$  was mobilized out of the leaves into the rest

of the plant. The initial decline in the TR of the laminae from A to 2 WAA was the most marked. From 6 WAA to PM the TR of the laminae of stressed plants increased marginally such that the TR of the laminae of stressed plants at PM was higher than that of non-stressed plants. It is unlikely that  $^{14}\text{C}$  was mobilized back into the leaves at PM so this trend in the stressed plants is likely to be due to sampling error. Initially at A the cob received more  $^{14}\text{C}$  than the grain in both stressed and non-stressed plants as evidenced by the higher TR of the cob at A than that of the grain. The TR of the cob and grain in the stressed plants at A was higher than that of the non-stressed plants. This may indicate that after 48 h without water the stressed plants translocated more of the  $^{14}\text{C}$  assimilated at A directly to the ear as a result of reduced assimilation of  $\text{CO}_2$ . From 4 WAA the TR of the grain exceeded that of the cob in both stressed and non-stressed plants as  $^{14}\text{C}$  was mobilized to the grain. The TR of the grain of stressed plants at PM was marginally higher than that of non-stressed plants. This may indicate that the stressed plants utilized the  $^{14}\text{C}$  assimilated at A to a greater extent for grain fill than did the non-stressed plants. The TR of the cob after initially increasing from A to 2 WAA remained fairly constant from 2 WAA to PM. This may indicate that as  $^{14}\text{C}$  was translocated from the cob to the grain it was replaced by  $^{14}\text{C}$  arriving from the rest of the plant. It may also indicate that much of the  $^{14}\text{C}$  assimilated at A was utilized for structural growth of the cob. The TR of the 2° ear peaked at A with the TR of the 2° ear of non-stressed plants higher at A than that of stressed plants. This may indicate that the non-stressed plants allocated more of the  $^{14}\text{C}$  assimilated at A to the 2° ear than did

the stressed plants. From A to 4 WAA the TR of the 2° ear declined, possibly as a result of the establishment of the primary ear as the major sink for photosynthate. From 4 WAA to PM the TR of the 2° ear increased again, possibly because as the rate of dry mass gain by the primary grain declined, some <sup>14</sup>C became available to the 2° ear. At PM the TR of the 2° ear of the non-stressed plants was 271,0 % higher than that of the stressed plants. Again this would appear to indicate that the non-stressed plants had more <sup>14</sup>C available in the segments of the whole shoot that could be translocated to the 2° ear during late grain fill. The TR of the tassel peaked at A, with the TR of the tassel of the non-stressed plants higher than that of the stressed plants. It appears therefore that the tassel still had a requirement for C at A, although relative to the other segments this requirement was small. The lower TR of the tassel of stressed plants compared to non-stressed plants at A is indicative of less <sup>14</sup>C being allocated to the non-grain parts of the plant under stress conditions. From A to PM the TR of the tassel declined as <sup>14</sup>C was utilized for respiration and mobilized out of the tassel and used for grain fill. The TR of the tassel of non-stressed plants at PM was higher than that of stressed plants which again indicates that less <sup>14</sup>C was available for non-grain parts of the plant under stress conditions. Of the stem segments including the shank, the B4 segment recorded the highest TR at A. The stressed plants recorded a higher TR of the A1, B3, B4 and shank segments at A than did the respective segments of the non-stressed plants. The higher TR of the A1 segment at A in stressed plants may indicate greater mobilization of <sup>14</sup>C out of the leaves attached to this segment for translocation to the

primary ear. The higher TR of the B3 and B4 stem segments of stressed plants may also indicate increased mobilization of  $^{14}\text{C}$  out of the leaves attached to these segments. The higher TR of the shank of stressed plants is indicative of the translocation of a greater amount of  $^{14}\text{C}$  directly to the primary ear under stress conditions. From A to 2 WAA the TR of the top, A1, B1, B2, B3, B4 and shank segments of non-stressed plants increased before declining from 2 WAA to PM. From A to 2 WAA only the TR of the B3 and B4 segments increased in the stressed plants before declining from 2 WAA to PM. The TR of the other stem segments of the stressed plants declined from A to PM, which is indicative of direct translocation of  $^{14}\text{C}$ , assimilated at A, to the grain under stress conditions. The increase in the TR of the stem segments of the non-stressed plants from A to 2 WAA may indicate that the mobilization of  $^{14}\text{C}$  out of the leaves did not occur as immediately as it did in the stressed plants. The increase in the TR of the B4 segment of the stressed plants from A to 2 WAA was most marked in comparison to that of the non-stressed plants. However, the physiological significance of this is not certain. The TR of all the stem segments except the B3 segment of stressed plants was lower at PM than that of non-stressed plants. This may indicate that the stressed plants mobilized more  $^{14}\text{C}$  out of the stem to the grain, than did the non-stressed plants.

When plants were labelled at 2 WAA, 15,8 and 12,1 % of the  $^{14}\text{C}$  recovered in the whole plant at PM in the stressed and non-stressed plants, respectively, occurred in the whole shoot (Section 4.3.6.3). This was the lowest proportion of  $^{14}\text{C}$  assimilated that remained in the shoot at PM for all the

labelling occasions. Thus it is clear that at 2 WAA the primary ear was established as the major sink for photosynthate, with much of the  $^{14}\text{C}$  assimilated by the plants at 2 WAA translocated to the grain. Averaged over the stressed and non-stressed plants the TR of the whole plant 48 h after labelling at 2 WAA was 2 526 851 dpm plant<sup>-1</sup> less than the TR of the whole plant 48 h after labelling at A. Thus the lower amount of  $^{14}\text{C}$  assimilated by the whole plant at 2 WAA, coupled with the tendency to translocate much of the assimilated  $^{14}\text{C}$  to the grain, resulted in the TR of the segments of the whole shoot for plants labelled at 2 WAA being generally less on all sampling occasions, in comparison to the TR of the segments of the whole shoot of plants labelled at A. However, the greater partitioning of  $^{14}\text{C}$  assimilated at 2 WAA to the grain resulted in the grain of plants labelled at 2 WAA recording the highest TR on all sampling occasions in comparison to the grain of plants labelled at A, 4 WAA and 6 WAA. When plants were labelled at 2 WAA, the stressed plants had already been exposed to two consecutive stress cycles. However, the whole plant TR of the stressed plants at 2 WAA of 14 749 517 dpm plant<sup>-1</sup> was marginally higher than the whole plant TR of 14 361 047 dpm plant<sup>-1</sup> of the non-stressed plants. It appears that the stressed plants recovered from the effects of the water deficits sufficiently enough at 2 WAA to assimilate marginally more  $^{14}\text{C}$  than the non-stressed plants. The grain recorded the highest TR 48 h after labelling at 2 WAA, with the TR of the grain of stressed plants higher than that of non-stressed plants. In fact the  $^{14}\text{C}$  in the grain at 2 WAA represented 59,0 and 51,8 % of the  $^{14}\text{C}$  recovered in the whole plant at 2 WAA in the stressed and non-stressed plants,

respectively. Thus it is clear that much of the  $^{14}\text{C}$  assimilated at 2 WAA was translocated directly to the grain with the stressed plants partitioning a greater proportion of the assimilated  $^{14}\text{C}$  to the grain. As indicated by the increase in the TR of the grain from 2 to 4 WAA most of the  $^{14}\text{C}$  which occurred in the grain was translocated to it during this period. The TR of the grain of stressed plants declined from 4 WAA to PM while in non-stressed plants it fluctuated from 4 WAA to PM but was higher at PM than at 4 WAA. The decline in the TR of the grain of stressed plants from 4 WAA to PM may indicate that the respiratory requirements of the grain were met by utilizing previously assimilated C to a greater extent as the assimilation of new C was reduced due to stress. The next highest TR at 2 WAA was recorded in the laminae of non-stressed plants. The TR of the laminae of non-stressed plants was higher than that of stressed plants at 2 WAA. This probably indicates that stressed plants had mobilized  $^{14}\text{C}$  out of the leaves more rapidly than non-stressed plants. From 2 WAA to PM the TR of the sheaths and laminae declined as  $^{14}\text{C}$  was mobilized into the rest of the plant. The initial decline in the TR of the sheaths and laminae from 2 to 4 WAA was the most marked and indicates further rapid translocation of  $^{14}\text{C}$  into the rest of the plant. At PM the TR of the sheaths and laminae of non-stressed plants was higher than that of stressed plants which probably indicates that stressed plants had mobilized  $^{14}\text{C}$  out of the leaves to a greater extent than non-stressed plants. The cob of stressed plants recorded a higher TR at 2 WAA than the laminae. The cob of the non-stressed plants recorded a higher TR at 2 WAA than that of the stressed plants. However, from 4 WAA to PM the TR of the cob of

stressed plants was higher than that of non-stressed plants. The TR of the cob of non-stressed plants declined from 2 to 6 WAA and then increased from 6 WAA to PM, while that of stressed plants declined from 2 to 4 WAA and then increased from 4 WAA to PM. The increase in the TR of the cob in the latter phase of grain fill, earlier in stressed plants than non-stressed plants, may indicate that  $^{14}\text{C}$  in excess of grain requirements accumulated in the cob as the rate of grain dry mass gain declined (Table 4.8 and Appendix 46). The higher TR of the cob of the stressed plants at PM and the earlier accumulation of  $^{14}\text{C}$  in the cob in comparison to the non-stressed plants, indicates that the rate of dry mass gain by the grain declined sooner and more rapidly under stress conditions than non-stress conditions (Section 4.3.3.8). On the other hand, the question may be posed as to why the rate of grain dry mass gain declined more rapidly under stress conditions when photosynthate was still available to be mobilized into the grain. As with plants labelled at A, the husks accumulated a large amount of the  $^{14}\text{C}$  assimilated at 2 WAA. The TR of the husks at 48 h was higher than that of the tassel, top, A1, B1, B2, B3, B4 and shank segments. The TR of the husks of the stressed plants was higher at 2 WAA than that of the non-stressed plants. This may indicate that the husks served as a reservoir for some of the  $^{14}\text{C}$  partitioned to the primary ear, and the more direct translocation of the assimilated  $^{14}\text{C}$  to the primary ear under stress conditions resulted in the higher TR. In contrast to the husks of the plants labelled at A, the TR of the husks was substantially less at PM than at 2 WAA. This indicates that much of the  $^{14}\text{C}$  assimilated by the husks at 2 WAA was available for mobilization to the grain. The TR of the

2° ear peaked at A, with the TR of the 2° ear of non-stressed plants higher than that of stressed plants. This would appear to indicate that the stressed plants partitioned less <sup>14</sup>C to the 2° ear at 2 WAA as more of the <sup>14</sup>C assimilated at 2 WAA was translocated directly to the primary grain. From 2 to 6 WAA the TR of the 2° ear declined in both stressed and non-stressed plants, probably as a result of <sup>14</sup>C being mobilized out of the 2° ear to the grain. From 6 WAA to PM, the TR of the 2° ear increased, with the TR of the 2° ear of non-stressed plants higher than that of stressed plants. This probably indicates that as the rate of dry mass gain by the primary grain declined in the latter phase of grain fill (Table 4.8 and Appendix 46), some <sup>14</sup>C became available for translocation to the 2° ear. The TR of the tassel peaked at 2 WAA, with the TR of the tassel of non-stressed plants higher than that of stressed plants. It appears therefore that the tassel still had a requirement for C at 2 WAA, although relative to the other segments this requirement was small. The higher TR of the tassel of non-stressed plants at 2 WAA in comparison to stressed plants is indicative of less <sup>14</sup>C being allocated to the non-grain parts of the plant under stress conditions. From 2 WAA to PM the TR of the tassel declined as <sup>14</sup>C was utilized for respiration and mobilized out of the tassel and used for grain fill. Of the stem segments, including the shank, the B3 followed by the B2 segment recorded the highest TR at 48 h after labelling at 2 WAA. Except for the B4 segment the TR of the stem segments of non-stressed plants was higher at 2 WAA than that of stressed plants. This is indicative of the more direct and rapid translocation of much of the <sup>14</sup>C assimilated at 2 WAA to the primary ear under stress

conditions. The physiological significance of the higher TR of the B4 segment at 2 WAA under stress conditions is not certain. From 2 WAA to PM the TR of the stem segments declined as  $^{14}\text{C}$  was translocated to the primary ear. The initial decline in the TR of the stem segments from 2 to 4 WAA was the most marked. This would appear to indicate that the bulk of the  $^{14}\text{C}$  which occurred as labile organic compounds in the stem segments was mobilized out of the stem soon after labelling. The TR of the A1, B1 and shank segments of the stressed plants at PM was higher than that of the non-stressed plants. The A1 and B1 segments are the internodes that occur above and below the primary ear and the shank serves as the conduit for photosynthate translocated from the shoot to the primary ear. Thus it appears that a greater amount of  $^{14}\text{C}$ , which was mobilized to the primary ear, remained in these stem segments at PM under stress conditions than under non-stress conditions. However, the stressed plants apparently mobilized more  $^{14}\text{C}$  out of the top, B2, B3, and B4 stem segments during grain fill, as the TR of these stem segments at PM was lower than that of the non-stressed plants.

When plants were labelled at 4 WAA, 20,3 and 19,7 % of the  $^{14}\text{C}$  recovered in the whole plant at PM in stressed and non-stressed plants, respectively, occurred in the whole shoot (Section 4.3.6.3). This was a greater proportion of assimilated  $^{14}\text{C}$  that remained in the segments of the whole shoot at PM than was the case for plants labelled at 2 WAA. It was, however, a smaller proportion in comparison to plants labelled at A. It is clear then that the primary grain was still established as the major sink for photosynthate at 4 WAA, however, to a lesser extent than

was the case at 2 WAA. Averaged over stressed and non-stressed plants the TR of the whole plant 48 h after labelling at 4 WAA was 6 914 836 and 9 441 687 dpm plant<sup>-1</sup> less than the TR of the whole plant 48 h after labelling at 2 WAA and at A, respectively. The lower amount of <sup>14</sup>C assimilated by the whole plant at 4 WAA coupled with the tendency to translocate much of the assimilated <sup>14</sup>C to the grain resulted in the TR of the segments of the whole shoot being less on all sampling occasions in comparison to segments of the whole shoot of plants labelled at A. On the other hand, the fact that the plants labelled at 4 WAA had a greater proportion of the whole plant <sup>14</sup>C in the shoot at PM, in comparison to plants labelled at 2 WAA, resulted in the TR of some of the segments of the shoot at each of the sampling occasions, exceeding that of the segments of the shoot of plants labelled at 2 WAA. The grain of the plants labelled at 4 WAA had a higher TR on all sampling occasions than the grain of plants labelled at A. However, the grain of plants labelled at 2 WAA had a higher TR on all sampling occasions than the grain of plants labelled at 4 WAA. When plants were labelled at A the TR of the grain of stressed and non-stressed plants was 3 900 109 and 3 557 571 dpm segment<sup>-1</sup> at PM, respectively. When plants were labelled at 2 WAA the TR of the grain of stressed and non-stressed plants at PM was 11 018 658 and 11 983 881 dpm segment<sup>-1</sup>, respectively. When plants were labelled at 4 WAA the TR of the grain of stressed and non-stressed plants at PM was 4 873 784 and 7 433 867 dpm segment<sup>-1</sup>, respectively. However, it will be recalled that the grain of the stressed, and particularly the non-stressed, plants labelled at 4 WAA and sampled at PM from replication one, recorded much higher SR than plants from the

other two replications. This may therefore have exaggerated the TR recorded in the grain at PM of plants labelled at 4 WAA. As mentioned earlier the stressed plants at 4 WAA had a lower leaf  $\Psi_w$  and stress resulted in greater leaf senescence (Sections 4.3.1 and 4.3.2). Both these factors would reduce the rate at which the stressed plants assimilated  $^{14}\text{C}$ . This was confirmed by the fact that the whole plant TR of the stressed plants 48 h after labelling at 4 WAA was 6 870 564 dpm plant<sup>-1</sup> in comparison to 8 410 327 dpm plant<sup>-1</sup> for non-stressed plants. Thus the lower TR for the stressed plants resulted in the TR of all segments, except the B4 segment, being lower on all sampling occasions in stressed plants than non-stressed plants. At 4 WAA the grain recorded the highest TR. The TR of the grain increased in both stressed and non-stressed plants as  $^{14}\text{C}$  was translocated from the rest of the plant to the grain. The laminae recorded the next highest TR at 4 WAA. From 4 to 6 WAA the TR of the sheaths and laminae declined sharply which indicates the further mobilization of  $^{14}\text{C}$  into the rest of the plant. The laminae of the stressed and non-stressed plants showed a slight increase in TR from 6 WAA to PM. Since the TR of the whole plant for stressed and non-stressed plants increased from 6 WAA to PM (Section 4.3.7.2) as a result of sampling error, the increase in the TR of the laminae from 6 WAA to PM was probably due to sampling error. The cob recorded the next highest TR at 4 WAA. From 4 WAA to PM the TR of the cob declined, with the initial decline from 4 to 6 WAA the most marked. This indicates that the  $^{14}\text{C}$  arriving in the cob from the rest of the plant was continually deposited in the grain, with the bulk of the  $^{14}\text{C}$  moving through the cob to the grain in the first two weeks after labelling at 4 WAA. The TR of the

husks of non-stressed plants declined from 4 to 6 WAA and then increased marginally from 6 WAA to PM. On the other hand, the TR of the husks of the stressed plants declined markedly from 4 to 6 WAA and then less markedly from 6 WAA to PM. This would appear to indicate that the husks of the stressed and non-stressed plants served as temporary reservoirs for  $^{14}\text{C}$  assimilated at 4 WAA. Under stress conditions  $^{14}\text{C}$  was continually mobilized out of the husks from 4 WAA to PM, presumably to be utilized mainly for grain fill requirements. On the other hand, under non-stress conditions  $^{14}\text{C}$  was initially mobilized out of the husks from 4 to 6 WAA but as the rate of dry mass gain by the grain declined (Table 4.8 and Appendix 46),  $^{14}\text{C}$  accumulated in the husks from 6 WAA to PM. Changes in the TR of the 2° ear under stress and non-stress conditions were somewhat variable from 4 WAA to PM. However, the TR of the 2° ear at PM under stress and non-stress conditions was less than at 4 WAA, indicating the mobilization of  $^{14}\text{C}$  out of the 2° ear into the rest of the plant. The TR of the tassel peaked at 4 WAA, indicating some requirement for C by the tassel as late as 4 WAA. However, based on the value of the TR recorded for the tassel at 4 WAA, this requirement was small relative to the other segments. From 4 to 6 WAA the TR of the tassel declined substantially under stress and non-stress conditions. This indicates the mobilization of  $^{14}\text{C}$  out of the tassel into the rest of the plant, presumably to be utilized primarily for grain fill requirements. However, from 6 WAA to PM the TR of the tassel increased substantially in non-stressed plants and marginally in stressed plants. This would seem to indicate that as the rate of grain dry mass gain declined, the tassel still provided a sink for

available  $^{14}\text{C}$ , particularly under non-stress conditions. Of the stem segments, including the shank, the B2 segment recorded the highest TR for stressed and non-stressed plants at 4 WAA. The B4 segment of the stressed plants, as with plants labelled at A and 2 WAA, recorded a higher TR than the B4 segment of the non-stressed plants 48 h after labelling at 4 WAA. It appears that there is a definite increase in the partitioning of  $^{14}\text{C}$  to the stem base as a result of stress. It is noteworthy, though, that the TR of the B4 segment of non-stressed plants increased from 4 to 6 WAA, while the TR of the B4 segment of stressed plants declined from 4 to 6 WAA. It appears that the non-stressed plants increased the partitioning of  $^{14}\text{C}$  to the stem base later than the stressed plants did. The TR of all the stem segments of the stressed plants, apart from the B4 segment, declined markedly from 4 to 6 WAA and then less markedly from 6 WAA to PM. This indicates the general mobilization of  $^{14}\text{C}$  out of the stem segments and into the grain. The TR of the B4 segment of stressed plants increased from 6 WAA to PM, after initially declining from 4 to 6 WAA. The physiological significance of this is uncertain as it was not repeated in the non-stressed plants. The changes in the TR of the stem segments of the non-stressed plants were somewhat variable from 4 WAA to PM. However, the TR of all stem segments at PM was less than at 4 WAA indicating an overall mobilization of  $^{14}\text{C}$  out of the stem into the grain. The TR of all the stem segments except the B4 and shank of the stressed plants was lower at PM than that of the non-stressed plants. This is indicative of the lower whole plant TR recorded for the stressed plants at 4 WAA. It is also indicative of the greater mobilization of  $^{14}\text{C}$  out of the stem to the grain,

under stress conditions. The higher TR of the shank of stressed plants at PM may indicate that the greater mobilization of  $^{14}\text{C}$  to the primary ear under stress conditions, resulted in a greater amount of  $^{14}\text{C}$  remaining in the shank as grain fill ceased at PM. The physiological significance of the higher TR of the B4 segment at PM under stress conditions is uncertain. It is noteworthy that the stem segments of plants labelled at 4 WAA generally had a higher TR at 6 WAA and at PM than the stem segments at 4 and 6 WAA and at PM of plants labelled at 2 WAA for stressed and, particularly, non-stressed plants.

When plants were labelled at 6 WAA, 32,4 and 33,0 % of the  $^{14}\text{C}$  recovered in the whole plant at PM in stressed and non-stressed plants, respectively, occurred in the whole shoot (Section 4.3.6.3). This was a greater proportion of assimilated  $^{14}\text{C}$  that remained in the shoot at PM, than was the case in plants labelled at 2 WAA and 4 WAA. It was, however, a smaller proportion in comparison to plants labelled at A. It is apparent therefore that the grain was still established as the major sink for photosynthate at 6 WAA but to a lesser extent than was the case at 2 and 4 WAA. Averaged over the stressed and non-stressed plants the whole plant TR 48 h after labelling at 6 WAA was 5 238 623, 12 153 459 and 14 680 310 dpm plant<sup>-1</sup> less than the TR of the whole plant 48 h after labelling at 4 WAA, 2 WAA and A, respectively. Thus the considerably lower amount of  $^{14}\text{C}$  assimilated by the whole plant at 6 WAA coupled with the tendency to translocate a large proportion of the assimilated  $^{14}\text{C}$  to the grain resulted in the TR of the whole shoot segments being generally less on all sampling occasions in comparison to

segments of the whole shoot of plants labelled at A, 2 WAA and 4 WAA and sampled on all occasions. The grain too, as a result of the low amount of  $^{14}\text{C}$  assimilated at 6 WAA, had a lower TR on all sampling occasions compared to the grain sampled on all occasions from plants labelled at A, 2 WAA and 4 WAA. When plants were labelled at 6 WAA, the stressed plants had already been exposed to six consecutive stress cycles which resulted in lower leaf  $\Psi_w$  (Section 4.3.1) and greater leaf senescence (Section 4.3.2) compared to the non-stressed plants. Thus the photosynthetic capacity of the stressed plants would be reduced at 6 WAA. This was confirmed by the lower whole plant TR recorded for the stressed plants of 2 063 377 dpm plant<sup>-1</sup>, 48 h after labelling at 6 WAA, compared to 2 740 269 dpm plant<sup>-1</sup> recorded for the non-stressed plants. Nonetheless, the marginally higher TR of the whole plant of non-stressed plants enabled them to establish a higher TR of all segments 48 h after labelling at 6 WAA than stressed plants. The grain recorded the highest TR at 6 WAA and the TR of the grain increased from 6 WAA to PM as  $^{14}\text{C}$  was translocated to the grain. The TR of the grain of the non-stressed plants was higher than that of the stressed plants at PM. The laminae of the non-stressed plants recorded the next highest TR at 6 WAA. The TR of the laminae of the non-stressed plants at 6 WAA was 233,5 % higher than that of the stressed plants. This is indicative of the rapid translocation of  $^{14}\text{C}$  out of the leaves of the stressed plants and also the lower amount of  $^{14}\text{C}$  assimilated by the stressed plants at 6 WAA. The TR of the sheaths and laminae declined from 6 WAA to PM with the TR of the sheaths and laminae of the non-stressed plants greater at PM than that of the stressed plants. The cob of the non-

stressed plants recorded the next highest TR at 6 WAA. The TR of the cob declined from 6 WAA to PM as  $^{14}\text{C}$  was translocated into the grain. The TR of the cob of stressed plants was higher at PM than that of non-stressed plants. This may indicate that the stressed plants continued to mobilize  $^{14}\text{C}$  from the shoot to the grain and as deposition of photosynthate into the grain ceased at PM a greater amount of  $^{14}\text{C}$  remained in the cob of the stressed plants. From 6 WAA to PM the TR of the husks of the non-stressed plants declined, while the TR of the husks of the stressed plants increased. In fact at PM the TR of the husks of stressed plants was higher than that of non-stressed plants. It is possible that the increased mobilization of  $^{14}\text{C}$  to the grain under stress conditions resulted in  $^{14}\text{C}$  accumulating in the husks as grain fill ceased at PM. The TR of the 2° ear declined from 6 WAA to PM with the non-stressed plants maintaining a higher TR of the 2° ear at PM than the stressed plants. The TR of the tassel also declined from 6 WAA to PM as  $^{14}\text{C}$  was respired and mobilized out of the tassel into the rest of the plant. The TR of the tassel of non-stressed plants was higher at PM than that of stressed plants. Of the stem segments, including the shank, the B3 segment of non-stressed plants recorded the highest TR at 6 WAA while the B2 segment of stressed plants recorded the highest TR at 6 WAA. The TR of all the stem segments declined from 6 WAA to PM, with the TR of all the stem segments of the non-stressed plants higher at PM than that of the stressed plants. This is indicative of the increased mobilization of  $^{14}\text{C}$  from the stem segments to the primary ear under stress conditions and also the lower amount of  $^{14}\text{C}$  assimilated by stressed plants at 6 WAA.

#### 4.3.4.3 Segment total radioactivity as a % of whole plant total radioactivity

Changes in the TR of a segment over sampling occasions are due to translocation of  $^{14}\text{C}$  in or out of the segment and are also due to respiration losses. By expressing the TR of each segment as a percentage of the TR of the whole plant on each sampling occasion the losses due to respiration are ignored assuming that the proportion of  $^{14}\text{C}$  lost from each segment due to respiration is the same as the proportion of  $^{14}\text{C}$  lost from the whole plant due to respiration. Thus changes in the percentage values calculated in this manner indicate losses or gains of  $^{14}\text{C}$  in a segment due to translocation. Superficially the changes in the percentage data of the segments (Figure 4.15a,b,c,d) resemble that of TR data (Figure 4.14a,b,c,d).

#### Labelling at A

When plants were labelled at A the husks recorded the highest percentage of whole plant  $^{14}\text{C}$  at 48 h after labelling at A (Figure 4.15a,b,c,d). The stressed plants recorded 21,2 % and the non-stressed plants 17,0 % of the whole plant  $^{14}\text{C}$  in the husks at A. This again illustrates the high C assimilation capacity of the husks at A. However, it is not certain how much of the  $^{14}\text{C}$  in the husks at A was assimilated through own photosynthesis and how much was translocated from the rest of the plant. The higher proportion of whole plant  $^{14}\text{C}$  in the husks of stressed plants may indicate the priority partitioning of  $^{14}\text{C}$  directly to the primary ear under stress conditions. From A to PM the percentage of  $^{14}\text{C}$

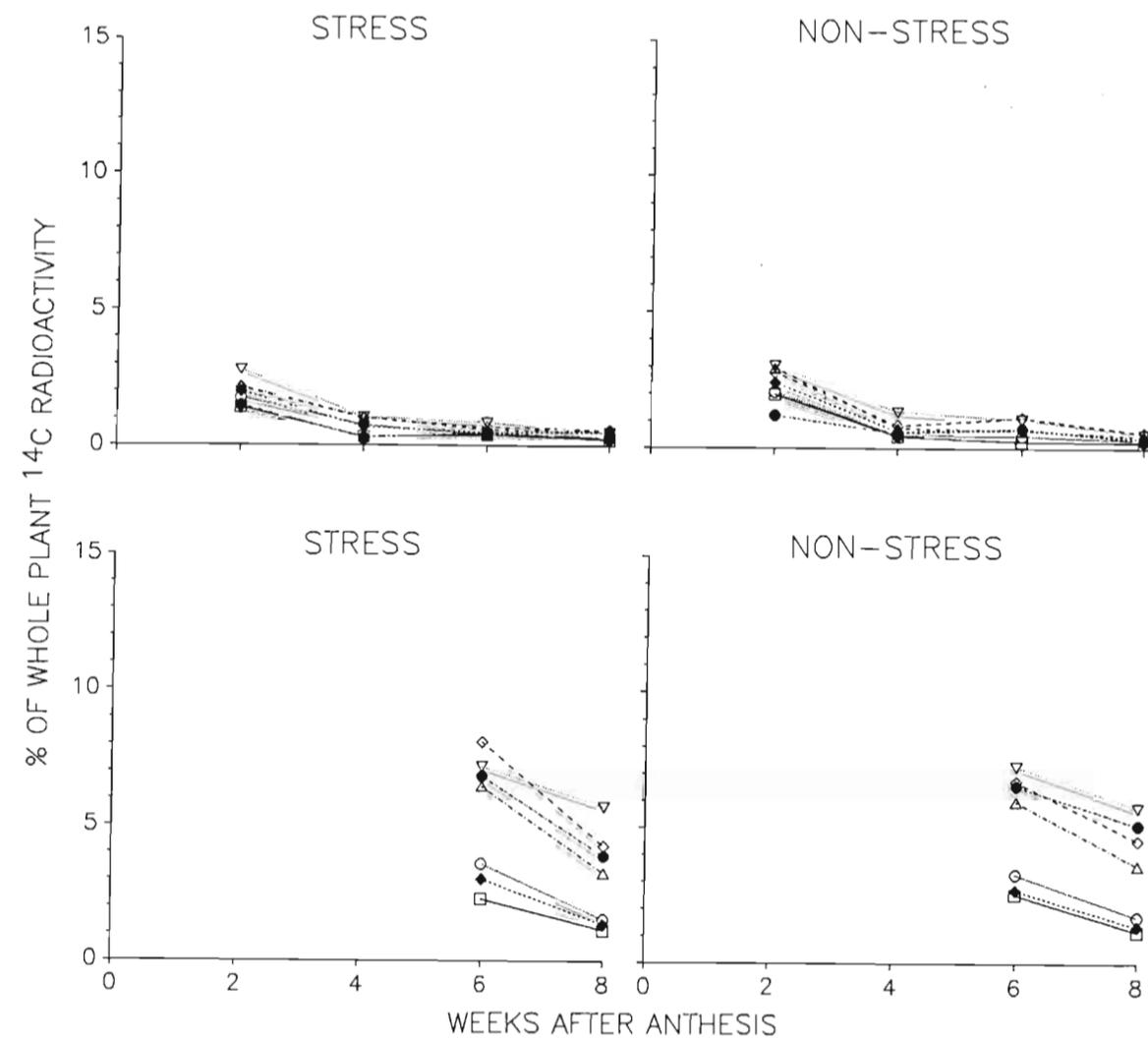
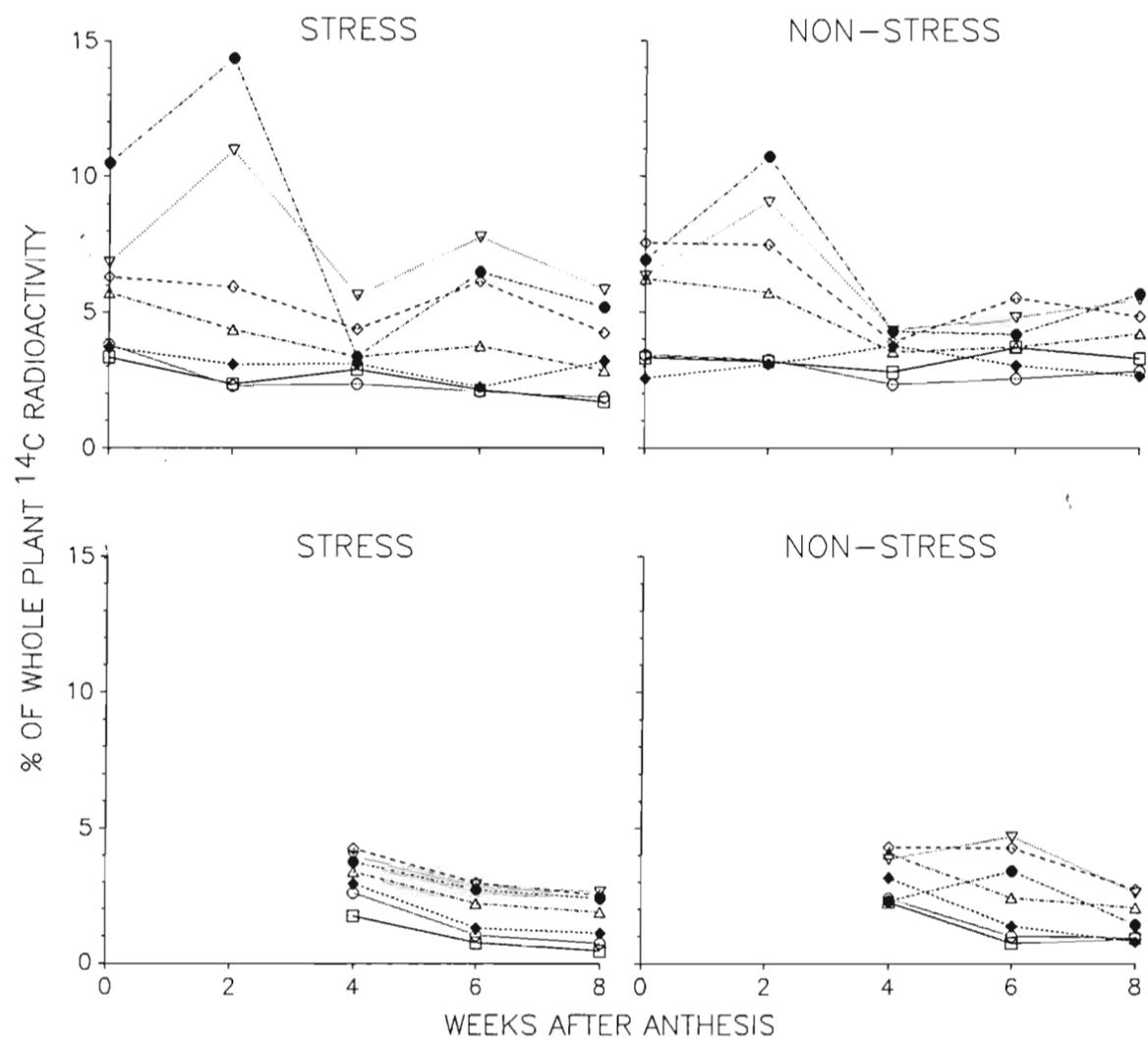


Figure 4.15a Effect of water stress during grain fill on the total radioactivity of each stem segment expressed as a percentage of whole plant <sup>14</sup>C total radioactivity from a maize hybrid labelled at anthesis, 2 ,4 and 6 weeks after anthesis and sampled at fortnightly intervals

Key: top □—□ , A1 ○—○ , B1 △—△ , B2 ◇—◇ , B3 ▽—▽ , B4 ●—● , shank ◆—◆

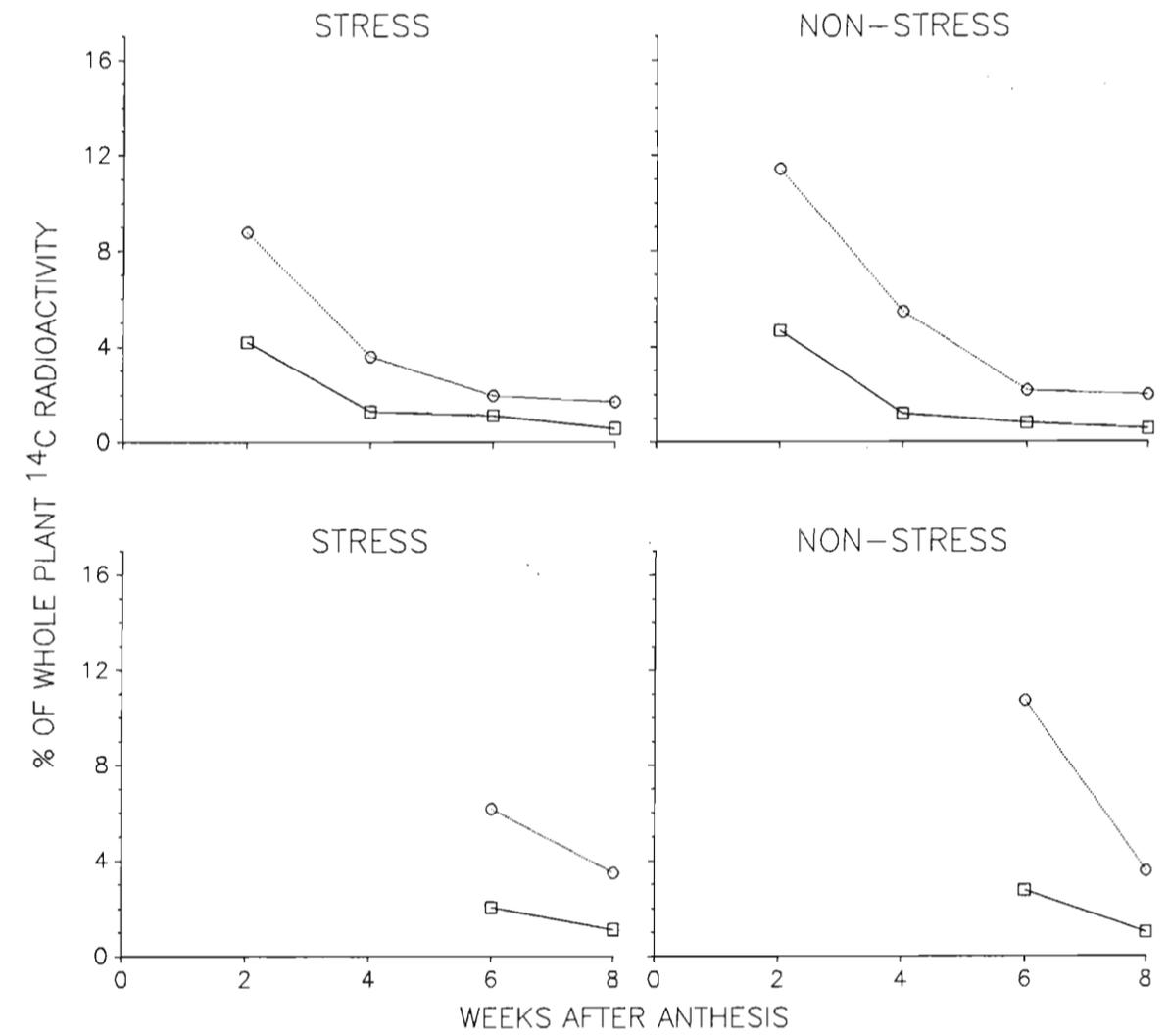
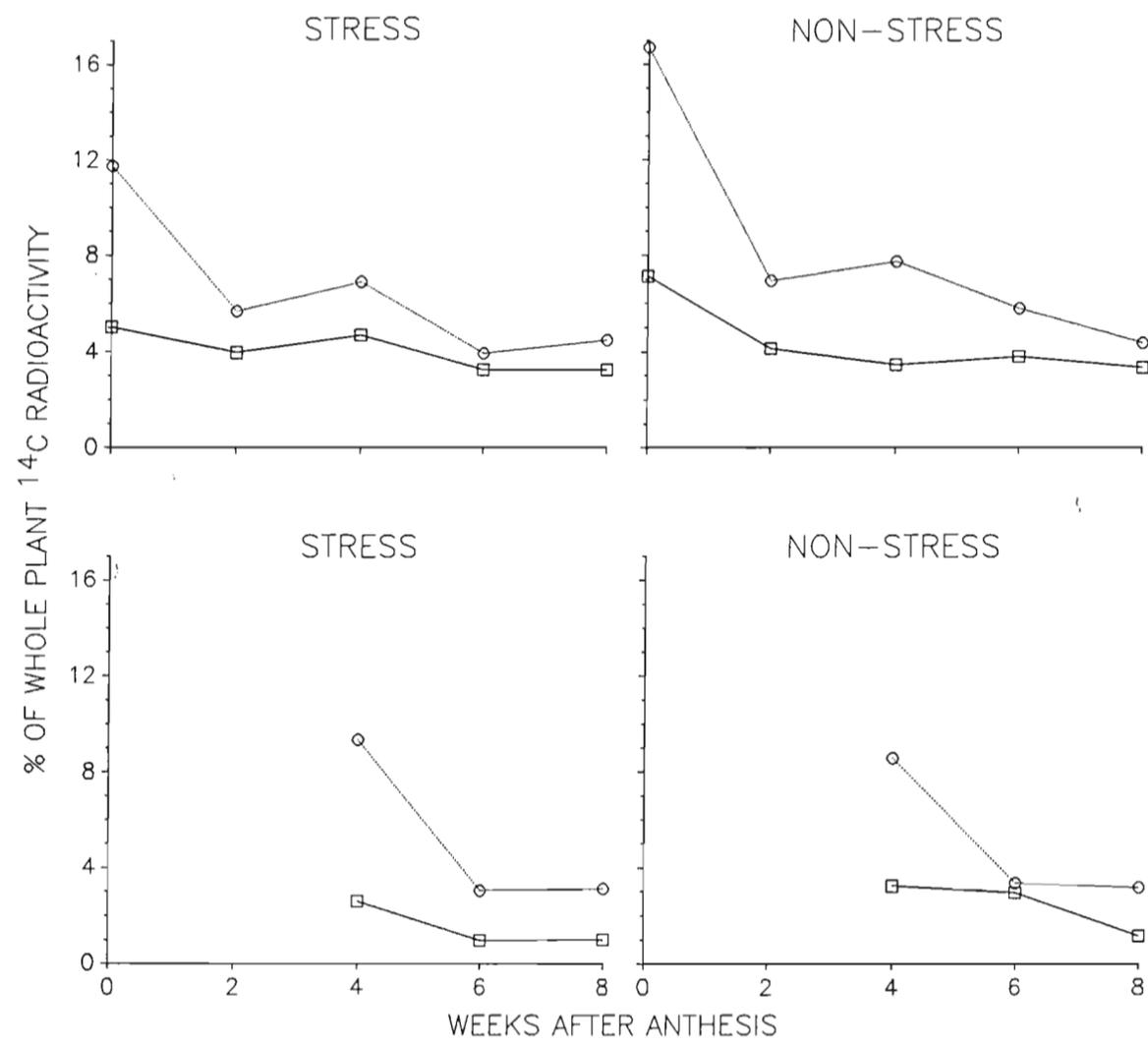


Figure 4.15b Effect of water stress during grain fill on the total radioactivity of leaves expressed as a percentage of whole plant  $^{14}\text{C}$  total radioactivity from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis and sampled at fortnightly intervals

Key: sheaths □—□, laminae ○—○

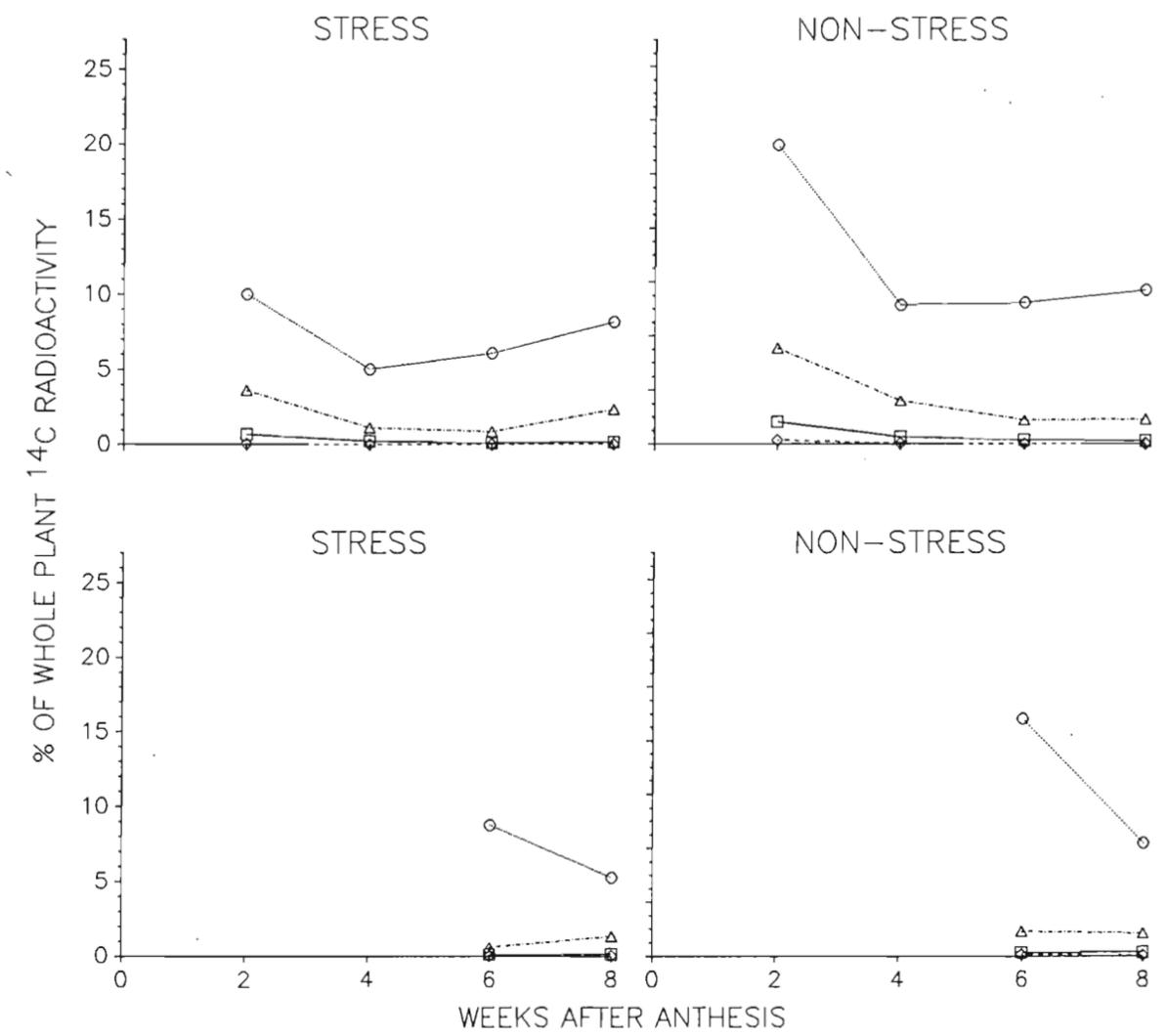
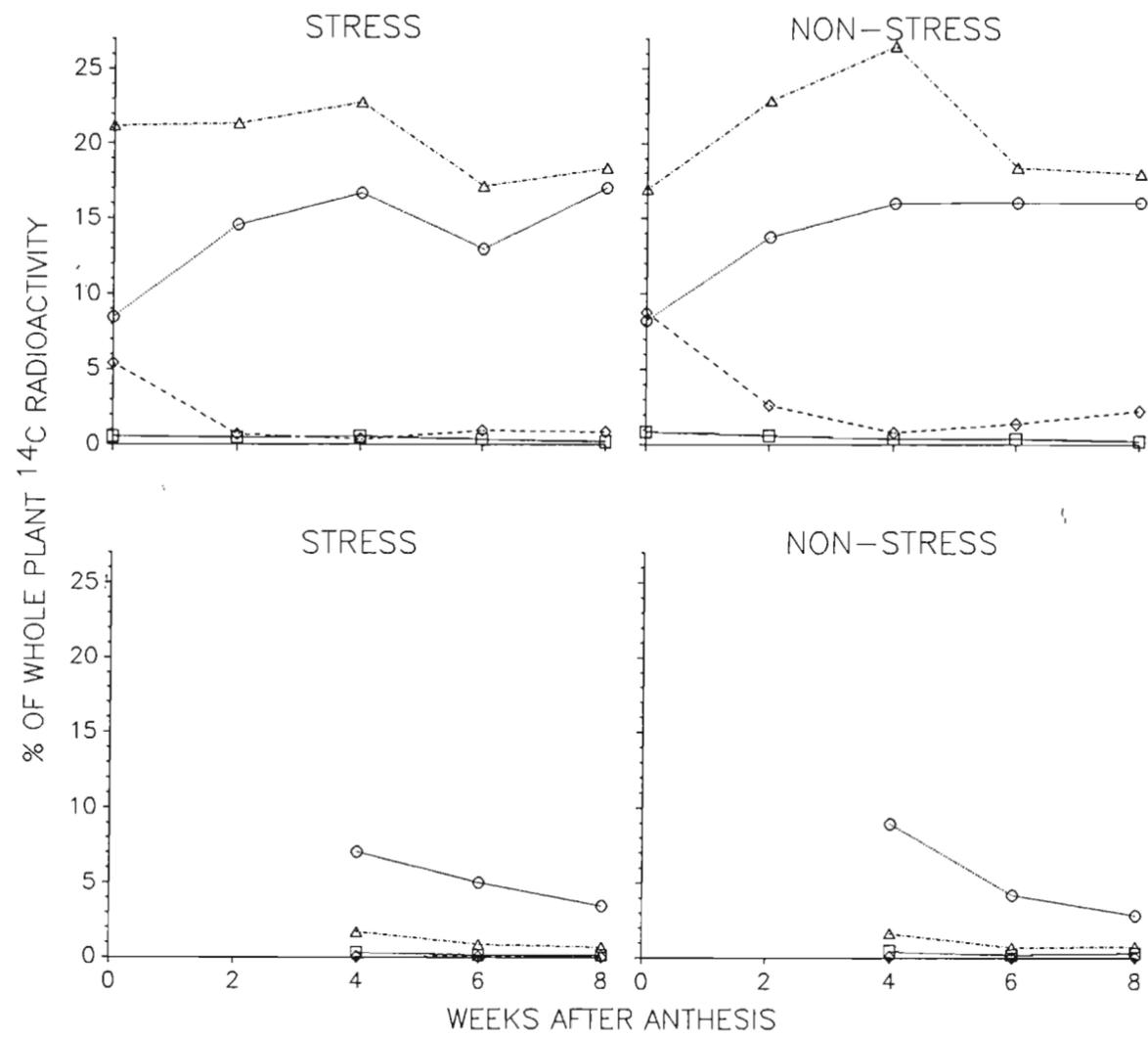


Figure 4.15c Effect of water stress during grain fill on the total radioactivity of segments expressed as a percentage of whole plant <sup>14</sup>C total radioactivity from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis and sampled at fortnightly intervals

Key: tassel □—□, cob ○—○, husks △—△, 2° ear ◇—◇

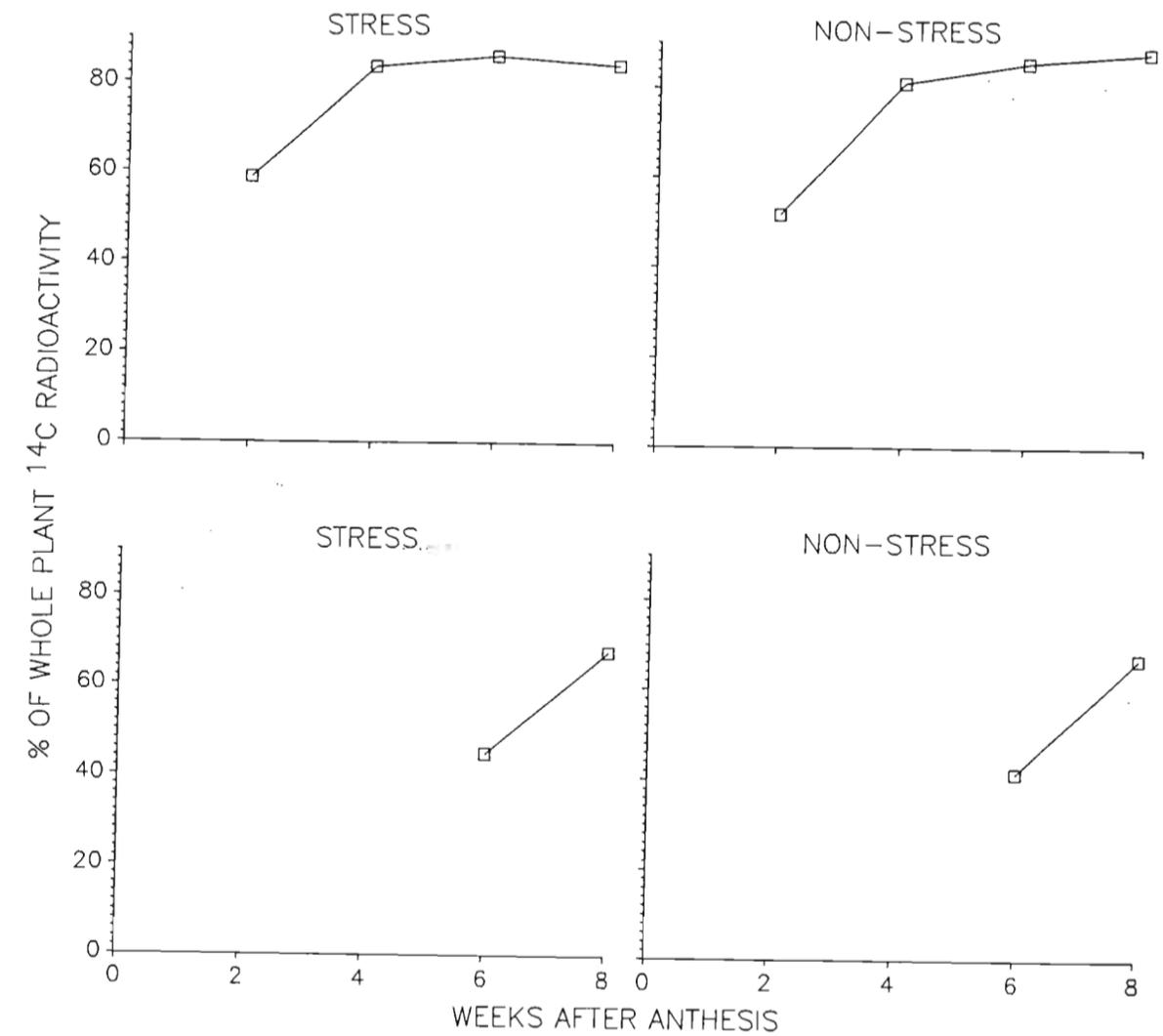
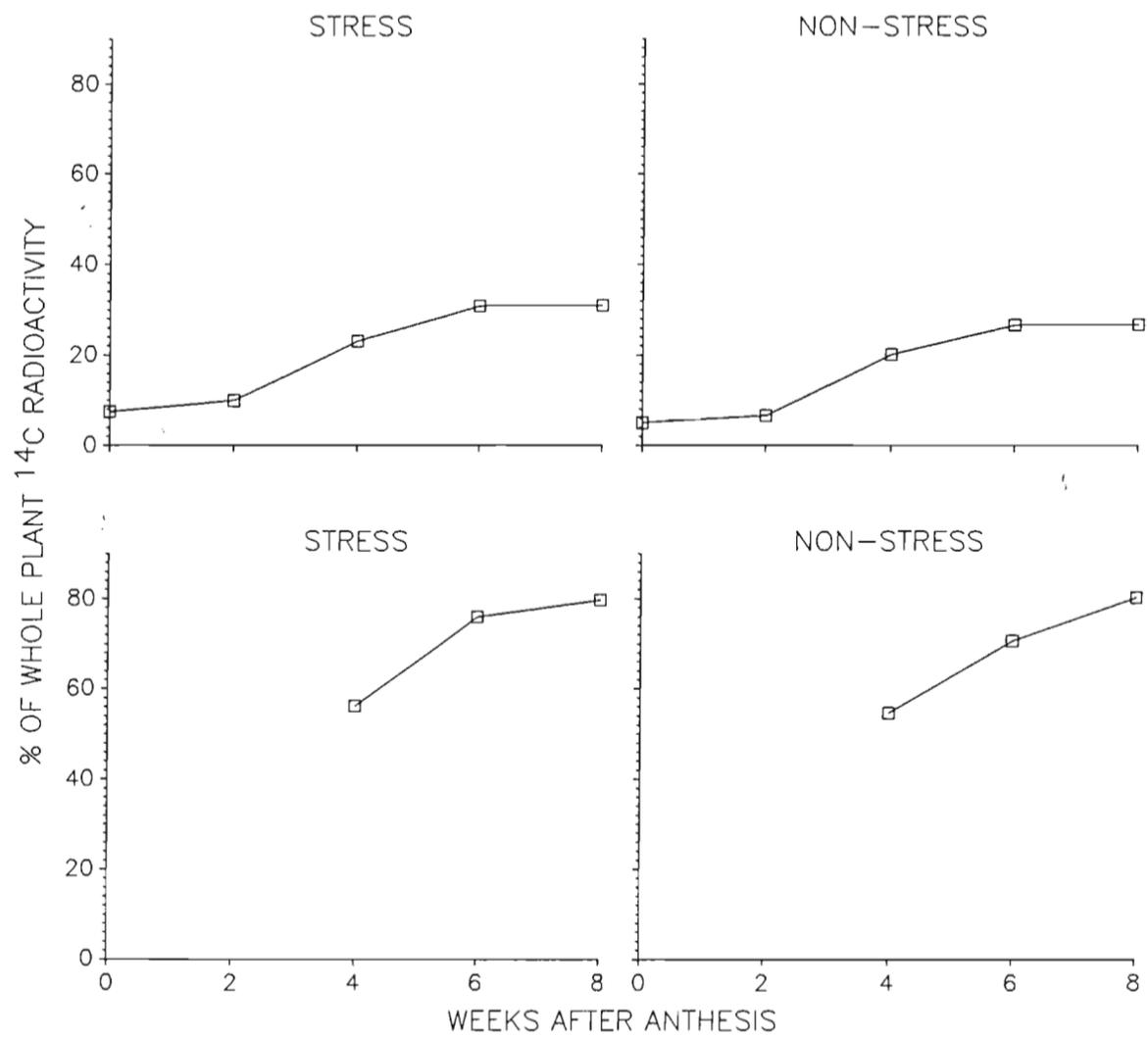


Figure 4.15d Effect of water stress during grain fill on the total radioactivity of grain expressed as a percentage of whole plant <sup>14</sup>C total radioactivity from a maize hybrid labelled at anthesis, 2 ,4 and 6 weeks after anthesis and sampled at fortnightly intervals

in the husks of non-stressed plants initially increased from A to 4 WAA reaching 26,5 % and then declined from 4 WAA to PM. The percentage of  $^{14}\text{C}$  in the husks of stressed plants also increased slightly from A to 4 WAA reaching 22,7 % and then declined from 4 WAA to PM. The percentage of  $^{14}\text{C}$  in the husks of stressed plants and non-stressed plants at PM was 18,3 and 18,0 %, respectively. It is clear that the husks retained most of the  $^{14}\text{C}$  assimilated at A and this probably points to the utilization of the  $^{14}\text{C}$  for the structural growth of the husks as the primary ear increased in volume and mass, particularly from A to 2 WAA. The laminae recorded the next highest percentage of  $^{14}\text{C}$  at A. The laminae of the stressed plants and non-stressed plants recorded 11,7 and 16,7 % of the whole plant  $^{14}\text{C}$  at A, respectively. The sheaths of the stressed and non-stressed plants recorded 5,0 and 7,1 % of the whole plant  $^{14}\text{C}$  at A, respectively. It is clear that the stressed plants mobilized more  $^{14}\text{C}$  out of the leaves within the 48 h after labelling at A. This again points to the more direct and rapid translocation of  $^{14}\text{C}$  to the grain under stress conditions. From A to PM the percentage of  $^{14}\text{C}$  in the leaves declined under stress and non-stress conditions as  $^{14}\text{C}$  was mobilized to the rest of the plant. The percentage of  $^{14}\text{C}$  in the sheaths and laminae of the stressed plants at PM was 3,2 and 4,5 %, respectively. In the non-stressed plants the sheaths and laminae recorded 3,4 and 4,4 % of the whole plant  $^{14}\text{C}$  at PM, respectively. There was apparently very little difference in the proportion of whole plant  $^{14}\text{C}$  that remained in the leaves at PM between stressed and non-stressed plants. At A the grain and cob of the stressed plants recorded 7,5 and 8,5 % respectively of the whole plant  $^{14}\text{C}$ , while the grain and cob of the non-stressed

plants recorded 5,0 and 8,2 % respectively of the whole plant  $^{14}\text{C}$ . Thus it is clear that at A the grain was not yet established as the major sink for photosynthate with the cob even assimilating more than the grain. Nonetheless the grain and cob of the stressed plants assimilated a greater proportion of the whole plant  $^{14}\text{C}$  at A. This once again points to the more direct translocation of  $^{14}\text{C}$  assimilated at A to the primary ear under stress conditions. From A to PM the percentage of  $^{14}\text{C}$  in the grain and cob increased with the stressed plants generally recording a higher percentage of the whole plant  $^{14}\text{C}$  in these segments on each sampling occasion than the non-stressed plants. At PM the grain and cob of the stressed plants recorded 31,0 and 17,0 % respectively of the whole plant  $^{14}\text{C}$ . The grain and cob of non-stressed plants at PM recorded 26,9 and 16,1 % respectively of the whole plant  $^{14}\text{C}$ . It is clear that much of the  $^{14}\text{C}$  assimilated at A was not translocated to the grain. Nonetheless the stressed plants translocated a greater amount of the  $^{14}\text{C}$  assimilated at A to the grain than did the non-stressed plants. The increase in the percentage of  $^{14}\text{C}$  in the cob from A to PM is indicative of  $^{14}\text{C}$  being translocated through it to the grain. It is also indicative of the  $^{14}\text{C}$  that was utilized for the structural growth of the cob. At A the 2° ear of the non-stressed plants recorded 8,8 % of the whole plant  $^{14}\text{C}$  which was higher than the 5,4 % recorded in the stressed plants. This indicates that the 2° ear at A was initially partitioned a fair proportion of the  $^{14}\text{C}$  assimilated at A. The stressed plants, however, partitioned a smaller proportion of the whole plant  $^{14}\text{C}$  at A to the 2° ear than did the non-stressed plants. From A to 4 WAA the percentage of  $^{14}\text{C}$  in the 2° ear initially declined and then increased from

4 WAA to PM under stress and non-stress conditions. At PM the stressed plants recorded 0,9 % and the non-stressed plants recorded 2,2 % of the whole plant  $^{14}\text{C}$  in the 2° ear. It is clear that once the primary ear became established as the major sink for photosynthate  $^{14}\text{C}$  was mobilized out of the 2° ear for grain fill. However, as the rate of dry mass gain by the primary grain declined from 4 WAA to PM  $^{14}\text{C}$  was translocated to the 2° ear. The 2° ear of non-stressed plants received a greater proportion of the whole plant  $^{14}\text{C}$  in the latter phase of grain fill in comparison to stressed plants. The tassel of stressed and non-stressed plants recorded 0,5 and 0,9 %, respectively, of the whole plant  $^{14}\text{C}$  at A. This was the lowest proportion of the whole plant  $^{14}\text{C}$  which occurred in the segments at A. From A to PM the percentage of whole plant  $^{14}\text{C}$  in the tassel declined to 0,2 % in both stressed and non-stressed plants. It is apparent that relative to the other segments the tassel was partitioned a small proportion of the  $^{14}\text{C}$  assimilated at A and during grain fill part of the  $^{14}\text{C}$  was mobilized out of the tassel into the rest of the plant. Of the stem segments the lower, and larger (by dry mass) B2, B3 and B4 stem segments recorded a higher proportion of the whole plant  $^{14}\text{C}$  at A than the upper top, A1 and B1 stem segments. At A the B3 and B4 segments of the stressed plants recorded 6,8 and 10,5 % of the whole plant  $^{14}\text{C}$  respectively, while the B3 and B4 segments of the non-stressed plants recorded 6,3 and 6,9 % respectively of the whole plant  $^{14}\text{C}$  at A. It appears that the lower stem segments particularly the B4 segment of the stressed plants assimilated a greater proportion of the whole plant  $^{14}\text{C}$  than they did in the non-stressed plants. From A to 2 WAA the percentage of  $^{14}\text{C}$  in the B3 and B4 segments increased before

declining from 2 WAA to PM in stressed and non-stressed plants. In stressed plants the percentages of whole plant  $^{14}\text{C}$  in the B3 and B4 segments of 11,0 and 14,4 % respectively at 2 WAA were particularly high. In comparison the percentages of  $^{14}\text{C}$  in the B3 and B4 segments of non-stressed plants at 2 WAA were 9,1 and 10,7 %, respectively. The basis for this increase in the proportion of whole plant  $^{14}\text{C}$  in the B3 and B4 segments is not certain but may indicate partitioning of photosynthate for final structural growth of the stem base as well as translocation of photosynthate to the roots. The percentage of  $^{14}\text{C}$  in the top, A1, B1 and B2 segments generally declined from A to PM indicating the mobilization of  $^{14}\text{C}$  out of the stem primarily to the grain. The proportion of  $^{14}\text{C}$  in the stem segments of non-stressed plants was generally higher than that in stressed plants on all sampling occasions from A to PM. This indicates that the stressed plants mobilized more  $^{14}\text{C}$  directly to the grain than did the non-stressed plants. It is important to point out that the decline in the percentage of  $^{14}\text{C}$  in the stem segments from A to PM under stress and non-stress conditions was not as great as was the case when plants were labelled at 2 WAA, 4 WAA and 6 WAA. This is indicative of the greater percentage of the whole plant  $^{14}\text{C}$  that occurred in the whole shoot at PM of plants labelled at A.

#### Labelling at 2 WAA

When plants were labelled at 2 WAA, the primary grain was established as the major sink for photosynthate. Not surprisingly therefore the grain recorded the highest percentage of the whole plant  $^{14}\text{C}$  at 2 WAA (Figure 4.15a,b,c,d). The grain

of stressed and non-stressed plants recorded 59,0 and 51,8 %, respectively, of the whole plant  $^{14}\text{C}$  at 2 WAA. This was a substantially greater proportion of whole plant  $^{14}\text{C}$  allocated to the grain than was the case for the grain of plants labelled at A even when sampled at PM. The higher percentage of whole plant  $^{14}\text{C}$  in the grain of stressed plants at 2 WAA is indicative of the greater proportion of  $^{14}\text{C}$  that was directly translocated to the grain under stress conditions. From 2 to 4 WAA the percentage of  $^{14}\text{C}$  in the grain of stressed and non-stressed plants increased to 83,6 and 81,2 %. While this increase in the proportion of whole plant  $^{14}\text{C}$  that occurred in the grain was substantial, it is clear that the bulk of the  $^{14}\text{C}$  translocated to the grain occurred within the first 48 h after labelling at 2 WAA. From 4 WAA to PM the percentage of whole plant  $^{14}\text{C}$  in the grain increased slightly to 87,9 % in the non-stressed plants. However, in the stressed plants the percentage of whole plant  $^{14}\text{C}$  in the grain increased to 86,0 % from 4 to 6 WAA and then declined to 84,2 % at PM. Since the method of calculating these percentage values discounts respiration losses the basis for the decline in the proportion of whole plant  $^{14}\text{C}$  in the grain of the stressed plants from 6 WAA to PM is not clear. It is clear, however, that at PM the bulk of the whole plant  $^{14}\text{C}$  occurred in the grain. At 2 WAA the cob of stressed and non-stressed plants recorded 10,0 and 11,1 %, respectively, of the whole plant  $^{14}\text{C}$ . From 2 to 6 WAA the percentage of  $^{14}\text{C}$  in the cob of the non-stressed plants declined to 5,2 % and then increased to 5,7 % at PM. In the stressed plants on the other hand, the percentage of whole plant  $^{14}\text{C}$  in the cob declined to 5,0 % from 2 to 4 WAA and then increased to 8,1 % at PM. The overall decline in the percentage of  $^{14}\text{C}$  in the cob

from 2 WAA to PM is indicative of  $^{14}\text{C}$  being mobilized through the cob to the grain from the rest of the plant. However, in stressed plants it appears that  $^{14}\text{C}$  mobilized to the primary ear from the rest of the plant began to accumulate in the cob from 6 WAA to PM. This may simply be due to the fact that the stressed plants generally mobilized more of the assimilated  $^{14}\text{C}$  directly to the grain and as the grain reached maturity more  $^{14}\text{C}$  remained and/or accumulated in the cob. On the other hand, it may indicate that stress reduced the sink strength of the grain and the cob served as an alternative sink for photosynthate. The cob of the non-stressed plants also showed an increase in the percentage of  $^{14}\text{C}$  at PM indicating that the cob may serve as an alternative sink for  $^{14}\text{C}$  mobilized to the grain as the grain reached maturity. In contrast to the 11,7 and 16,7 % of the whole plant  $^{14}\text{C}$  which occurred in the laminae of stressed and non-stressed plants respectively 48 h after labelling at A, the laminae at 48 h after labelling at 2 WAA recorded 8,8 and 11,4 % of the whole plant  $^{14}\text{C}$  in stressed and non-stressed plants respectively. It is clear that the  $^{14}\text{C}$  assimilated at 2 WAA was mobilized more rapidly out of the laminae than was the case for  $^{14}\text{C}$  assimilated at A. From 2 to 4 WAA the percentage of  $^{14}\text{C}$  in the sheaths and laminae of the stressed plants declined markedly and then less markedly from 4 WAA to PM. In the non-stressed plants the percentage of  $^{14}\text{C}$  in the laminae declined markedly from 2 to 6 WAA and then declined slightly from 6 WAA to PM. The percentage of  $^{14}\text{C}$  in the sheaths of the non-stressed plants declined sharply from 2 to 4 WAA and then declined slightly from 4 WAA to PM. The bulk of the  $^{14}\text{C}$  assimilated at 2 WAA by the leaves appears to be mobilized out of the leaves of stressed

plants from 2 to 4 WAA while in the non-stressed plants  $^{14}\text{C}$  continued to be mobilized out of the laminae to a greater extent from 2 to 6 WAA. At PM the proportion of whole plant  $^{14}\text{C}$  in the sheaths and laminae was similar under stress and non-stress conditions. As with the leaves the percentage of  $^{14}\text{C}$  that occurred in the tassel, husks, 2° ear and stem segments on all sampling occasions of plants labelled at 2 WAA was less than that of the same segments sampled on all occasions from plants labelled at A. This reflects the greater proportion of  $^{14}\text{C}$  assimilated at 2 WAA that was mobilized directly to the grain. The husks of stressed plants recorded 3,6 % and that of non-stressed plants 3,5 % of the whole plant  $^{14}\text{C}$  at 2 WAA. The higher percentage of  $^{14}\text{C}$  in the husks of stressed plants may reflect the increased mobilization of  $^{14}\text{C}$  to the primary ear under stress conditions. From 2 to 6 WAA the percentage of  $^{14}\text{C}$  in the husks declined to 0,9 % in both stressed and non-stressed plants and then increased to 2,3 % in stressed plants at PM while remaining constant in non-stressed plants. The increase in the percentage of  $^{14}\text{C}$  in the husks of stressed plants may be due to the same reasons as suggested for the cob. The percentage of  $^{14}\text{C}$  in the 2° ear at 2 WAA was the lowest of all the segments. It is clear then that at 2 WAA the primary grain was established as the major sink for photosynthate and very little of the assimilated  $^{14}\text{C}$  was translocated to the 2° ear. Non-stressed plants recorded a higher percentage of  $^{14}\text{C}$  in the 2° ear at 2 WAA than did stressed plants. This further reflects the increased translocation of assimilated  $^{14}\text{C}$  to the primary grain under stress conditions. From 2 to 6 WAA the percentage of  $^{14}\text{C}$  in the 2° ear declined and then increased from 6 WAA to PM in both stressed and non-stressed

plants. The increase in percentage  $^{14}\text{C}$  from 6 WAA to PM was, however, slight with the non-stressed plants recording a higher percentage of  $^{14}\text{C}$  in the 2° ear than the stressed plants. The tassel of stressed and non-stressed plants recorded 0,7 and 0,8 %, respectively, of the whole plant  $^{14}\text{C}$  at 2 WAA. From 2 WAA to PM the percentage of whole plant  $^{14}\text{C}$  in the tassel declined to 0,1 % in both stressed and non-stressed plants. It is apparent that relative to the other segments the tassel was partitioned a small proportion of the  $^{14}\text{C}$  assimilated at 2 WAA and from 2 WAA to PM part of the  $^{14}\text{C}$  was mobilized out of the tassel into the rest of the plant. Of the stem segments the B3 segment recorded the highest percentage of whole plant  $^{14}\text{C}$  at 2 WAA. The percentage of  $^{14}\text{C}$  in the B3 segment at 2 WAA in stressed and non-stressed plants was 2,8 and 3,0 %, respectively. Although the B3 segment had a slightly smaller dry mass than the B4 segment, the large size of the B3 segment coupled with the fact that it had photosynthesising leaves attached to it at 2 WAA resulted in a greater proportion of  $^{14}\text{C}$  occurring in it at 2 WAA. From 2 WAA to PM the percentage of  $^{14}\text{C}$  in the stem segments declined as  $^{14}\text{C}$  was mobilized to the grain. The initial decline in the percentage of  $^{14}\text{C}$  in the stem segments from 2 to 4 WAA was the most marked. This indicates that the bulk of the  $^{14}\text{C}$  assimilated at 2 WAA was mobilized out of the stem to the grain within the first two weeks of labelling.

### Labelling at 4 WAA

When plants were labelled at 4 WAA the primary grain was still established as the major sink for photosynthate. Not surprisingly therefore the grain recorded the highest percentage of whole plant  $^{14}\text{C}$  at 4 WAA (Figure 4.15a,b,c,d). The grain of stressed and non-stressed plants recorded 56,2 and 54,6 %, respectively, of the whole plant  $^{14}\text{C}$  at 4 WAA. This was already a greater proportion of whole plant  $^{14}\text{C}$  allocated to the grain than was the case for the grain of plants labelled at A even when sampled at PM. On the other hand, for stressed plants it was just less than the proportion of whole plant  $^{14}\text{C}$  that occurred in the grain of stressed plants 48 h after labelling at 2 WAA, while for non-stressed plants it was marginally higher than the proportion of whole plant  $^{14}\text{C}$  that occurred in the grain of non-stressed plants 48 h after labelling at 2 WAA. Although the plants labelled at 4 WAA assimilated less  $^{14}\text{C}$  than the plants labelled at 2 WAA (Section 4.3.7.2) it is clear that at 4 WAA the plants partitioned a similar proportion of assimilated  $^{14}\text{C}$  to the grain as did the plants at 2 WAA. Once again the higher percentage of whole plant  $^{14}\text{C}$  in the grain of stressed plants at 4 WAA is indicative of the greater proportion of  $^{14}\text{C}$  that was directly translocated to the grain under stress conditions. From 4 WAA to PM the percentage of whole plant  $^{14}\text{C}$  in the grain of stressed and non-stressed plants increased to 79,7 and 80,2 %, respectively. Averaged over the stressed and non-stressed plants this represents an increase of 24,6 % of the whole plant  $^{14}\text{C}$  that occurred in the grain. It is clear, however, that the bulk of the translocation of  $^{14}\text{C}$  to the grain occurred within the first

48 h after labelling at 4 WAA. It is also clear that at PM the bulk of the whole plant  $^{14}\text{C}$  occurred in the grain of both stressed and non-stressed plants. The proportion of  $^{14}\text{C}$  in the grain at PM was just less than that in the grain at PM of plants labelled at 2 WAA. At 4 WAA the cob of stressed and non-stressed plants recorded the next highest percentages of 7,1 and 9,0 %, respectively. From 4 WAA to PM the percentage of  $^{14}\text{C}$  in the cob of stressed and non-stressed plants declined to 3,5 and 2,8 %, respectively. This overall decline in the percentage of  $^{14}\text{C}$  in the cob is indicative of the translocation of  $^{14}\text{C}$  through the cob to the grain with the bulk of the  $^{14}\text{C}$  being translocated through the cob at 4 WAA. The higher percentage of whole plant  $^{14}\text{C}$  that occurred in the cob of stressed plants at PM in comparison to non-stressed plants may be due to the same reasons suggested for the same phenomenon that occurred in the cob at PM of plants labelled at 2 WAA. The percentage of whole plant  $^{14}\text{C}$  in the sheaths and laminae of the stressed plants at 4 WAA was 2,6 and 9,4 %, respectively. While in the sheaths and laminae of the non-stressed plants it was 3,2 and 8,6 %, respectively. From 4 WAA to PM the percentage of  $^{14}\text{C}$  in the leaves declined, most markedly from 4 to 6 WAA in the sheaths and laminae of stressed plants and the laminae of non-stressed plants. The percentage of  $^{14}\text{C}$  in the sheaths of the non-stressed plants declined more markedly from 6 WAA to PM. At PM the percentage of whole plant  $^{14}\text{C}$  in the sheaths and laminae of stressed plants was 1,0 and 3,1 % respectively, while that in the sheaths and laminae of non-stressed plants was 1,2 and 3,2 %, respectively. This was marginally higher than the percentage of whole plant  $^{14}\text{C}$  that occurred in the sheaths and laminae at PM of stressed and non-

stressed plants labelled at 2 WAA. It was, however, less than that in the sheaths and laminae at PM of plants labelled at A. The percentage of  $^{14}\text{C}$  that occurred in the tassel, husks and 2° ear on all sampling occasions of plants labelled at 4 WAA was generally less than that of the same segments sampled on all occasions from plants labelled at A and 2 WAA. It is apparent therefore that a smaller proportion of  $^{14}\text{C}$  assimilated at 4 WAA was partitioned to these segments in comparison to plants labelled at A and 2 WAA. The non-stressed plants generally had a higher percentage of whole plant  $^{14}\text{C}$  in the tassel and 2° ear than the stressed plants from 4 WAA to PM. The percentage of  $^{14}\text{C}$  declined in these segments from 4 to 6 WAA which is indicative of the mobilization of  $^{14}\text{C}$  to the grain. However, from 6 WAA to PM the percentage of  $^{14}\text{C}$  in these segments increased. This indicates that as grain fill ceased at PM,  $^{14}\text{C}$  was translocated to these organs. The husks generally declined in the percentage of  $^{14}\text{C}$  from 4 WAA to PM in both stressed and non-stressed plants. The percentage of  $^{14}\text{C}$  in the husks was very similar for stressed and non-stressed plants on all sampling occasions. Of the stem segments the B2 segment recorded the highest percentage of whole plant  $^{14}\text{C}$  at PM for both stressed and non-stressed plants. Apart from the B4 segment the percentage of  $^{14}\text{C}$  in the stem segments of non-stressed plants was generally higher than that of stressed plants from 4 WAA to PM. The B4 segment of stressed plants had a higher percentage of  $^{14}\text{C}$  than non-stressed plants from 4 WAA to PM. The physiological significance for this has been discussed in Sections 4.3.4.1 and 4.3.4.2. From 4 WAA to PM the percentage of  $^{14}\text{C}$  in the stem segments generally declined as  $^{14}\text{C}$  was mobilized to the grain. The higher percentage of  $^{14}\text{C}$  in the stem segments

of non-stressed plants (apart from the B4 segment) in comparison to stressed plants is probably indicative of a smaller proportion of the whole plant  $^{14}\text{C}$  remaining in the stem under stress conditions as a greater proportion was utilized for grain fill. The slightly smaller proportion of  $^{14}\text{C}$  that occurred in the grain at PM for plants labelled at 4 WAA compared to plants labelled at 2 WAA resulted in the proportion of  $^{14}\text{C}$  that occurred in the stem segments on all sampling occasions of stressed and non-stressed plants labelled at 4 WAA being generally higher than that of plants labelled at 2 WAA. However, the proportion of  $^{14}\text{C}$  in the stem segments of plants labelled at 4 WAA was generally less than that of plants labelled at A.

#### Labelling at 6 WAA

When plants were labelled at 6 WAA the primary grain was still established as the major sink for photosynthate, however to a lesser extent than was the case at 2 and 4 WAA. The grain recorded the highest percentage of whole plant  $^{14}\text{C}$  at 6 WAA (Figure 4.15a,b,c,d). The grain of stressed and non-stressed plants recorded 44,8 and 41,6 %, respectively, of the whole plant  $^{14}\text{C}$  at 6 WAA. This was already a greater proportion of the whole plant  $^{14}\text{C}$  allocated to the grain than was the case for the grain of plants labelled at A even when sampled at PM. On the other hand, for stressed and non-stressed plants it was a smaller proportion than that which occurred in the grain 48 h after plants were labelled at 2 WAA and at 4 WAA. Once again the higher percentage of whole plant  $^{14}\text{C}$  in the grain of stressed plants at 6 WAA is indicative of the greater proportion of  $^{14}\text{C}$

that was directly translocated to the grain under stress conditions. From 6 WAA to PM the percentage of whole plant  $^{14}\text{C}$  in the grain of stressed and non-stressed plants increased to 67,6 and 67,0 %, respectively. Averaged over the stressed and non-stressed plants this represents an increase of 24,1 % of the whole plant  $^{14}\text{C}$  that occurred in the grain. It is clear therefore that the bulk of the translocation of  $^{14}\text{C}$  to the grain occurred within the first 48 h after labelling at 6 WAA. It is also clear that at PM the bulk of the whole plant  $^{14}\text{C}$  occurred in the grain of both stressed and non-stressed plants. However, the proportion of whole plant  $^{14}\text{C}$  in the grain at PM was, averaged over stressed and non-stressed plants, 18,7 and 12,7 % less than that at PM when plants were labelled at 2 WAA and at 4 WAA. At 6 WAA the cob of stressed and non-stressed plants recorded 8,7 and 8,8 %, respectively of the whole plant  $^{14}\text{C}$ . From 6 WAA to PM the percentage of  $^{14}\text{C}$  in the cob of stressed and non-stressed plants declined to 5,3 and 4,2 %, respectively. This overall decline in the percentage of  $^{14}\text{C}$  in the cob is indicative of the translocation of  $^{14}\text{C}$  through the cob to the grain with the bulk of the  $^{14}\text{C}$  being translocated through the cob at 6 WAA. The higher percentage of whole plant  $^{14}\text{C}$  that occurred in the cob of the stressed plants at PM in comparison to non-stressed plants may be due to the same reasons suggested for the same phenomenon that occurred in the cob at PM of plants labelled at 2 WAA and at 4 WAA. The percentage of the whole plant  $^{14}\text{C}$  in the sheaths and laminae of stressed plants at 6 WAA was 2,0 and 6,2 %, respectively. While in the sheaths and laminae of the non-stressed plants it was 2,8 and 10,7 %, respectively. Thus the percentage of whole plant  $^{14}\text{C}$  in the laminae of the non-stressed

plants was higher than that in the cob at 6 WAA. The higher percentage in the laminae than the cob at 6 WAA is indicative of the decline in the proportion of  $^{14}\text{C}$  translocated to the grain at 6 WAA. The lower percentage of whole plant  $^{14}\text{C}$  in the sheaths and particularly the laminae of the stressed plants at 6 WAA is again indicative of the more direct and rapid translocation of assimilated  $^{14}\text{C}$  to the grain under stress conditions. At PM the percentage of  $^{14}\text{C}$  in the sheaths and laminae of the stressed plants was 1,1 and 3,5 % respectively, while that in the sheaths and laminae of the non-stressed plants was 1,0 and 3,6 %, respectively. These were similar percentages to those recorded in the sheaths and laminae at PM of stressed and non-stressed plants labelled at 4 WAA. It was, however, less than that in the sheaths and laminae at PM of plants labelled at A. The percentage of  $^{14}\text{C}$  in the tassel in both stressed and non-stressed plants increased marginally from 6 WAA to PM with the percentage in non-stressed plants higher than that in stressed plants on both sampling occasions. This may indicate translocation of  $^{14}\text{C}$  to the tassel as late as at PM as grain fill ceased, with the non-stressed plants partitioning a greater proportion of the whole plant  $^{14}\text{C}$  to the tassel than the stressed plants. The percentage of  $^{14}\text{C}$  in the 2° ear was the lowest of all the segments with the tassel recording the second lowest percentage of  $^{14}\text{C}$ . In contrast to the tassel the percentage of  $^{14}\text{C}$  in the 2° ear declined from 6 WAA to PM with the percentage of  $^{14}\text{C}$  in the 2° ear of the non-stressed plants higher than that of the stressed plants on both sampling occasions. The percentage of  $^{14}\text{C}$  in the husks of stressed plants increased from 0,6 to 1,3 % from 6 WAA to PM while it declined from 0,9 to 0,8 % in non-stressed plants.

The increase in the percentage of  $^{14}\text{C}$  in the husks of stressed plants from 6 WAA to PM may be due to the same reasons suggested for the same phenomenon that occurred in the cob at PM. Of the stem segments the B2 segment of stressed plants recorded the highest percentage of whole plant  $^{14}\text{C}$  of 8,1 % while the B3 segment of the non-stressed plants had the highest percentage of 7,3 %. A noticeable feature of the proportional distribution of  $^{14}\text{C}$  in the stem segments of stressed and non-stressed plants labelled at 6 WAA is that at 6 WAA and at PM the B1, B2, B3 and B4 segments had higher percentages of  $^{14}\text{C}$  than the top, A1 and shank segments which had similar percentages. From 6 WAA to PM the percentage of  $^{14}\text{C}$  declined in the stem segments of both stressed and non-stressed plants. At PM the percentage of  $^{14}\text{C}$  in the stem segments of the stressed plants was lower than that of the non-stressed plants which is indicative of a greater proportion of  $^{14}\text{C}$  mobilized out of the stem to the primary ear under stress conditions. The smaller percentage of whole plant  $^{14}\text{C}$  that occurred in the grain at PM for plants labelled at 6 WAA compared to plants labelled at 2 WAA and at 4 WAA resulted in the proportion of  $^{14}\text{C}$  that occurred in the stem segments on all sampling occasions of stressed and non-stressed plants labelled at 6 WAA being generally higher than that in the stem segments of plants labelled at 2 WAA and at 4 WAA. Particularly at 6 WAA the proportion of  $^{14}\text{C}$  in the stem segment of plants labelled at 6 WAA was high and often equalling that of the stem segments of plants labelled at A.

#### 4.3.4.4 Total radioactivity of the stem segments as a % of whole stem total radioactivity

As  $^{14}\text{C}$ , assimilated primarily by the leaves, is mobilized out of the leaves and into the stem some remains in the stem while the rest is translocated predominantly to the primary ear with some being mobilized to the tassel and 2° ear. Thus generally the TR of the whole stem peaked just after labelling for all labelling occasions and then declined on each sampling occasion as  $^{14}\text{C}$  was mobilized to the rest of the plant, particularly the primary grain, and lost through respiration. Therefore the proportion of the whole stem  $^{14}\text{C}$  in each segment on each sampling occasion reflects  $^{14}\text{C}$  as labile organic compounds which could potentially be translocated to the grain and it also represents  $^{14}\text{C}$  that has been utilized within that stem segment for cell growth and maintenance.

#### Labelling at A

When plants were labelled at A the TR of the whole stem at PM was higher than that in the whole stem at PM of plants labelled at 2 WAA, 4 WAA and 6 WAA (Section 4.3.5.2). It is clear then that a greater proportion of the  $^{14}\text{C}$  assimilated at A was utilized irreversibly for the final structural growth of the stem tissue. Thus for plants labelled at A the proportion of whole stem  $^{14}\text{C}$  in each segment, particularly from 4 WAA to PM, represents to a greater extent than was the case for plants labelled on the other subsequent occasions,  $^{14}\text{C}$  incorporated into the structure of the stem tissue. Forty-eight hours after labelling at A the B4

segment for stressed plants recorded the highest percentage of whole stem  $^{14}\text{C}$  of 24,9 %, but in non-stressed plants the B2 segment recorded the highest percentage of 20,9 % (Figure 4.16). However, at 2 WAA the B4 segment did record the highest percentage of whole stem  $^{14}\text{C}$  for the non-stressed plants of 24,4 %. The percentage of whole stem  $^{14}\text{C}$  in the B4 segment of the stressed plants increased to 31,2 % at 2 WAA and was again the highest recorded percentage. From 2 WAA to PM the percentage of whole stem  $^{14}\text{C}$  in the B4 segment of stressed and non-stressed plants declined to 20,2 and 19,9 %, respectively. The B3 segment of stressed plants also increased in percentage of  $^{14}\text{C}$  from 16,6 % at A to 25,1 % at 2 WAA while that in the non-stressed plants increased from 17,2 % at A to 20,5 % at 2 WAA. From 2 WAA to PM the percentage of  $^{14}\text{C}$  in the B3 segment of stressed and non-stressed plants declined to 21,7 and 18,3 %, respectively. At PM the B3 and B4 segments of stressed and non-stressed plants still recorded the highest percentage of whole stem  $^{14}\text{C}$  in comparison to the other stem segments. The fact that the B4 segment recorded the highest percentage of whole stem  $^{14}\text{C}$  at A in the stressed plants while the B2 segment recorded the highest percentage in the non-stressed plants is not easy to explain. It may indicate that the stressed plants mobilized more  $^{14}\text{C}$  assimilated at A directly to the stem base to be utilized for structural growth of the stem base as well as supplying the carbohydrate requirements of the roots. The increase in the percentage of whole stem  $^{14}\text{C}$  that occurred in the B3 and B4 segments from A to 2 WAA in both the stressed and non-stressed plants is also not easy to explain. Since this increase was due to an actual increase in the TR of the segments during this

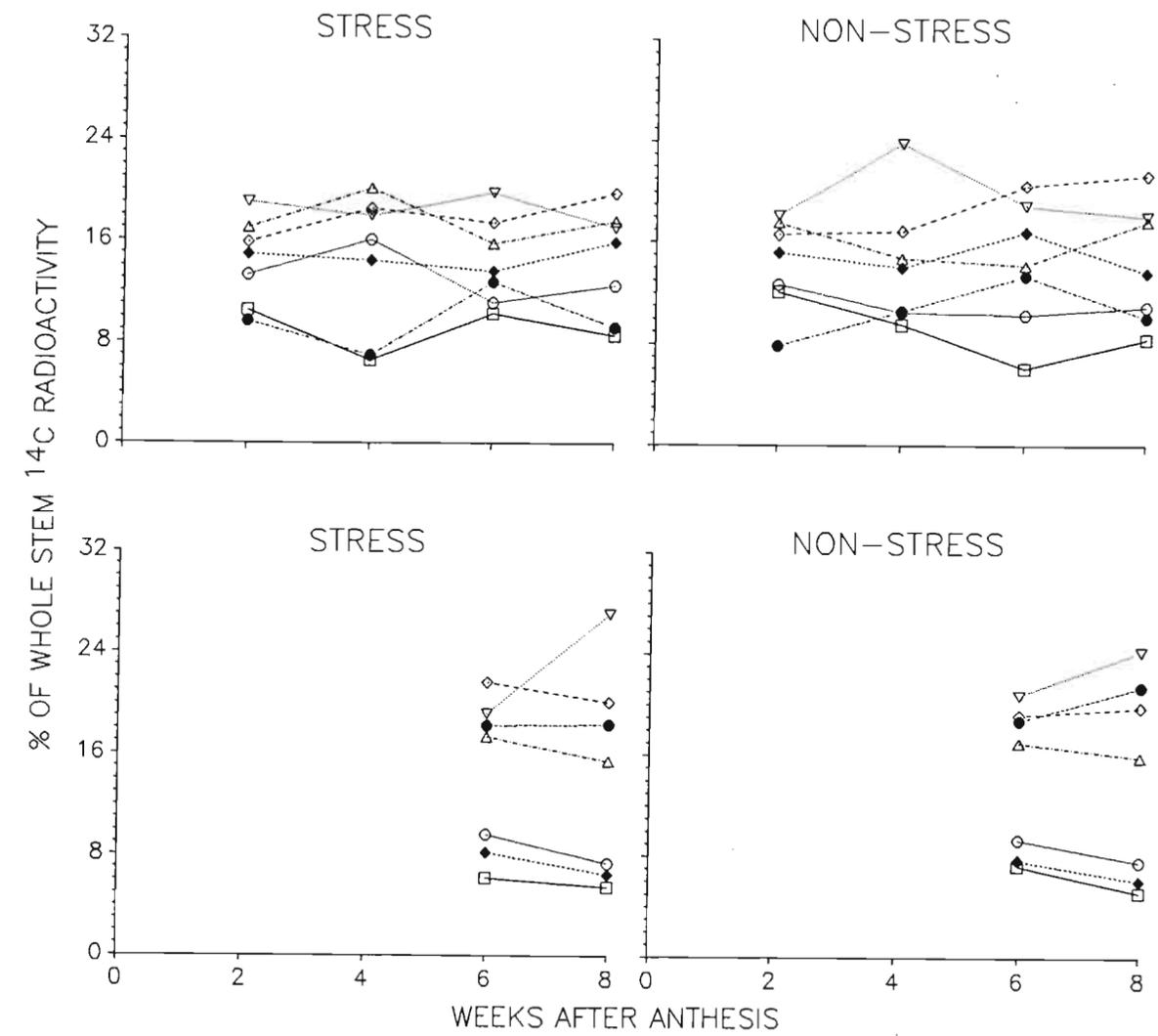
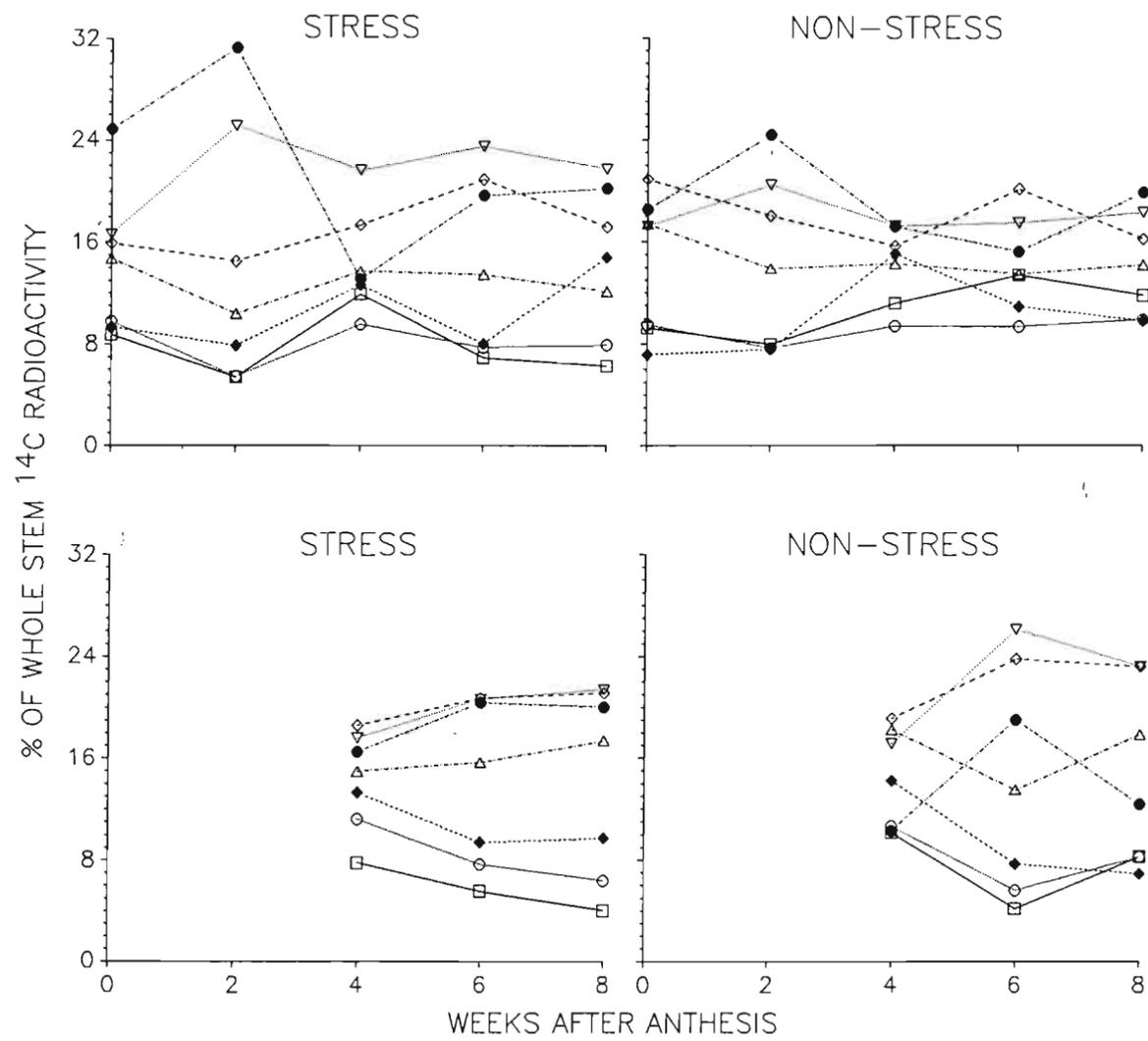


Figure 4.16 Effect of water stress during grain fill on the total radioactivity of each stem segment expressed as a percentage of whole stem <sup>14</sup>C total radioactivity from a maize hybrid labelled at anthesis, 2, 4 and 6 weeks after anthesis and sampled at fortnightly intervals

Key: top □—□, A1 ○—○, B1 △—△, B2 ◇—◇, B3 ▽—▽, B4 ●—●, shank ◆—◆

period (Section 4.3.4.2) it appears that the  $^{14}\text{C}$  did specifically accumulate in these stem segments from A to 2 WAA. Since the B3 segment still had actively photosynthesising leaves attached to it the increase in the amount of  $^{14}\text{C}$  located in it may have been due to the further mobilization of  $^{14}\text{C}$  out of the leaves attached to it and into the B3 segment. On the other hand, at A the B4 segment had leaves attached to it which were largely senesced and so the increase in the amount of  $^{14}\text{C}$  in it from A to 2 WAA would indicate translocate from the upper photosynthesising leaves. Clearly within the first two weeks after A photosynthate was partitioned to the stem base. The B3 and B4 segments also had the greatest proportion of whole stem  $^{14}\text{C}$  at PM and this was probably due to their large size (by dry mass) and since they are not in close proximity to the primary ear less of the available labile  $^{14}\text{C}$  would be mobilized out of them and utilized for grain fill (Palmer et al., 1973). The percentage of whole stem  $^{14}\text{C}$  in the A1 segment of stressed and non-stressed plants at A was 9,8 and 9,5 %, respectively. At PM the percentage of whole stem  $^{14}\text{C}$  in the A1 segment of stressed and non-stressed plants was 7,9 and 9,9 %, respectively. It is clear that a greater proportion of the whole stem  $^{14}\text{C}$  occurred in the A1 segment at PM of non-stressed plants than stressed plants. At A the percentage of whole stem  $^{14}\text{C}$  in the B1 segment of stressed and non-stressed plants was 14,7 and 17,4 %, respectively. At PM the percentage of whole stem  $^{14}\text{C}$  in the B1 segment was 12,1 and 14,2 % in stressed and non-stressed plants, respectively. It is apparent that a greater proportion of the whole stem  $^{14}\text{C}$  occurred in the B1 segment at PM of non-stressed plants than stressed plants. Thus it appears that the stressed plants mobilized more of the

$^{14}\text{C}$  assimilated at A out of the stem segments in closest proximity to the primary ear in the A1 and B1 segments for grain fill than did the non-stressed plants. At A the proportion of whole stem  $^{14}\text{C}$  in the shank of stressed and non-stressed plants was 9,8 and 7,2 %, respectively. The higher percentage in the shank of stressed plants reflects the more direct translocation of  $^{14}\text{C}$  to the primary ear in comparison to non-stressed plants. From A to 2 WAA the percentage of  $^{14}\text{C}$  in the shank of stressed and non-stressed plants remained fairly constant. But then, from 2 to 4 WAA the percentage of  $^{14}\text{C}$  in the shank of stressed plants increased to 12,7 % while that in non-stressed plants increased sharply to 15,1 %. It appears that initially from A to 2 WAA the  $^{14}\text{C}$  mobilized from the rest of the plant through the shank was utilized by the shank itself for growth and respiration requirements and by the cob and husks for growth and respiration requirements. However, once the lag phase of grain fill was completed the primary grain became established as a major sink for photosynthate and the  $^{14}\text{C}$  which still occurred as labile organic compounds in the rest of the plant was mobilized to the primary grain. Thus the proportion of whole stem  $^{14}\text{C}$  increased in the shank, however, to a greater extent in non-stressed plants. This may once again reflect the earlier mobilization of  $^{14}\text{C}$  to the primary ear i.e. from A to 2 WAA that occurred in stressed plants (Sections 4.3.4.1 and 4.3.4.2). From 4 WAA the percentage of  $^{14}\text{C}$  in the shank of non-stressed plants declined to 9,8 % at PM while that in the stressed plants after initially declining to 8,0 % from 4 to 6 WAA increased to 14,8 % at PM. This may indicate that stressed plants were forced to continue mobilizing more of the  $^{14}\text{C}$  assimilated at A to the primary ear

during grain fill and as grain fill ceased at PM this  $^{14}\text{C}$  accumulated in the shank. Interestingly, in non-stressed plants the percentage of  $^{14}\text{C}$  in the top segment increased from 9,2 % at A to 11,8 % at PM. Since this was associated with an overall decline in the TR of this segment during the same period this would seem to indicate that a smaller proportion of  $^{14}\text{C}$  was mobilized out of the top segment to the grain under non-stress conditions. On the other hand, the percentage of  $^{14}\text{C}$  in the top segment of stressed plants declined from 8,7 % at A to 6,2 % at PM. It is clear that the stressed plants partitioned less  $^{14}\text{C}$  assimilated at A to the top segment and mobilized more of the  $^{14}\text{C}$  in the top segment to the primary grain for grain fill than did non-stressed plants.

#### Labelling at 2 WAA

When plants were labelled at 2 WAA, what is immediately apparent from the percentage distribution of whole stem  $^{14}\text{C}$  among the stem segments at 2 WAA is that the B4 segment of stressed and non-stressed plants recorded 9,6 and 7,8 %, respectively (Figure 4.16). This is much less than the percentage of  $^{14}\text{C}$  in the B4 segment at 48 h after labelling at A. It is clear that less of the  $^{14}\text{C}$  assimilated at 2 WAA which occurred in the whole stem was partitioned to the stem base as was the case for  $^{14}\text{C}$  assimilated at A. However, the stressed plants still initially partitioned more of the  $^{14}\text{C}$  assimilated at 2 WAA to the B4 segment within 48 h after labelling than did the non-stressed plants. However, from 4 WAA to PM the non-stressed plants generally maintained a higher percentage of whole stem  $^{14}\text{C}$  in the B4 segment than did the

stressed plants. The B3 segment of both stressed and non-stressed plants recorded the highest percentage of whole stem  $^{14}\text{C}$  at 2 WAA which was 18,9 and 18,1 %, respectively. The B1 and B2 segments recorded just less than this while the A1 segment at 2 WAA recorded 13,2 and 12,7 % in stressed and non-stressed plants, respectively. From 2 WAA to PM the percentage of whole stem  $^{14}\text{C}$  in the B3 segment of stressed plants declined to 17,0 % while that in non-stressed plants increased to 23,8 % at 4 WAA before declining to 18,1 %. The physiological significance of the increase in the proportion of  $^{14}\text{C}$  in the B3 segment of non-stressed plants from 2 to 4 WAA is not certain, however it may indicate that  $^{14}\text{C}$  was mobilized out of the leaves attached to this segment at a later stage than in the stressed plants. From 2 WAA to PM the percentage of whole stem  $^{14}\text{C}$  in the A1, B1 and B2 segments fluctuated somewhat with the percentage of whole stem  $^{14}\text{C}$  in the A1 and B1 segments at PM similar to that at 2 WAA, while the percentage of whole stem  $^{14}\text{C}$  in the B2 segment at PM was higher than at 2 WAA. The top segment recorded the lowest percentage of whole stem  $^{14}\text{C}$  from 2 WAA to PM in comparison to the other segments with the percentage of  $^{14}\text{C}$  in the top segment of stressed plants generally less than that of non-stressed plants. Again this may indicate the reduced accumulation of  $^{14}\text{C}$  in the top segment under stress conditions. In contrast to the percentage of whole stem  $^{14}\text{C}$  recorded in the shank of plants labelled at A, the shank of stressed and non-stressed plants recorded 14,9 and 15,2 % respectively at 48 h after labelling at 2 WAA. These proportions of whole stem  $^{14}\text{C}$  in the shank were generally maintained from 2 WAA to PM with percentages in stressed and non-stressed plants at PM being 15,8 and 13,6 %, respectively. This

is indicative of the greater mobilization of  $^{14}\text{C}$  assimilated at 2 WAA to the grain as the grain had become established as the major sink for photosynthate at 2 WAA. The percentage of whole stem  $^{14}\text{C}$  in the shank in fact increased from 6 WAA to PM in the stressed plants. This again indicates that the stressed plants mobilized more of the  $^{14}\text{C}$  assimilated at 2 WAA to the primary ear during grain fill and as grain fill ceased at PM this  $^{14}\text{C}$  remained in the shank.

#### Labelling at 4 WAA

When plants were labelled at 4 WAA the percentage of whole stem  $^{14}\text{C}$  in the B4 segment of stressed and non-stressed plants was 16,5 and 10,3 % respectively at 4 WAA (Figure 4.16). The percentage of  $^{14}\text{C}$  in the B4 segment of stressed plants increased to 20,0 % at PM while that in non-stressed plants increased to 19,0 % at 6 WAA and then declined to 12,4 % at PM. Although the percentage of  $^{14}\text{C}$  in the B4 segment was generally not as high as was the case with plants labelled at A, it is clear that the B4 segment had a greater proportion of whole stem  $^{14}\text{C}$  in it than was the case for plants labelled at 2 WAA. The higher percentage of whole stem  $^{14}\text{C}$  in the B4 segment of the stressed plants is not easy to explain. It may indicate that the C requirements of the roots are greater under stress conditions than under non-stress conditions. In contrast to plants labelled at 2 WAA, the B2 segment recorded the highest percentage of whole stem  $^{14}\text{C}$  at 48 h after labelling at 4 WAA which was 18,6 and 19,1 % in stressed and non-stressed plants, respectively. The percentage of whole stem  $^{14}\text{C}$  in the B1 and B3 segments at 4 WAA was just less than

that recorded in the B2 segment. From 4 WAA to PM the percentage of whole stem  $^{14}\text{C}$  in the B2 segment of stressed and non-stressed plants increased to 21,1 and 23,2 %, respectively. The percentage of whole stem  $^{14}\text{C}$  in the B3 segment of stressed plants increased from 17,6 % at 4 WAA to 21,4 % at PM, while that in the B3 segment of the non-stressed plants increased sharply from 17,2 % at 4 WAA to 26,1 % at 6 WAA before declining to 23,2 % at PM. The physiological significance for the sharp increase in the percentage of whole stem  $^{14}\text{C}$  in the B3 segment of non-stressed plants from 4 to 6 WAA is not certain. However, it may as with plants labelled at 2 WAA, indicate that  $^{14}\text{C}$  was mobilized out of the leaves attached to this segment at a later stage than in the stressed plants. At 4 WAA the percentage of  $^{14}\text{C}$  in the A1 segment of stressed and non-stressed plants was 11,2 and 10,7 %, respectively. This was less than the percentage of whole stem  $^{14}\text{C}$  recorded 48 h after plants were labelled at 2 WAA. It appears that a smaller proportion of  $^{14}\text{C}$  assimilated at 4 WAA was partitioned to the A1 segment than was the case for plants labelled at 2 WAA. The slightly higher percentage of whole stem  $^{14}\text{C}$  recorded in the A1 segment of stressed plants 48 h after labelling at 4 WAA than that in non-stressed plants is probably indicative of the more direct and rapid translocation of  $^{14}\text{C}$  to the primary ear. Since the A1 segment is in close proximity to the primary ear it may be expected that this tendency would result in a higher proportion of  $^{14}\text{C}$  in the A1 segment of stressed than non-stressed plants. From 4 WAA to PM the percentage of  $^{14}\text{C}$  in the A1 segment of stressed plants declined to 6,4 % while that in the A1 segment of non-stressed plants initially decreased to 5,6 % from 4 to 6 WAA and then increased to 8,2 % at PM. The

lower percentage of whole stem  $^{14}\text{C}$  in the A1 segment from 6 WAA to PM than at 4 WAA in both stressed and non-stressed plants may be indicative of less  $^{14}\text{C}$  being mobilized through it to the primary ear. At 4 WAA the percentage of whole stem  $^{14}\text{C}$  in the shank peaked in stressed and non-stressed plants at 13,3 and 14,2 %, respectively. This was just less than the percentage of whole stem  $^{14}\text{C}$  recorded in the shank at 48 h after labelling at 2 WAA and more than that recorded in the shank at 48 h after labelling at A. This is indicative of the rapid mobilization of  $^{14}\text{C}$  through the shank to the grain shortly after labelling at 4 WAA. The percentage of whole stem  $^{14}\text{C}$  in the shank of non-stressed plants declined to 7,7 % at 6 WAA and then to 6,9 % at PM, while that in the shank of stressed plants declined to 9,4 % at 6 WAA and then increased marginally to 9,7 %. Thus it appears that the stressed plants continued to mobilize proportionately more  $^{14}\text{C}$  to the grain and thus maintained a greater proportion of the whole stem  $^{14}\text{C}$  in the shank than did the non-stressed plants. As with plants labelled at 2 WAA the top segment recorded the lowest percentage of whole stem  $^{14}\text{C}$  from 4 WAA to PM in comparison to the other segments, with the percentage of  $^{14}\text{C}$  in the top segment of stressed plants generally less than that of non-stressed plants.

#### Labelling at 6 WAA

When plants were labelled at 6 WAA, the primary grain was still established as the major sink for photosynthate, however, to a lesser extent than was the case when plants were labelled at 2 WAA and 4 WAA (Sections 4.3.4.1 and 4.3.4.2). At 6 WAA the B2

segment of stressed plants recorded the highest percentage of whole stem  $^{14}\text{C}$  of 21,6 % with the percentage in the B1, B3 and B4 segments marginally less than that of the B2 segment (Figure 4.16). In the non-stressed plants the B3 segment recorded the highest percentage of whole stem  $^{14}\text{C}$  of 20,8 % with the percentage in the B1, B2 and B4 segments just less than that of the B3 segment. As the percentage of whole stem  $^{14}\text{C}$  in the top, A1, B1 and B2 segments of stressed plants declined from 6 WAA to PM the percentage in the B3 and B4 segments increased. The increase from 19,1 to 27,1 % in the B3 segment was particularly marked. In the non-stressed plants the percentage of whole stem  $^{14}\text{C}$  in the top, A1, B1 and shank segments declined from 6 WAA to PM while that of the B2, B3 and B4 segments increased. The percentage of the whole stem  $^{14}\text{C}$  in the shank of stressed and non-stressed plants at 6 WAA was 8,1 and 7,7 %, respectively. The marginally higher percentage in the shank of the stressed plants again reflects the more direct and rapid translocation of the  $^{14}\text{C}$  assimilated at 6 WAA through the shank to the grain. At PM the percentage of whole stem  $^{14}\text{C}$  in the shank declined to 6,4 and 6,1 % in stressed and non-stressed plants, respectively. It is apparent that the percentage of  $^{14}\text{C}$  in the shank of stressed and non-stressed plants labelled at 6 WAA was generally less on all sampling occasions than that recorded in plants labelled at 2 WAA and 4 WAA. This reflects the reduced mobilization of  $^{14}\text{C}$  through the shank to the grain at 6 WAA as the rate of dry mass gain by the grain declined from 6 WAA to PM (Table 4.8 and Appendix 46). Although the primary grain was not established as the major sink for photosynthate when plants were labelled at A the percentage of whole stem  $^{14}\text{C}$  in the shank from A to 2 WAA was

similar to that in the shank of the plants labelled at 6 WAA from 6 WAA to PM. However, once the primary grain was established as the major sink for photosynthate the percentage of <sup>14</sup>C in the shank of the plants labelled at A from 4 WAA to PM generally exceeded that in the shank of plants labelled at 6 WAA from 6 WAA to PM. This indicates that plants labelled at A mobilized a greater proportion of whole stem <sup>14</sup>C through the shank once the primary grain became established as the major sink for photosynthate than did plants labelled at 6 WAA from 6 WAA to PM.

4.3.5 Radioactivity analysis of whole stem

4.3.5.1 Specific radioactivity

Labelling at A

The main effect for stress treatment was non-significant (Table 4.23 and Appendix 37.1). The SR of the stem under stress

Table 4.23 Effect of water stress (S) and lack of water stress (NS) on whole stem specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) meaned over five growth periods during grain fill for a maize hybrid labelled at anthesis

Stress treatment	
S	NS
86,32	82,40
LSD (0,05)	NS
LSD (0,01)	NS

conditions was marginally higher than that under non-stress conditions. Whole plant TR was higher in stressed plants than non-stressed plants 48 h after labelling at A (Section 4.3.7.2). At A the primary ear was not yet established as the major sink for photosynthate. The stem, however, underwent a further dry mass increase from A to 2 WAA (Table 4.24 and Appendix 47), more so in the non-stressed plants than the stressed plants. Thus initially a considerable proportion of the  $^{14}\text{C}$  assimilated at A was used irreversibly for synthesis of structural compounds in the stem. It would be expected that because of their reduced photosynthetic rate the stressed plants would be forced to utilize available labile  $^{14}\text{C}$  organic compounds in the vegetative organs, in particular that in the stem, to meet the photosynthate requirements of the grain. This would in turn reduce the TR of the stem under stress conditions. This did indeed occur (Section 4.3.5.2). However, stressed plants maintained a higher SR of the stem because of the reduced dry mass of the whole stem (Table 4.24 and Appendix 47) and because in contrast to the non-stressed

Table 4.24 Whole stem dry mass ( $\text{g stem}^{-1}$ ), meaned over corresponding sampling occasions from each labelling occasion, from a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill

Stress treatment	Weeks after anthesis				
	0	2	4	6	8
S	58,7	55,2	51,1	60,6	57,4
NS	57,0	57,1	50,8	65,7	62,6

plants it is likely that less  $^{12}\text{C}$  was used for structural growth of the stem after labelling.

The main effect for WAA was significant (Table 4.25). There was a significant negative linear effect which indicates that the SR of the stem generally declined from A to PM. Initially, however, the SR of the stem increased from A to 2 WAA which was largely due to the high TR recorded for the stem of non-stressed plants at 2 WAA (Section 4.3.5.2). This may be a real trend reflecting the further mobilization of  $^{14}\text{C}$  from the leaves into the stem or it may be due to sampling error. Generally, however, SR of the stem declined from A to PM with SR at A significantly ( $p = 0,01$ ) higher than at PM. This reflects the general decline in  $^{14}\text{C}$  in the stem as photosynthate was mobilized to the grain and utilized for respiratory requirements. It also reflects the dilution effect as new non-radioactive photosynthate was utilized for final structural growth of the stem from A to 2 WAA and non-radioactive labile organic compounds accumulated in the stem

Table 4.25 Specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) of whole stem meaned over water stress treatments from anthesis to eight weeks after anthesis (WAA) for a maize hybrid labelled at anthesis

	WAA				
	0	2	4	6	8
	116,67	123,69	63,46	62,84	55,16
LSD (0,05)		31,61			
LSD (0,01)		43,56			

towards the end of grain fill, particularly under non-stress conditions.

#### Labelling at 2 WAA

The main effect for stress treatment was non-significant (Table 4.26 and Appendix 37.2). The SR of the stem under stress conditions was non-significantly lower than that under non-stress conditions. When the plants were labelled at 2 WAA the stressed plants had already undergone two consecutive stress cycles. Although stressed plants had a higher whole plant TR 48 h after labelling at 2 WAA (Section 4.3.7.2), the TR of the stem under stress conditions (Section 4.3.5.2) was lower. At 2 WAA the primary ear was established as the major sink for photosynthate. Thus under stress conditions it would possibly be expected that much of the assimilated  $^{14}\text{C}$  would be translocated directly to the grain with less initially accumulating in the stem tissue.

Table 4.26 Effect of water stress (S) and lack of water stress (NS) on whole stem specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over four growth periods during grain fill for a maize hybrid labelled at two weeks after anthesis

Stress treatment	
S	NS
18,39	19,62
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.27). There was a significant negative linear effect superimposed with a significant positive quadratic effect which indicates that the SR of the stem declined markedly from 2 to 4 WAA and then declined less markedly from 4 WAA to PM. This reflects the general decline in <sup>14</sup>C in the stem as photosynthate was mobilized to the grain and utilized for respiratory requirements. The SR declined most markedly in the first two weeks after labelling which indicates that <sup>14</sup>C which occurred as labile organic compounds in the stem was rapidly utilized for respiratory and predominantly grain requirements. In the period from 4 WAA to PM the SR of the stem declined less rapidly as there was little <sup>14</sup>C available as labile compounds in the stem for mobilization to the grain.

Table 4.27 Specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of whole stem meaned over water stress treatments from two weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at two weeks after anthesis

WAA			
2	4	6	8
43,94	16,17	9,14	6,77
LSD (0,05)	11,46		
LSD (0,01)	15,91		

### Labelling at 4 WAA

The main effect for stress treatment was non-significant (Table 4.28 and Appendix 37.3). The SR of the stem under stress conditions was non-significantly lower than that under non-stress conditions. This is an indication of the lower whole plant TR recorded in the stressed plants 48 h after labelling at 4 WAA (Section 4.3.7.2) and it is also an indication of the more direct translocation of assimilated  $^{14}\text{C}$  to the primary ear under stress conditions. The primary ear at 4 WAA was still a major sink for photosynthate.

Table 4.28 Effect of water stress (S) and lack of water stress (NS) on whole stem specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over three growth periods during grain fill for a maize hybrid labelled at four weeks after anthesis

Stress treatment	
S	NS
18,58	25,04
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.29). There was a significant negative linear effect superimposed with a significant positive quadratic effect which indicates that the SR of the stem declined markedly from 4 to 6 WAA and then less markedly from 6 WAA to PM. The marked decline in the SR of the

stem from 4 to 6 WAA reflects the rapid utilization of  $^{14}\text{C}$ , which occurred as labile organic compounds in the stem, for respiratory and predominantly grain requirements. In the period from 6 WAA to PM the SR of the stem declined less rapidly there was less  $^{14}\text{C}$  available as labile compounds in the stem for mobilization to the grain.

Table 4.29 Specific radioactivity (dpm  $\times 10^{-3} \text{ g}^{-1}$ ) of whole stem meaned over water stress treatments from four weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at four weeks after anthesis

	WAA		
	4	6	8
	33,78	16,85	14,80
LSD (0,05)		2,76	
LSD (0,01)		4,01	

#### Labelling at 6 WAA

The main effect for stress treatment was non-significant (Table 4.30 and Appendix 37.4). The SR of the stem under stress conditions was non-significantly lower than that under non-stress conditions. This is an indication of the lower whole plant TR recorded in the stressed plants at 48 h after labelling at 6 WAA (Section 4.3.7.2), and it is also an indication of the more direct translocation of the assimilated  $^{14}\text{C}$  to the primary ear under stress conditions. Although whole plant photosynthetic

activity was much less at 6 WAA than earlier on in grain fill (Section 4.3.7.2) the primary ear was still the major sink for photosynthate.

Table 4.30 Effect of water stress (S) and lack of water stress (NS) on whole stem specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) meaned over two growth periods during grain fill for a maize hybrid labelled at six weeks after anthesis

Stress treatment	
S	NS
9,60	11,61
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.31). The SR of the stem declined from 6 WAA to PM, with the SR at 6 WAA significantly ( $p = 0,01$ ) higher than that at PM. In fact SR of the stem at PM was only half that at 6 WAA. Since the dry mass of the stem remained constant from 6 WAA to PM (Table 4.24 and Appendix 47) the decline in SR from 6 WAA to PM reflects the mobilization of <sup>14</sup>C labile organic compounds in the stem to the grain. There would, of course, also be losses due to respiration.

Table 4.31 Specific radioactivity (dpm x 10<sup>3</sup> g<sup>-1</sup>) of whole stem meaned over water stress treatments from six weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at six weeks after anthesis

WAA	
6	8
14,15	7,06
LSD (0,05) 3,07	
LSD (0,01) 5,09	

First order interactions for labelling at A, 2 WAA, 4 WAA and 6 WAA

Each first order interaction of stress treatment with WAA for labelling at A, 2 WAA, 4 WAA and 6 WAA was non-significant (Figure 4.17). There were no significant components of each interaction either. However, the apparent trends of these first order interactions are discussed.

Stressed and non-stressed plants labelled at A maintained a higher SR of the stem on all sampling occasions than plants labelled at 2 WAA, 4 WAA and 6 WAA (Figure 4.17). The reason for this was twofold, namely: (i) plants labelled at A recorded the highest TR of the whole plant 48 h after labelling compared to plants labelled on the other three occasions; and (ii) the percentage of whole plant <sup>14</sup>C recovered in the stem at PM was the highest for all labelling occasions, namely 24,9 and 28,9 % in

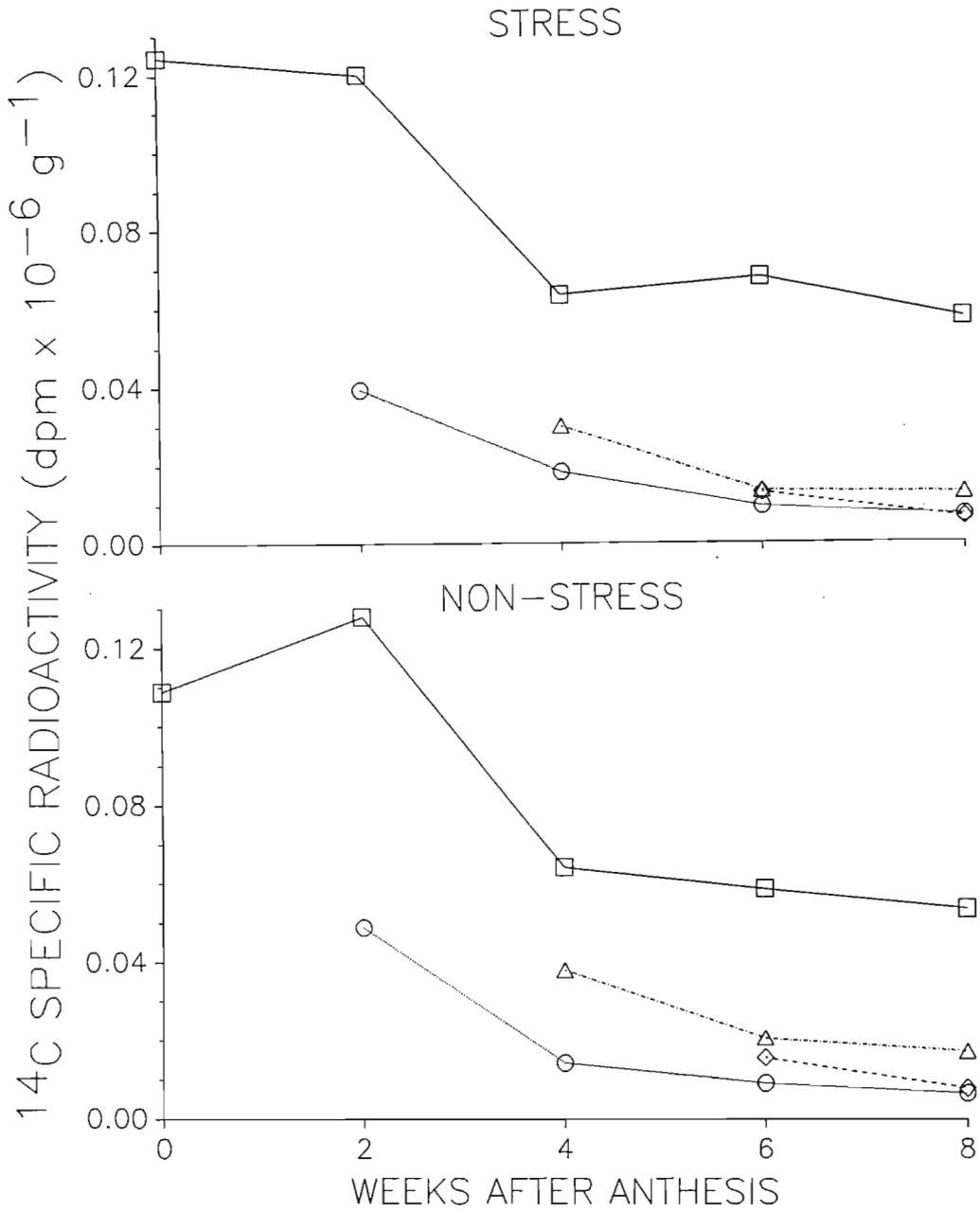


Figure 4.17 Effect of water stress during grain fill on specific radioactivity of the whole stem sampled at fortnightly intervals from a maize hybrid labelled at anthesis ( $\square-\square$ ), 2 ( $\circ-\circ$ ), 4 ( $\triangle-\triangle$ ) and 6 ( $\diamond-\diamond$ ) weeks after anthesis

stressed and non-stressed plants, respectively. This reflects the greater 'irreversible' utilization of  $^{14}\text{C}$  assimilated at A for the growth of stem cells. The SR of the stem of stressed and non-stressed plants at A was 124 438 and 108 905 dpm  $\text{g}^{-1}$ , respectively. At PM the SR of the stem of stressed and non-stressed plants was 57 110 and 53 207 dpm  $\text{g}^{-1}$ , respectively. It is clear that the SR of the stem declined as  $^{14}\text{C}$  was mobilized out of the stem to the primary grain. The most marked decline in the SR of the stem of stressed and non-stressed plants occurred from 2 to 4 WAA once the primary grain was established as the major sink for photosynthate. It would be expected that as a result of their reduced photosynthetic rate the stressed plants would be forced to utilize labile  $^{14}\text{C}$  organic compounds in the stem to meet the photosynthate requirements of the grain. This would in turn reduce the TR of the stem under stress conditions. This did indeed occur (Section 4.3.5.2). However, stressed plants maintained a higher SR of the stem because of the reduced size (by dry mass) of the whole stem (Table 4.24 and Appendix 47) and because in contrast to non-stressed plants less  $^{12}\text{C}$  organic compounds accumulated in the stem after labelling at A.

When plants were labelled at 2 WAA the SR of the stem on all sampling occasions was less than that of plants labelled at A, 4 WAA and 6 WAA (Figure 4.17). This reflects the low percentage of whole plant  $^{14}\text{C}$  recovered in the stem at PM of plants labelled at 2 WAA, namely 3,0 and 2,8 % in stressed and non-stressed plants, respectively. This further reflects the high percentage of whole plant  $^{14}\text{C}$  recovered in the grain at PM of plants labelled at 2 WAA namely 84,2 and 87,9 % in stressed and non-stressed

plants, respectively. The SR of the stem of stressed and non-stressed plants at 2 WAA was 39 176 and 48 694 dpm g<sup>-1</sup> respectively, which declined sharply to 18 149 and 14 185 dpm g<sup>-1</sup> in stressed and non-stressed plants, respectively, at 4 WAA. From 4 WAA to PM the SR of the stem declined less markedly and at PM it was 6 979 and 6 570 dpm g<sup>-1</sup> in stressed and non-stressed plants, respectively. Thus initially at 2 WAA the SR of the stem of non-stressed plants was higher than that of the stressed plants but from 4 WAA to PM the SR of the stem of stressed plants was higher than that of the non-stressed plants although the difference was marginal. This would appear to indicate that soon after labelling the stressed plants mobilized more of the <sup>14</sup>C directly to the grain with less accumulating in the stem tissue. However, from 4 WAA to PM the non-stressed plants assimilated more <sup>12</sup>C than the stressed plants. As the dry mass of the stem continued to increase to a greater extent during grain fill in the non-stressed plants than the stressed plants (Table 4.24 and Appendix 47) the <sup>14</sup>C in the stem was diluted to a greater extent by <sup>12</sup>C photosynthate than was the case for the stressed plants.

When plants were labelled at 4 WAA the SR of the stem on all sampling occasions was marginally higher than that of plants labelled at 2 WAA and 6 WAA but less than that of plants labelled at A (Figure 4.17). The SR of the stem for plants labelled at 4 WAA was greater than that of plants labelled at 2 WAA even though the TR of the whole plant at 48 h after labelling at 4 WAA was, averaged over stressed and non-stressed plants, 52,5 % of the TR of the whole plant at 48 h after labelling at 2 WAA. This reflects the higher percentage of whole plant <sup>14</sup>C recovered in the

stem at PM of plants labelled at 4 WAA namely 11,8 and 11,5 % in stressed and non-stressed plants, respectively. The SR of the stem of stressed and non-stressed plants at 4 WAA was 29 829 and 37 729 dpm g<sup>-1</sup> respectively, which declined sharply to 13 285 and 20 404 dpm g<sup>-1</sup> in stressed and non-stressed plants respectively, at 6 WAA. From 6 WAA to PM the SR of the stem declined less markedly and at PM it was 12 618 and 16 984 dpm g<sup>-1</sup> in stressed and non-stressed plants, respectively. The overall decline in the SR of the stem reflects the mobilization of <sup>14</sup>C to the grain with the bulk of <sup>14</sup>C being translocated to the grain in the first two weeks after labelling at 4 WAA. The lower SR of the stem of stressed plants on all sampling occasions reflects the lower TR of the whole plant and whole stem recorded in the stressed plants on all sampling occasions in comparison to non-stressed plants and the more direct translocation of <sup>14</sup>C to the grain.

When plants were labelled at 6 WAA the SR of the stem on all sampling occasions was marginally higher than that of plants labelled at 2 WAA, marginally less than that of plants labelled at 4 WAA and substantially less than that of plants labelled at A (Figure 4.17). The SR of the stem for plants labelled at 4 WAA was marginally higher than that of plants labelled at 2 WAA even though the TR of the whole plant at 48 h after labelling at 6 WAA was, averaged over stressed and non-stressed plants, 16,5 % of the TR of the whole plant at 48 h after labelling at 2 WAA. This reflects the higher percentage of whole plant <sup>14</sup>C recovered in the stem at PM namely 21,1 and 23,2 % in stressed and non-stressed plants, respectively. Although the percentage of whole plant <sup>14</sup>C recovered at PM in the stem of plants labelled at 4 WAA was less

than that of plants labelled at 6 WAA (Section 4.3.5.3), the TR of the whole plant at 48 h after labelling at 6 WAA was, averaged over stressed and non-stressed plants, 31,4 % of the TR of the whole plant at 48 h after labelling at 4 WAA. This resulted in the SR of the stem of stressed and non-stressed plants labelled at 6 WAA being marginally less than that of plants labelled at 4 WAA on all sampling occasions. The SR of the stem at 6 WAA was 12 845 and 15 457 dpm g<sup>-1</sup> which declined to 6 350 and 7 765 dpm g<sup>-1</sup> at PM in stressed and non-stressed plants, respectively. The overall decline in the SR of the stem reflects the mobilization of <sup>14</sup>C to the grain. The lower SR of the stem of stressed plants on all sampling occasions reflects the lower TR of the whole plant and whole stem recorded in stressed plants on all sampling occasions in comparison to non-stressed plants. It also reflects the more direct translocation of assimilated <sup>14</sup>C to the grain under stress conditions.

#### 4.3.5.2 Total radioactivity

##### Labelling at A

The main effect for stress treatment was non-significant (Table 4.32 and Appendix 38.1). The TR of the stem under stress conditions was marginally lower than that under non-stress conditions. It would appear that averaged over sampling occasions stressed plants incorporated marginally less <sup>14</sup>C into structural components of the stem and once the primary ear was established as the major sink for photosynthate more <sup>14</sup>C was mobilized out of the stem of stressed plants to the grain. It

would be expected that stressed plants would respire less than non-stressed plants (Boyer, 1970a; Boyer and McPherson, 1975). However, since the  $^{14}\text{C}$  assimilated at A would be in the plant for the entire grain filling period, eventually the stressed plants would respire a great deal of the  $^{14}\text{C}$  because they would have to utilize previously assimilated C for respiration requirements as the assimilation rate of  $^{12}\text{C}$  after labelling would be reduced as a result of stress.

Table 4.32 Effect of water stress (S) and lack of water stress (NS) on whole stem total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over five growth periods during grain fill for a maize hybrid labelled at anthesis

Stress treatment	
S	NS
4 965	5 089
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.33). There was a significant negative linear effect superimposed with a significant positive cubic effect which indicates that the TR of the stem fluctuated somewhat as it generally declined from A to PM. The TR of the stem was significantly ( $p = 0,01$ ) lower at PM than at A. The decline in TR from A to 4 WAA was the most marked and perhaps indicates that most of the  $^{14}\text{C}$  assimilated at A, which accumulated as labile organic compounds within the stem, was mobilized to the grain within the first four weeks of grain fill.

The non-significant increase in stem TR from A to 2 WAA was largely due to the high TR recorded for the stem of non-stressed plants at 2 WAA. This may be a real trend reflecting the further mobilization of  $^{14}\text{C}$  from the leaves into the stem in the two weeks following labelling at A as the primary ear was established as the major sink for photosynthate or it may be due to sampling error.

Table 4.33 Total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) of whole stem meaned over water stress treatments from anthesis to eight weeks after anthesis (WAA) for a maize hybrid labelled at anthesis

	WAA				
	0	2	4	6	8
	6 603	7 608	3 307	4 094	3 526
LSD (0,05)		1 736			
LSD (0,01)		2 392			

#### Labelling at 2 WAA

The main effect for stress treatment was non-significant (Table 4.34 and Appendix 38.2). The TR of the stem under stress conditions was lower than that under non-stress conditions. When the plants were labelled at 2 WAA the stressed plants had already undergone two consecutive stress cycles, however, the TR of the whole plant at 48 h after labelling at 2 WAA was marginally higher in stressed plants than non-stressed plants. At 2 WAA the primary ear was established as the major sink for photosynthate. Thus lower TR of the whole stem under stress conditions would

appear to reflect the more direct translocation of assimilated  $^{14}\text{C}$  to the grain with less being incorporated into labile pools in vegetative tissue such as the stem.

Table 4.34 Effect of water stress (S) and lack of water stress (NS) on whole stem total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over four growth periods during grain fill for a maize hybrid labelled at two weeks after anthesis

Stress treatment	
S	NS
975	1 021
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.35). There was a significant negative linear effect superimposed with a significant positive quadratic effect which indicates that the

Table 4.35 Total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) of whole stem meaned over water stress treatments from two weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at two weeks after anthesis

WAA			
2	4	6	8
2 214	801	589	388
LSD (0,05)	552		
LSD (0,01)	766		

TR of the stem declined markedly from 2 to 4 WAA and then declined less markedly from 4 WAA to PM. In fact from 2 to 4 WAA TR declined by 63,8 %. This indicates that <sup>14</sup>C which occurred as labile organic compounds in the stem was rapidly utilized for respiratory and predominantly grain requirements within the first two weeks after labelling.

Labelling at 4 WAA

The main effect for stress treatment was non-significant (Table 4.36 and Appendix 38.3). The TR of the stem under stress conditions was marginally lower than that under non-stress conditions. This reflects the lower amount of <sup>14</sup>C assimilated by the whole plant at 4 WAA under stress conditions and it also reflects the more direct translocation of assimilated <sup>14</sup>C to the primary ear under stress conditions. The primary ear at 4 WAA was still a major sink for photosynthate.

Table 4.36 Effect of water stress (S) and lack of water stress (NS) on whole stem total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) meaned over three growth periods during grain fill for a maize hybrid labelled at four weeks after anthesis

Stress treatment	
S	NS
1 025	1 396
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.37). There was a significant negative linear effect superimposed with a significant positive quadratic effect which indicates that the TR of the stem declined markedly from 4 to 6 WAA and then less markedly from 6 WAA to PM. The marked decline in the TR of the stem from 4 to 6 WAA reflects the rapid utilization of  $^{14}\text{C}$ , which occurred as labile organic compounds in the stem, for respiratory and predominantly grain requirements. In the period from 6 WAA to PM the TR of the stem declined less rapidly as there was less  $^{14}\text{C}$  available as labile compounds in the stem for mobilization to the grain.

Table 4.37 Total radioactivity (dpm  $\times 10^{-3} \text{ g}^{-1}$ ) of whole stem meaned over water stress treatments from four weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at four weeks after anthesis

	WAA		
	4	6	8
	1 703	1 063	865
LSD (0,05)	140		
LSD (0,01)	204		

#### Labelling at 6 WAA

The main effect for stress treatment was non-significant (Table 4.38 and Appendix 38.4). The TR of the stem under stress conditions was non-significantly lower than that under non-stress

conditions. This reflects the lower amount of  $^{14}\text{C}$  assimilated by the whole plant at 6 WAA under stress conditions and it also reflects the more direct translocation of assimilated  $^{14}\text{C}$  to the primary ear under stress conditions. At 6 WAA the primary ear remained a major sink for photosynthate.

Table 4.38 Effect of water stress (S) and lack of water stress (NS) on whole stem total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over two growth periods during grain fill for a maize hybrid labelled at six weeks after anthesis

Stress treatment	
S	NS
573	720
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.39). The TR of the stem declined from 6 WAA to PM, with the TR at 6 WAA significantly ( $p = 0,01$ ) higher than that at PM. In fact, the TR of the stem at PM was 49,5 % of that at 6 WAA. The decline in the TR of the stem reflects the mobilization of  $^{14}\text{C}$  labile organic compounds in the stem to the primary grain as well as losses due to respiration.

Table 4.39 Total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of whole stem meaned over water stress treatments from six weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at six weeks after anthesis

WAA	
6	8
865	428
LSD (0,05)	191
LSD (0,01)	316

First order interactions for labelling at A, 2 WAA, 4 WAA and 6 WAA

Each first order interaction of stress treatment with WAA for labelling at A, 2 WAA, 4 WAA and 6 WAA was non-significant (Figure 4.18). There were no significant components of each interaction either. However, the apparent trends of these first order interactions are discussed.

The patterns in the changes of the TR of the stem on all sampling occasions for each of the labelling occasions are very similar to that of the SR of the stem (Figure 4.17).

Stressed and non-stressed plants labelled at A maintained a higher TR of the stem on all sampling occasions than plants labelled at 2 WAA, 4 WAA and 6 WAA (Figure 4.18). The reason for this is twofold, namely: (i) plants labelled at A recorded the highest TR of the whole plant 48 h after labelling compared to

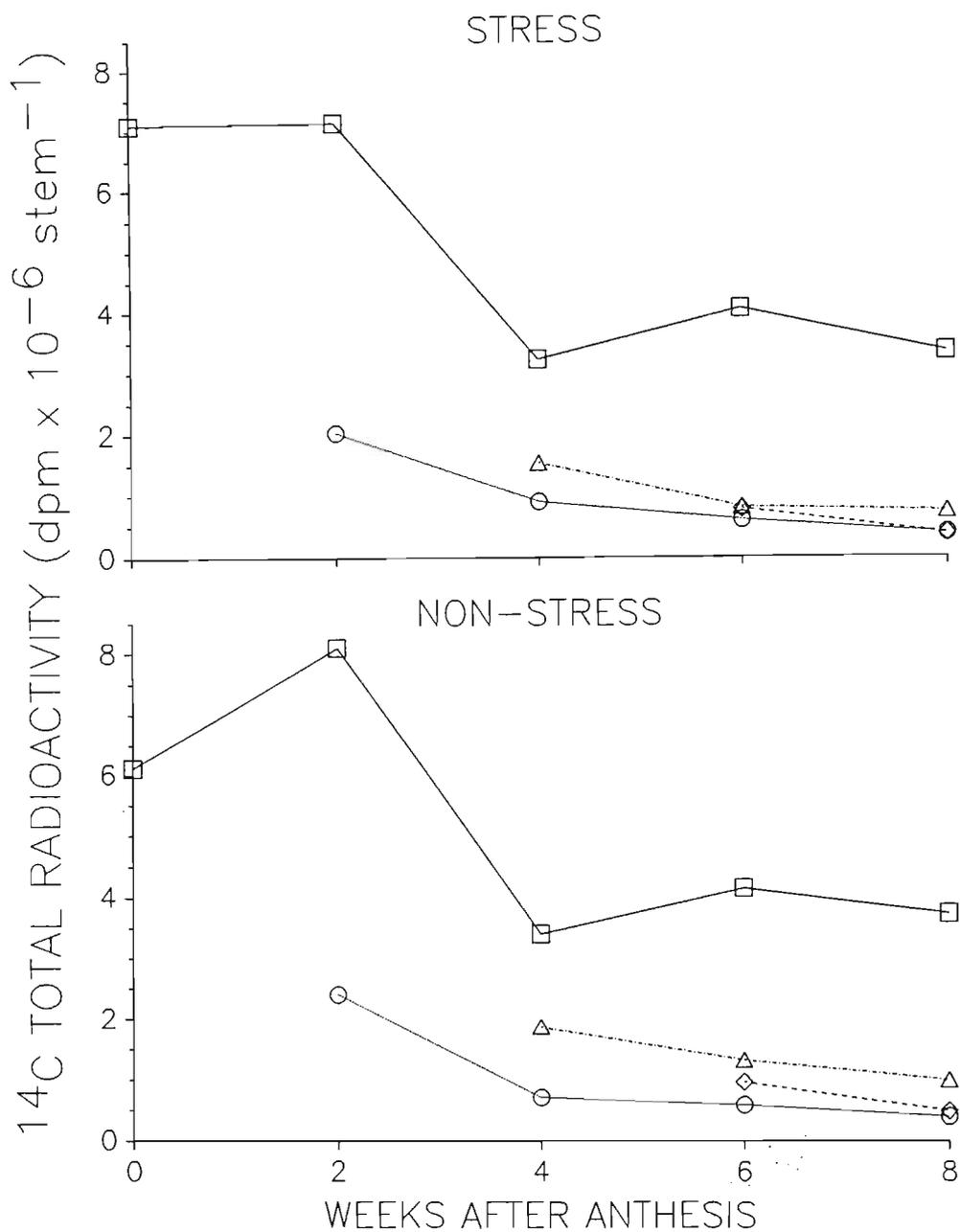


Figure 4.18 Effect of water stress during grain fill on total radioactivity of the whole stem sampled at fortnightly intervals from a maize hybrid labelled at anthesis ( $\square-\square$ ), 2 ( $\circ-\circ$ ), 4 ( $\triangle-\triangle$ ) and 6 ( $\diamond-\diamond$ ) weeks after anthesis

the plants labelled on the other three occasions; and (ii) the percentage of whole plant  $^{14}\text{C}$  recovered in the stem at PM was the highest for all labelling occasions, namely 24,9 and 28,9 % in stressed and non-stressed plants, respectively. This reflects the greater irreversible utilization of  $^{14}\text{C}$  assimilated at A for the growth of the stem cells. The TR of the stem of stressed and non-stressed plants at A was 7 092 915 and 6 113 300 dpm stem<sup>-1</sup>, respectively. The TR of the stem increased from A to 2 WAA to 7 125 863 and 8 089 401 dpm stem<sup>-1</sup> in stressed and non-stressed plants, respectively. The marked increase in the TR of the stem of the non-stressed plants from A to 2 WAA may reflect a real phenomenon where  $^{14}\text{C}$  was mobilized out of the leaves and into the stem at a later stage than occurred in the stressed plants. On the other hand, it may be due to sampling error. From 2 to 4 WAA the TR of the stem of stressed and non-stressed plants declined sharply to 3 221 546 and 3 391 861 dpm stem<sup>-1</sup>, respectively. This probably reflects the mobilization of  $^{14}\text{C}$  which occurred as labile organic compounds in the stem to the primary grain which had become established as the major sink for photosynthate. From 4 WAA to PM the TR of the stem fluctuated somewhat and at PM the TR of the stem of stressed and non-stressed plants was 3 335 187 and 3 716 273 dpm stem<sup>-1</sup>, respectively. Initially the TR of the stem of the stressed plants was higher than that of non-stressed plants at A. This reflects the higher TR of the whole plant of the stressed plants recorded at A (Section 4.3.7.2). However, from 2 WAA to PM the TR of the stem of the stressed plants was less than that of the non-stressed plants. This reflects the greater mobilization of  $^{14}\text{C}$  to the grain under stress conditions due to the reduced photosynthetic rate of the stressed plants.

When plants were labelled at 2 WAA the TR of the stem on all sampling occasions was less than that of plants labelled at A, 4 WAA and 6 WAA (Figure 4.18). The reasons for this were as for the SR of the stem of plants labelled at 2 WAA. The TR of the stem of stressed and non-stressed plants at 2 WAA was 2 026 631 and 2 401 125 dpm stem<sup>-1</sup> respectively, which declined sharply to 893 509 and 709 270 dpm stem<sup>-1</sup> at 4 WAA in stressed and non-stressed plants, respectively. From 4 WAA to PM the TR of the stem declined less markedly and at PM it was 385 010 and 390 035 dpm stem<sup>-1</sup> in stressed and non-stressed plants, respectively. Initially at 2 WAA the TR of the stem of the non-stressed plants was higher than that of stressed plants but from 4 to 6 WAA the TR of the stem of stressed plants was higher than that of non-stressed plants but at PM the TR of the stem of non-stressed plants was higher than that of stressed plants. Thus it would appear that stressed plants mobilized more <sup>14</sup>C to the grain within the 48 h after labelling with the result that less <sup>14</sup>C accumulated in the stem. From 4 to 6 WAA the TR of the stem of non-stressed plants was less than that of stressed plants as <sup>14</sup>C was mobilized to the grain at a later stage than the stressed plants. Also the lower TR of the stem of non-stressed plants from 2 to 4 WAA reflects the lower TR of the whole plant recorded for the non-stressed plants during the same period (Section 4.3.7.2). This may reflect greater respiration losses from the non-stressed plants during this period. However, at PM the TR of the stem of non-stressed plants was marginally higher than that of stressed plants.

When plants were labelled at 4 WAA the TR of the stem on all sampling occasions was marginally higher than that of plants labelled at 2 WAA and 6 WAA, and substantially less than that of plants labelled at A (Figure 4.18). The reasons for this were as for the SR of the stem of plants labelled at 4 WAA. The TR of the stem of stressed and non-stressed plants at 4 WAA was 1 532 814 and 1 872 831 dpm stem<sup>-1</sup> respectively, which declined to 807 424 and 1 318 605 dpm stem<sup>-1</sup> at 6 WAA in stressed and non-stressed plants, respectively. From 6 WAA to PM the TR of the stem declined further and at PM it was 734 901 and 995 841 dpm stem<sup>-1</sup> in stressed and non-stressed plants, respectively. The overall decline in the TR of the stem reflects the mobilization of <sup>14</sup>C to the grain with the bulk of the <sup>14</sup>C being translocated to the grain in the first two weeks after labelling at 4 WAA. The lower TR of the stem of the stressed plants on all sampling occasions reflects the lower TR of the whole plant recorded in the stressed plants on all sampling occasions in comparison to non-stressed plants (Section 4.3.7.2). It also reflects the more direct and rapid translocation of <sup>14</sup>C assimilated at 4 WAA to the grain under stress conditions.

When plants were labelled at 6 WAA the TR of the stem on all sampling occasions was marginally higher than that of plants labelled at 2 WAA, marginally less than that of plants labelled at 4 WAA and substantially less than that of plants labelled at A. The reasons for this were as for the SR of the stem of plants labelled at 6 WAA. The TR of the stem of stressed and non-stressed plants at 6 WAA was 773 088 and 957 137 dpm stem<sup>-1</sup> respectively, which declined to 372 791 and 483 021 dpm stem<sup>-1</sup> in

stressed and non-stressed plants, respectively, at PM. The overall decline in the TR of the stem reflects the mobilization of  $^{14}\text{C}$  to the grain. The lower TR of the stem of stressed plants on all sampling occasions reflects the lower TR of the whole plant recorded in the stressed plants on all sampling occasions in comparison to non-stressed plants. It also reflects the more direct translocation of assimilated  $^{14}\text{C}$  to the grain under stress conditions.

#### 4.3.5.3 Whole stem total radioactivity as a % of whole plant total radioactivity

As the leaf  $\Psi_w$  of the stressed plants declined the photosynthetic capacity of the stressed plants declined as evidenced by the decline in the TR of the whole plant recorded on subsequent labelling occasions during grain fill (Section 4.3.7.2). As mentioned the stressed and non-stressed plants were watered in the morning of the day on which labelling took place. This enabled the stressed plants at 2 WAA to recover fully to assimilate marginally more  $^{14}\text{C}$  than the non-stressed plants as judged by the higher whole plant TR recorded for the stressed plants at 48 h after labelling at 2 WAA. However, at 4 WAA and 6 WAA the stressed plants assimilated less  $^{14}\text{C}$  than the non-stressed plants as judged by the lower whole plant TR recorded at 48 h after each labelling occasion. Thus the lower TR of the stem recorded on all sampling occasions for stressed plants labelled at 4 WAA and 6 WAA in comparison to non-stressed plants could simply reflect the lower TR of the whole plant and not necessarily indicate a greater mobilization of  $^{14}\text{C}$  out of the stem

to the grain under stress conditions. By expressing the TR of the stem as a percentage of the TR of the whole plant on each sampling occasion an assessment can be made of the proportion of whole plant  $^{14}\text{C}$  that was retained in the stem under stress and non-stress conditions.

#### Labelling at A

Stressed and non-stressed plants labelled at A maintained a higher percentage of whole plant  $^{14}\text{C}$  in the stem on all sampling occasions than did plants labelled at 2 WAA and 4 WAA (Figure 4.19). However, plants labelled at 6 WAA had a higher percentage of whole plant  $^{14}\text{C}$  in the stem at 48 h after labelling than did plants labelled at A when sampled at 4 and 6 WAA and at PM. This reflects the low percentage of whole plant  $^{14}\text{C}$  recovered in the grain at PM of plants labelled at A, which was the lowest for all labelling occasions, namely 31,0 and 26,9 % in stressed and non-stressed plants, respectively. The percentage of whole plant  $^{14}\text{C}$  in the stem at A was 40,2 and 36,4 % in stressed and non-stressed plants, respectively. This increased to 43,3 and 42,4 % in stressed and non-stressed plants, respectively, at 2 WAA before declining sharply to 25,1 and 24,9 % at 4 WAA in stressed and non-stressed plants, respectively. From 4 to 6 WAA the percentage of whole plant  $^{14}\text{C}$  in the stem of stressed plants increased to 30,6 % and then declined to 24,9 % at PM. In non-stressed plants, on the other hand, the percentage of whole plant  $^{14}\text{C}$  in the stem increased to 27,5 % at 6 WAA and then increased marginally to 28,9 % at PM. The general decline in the percentage of whole plant  $^{14}\text{C}$  in the stem from A to PM reflects

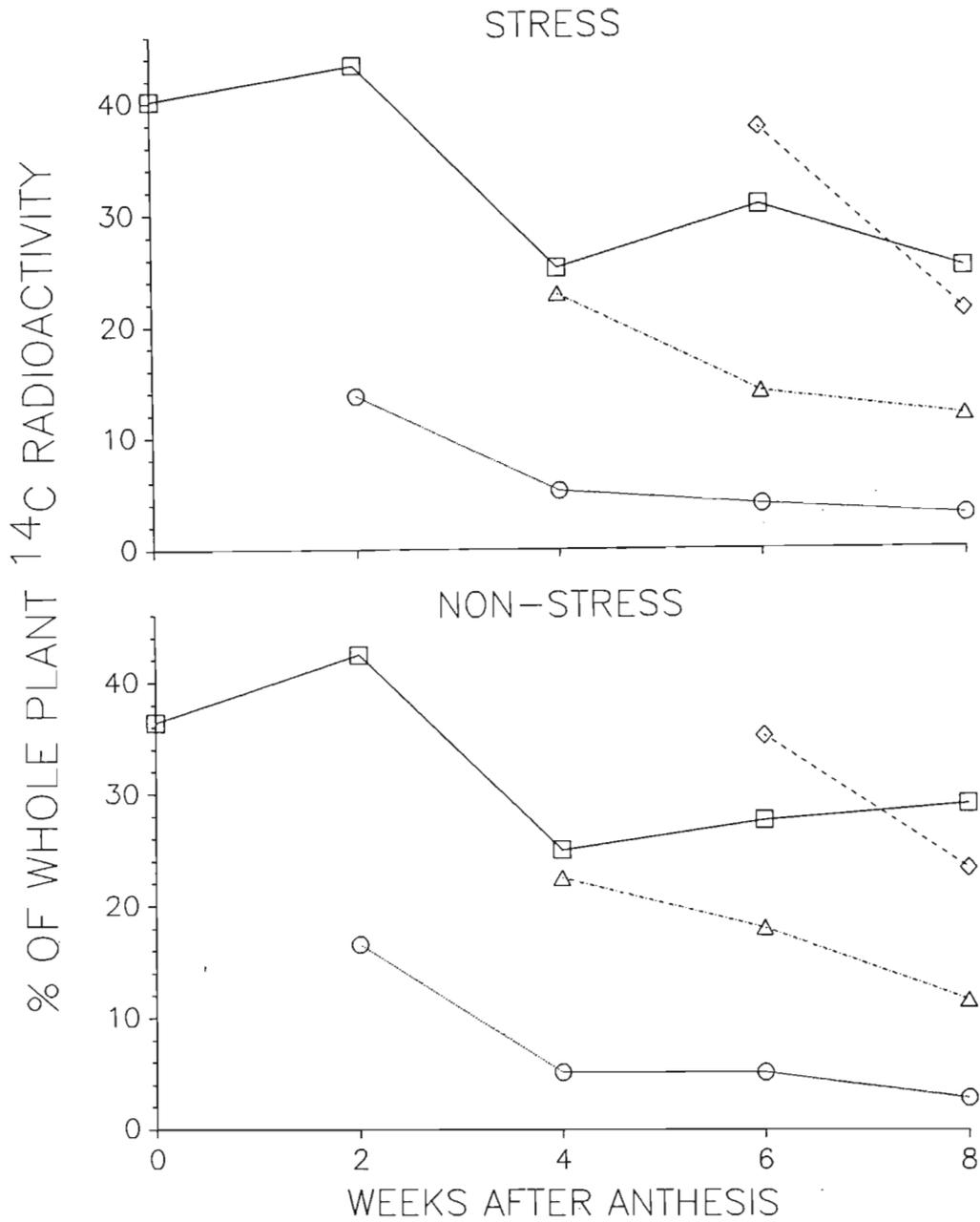


Figure 4.19 Effect of water stress during grain fill on total radioactivity of the whole stem expressed as a percentage of whole plant <sup>14</sup>C total radioactivity from a maize hybrid labelled at anthesis ( $\square$ — $\square$ ), 2 ( $\circ$ — $\circ$ ), 4 ( $\triangle$ — $\triangle$ ) and 6 ( $\diamond$ — $\diamond$ ) weeks after anthesis and sampled at fortnightly intervals

the mobilization of  $^{14}\text{C}$  to the grain. The most marked decline in the percentage of whole plant  $^{14}\text{C}$  in the stem occurred from 2 to 4 WAA as the primary grain became established as a major sink for photosynthate. Interestingly, the stressed plants maintained a higher proportion of whole plant  $^{14}\text{C}$  in the stem from A to 6 WAA than did the non-stressed plants. This is in direct contrast to the trend observed in the TR of the stem where the non-stressed plants maintained a higher TR of the stem from 2 WAA to PM compared to the stressed plants. The physiological significance of this is uncertain, although it may reflect greater mobilization of  $^{14}\text{C}$  out of the other vegetative segments i.e. the leaves and tassel as well as decreased mobilization of  $^{14}\text{C}$  to the 2° ear under stress conditions. It will also be recalled that the stressed plants accumulated a greater proportion of whole plant  $^{14}\text{C}$  in the B4 segment of the stem (Section 4.3.4.3).

#### Labelling at 2 WAA

Stressed and non-stressed plants labelled at 2 WAA maintained the lowest percentage of whole plant  $^{14}\text{C}$  in the stem on all sampling occasions than plants labelled on any of the other three occasions. This reflects the high percentage of whole plant  $^{14}\text{C}$  recovered in the grain at PM which was the highest for all labelling occasions, namely 84,2 and 87,9 % in stressed and non-stressed plants, respectively (Figure 4.19). The percentage of whole plant  $^{14}\text{C}$  in the stem at A was 13,7 and 16,5 % in stressed and non-stressed plants respectively which declined sharply to 5,1 % in both stressed and non-stressed plants at 4 WAA. From

4 WAA to PM the percentage of whole plant  $^{14}\text{C}$  in the stem declined further but less markedly and at PM the percentages were 3,0 and 2,8 % in the stressed and non-stressed plants, respectively. The overall decline in the percentage of whole plant  $^{14}\text{C}$  in the stem from 2 WAA to PM reflects the mobilization of  $^{14}\text{C}$  to the grain with the bulk of the  $^{14}\text{C}$  being mobilized to the grain within 48 h after labelling with a further marked mobilization occurring up to 4 WAA. The lower percentage of whole plant  $^{14}\text{C}$  in the stem of stressed plants at 2 WAA reflects the more direct mobilization of  $^{14}\text{C}$  to the grain under stress conditions.

#### Labelling at 4 WAA

When plants were labelled at 4 WAA the percentage of whole plant  $^{14}\text{C}$  in the stem on all sampling occasions was greater than that of plants labelled at 2 WAA but less than that of plants labelled at A and 6 WAA (Figure 4.19). This reflects the fact that percentage of whole plant  $^{14}\text{C}$  recovered in the grain at PM which was 79,7 and 80,3 % in stressed and non-stressed plants respectively, was less than that for plants labelled at 2 WAA but more than that for plants labelled at A and 6 WAA. The percentage of whole plant  $^{14}\text{C}$  in the stem at 4 WAA was 22,8 and 22,4 % in stressed and non-stressed plants, respectively. This declined to 14,0 and 17,9 % at 6 WAA and then declined further to 11,8 and 11,5 % at PM in stressed and non-stressed plants, respectively. The overall decline in the percentage of whole plant  $^{14}\text{C}$  in the stem from 4 WAA to PM reflects the mobilization of  $^{14}\text{C}$  to the grain with stressed plants showing a more marked

decline from 4 to 6 WAA and non-stressed plants showing a more marked decline from 6 WAA to PM.

#### Labelling at 6 WAA

When plants were labelled at 6 WAA the percentage of whole plant  $^{14}\text{C}$  in the stem 48 h after labelling was higher than that in stem of plants labelled at A when sampled at 4 and 6 WAA and at PM (Figure 4.19). However, at PM the percentage of whole plant  $^{14}\text{C}$  in the stem was less than that in the stem on all sampling occasions of plants labelled at A. The percentage of whole plant  $^{14}\text{C}$  in the stem on all sampling occasions was, however, greater than that in the stem of plants labelled at 2 WAA and 4 WAA. This reflects the fact that percentage of whole plant  $^{14}\text{C}$  recovered in the grain at PM in stressed and non-stressed plants of 67,6 and 67,0 % respectively, was less than that for plants labelled at 2 WAA and 4 WAA, but more than that for plants labelled at A. The percentage of whole plant  $^{14}\text{C}$  in the stem at 6 WAA was 37,5 and 35,1 % in stressed and non-stressed plants, respectively. This declined to 21,1 and 23,2 % in stressed and non-stressed plants at PM. The overall decline in the percentage of whole plant  $^{14}\text{C}$  in the stem from 6 WAA to PM reflects the mobilization of  $^{14}\text{C}$  to the grain. Only at PM, however, did the stressed plants maintain a lower percentage of whole plant  $^{14}\text{C}$  in the stem indicating a greater mobilization of  $^{14}\text{C}$  to the primary ear from 6 WAA to PM.

#### 4.3.6 Radioactivity analysis of whole shoot

##### 4.3.6.1 Specific radioactivity

It will be recalled (Section 4.2) that the whole shoot was defined as all the aboveground plant parts excluding the primary grain.

##### Labelling at A

The main effect for stress treatment was non-significant (Table 4.40 and Appendix 39.1). The SR of the shoot under stress conditions was marginally higher than that under non-stress conditions. Whole plant TR was higher in stressed plants than non-stressed plants 48 h after labelling at A (Section 4.3.7.2). At A the primary ear was not yet established as the major sink

Table 4.40 Effect of water stress (S) and lack of water stress (NS) on whole shoot specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over five growth periods during grain fill for a maize hybrid labelled at anthesis

Stress treatment	
S	NS
83,12	82,24
LSD (0,05)	NS
LSD (0,01)	NS

for photosynthate. The whole shoot, on the other hand, underwent a further increase in dry mass from A to 2 WAA (Table 4.41 and Appendix 48), more so in non-stressed plants than stressed plants. The non-stressed plants also maintained a higher shoot dry mass throughout the grain filling period. Thus initially a considerable proportion of the  $^{14}\text{C}$  assimilated at A was used irreversibly for structural growth of the whole shoot. However, as the primary ear became established as the major sink for photosynthate it would be expected that, as a result of their reduced photosynthetic rate, the stressed plants would be forced to utilize labile  $^{14}\text{C}$  organic compounds in the shoot to meet the photosynthate requirements of the grain. This would in turn reduce the TR of the shoot under stress conditions; this did indeed occur (Section 4.3.6.2). However, stressed plants maintained a higher SR of the shoot because of the reduced size of the whole shoot (Table 4.41 and Appendix 48) and because in contrast to the non-stressed plants less  $^{12}\text{C}$  was used for structural growth of the shoot after labelling.

Table 4.41 Whole shoot dry mass ( $\text{g shoot}^{-1}$ ), meaned over corresponding sampling occasions from each labelling occasion, from a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill

Stress treatment	Weeks after anthesis				
	0	2	4	6	8
S	138,1	145,9	138,9	140,3	133,6
NS	143,8	161,0	149,7	156,3	147,4

The main effect for WAA was significant (Table 4.42). There was a significant negative linear effect superimposed with a significant positive quadratic effect which indicates that the SR of the shoot declined slightly from A to 2 WAA, more markedly from 2 to 4 WAA and then declined gradually from 4 WAA to PM. The SR of the shoot at A was non-significantly higher than that at 2 WAA but the SR of the shoot at A and 2 WAA was significantly ( $p = 0,01$ ) higher than that at 4 and 6 WAA and at PM. The TR of the shoot at 2 WAA was non-significantly higher than that at A (Section 4.3.6.2). This can only be attributed to sampling error as it is highly unlikely that  $^{14}\text{C}$  was mobilized out of the primary grain back to the whole shoot. Nonetheless it would appear that the  $^{14}\text{C}$  assimilated at A remained fairly constant in the shoot until 2 WAA whereupon it declined markedly from 2 to 4 WAA. Thus the concomitant marked decline in the SR of the shoot from 2 to 4 WAA occurred as the primary ear was established as the major sink and final increases in shoot dry mass had been completed. The general decline in the SR of the shoot from A to

Table 4.42 Specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) of whole shoot meaned over water stress treatments from anthesis to eight weeks after anthesis (WAA) for a maize hybrid labelled at anthesis

		WAA				
		0	2	4	6	8
		113,66	103,32	70,22	64,03	62,17
LSD	(0,05)		12,96			
LSD	(0,01)		17,86			

PM not only indicates the mobilization of  $^{14}\text{C}$  to the grain and utilization for respiratory requirements, but it also reflects the assimilation of new non-radioactive C in the whole shoot.

#### Labelling at 2 WAA

The main effect for stress treatment was non-significant (Table 4.43 and Appendix 39.2). The SR of the shoot under stress conditions was marginally higher than that under non-stress conditions. It will be recalled that the main effect for stress treatment for labelling at 2 WAA indicated that the SR of the stem under stress conditions was lower than that under non-stress conditions (Section 4.3.5.1). It will also be recalled that stressed plants labelled at 2 WAA on average maintained a higher SR of the cob and husks than non-stressed plants as a result of the concentrating effects of stress (Section 4.3.4.1). Thus when all segments of the shoot are considered together i.e. including

Table 4.43 Effect of water stress (S) and lack of water stress (NS) on whole shoot specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over four growth periods during grain fill for a maize hybrid labelled at two weeks after anthesis

Stress treatment	
S	NS
22,64	21,66
LSD (0,05)	NS
LSD (0,01)	NS

the cob and husks, the SR of the shoot of stressed plants was higher than that of non-stressed plants. Also stressed plants had a lower shoot dry mass than non-stressed plants during grain fill which would tend to concentrate the  $^{14}\text{C}$  in the shoot (Table 4.41 and Appendix 48).

The main effect for WAA was significant (Table 4.44). There was a significant negative linear effect superimposed with a significant positive quadratic effect which indicates that the SR of the shoot declined markedly from 2 to 4 WAA and then declined less markedly from 4 WAA to PM. The SR of the shoot was significantly ( $p = 0,01$ ) higher at 2 WAA than at 4 and 6 WAA and at PM. The marked decline in the SR of the shoot in the first two weeks after labelling indicates that  $^{14}\text{C}$  which occurred as labile organic compounds in the shoot was rapidly utilized for respiratory and predominantly grain requirements. In the period

Table 4.44 Specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) of whole shoot meaned over water stress treatments from two weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at two weeks after anthesis

	WAA			
	2	4	6	8
	43,52	18,76	12,76	13,58
LSD (0,05)		7,70		
LSD (0,01)		10,69		

from 4 WAA to PM the decline in the SR of the shoot was less marked as there was little  $^{14}\text{C}$  available as labile compounds in the shoot for mobilization to the grain.

Labelling at 4 WAA

The main effect for stress treatment was significant (Table 4.45 and Appendix 39.3). The SR of the shoot under stress conditions was significantly less than that under non-stress conditions. When the plants were labelled at 4 WAA the stressed plants had already undergone four consecutive stress cycles. Thus the lower SR of the shoot under stress conditions reflects the lower amount of  $^{14}\text{C}$  assimilated by the whole plant at 4 WAA (Section 4.3.7.2) under stress conditions and it also reflects the more direct translocation of the assimilated  $^{14}\text{C}$  to the primary ear under stress conditions. Clearly with the mathematics of calculating the SR of the shoot there is a threshold level of TR that must

Table 4.45 Effect of water stress (S) and lack of water stress (NS) on whole shoot specific radioactivity (dpm x  $10^{-3}$  g $^{-1}$ ) meaned over three growth periods during grain fill for a maize hybrid labelled at four weeks after anthesis

Stress treatment	
S	NS
13,45	18,15
LSD (0,05)	3,00
LSD (0,01)	4,26

occur in the shoot, lower than which, even with the influence of the concentrating effects of stress, the SR of the shoot will be lower under stress conditions than under non-stress conditions.

The main effect for WAA was significant (Table 4.46). There was a significant negative linear effect superimposed with a significant positive quadratic effect which indicates that the SR of the shoot declined markedly from 4 to 6 WAA and then less markedly from 6 WAA to PM. The SR of the shoot at 4 WAA was significantly ( $p = 0,01$ ) higher than that at 6 WAA and at PM. The marked decline in the SR of the shoot from 4 to 6 WAA reflects the rapid utilization of  $^{14}\text{C}$ , which occurred as labile organic compounds in the shoot, for respiratory and predominantly grain requirements. In the period from 6 WAA to PM, the SR of the shoot declined less rapidly as there was less  $^{14}\text{C}$  available as labile compounds in the shoot for mobilization to the grain.

Table 4.46 Specific radioactivity (dpm  $\times 10^{-3} \text{ g}^{-1}$ ) of whole shoot meaned over water stress treatments from four weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at four weeks after anthesis

	WAA		
	4	6	8
	23,90	12,08	11,41
LSD (0,05)		3,67	
LSD (0,01)		5,22	

### Labelling at 6 WAA

The main effect for stress treatment was non-significant (Table 4.47 and Appendix 39.4). The SR of the shoot under stress conditions was non-significantly lower than that under non-stress conditions. This reflects the lower whole plant TR recorded in the stressed plants at 48 h after labelling at 6 WAA (Section 4.3.7.2) and it also reflects the more direct translocation of the assimilated  $^{14}\text{C}$  to the primary ear under stress conditions. Although whole plant photosynthetic activity was much less at 6 WAA than earlier on in grain fill (Section 4.3.7.2), the primary ear still remained as the major sink for photosynthate.

Table 4.47 Effect of water stress (S) and lack of water stress (NS) on whole shoot specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over two growth periods during grain fill for a maize hybrid labelled at six weeks after anthesis

Stress treatment	
S	NS
6,28	7,55
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.48). The SR of the shoot declined from 6 WAA to PM, with SR at 6 WAA significantly ( $p = 0,01$ ) higher than that at PM. In fact the SR of the shoot at PM was only 47,6 % of that at 6 WAA. Since the

dry mass of the shoot declined from 6 WAA to PM (Table 4.41 and Appendix 48) the decline in SR from 6 WAA to PM reflects the mobilization of  $^{14}\text{C}$  labile organic compounds in the shoot to grain as well as losses due to respiration.

Table 4.48 Specific radioactivity (dpm  $\times 10^{-3} \text{ g}^{-1}$ ) of whole shoot meaned over water stress treatments from six weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at six weeks after anthesis

WAA	
6	8
9,37	4,46
LSD (0,05) 1,94	
LSD (0,01) 4,46	

First order interactions for labelling at A, 2 WAA, 4 WAA and 6 WAA

Each first order interaction of stress treatment with WAA for labelling at A, 2 WAA, 4 WAA and 6 WAA was non-significant (Figure 4.20). There were no significant components of each interaction either. However, the apparent trends of these first order interactions are discussed.

The stressed and non-stressed plants labelled at A maintained a higher SR of the shoot on all sampling occasions than did plants labelled at 2 WAA, 4 WAA and 6 WAA (Figure 4.20). The reason for

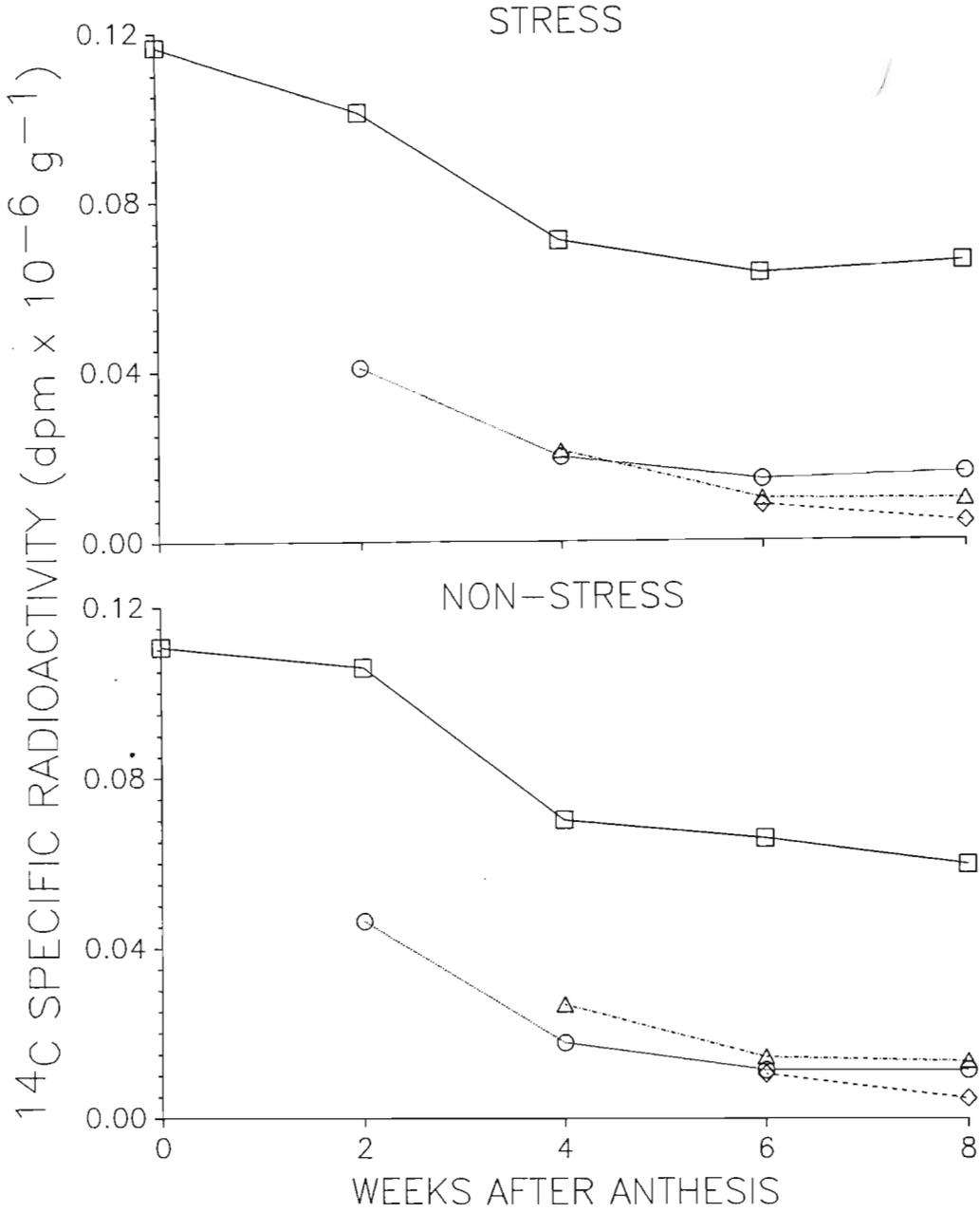


Figure 4.20 Effect of water stress during grain fill on specific radioactivity of the whole shoot sampled at fortnightly intervals from a maize hybrid labelled at anthesis ( $\square-\square$ ), 2 ( $\circ-\circ$ ), 4 ( $\triangle-\triangle$ ) and 6 ( $\diamond-\diamond$ ) weeks after anthesis

this was twofold, namely: (i) plants labelled at A recorded the highest TR of the whole plant 48 h after labelling compared to plants labelled on the other three occasions; and (ii) the percentage of whole plant  $^{14}\text{C}$  recovered in the shoot at PM was the highest for all labelling occasions, namely 69,0 and 73,2 % in stressed and non-stressed plants, respectively. This reflects the greater irreversible utilization of  $^{14}\text{C}$  assimilated at A for growth of shoot cells. The SR of the shoot of the stressed and non-stressed plants at A was 116 640 and 110 675 dpm  $\text{g}^{-1}$ , respectively. This declined slightly to 100 923 and 105 719 dpm  $\text{g}^{-1}$  in stressed and non-stressed plants respectively at 2 WAA, and then declined sharply to 70 446 and 69 997 dpm  $\text{g}^{-1}$  in stressed and non-stressed plants respectively, at 4 WAA. From 4 to 6 WAA the SR of the shoot declined to 62 553 dpm  $\text{g}^{-1}$  in stressed plants and then increased to 65 035 dpm  $\text{g}^{-1}$  at PM. In non-stressed plants the SR of the shoot declined steadily from 4 WAA to PM and at PM the SR of the shoot was 59 301 dpm  $\text{g}^{-1}$ . It is clear that the SR of the shoot declined as  $^{14}\text{C}$  was mobilized out of the shoot to the primary grain and lost through respiration. The most marked decline in the SR of the shoot of stressed and non-stressed plants occurred from 2 to 4 WAA once the primary grain was established as the major sink for photosynthate. However, the stressed plants did show a greater decline in the SR of the shoot from A to 2 WAA than did the non-stressed plants. It would be expected that as a result of their reduced photosynthetic rate the stressed plants would be forced to utilize labile  $^{14}\text{C}$  organic compounds in the shoot to meet the photosynthate requirements of the grain. This would in turn reduce the TR of the shoot under stress conditions; this did

indeed occur (Section 4.3.6.2). However, the shoot of non-stressed plants increased in dry mass by 17,2 g shoot<sup>-1</sup> from A to 2 WAA whereas the shoot of stressed plants increased by only 7,8 g shoot<sup>-1</sup> during the same period (Table 4.41 and Appendix 48). The stressed plants also maintained a lower shoot mass throughout grain fill than did the non-stressed plants. It is clear that stressed plants incorporated less <sup>12</sup>C photosynthate into the dry mass of the shoot during grain fill and therefore <sup>14</sup>C in the shoot was diluted to a lesser extent than was the case with non-stressed plants.

When plants were labelled at 2 WAA the SR of the shoot on all sampling occasions was less than that of plants labelled at A (Figure 4.20). The SR of the shoot of stressed plants labelled at 2 WAA was also, on all sampling occasions, higher than that of plants labelled at 4 WAA and 6 WAA. However, in non-stressed plants labelled at 2 WAA, the SR of the shoot on all sampling occasions was marginally less than that of plants labelled at 4 WAA and marginally greater than that of plants labelled at 6 WAA. The SR of the shoot of stressed and non-stressed plants at 2 WAA was 40 736 and 46 298 dpm g<sup>-1</sup> respectively, which declined sharply to 19 741 and 17 784 dpm g<sup>-1</sup> respectively, at 4 WAA. From 4 WAA to PM the SR of the shoot fluctuated as it declined less markedly than from 2 to 4 WAA. At PM the SR of the shoot of stressed and non-stressed plants was 15 826 and 11 328 dpm g<sup>-1</sup>, respectively. Thus initially at 2 WAA the SR of the shoot of non-stressed plants was higher than that of stressed plants, but from 4 WAA to PM the SR of the shoot of stressed plants was higher than that of non-stressed plants. These

patterns in the SR of the shoot of stressed and non-stressed plants reflect the changes in the TR of the shoot (Section 4.3.6.2). It is possible that the lower SR of the shoot of stressed plants at 2 WAA is an indication that stressed plants mobilized a greater proportion of the  $^{14}\text{C}$  assimilated at 2 WAA directly to the primary grain soon after labelling. This is supported by the fact that percentage of whole plant  $^{14}\text{C}$  in the grain of stressed plants 48 h after labelling was 59,0 % as opposed to 51,8 % in non-stressed plants 48 h after labelling. However, the proportion of whole plant  $^{14}\text{C}$  in the grain of non-stressed plants at 4 WAA increased sharply to 81,2 % while that in stressed plants increased to 83,6 %. Thus it would appear that the non-stressed plants mobilized a greater proportion of  $^{14}\text{C}$  to the grain later than the stressed plants did. This explains the lower SR (and TR) of the shoot of non-stressed plants from 4 WAA to PM. The non-stressed plants also maintained a higher shoot dry mass than the stressed plants (Section 4.41 and Appendix 48) so more non-radioactive photosynthate was incorporated into the dry mass of the shoot under non-stress conditions which diluted the  $^{14}\text{C}$  in the shoot.

When plants were labelled at 4 WAA, the SR of the shoot of stressed plants on all sampling occasions was less than that of plants labelled at A and 2 WAA but greater than that of plants labelled at 6 WAA (Figure 4.20). The SR of the shoot of non-stressed plants on all sampling occasions was less than that of plants labelled at A but greater than that of plants labelled at 2 WAA and 6 WAA. The SR of the shoot of stressed and non-stressed plants at 4 WAA was 21 116 and 26 690 dpm  $\text{g}^{-1}$

respectively, which declined sharply at 6 WAA to 9 791 and 14 376 dpm g<sup>-1</sup> in stressed and non-stressed plants, respectively. From 6 WAA to PM the SR of the shoot declined slightly and at PM it was 9 440 and 13 378 dpm g<sup>-1</sup> in stressed and non-stressed plants, respectively. The overall decline in the SR of the shoot reflects the mobilization of <sup>14</sup>C to the grain with the bulk of the <sup>14</sup>C being mobilized to the grain within the first two weeks after labelling at 4 WAA. The lower SR of the shoot of the stressed plants on all sampling occasions reflects the lower TR of the whole plant recorded in stressed plants on all sampling occasions compared to non-stressed plants. It also reflects the more direct and rapid translocation of <sup>14</sup>C assimilated at 4 WAA to the grain under stress conditions.

When plants were labelled at 6 WAA the SR of the shoot of stressed and non-stressed plants on all sampling occasions was less than that of plants labelled at 2 WAA and 4 WAA and substantially less than that of plants labelled at A (Figure 4.20). The SR of the shoot of stressed and non-stressed plants at 6 WAA was 8 299 and 10 434 dpm g<sup>-1</sup> respectively, which declined to 4 255 and 4 672 dpm g<sup>-1</sup> in stressed and non-stressed plants, respectively, at PM. The overall decline in the SR of the shoot reflects the mobilization of <sup>14</sup>C to the grain. The lower SR of the shoot of stressed plants on all sampling occasions reflects the lower TR of the whole plant recorded in the stressed plants on all sampling occasions in comparison to non-stressed plants. It also reflects the more direct translocation of assimilated <sup>14</sup>C to the grain under stress conditions.

#### 4.3.6.2 Total Radioactivity

##### Labelling at A

The main effect for stress treatment was non-significant (Table 4.49 and Appendix 40.1). The TR of the shoot under stress conditions was non-significantly lower than that under non-stress conditions. Data from the non-significant interaction of stress treatment with WAA indicates that 48 h after labelling at A, the stressed plants had higher TR of the shoot than the non-stressed plants. However, the data from this interaction also indicates that from 2 WAA to PM non-stressed plants maintained a higher TR of the shoot than did stressed plants. Shoot dry mass increased from A to 2 WAA (Table 4.41 and Appendix 48) more so in non-stressed plants than stressed plants. The non-stressed plants also maintained a higher shoot dry mass than the stressed plants throughout grain fill. It would appear that the stressed plants incorporated less  $^{14}\text{C}$  into structural components of the shoot. Once the primary ear became established as the major sink for photosynthate stressed plants would be forced to mobilize more  $^{14}\text{C}$  out of the shoot to the grain as a result of their reduced assimilation of new C. This would in turn reduce the TR of the shoot under stress conditions. This did indeed occur as indicated by the data of the non-significant interaction of stress treatment with WAA mentioned above. It would be expected that stressed plants would respire less than non-stressed plants. However, since the  $^{14}\text{C}$  assimilated at A would be in the plants for the entire grain filling period, eventually the stressed plants would respire a great deal of the  $^{14}\text{C}$  because they would have to

utilize previously assimilated C for respiration requirements as the assimilation rate of new C would be reduced as a result of stress (Section 4.3.7.2).

Table 4.49 Effect of water stress (S) and lack of water stress (NS) on whole shoot total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) meaned over five growth periods during grain fill for a maize hybrid labelled at anthesis

Stress treatment	
S	NS
11 631	13 038
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.50). There was a large significant negative linear effect superimposed with a significant positive cubic effect and a significant deviations from linear, quadratic and cubic effect. These effects indicate that the TR of the shoot initially increased from A to 2 WAA then declined markedly from 2 to 4 WAA and then declined gradually from 4 WAA to PM. The TR of the shoot at 2 WAA was non-significantly higher than that at A. This can only be attributed to sampling error, as it is highly unlikely that <sup>14</sup>C was mobilized out of the primary grain back to the whole shoot during the first two weeks after labelling at A. Nonetheless it would appear that the <sup>14</sup>C assimilated at A remained fairly constant in the shoot until 2 WAA whereupon it declined markedly from 2 to 4 WAA. This marked decline from 2 to 4 WAA may be coincident with the

establishment of the primary ear as the major sink for photosynthate and would therefore reflect mobilization of  $^{14}\text{C}$  out of the shoot and into the grain. The less marked decline in the TR of the shoot from 4 WAA to PM would seem to indicate that much of the  $^{14}\text{C}$  available as labile organic compounds in the shoot had already been mobilized to the grain from 2 to 4 WAA.

Table 4.50 Total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) of whole shoot meaned over water stress treatments from anthesis to eight weeks after anthesis (WAA) for a maize hybrid labelled at anthesis

	WAA				
	0	2	4	6	8
	15 999	16 083	10 399	9 942	9 248
LSD (0,05)		1 837			
LSD (0,01)		2 531			

#### Labelling at 2 WAA

The main effect for stress treatment was non-significant (Table 4.51 and Appendix 40.2). The TR of the shoot under stress conditions was marginally less than that under non-stress conditions. With the primary ear established as the major sink for photosynthate by 2 WAA, the stressed plants would translocate much of the assimilated  $^{14}\text{C}$  directly to the primary ear. However, it will be recalled from Section 4.3.4.2 that the stressed plants labelled at 2 WAA retained, on average over grain fill, higher TR of the cob and husks than the non-stressed plants. Thus not

all the  $^{14}\text{C}$  assimilated at 2 WAA and translocated to the ear was deposited in the grain of the stressed plants.

Table 4.51 Effect of water stress (S) and lack of water stress (NS) on whole shoot total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over four growth periods during grain fill for a maize hybrid labelled at two weeks after anthesis

Stress treatment	
S	NS
3 234	3 255
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.52). There was a significant negative linear effect superimposed with a significant positive quadratic effect which indicates that the TR of the shoot declined markedly from 2 to 4 WAA and then declined less markedly from 4 WAA to PM. The TR of the shoot was significantly ( $p = 0,01$ ) higher at 2 WAA than at 4 and 6 WAA and at PM. The marked decline in the first two weeks after labelling indicates that  $^{14}\text{C}$  which occurred as labile organic compounds in the shoot was rapidly utilized for respiratory and predominantly grain requirements. In the period from 4 WAA to PM the decline in the TR of the shoot was less marked as there was little  $^{14}\text{C}$  available as labile compounds in the shoot for mobilization to the grain.

Table 4.52 Total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of whole shoot meaned over water stress treatments from two weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at two weeks after anthesis

WAA			
2	4	6	8
6 519	2 716	1 891	1 852
LSD (0,05)	982		
LSD (0,01)	1 363		

#### Labelling at 4 WAA

The main effect for stress treatment was significant (Table 4.53 and Appendix 40.3). The TR of the shoot under stress conditions was significantly ( $p = 0,01$ ) less than that under non-stress conditions. When the plants were labelled at 4 WAA the stressed

Table 4.53 Effect of water stress (S) and lack of water stress (NS) on whole shoot total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) meaned over three growth periods during grain fill for a maize hybrid labelled at four weeks after anthesis

Stress treatment	
S	NS
1 865	2 599
LSD (0,05)	425
LSD (0,01)	604

plants had already undergone four consecutive stress cycles. Thus the lower TR of the shoot under stress conditions reflects the lower total  $^{14}\text{C}$  assimilated by the stressed whole plant at 4 WAA (Section 4.3.7.2) and it also reflects the more direct translocation of much of the assimilated  $^{14}\text{C}$  to the grain under stress conditions.

The main effect for WAA was significant (Table 4.54). There was a significant negative linear effect superimposed with a significant positive quadratic effect which indicates that the TR of the shoot declined markedly from 4 to 6 WAA and then less markedly from 6 WAA to PM. The TR of the shoot at 4 WAA was significantly ( $p = 0,01$ ) higher than at 6 WAA and at PM. The marked decline in the TR of the shoot from 4 to 6 WAA reflects the rapid utilization of  $^{14}\text{C}$ , which occurred as labile organic compounds in the shoot, for respiratory and predominantly grain requirements. In the period from 6 WAA to PM, TR of the shoot

Table 4.54 Total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) of whole shoot meaned over water stress treatments from four weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at four weeks after anthesis

	WAA		
	4	6	8
	3 394	1 788	1 514
LSD (0,05)		520	
LSD (0,01)		740	

declined less rapidly as obviously there was less  $^{14}\text{C}$  available as labile organic compounds in the shoot for mobilization to the grain.

#### Labelling at 6 WAA

The main effect for stress treatment was non-significant (Table 4.55 and Appendix 40.4). The TR of the shoot under stress conditions was non-significantly lower than that under non-stress conditions. This reflects the lower whole plant TR recorded for the stressed plants at 48 h after labelling at 6 WAA (Section 4.3.7.2), and it also reflects the more direct translocation of much of the  $^{14}\text{C}$  to the primary ear under stress conditions. Although whole plant photosynthetic activity was much less at 6 WAA than earlier on in grain fill (Section 4.3.7.2), the primary ear still remained as the major sink for photosynthate.

Table 4.55 Effect of water stress (S) and lack of water stress (NS) on whole shoot total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over two growth periods during grain fill for a maize hybrid labelled at six weeks after anthesis

Stress treatment	
S	NS
856	1 143
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.56). The TR of the shoot declined from 6 WAA to PM with the TR at 6 WAA significantly ( $p = 0,01$ ) higher than at PM. In fact the TR of the shoot at PM was only 45,7 % of that at 6 WAA. The decline in the TR of the shoot from 6 WAA to PM reflects the mobilization of  $^{14}\text{C}$  labile organic compounds in the shoot to the grain as well as losses due to respiration.

Table 4.56 Total radioactivity (dpm x  $10^{-3}$  g $^{-1}$ ) of whole shoot meaned over water stress treatments from six weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at six weeks after anthesis

WAA	
6	8
1 372	627
LSD (0,05) 337	
LSD (0,01) 558	

First order interactions for labelling at A, 2 WAA, 4 WAA and 6 WAA

Each first order interaction of stress treatment with WAA for labelling at A, 2 WAA, 4 WAA and 6 WAA was non-significant (Figure 4.21). There were no significant components of each interaction either. However, the apparent trends of these first order interactions are discussed.

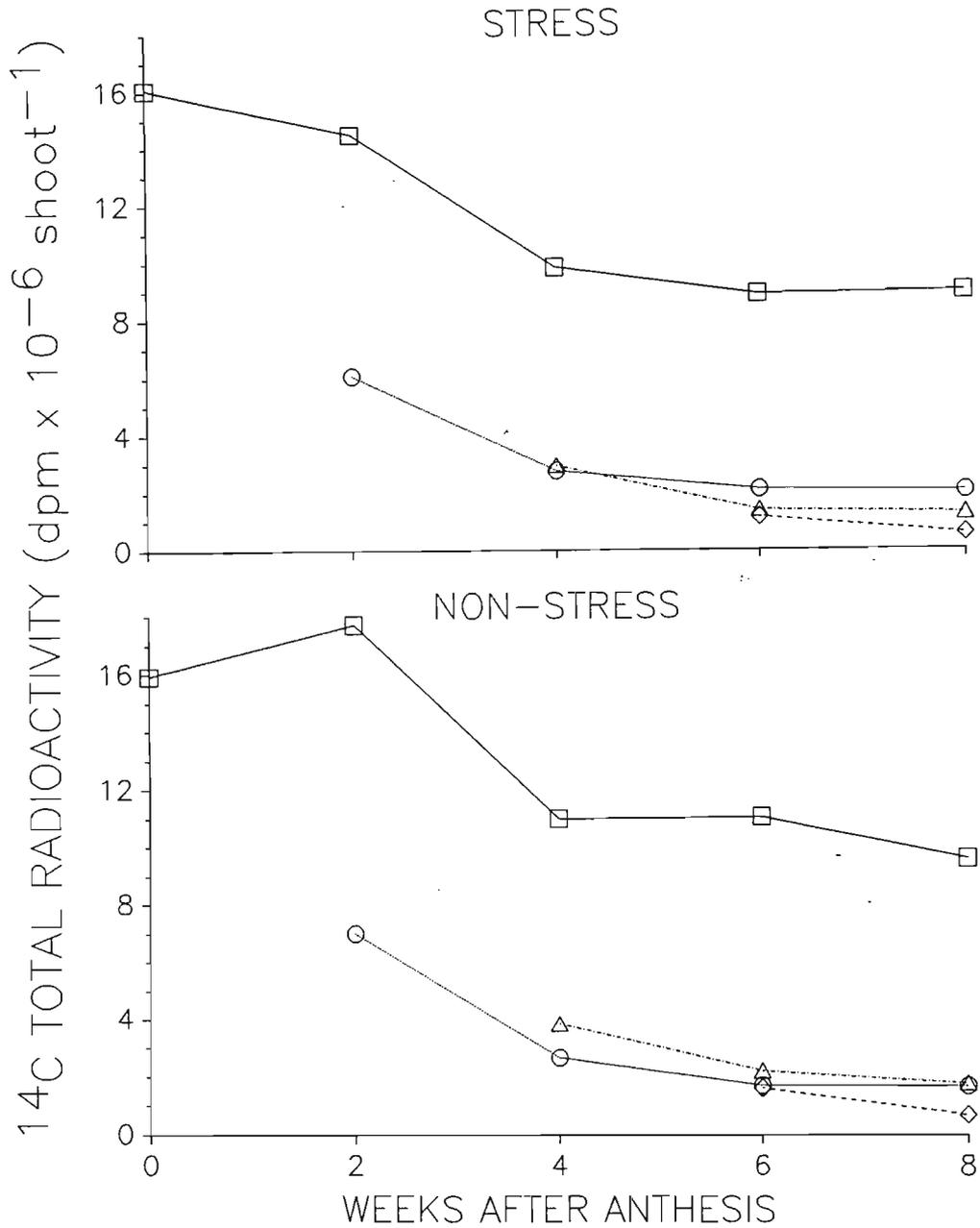


Figure 4.21 Effect of water stress during grain fill on total radioactivity of the whole shoot sampled at fortnightly intervals from a maize hybrid labelled at anthesis (□—□), 2 (○—○), 4 (△—△) and 6 (◇—◇) weeks after anthesis

The patterns in the changes of the TR of the shoot on all sampling occasions for each of the labelling occasions are very similar to that of the SR of the shoot (Figure 4.20).

The stressed and non-stressed plants labelled at A maintained a higher TR of the shoot on all sampling occasions than did plants labelled at 2 WAA, 4 WAA and 6 WAA (Figure 4.21). The reason for this was twofold, namely: (i) plants labelled at A recorded the highest TR of the whole plant 48 h after labelling compared to plants labelled on the other three occasions; and (ii) the percentage of whole plant  $^{14}\text{C}$  recovered in the shoot at PM was the highest for all labelling occasions, namely 69,0 and 73,2 % in stressed and non-stressed plants, respectively. This reflects the greater irreversible utilization of  $^{14}\text{C}$  assimilated at A for growth of shoot cells. The TR of the shoot of stressed and non-stressed plants at A was 16 070 323 and 15 927 955 dpm shoot<sup>-1</sup>, respectively. This declined slightly to 14 470 554 dpm shoot<sup>-1</sup> in stressed plants and increased to 17 695 995 dpm shoot<sup>-1</sup> in non-stressed plants at 2 WAA. The TR of the shoot then declined sharply to 9 821 895 and 10 975 496 dpm shoot<sup>-1</sup> in stressed and non-stressed plants, respectively, at 4 WAA and then declined to 8 859 546 dpm shoot<sup>-1</sup> in stressed plants and increased to 11 024 902 dpm shoot<sup>-1</sup> in non-stressed plants at 6 WAA. From 6 WAA to PM the TR increased to 8 930 935 dpm shoot<sup>-1</sup> in the stressed plants and decreased to 9 564 637 dpm shoot<sup>-1</sup> in the non-stressed plants. The overall decline in the TR of the shoot reflects the mobilization of  $^{14}\text{C}$  out of the shoot to the grain. The most marked decline in the TR of the shoot from 2 to 4 WAA occurred once the primary grain was established as the major sink

for photosynthate. However, the stressed plants did show a decline in the TR of the shoot from A to 2 WAA. The increase in the TR of the shoot of non-stressed plants from A to 2 WAA as well as the increases in the TR of the shoot which occurred later on in stressed and non-stressed plants was due to sampling error as it is unlikely that  $^{14}\text{C}$  was mobilized out of the primary grain back into the shoot. Initially at A the stressed plants had a higher TR of the shoot than the non-stressed plants which reflects the higher TR of the whole plant recorded for the stressed plants at A. However, as the primary ear was established as the major sink for photosynthate the TR of the shoot of stressed plants declined to lower than that of the non-stressed plants from 2 WAA to PM as  $^{14}\text{C}$  was mobilized out of the shoot to the grain to a greater extent than in the non-stressed plants. This indicates that the stressed plants were forced to mobilize more  $^{14}\text{C}$  assimilated at A to the grain as a result of their reduced photosynthetic capacity.

When plants were labelled at 2 WAA the TR of the shoot on all sampling occasions was less than that of plants labelled at A. The TR of the shoot of stressed plants labelled at 2 WAA was also, on all sampling occasions, higher than that of plants labelled at 4 WAA and 6 WAA (Figure 4.21). However, in non-stressed plants labelled at 2 WAA the TR of the shoot on all sampling occasions was marginally less than that of plants labelled at 4 WAA and marginally greater than that of plants labelled at 6 WAA. The TR of the shoot of stressed and non-stressed plants at 2 WAA was 6 048 576 and 6 989 005 dpm shoot<sup>-1</sup> respectively, which declined sharply to 2 762 909 and

2 668 243 dpm shoot<sup>-1</sup> in stressed and non-stressed plants, respectively, at 4 WAA. From 4 to 6 WAA the TR of the shoot declined to 2 096 843 and 1 685 574 dpm shoot<sup>-1</sup> and then declined slightly to 2 026 555 and 1 677 019 dpm shoot<sup>-1</sup> at PM in stressed and non-stressed plants, respectively. Thus initially at 2 WAA the TR of the shoot of non-stressed plants was higher than that of the stressed plants, but from 4 WAA to PM the TR of the shoot of stressed plants was higher than that of non-stressed plants. It is possible that the lower TR of the shoot of stressed plants at 2 WAA was an indication that stressed plants mobilized a greater proportion of the <sup>14</sup>C assimilated at 2 WAA directly to the primary grain soon after labelling. This is supported by the fact that the percentage of whole plant <sup>14</sup>C in the grain of stressed plants 48 h after labelling was 59,0 % as opposed to 51,8 % in non-stressed plants 48 h after labelling. However, the proportion of whole plant <sup>14</sup>C at 4 WAA in the grain of non-stressed plants increased sharply to 81,2 % while that in stressed plants increased to 83,6 %. Thus it would appear that non-stressed plants mobilized a greater proportion of <sup>14</sup>C to the grain later than the stressed plants did. This explains the lower TR of the shoot of the non-stressed plants from 4 WAA to PM. It also explains why the ratio of grain TR to shoot TR continued to increase markedly from 4 WAA to PM in non-stressed plants while the ratio increased much less markedly during the same period in stressed plants (Section 4.3.6.4).

When plants were labelled at 4 WAA, the TR of the shoot of stressed plants on all sampling occasions was less than that of plants labelled at A and 2 WAA but greater than that of plants

labelled at 6 WAA (Figure 4.21). The TR of the shoot of non-stressed plants on all sampling occasions was less than that of plants labelled at A, but greater than that of plants labelled at 2 WAA and 6 WAA. The TR of the shoot at 4 WAA was 2 974 017 and 3 840 524 dpm shoot<sup>-1</sup>, which declined sharply at 6 WAA to 1 386 062 and 2 190 933 dpm shoot<sup>-1</sup> in stressed and non-stressed plants, respectively. From 6 WAA to PM the TR of the shoot declined further to 1 261 961 and 1 766 507 dpm shoot<sup>-1</sup> in stressed and non-stressed plants, respectively. The overall decline in the TR of the shoot reflects the mobilization of <sup>14</sup>C to the grain with the bulk of the <sup>14</sup>C being mobilized to the grain within the first two weeks after labelling at 4 WAA. The lower TR of the shoot of stressed plants on all sampling occasions reflects the lower TR of the whole plant recorded in stressed plants on all sampling occasions compared to non-stressed plants. It also reflects the more direct and rapid translocation of a greater proportion of the <sup>14</sup>C assimilated at 4 WAA to the primary grain soon after labelling under stress conditions.

When plants were labelled at 6 WAA the TR of the shoot was less than that of plants labelled at 2 WAA and 4 WAA and substantially less than that of plants labelled at A (Figure 4.21). The TR of the shoot of stressed and non-stressed plants at 6 WAA was 1 140 830 and 1 602 835 dpm shoot<sup>-1</sup> respectively, which declined to 572 167 and 682 810 dpm shoot<sup>-1</sup> in stressed and non-stressed plants respectively at PM. The overall decline in the TR of the shoot reflects the mobilization of <sup>14</sup>C to the grain. The lower TR of the shoot of the stressed plants on all sampling occasions reflects the lower TR of the whole plant recorded in the stressed

plants on all sampling occasions in comparison to non-stressed plants. It also reflects the more direct and rapid translocation of a greater proportion of the  $^{14}\text{C}$  assimilated at 6 WAA to the primary grain soon after labelling under stress conditions.

It is of interest to determine what proportion of the  $^{14}\text{C}$  that was lost from the shoot from labelling to PM was translocated to the grain.

When plants were labelled at A, the TR of the shoot of stressed plants declined by 7 139 388 dpm shoot<sup>-1</sup> from A to PM while the TR of the grain increased by 2 622 957 dpm segment<sup>-1</sup> during the same period. This means that 36,7 % of the  $^{14}\text{C}$  lost from the shoot from A to PM was translocated to the grain of stressed plants. The TR of the shoot of non-stressed plants declined by 6 363 318 dpm shoot<sup>-1</sup> from A to PM while the TR of the grain increased by 2 668 733 dpm segment<sup>-1</sup> during the same period. This means that 41,9 % of the  $^{14}\text{C}$  lost from the shoot from A to PM was translocated to the grain of non-stressed plants.

When plants were labelled at 2 WAA, the TR of the shoot of stressed plants declined by 4 022 021 dpm shoot<sup>-1</sup> from 2 WAA to PM while the TR of the grain increased by 2 317 717 dpm segment<sup>-1</sup>. This means that 57,6 % of the  $^{14}\text{C}$  lost from the shoot from 2 WAA to PM was translocated to the grain of stressed plants. The TR of the shoot of non-stressed plants declined by 5 311 986 dpm shoot<sup>-1</sup> while the TR of the grain increased by 4 611 838 dpm segment<sup>-1</sup> during the same period. This means that

86,8 % of the  $^{14}\text{C}$  lost from the shoot from 2 WAA to PM was translocated to the grain of non-stressed plants.

When plants were labelled at 4 WAA, the TR of the shoot of stressed plants declined by 1 685 056 dpm shoot<sup>-1</sup> from 4 WAA to PM while the TR of the grain increased by 950 236 dpm segment<sup>-1</sup> during the same period. This means that 56,4 % of the  $^{14}\text{C}$  lost from the shoot from 4 WAA to PM was translocated to the grain of stressed plants. The TR of the shoot of the non-stressed plants declined by 2 074 017 dpm shoot<sup>-1</sup> from 4 WAA to PM while the TR of the grain increased by 1 417 213 dpm segment<sup>-1</sup>. (Here the mean TR of the grain from replications two and three has been used because of the very high value obtained for the grain of replication one). This means that 68,3 % of the  $^{14}\text{C}$  lost from the shoot from 4 WAA to PM was translocated to the grain of the non-stressed plants.

When plants were labelled at 6 WAA the TR of the shoot of stressed plants declined by 568 663 dpm shoot<sup>-1</sup> from 6 WAA to PM while the TR of the grain increased by 268 879 dpm segment<sup>-1</sup> during the same period. This means that 47,3 % of the  $^{14}\text{C}$  lost from the shoot from 6 WAA to PM was translocated to the grain of stressed plants. The TR of the shoot of non-stressed plants declined by 920 025 dpm shoot<sup>-1</sup> from 6 WAA to PM, while the TR of the grain increased by 237 663 dpm segment<sup>-1</sup> during the same period. This means that 25,8 % of the  $^{14}\text{C}$  lost from the shoot from 6 WAA to PM was translocated to the grain of the non-stressed plants.

#### 4.3.6.3 Whole shoot total radioactivity as a % of whole plant total radioactivity

##### Labelling at A

Stressed and non-stressed plants labelled at A maintained a higher percentage of whole plant  $^{14}\text{C}$  in the shoot on all sampling occasions than did plants labelled at 2 WAA, 4 WAA and 6 WAA (Figure 4.22). This reflects the low percentage of whole plant  $^{14}\text{C}$  recovered in the grain at PM which was the lowest for all labelling occasions namely 31,0 and 26,9 % in the stressed and non-stressed plants, respectively. The percentage of whole plant  $^{14}\text{C}$  in the shoot at A was 92,5 and 95,0 % in the stressed and non-stressed plants, respectively. This declined to 90,1 and 93,4 % at 2 WAA; 77,0 and 79,9 % at 4 WAA; 69,1 and 73,3 % at 6 WAA; and 69,0 and 73,1 % at PM in the stressed and non-stressed plants, respectively. The general decline in the percentage of whole plant  $^{14}\text{C}$  in the shoot from A to PM reflects the mobilization of  $^{14}\text{C}$  from the shoot to the grain. The most marked decline in percentage of whole plant  $^{14}\text{C}$  in the shoot occurred from 2 to 4 WAA as the primary grain became established as a major sink for photosynthate. It is clear that the stressed plants maintained a lower proportion of whole plant  $^{14}\text{C}$  in the shoot throughout grain fill which is indicative of the greater mobilization of the  $^{14}\text{C}$  assimilated at A to the grain under stress conditions. The high percentage of whole plant  $^{14}\text{C}$  retained in the shoot of both stressed and non-stressed plants once again reflects the utilization of  $^{14}\text{C}$  assimilated at A irreversibly for structural growth of the shoot.

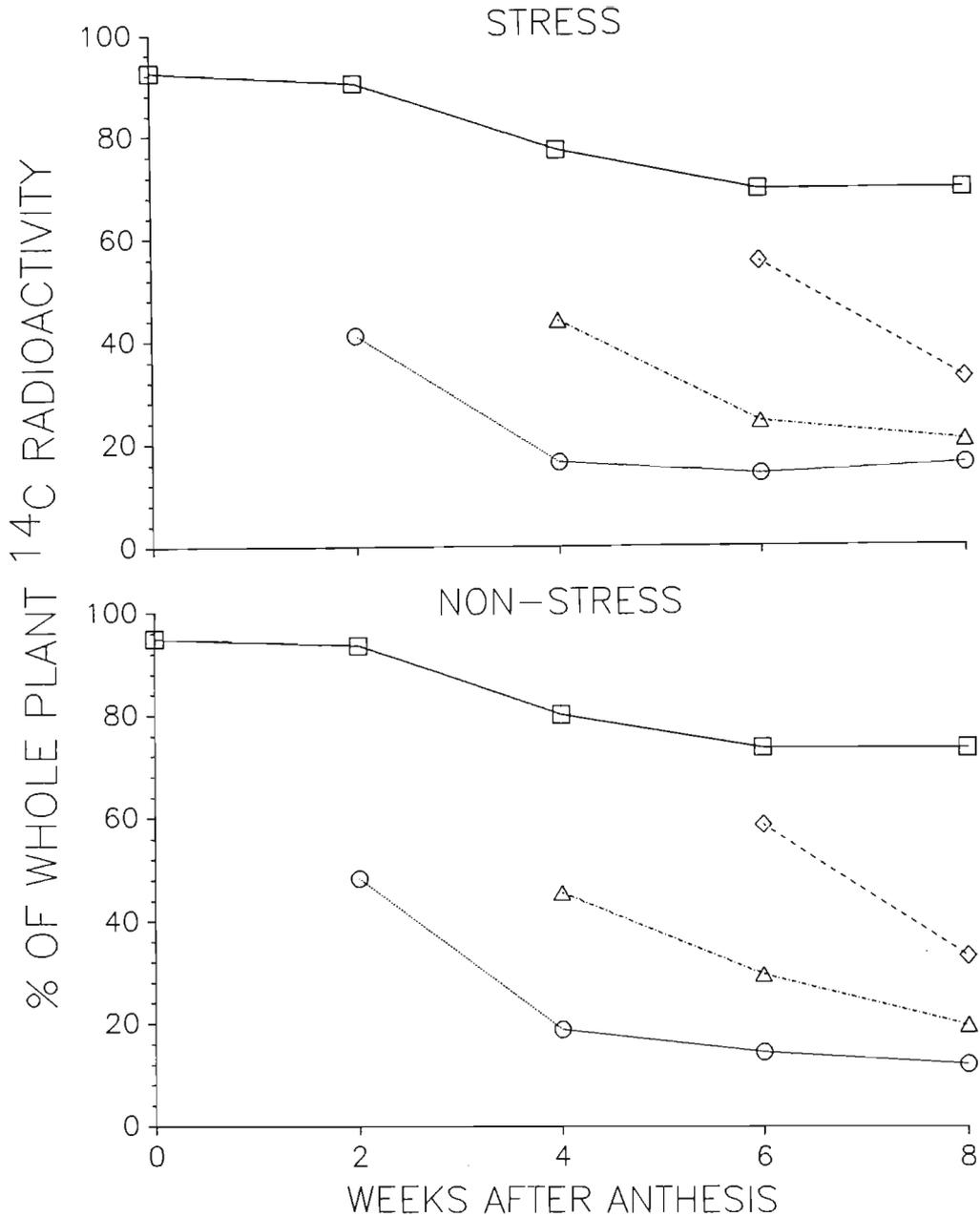


Figure 4.22 Effect of water stress during grain fill on total radioactivity of the whole shoot expressed as a percentage of whole plant <sup>14</sup>C total radioactivity from a maize hybrid labelled at anthesis (□—□), 2 (○—○), 4 (△—△) and 6 (◇—◇) weeks after anthesis and sampled at fortnightly intervals

## Labelling at 2 WAA

Stressed and non-stressed plants labelled at 2 WAA maintained the lowest percentage of whole plant  $^{14}\text{C}$  in the shoot on all sampling occasions than plants labelled on any of the other three occasions (Figure 4.22). This reflects the high percentage of whole plant  $^{14}\text{C}$  recovered in the grain at PM which was the highest for all the labelling occasions, namely 84,2 and 87,9 % in stressed and non-stressed plants, respectively. The percentage of whole plant  $^{14}\text{C}$  in the shoot at A was 41,0 and 48,2 % in stressed and non-stressed plants respectively, which then declined sharply to 16,4 and 18,8 % in stressed and non-stressed plants at 4 WAA. Thereafter the percentage of whole plant  $^{14}\text{C}$  in the shoot declined further, but less markedly, to 14,0 and 14,4 % at 6 WAA and then increased to 15,8 % and decreased to 12,1 % at PM in stressed and non-stressed plants, respectively. The overall decline in the percentage of whole plant  $^{14}\text{C}$  in the shoot from 2 WAA to PM reflects the mobilization of  $^{14}\text{C}$  to the grain with the bulk of the  $^{14}\text{C}$  being mobilized to the grain within 48 h after labelling with a further marked mobilization occurring up to 4 WAA. The lower percentage of  $^{14}\text{C}$  in the shoot of stressed plants at 2 WAA reflects the more direct and rapid translocation of  $^{14}\text{C}$  assimilated at 2 WAA to the grain soon after labelling. However, the percentage of whole plant  $^{14}\text{C}$  in the shoot of non-stressed plants declined more rapidly than stressed plants from 2 WAA to PM indicating that non-stressed plants translocated  $^{14}\text{C}$  out of the shoot at a later stage than stressed plants.

### Labelling at 4 WAA

When plants were labelled at 4 WAA the percentage of whole plant  $^{14}\text{C}$  in the shoot on all sampling occasions was greater than that of plants labelled at 2 WAA but less than that of plants labelled at A and 6 WAA (Figure 4.22). This reflects the fact that percentage of whole plant  $^{14}\text{C}$  recovered in the grain at PM, namely 79,7 and 80,3 % in the stressed and non-stressed plants respectively, was less than that for plants labelled at 2 WAA but more than that for plants labelled at A and 6 WAA. The percentage of whole plant  $^{14}\text{C}$  in the shoot at 4 WAA was 43,8 and 45,4 % in stressed and non-stressed plants, respectively. This declined to 24,1 and 29,4 % in stressed and non-stressed plants respectively at 6 WAA and then declined further to 20,3 and 19,7 % in stressed and non-stressed plants respectively, at PM. The overall decline in the percentage of whole plant  $^{14}\text{C}$  in the shoot from 4 WAA to PM reflects the mobilization of  $^{14}\text{C}$  to the grain with stressed plants showing a more marked decline from 4 to 6 WAA while non-stressed plants declined more markedly from 6 WAA to PM. Thus it appears that the stressed plants mobilized a greater proportion of  $^{14}\text{C}$  assimilated at 4 WAA directly to the grain from 4 to 6 WAA than did the non-stressed plants. However, the percentage of  $^{14}\text{C}$  in the shoot of non-stressed plants declined more rapidly from 6 WAA to PM than stressed plants indicating that non-stressed plants translocated a greater amount of  $^{14}\text{C}$  out of the shoot to the grain at a later stage than the stressed plants.

### Labelling at 6 WAA

When plants were labelled at 6 WAA the percentage of whole plant  $^{14}\text{C}$  in the shoot was lower than that on all sampling occasions of plants labelled at A, but greater than that of plants labelled at 2 WAA and 4 WAA (Figure 4.22). This reflects the fact that the percentage of whole plant  $^{14}\text{C}$  recovered in the grain at PM in stressed and non-stressed plants of 67,6 and 67,0 % respectively, was less than that for plants labelled at 2 WAA and 4 WAA, but more than that for plants labelled at A. The percentage of whole plant  $^{14}\text{C}$  in the shoot at 6 WAA was 55,2 and 58,4 % in stressed and non-stressed plants, respectively. This declined to 32,4 and 33,0 % in stressed and non-stressed plants respectively, at PM. The overall decline in the percentage of whole plant  $^{14}\text{C}$  in the shoot from 6 WAA to PM reflects the mobilization of  $^{14}\text{C}$  to the grain. The lower percentage of whole plant  $^{14}\text{C}$  in the shoot of stressed plants at 6 WAA is indicative of the more direct and rapid translocation of  $^{14}\text{C}$  to the grain soon after labelling. However, the non-stressed plants had a similar percentage of whole plant  $^{14}\text{C}$  in the shoot at PM compared to the stressed plants which indicates that the non-stressed plants mobilized a greater proportion of  $^{14}\text{C}$  to the grain at a later stage than the stressed plants.

#### 4.3.6.4 Ratio of total radioactivity in the grain to total radioactivity in the shoot

##### Labelling at A

Plants labelled at A maintained the lowest grain to shoot ratio on all sampling occasions compared to plants labelled on the other three occasions (Figure 4.23). This again reflects the higher percentage of  $^{14}\text{C}$  assimilated at A retained in the shoot of stressed and non-stressed plants. At A the grain to shoot ratio of stressed and non-stressed plants was 0,08 and 0,05, respectively. This increased to 0,45 and 0,37 in stressed and non-stressed plants respectively at PM, with the stressed plants maintaining a higher ratio throughout grain fill. This indicates that during grain fill the stressed plants partitioned a greater amount of whole plant  $^{14}\text{C}$  assimilated at A to the grain than did the non-stressed plants.

##### Labelling at 2 WAA

Plants labelled at 2 WAA maintained the highest grain to shoot ratio on all sampling occasions compared to plants labelled on the other three occasions (Figure 4.23). This reflects the fact that plants labelled at 2 WAA translocated the highest proportion of assimilated  $^{14}\text{C}$  to the grain than plants labelled on the other three occasions. At 2 WAA the grain to shoot ratio of stressed and non-stressed plants was 1,44 and 1,09, respectively. This increased markedly to 5,41 and 4,51 at 4 WAA, less markedly to 6,32 and 6,11 at 6 WAA and then increased to 6,50 and 7,31 at PM

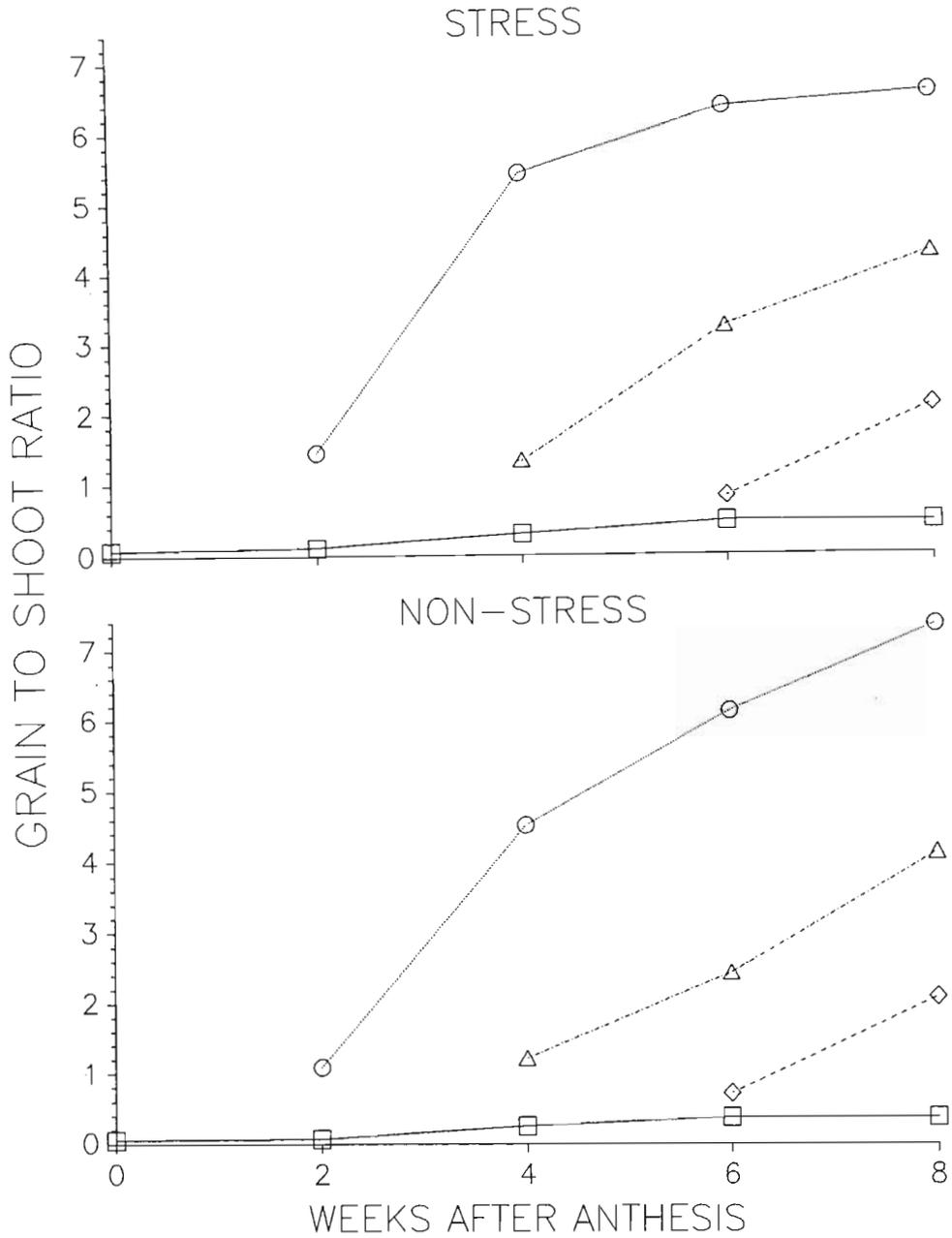


Figure 4.23 Effect of water stress during grain fill on grain to shoot total radioactivity ratio of a maize hybrid labelled at anthesis (□—□), 2 (○—○), 4 (△----△) and 6 (◇----◇) weeks after anthesis and sampled at fortnightly intervals

in stressed and non-stressed plants, respectively. Thus initially from 2 to 4 WAA the stressed plants partitioned a greater amount of whole plant  $^{14}\text{C}$  to the grain than the non-stressed plants. This was an indication of the more direct and rapid mobilization of  $^{14}\text{C}$  to the grain under stress conditions. Both the stressed and non-stressed plants showed a marked increase in the grain to shoot ratio from 2 to 4 WAA. However, from 4 WAA to PM the grain to shoot ratio increased less markedly in the stressed plants whereas it continued to increase markedly in the non-stressed plants. Thus although the stressed plants apparently translocated a greater amount of the  $^{14}\text{C}$  assimilated at 2 WAA to the grain from 2 to 4 WAA than the non-stressed plants, from 4 to 6 WAA the non-stressed plants continued to translocate  $^{14}\text{C}$  to the grain to a greater extent than the stressed plants.

#### Labelling at 4 WAA

Plants labelled at 4 WAA maintained the second highest grain to shoot ratio on all sampling occasions compared to plants labelled on the other three occasions (Figure 4.23). This reflects the fact that plants labelled at 4 WAA translocated the second highest proportion of assimilated  $^{14}\text{C}$  to the grain than plants labelled on the other three occasions. At 4 WAA the grain to shoot ratio of stressed and non-stressed plants was 1,32 and 1,22, respectively. This increased to 3,21 and 2,43 at 6 WAA and then to 4,25 and 4,11 at PM in stressed and non-stressed plants, respectively. The fact that the grain to shoot ratio was higher in stressed plants than non-stressed plants on all sampling

occasions indicates the greater mobilization of  $^{14}\text{C}$  assimilated at 4 WAA to the grain under stress conditions. The initial increase in the grain to shoot ratio of stressed plants from 4 to 6 WAA was more marked than that of non-stressed plants. This indicates the more direct and rapid translocation of  $^{14}\text{C}$  assimilated at 4 WAA to the grain under stress conditions. However, the increase in the grain to shoot ratio of non-stressed plants from 6 WAA to PM was greater than that of stressed plants which indicates that non-stressed plants translocated a greater amount of  $^{14}\text{C}$  to the grain at a later stage than stressed plants.

#### Labelling at 6 WAA

Plants labelled at 6 WAA maintained the third highest grain to shoot ratio on all sampling occasions compared to plants labelled on the other three occasions (Figure 4.23). This reflects the fact that the plants labelled at 6 WAA translocated the third highest proportion of assimilated  $^{14}\text{C}$  to the grain than plants labelled on the other three occasions. At 6 WAA the grain to shoot ratio of stressed and non-stressed plants was 0,81 and 0,71 respectively and this increased markedly to 2,09 and 2,08 in stressed and non-stressed plants, respectively. The marginally higher grain to shoot ratio in stressed plants on all sampling occasions indicates the greater mobilization of  $^{14}\text{C}$  assimilated at 6 WAA to the grain under stress conditions. However, the greater increase in the ratio of the non-stressed plants from 6 WAA to PM indicates that the non-stressed plants translocated a greater amount of  $^{14}\text{C}$  to the grain at a later stage than the stressed plants.

For interest the grain dry mass to shoot dry mass ratio is presented for the plants sampled for each labelling occasion in Figure 4.24. It is apparent that on average the non-stressed plants maintained a higher grain to shoot ratio than the stressed plants. This indicates that the stressed plants did not utilize the labile compounds which contribute to the dry mass of the shoot for grain fill requirements to a greater extent than the non-stressed plants.

4.3.7 Radioactivity analysis of whole plant

4.3.7.1 Specific radioactivity

Labelling at A

The main effect for stress treatment was non-significant (Table 4.57 and Appendix 41.1). The SR of the whole plant under stress conditions was non-significantly higher than that under non-

Table 4.57 Effect of water stress (S) and lack of water stress (NS) on whole plant specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) meaned over five growth periods during grain fill for a maize hybrid labelled at anthesis

Stress treatment	
S	NS
78,02	75,64
LSD (0,05)	NS
LSD (0,01)	NS

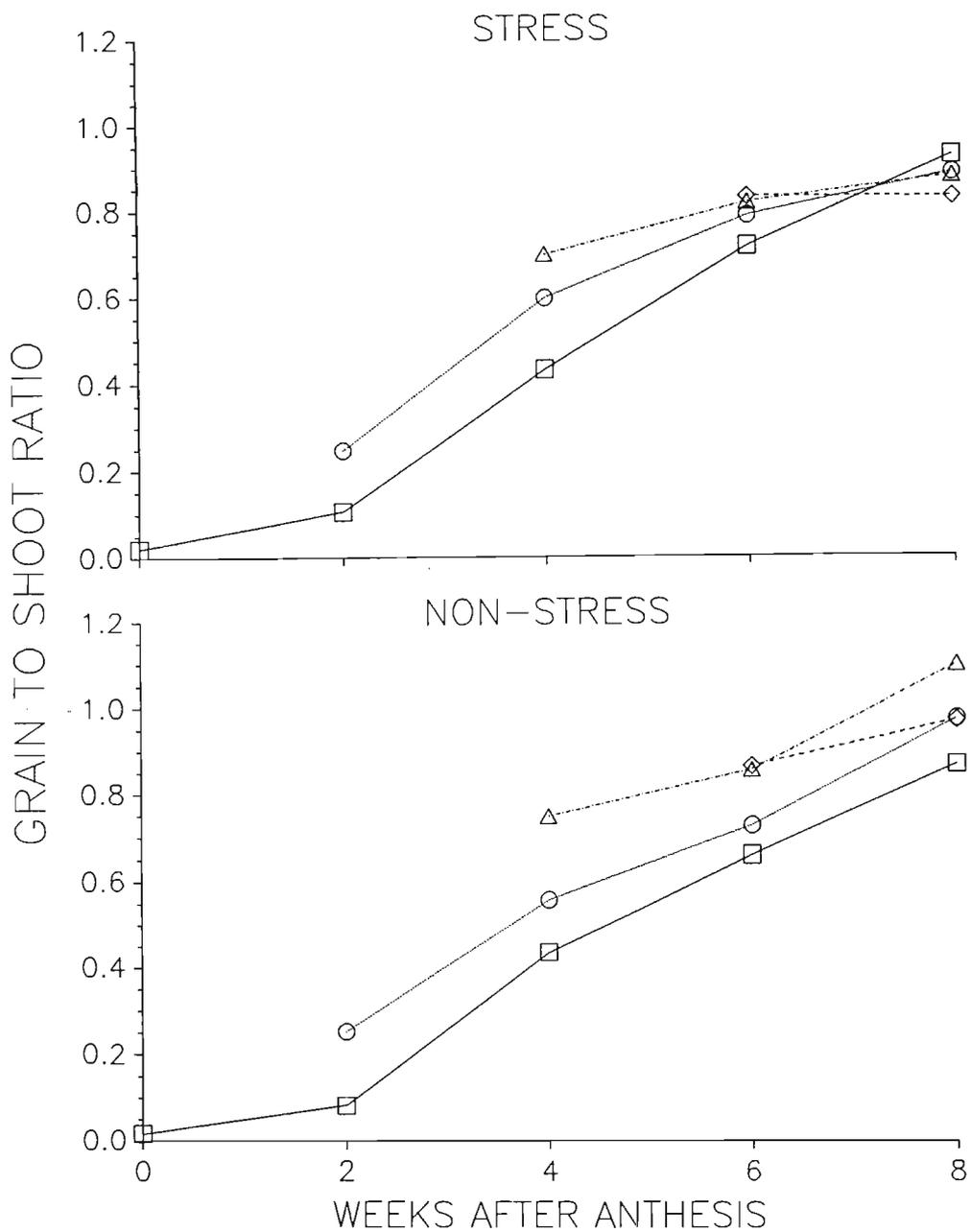


Figure 4.24 Effect of water stress during grain fill on grain to shoot dry mass ratio of a maize hybrid sampled at fortnightly intervals from anthesis (□—□), 2 (○—○), 4 (△—△) and 6 (◇—◇) weeks after anthesis

stress conditions. Averaged over the entire grain filling period, however, the TR of the whole plant under non-stress conditions was non-significantly higher than that under stress conditions (Section 4.3.7.2). Nonetheless, the stressed plants had the higher whole plant SR because the dry mass of the whole plant during grain fill under stress conditions was less than that under non-stress conditions (Table 4.58 and Appendix 49). Thus in contrast to non-stressed plants, the stressed plants incorporated less  $^{12}\text{C}$  into the dry mass of the whole plant during grain fill.

Table 4.58 Whole plant dry mass ( $\text{g plant}^{-1}$ ), meaned over corresponding sampling occasions from each labelling occasion, from a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill

Stress treatment	Weeks after anthesis				
	0	2	4	6	8
S	140,8	171,9	218,6	250,1	250,3
NS	146,2	187,2	235,6	276,9	289,8

The main effect for WAA was significant (Table 4.59). There was a significant negative linear effect superimposed with a positive quadratic effect which indicates that the SR of the whole plant declined slightly from A to 2 WAA and then markedly from 2 to 4 WAA and then more gradually from 4 WAA to PM. The TR of the whole plant at 2 WAA was non-significantly higher than at A (Section 4.3.7.2). This can only be attributed to sampling error

for the amount of  $^{14}\text{C}$  in the plants labelled at A should generally have declined from A to PM as a result of respiration losses. It is therefore likely that the SR of the whole plant declined more markedly from A to 2 WAA than what the data obtained indicate. The general decline in the SR of the whole plant from A to PM reflects the increase in the dry mass of the whole plant particularly as a result of the dry mass gain of the grain (Table 4.58 and Appendix 49). As the whole plant increased in dry mass new non-radioactive photosynthate was synthesized and incorporated into the dry mass of the whole plant. Thus the  $^{14}\text{C}$  in the whole plant was diluted. The decline in the SR of the whole plant also reflects the general loss of  $^{14}\text{C}$  due to respiration.

Table 4.59 Specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) of whole plant meaned over water stress treatments from anthesis to eight weeks after anthesis (WAA) for a maize hybrid labelled at anthesis

		WAA				
		0	2	4	6	8
		119,18	102,84	62,53	53,40	46,20
LSD	(0,05)		13,72			
LSD	(0,01)		18,80			

Labelling at 2 WAA

The main effect for stress treatment was just non-significant (Table 4.60 and Appendix 41.2). The SR of the whole plant under stress conditions was non-significantly higher than that under

non-stress conditions. Averaged over 2 WAA to PM the TR of the whole plant under stress conditions was higher than under non-stress conditions (Section 4.3.7.2) and this coupled with the lower whole plant dry mass under stress conditions than under non-stress conditions (Table 4.58 and Appendix 49) provided for the higher SR of the whole plant under stress than non-stress conditions. It is also likely that in contrast to non-stressed plants the stressed plants incorporated less  $^{12}\text{C}$  into the dry mass of the whole plant from 2 WAA to PM.

Table 4.60 Effect of water stress (S) and lack of water stress (NS) on whole plant specific radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over four growth periods during grain fill for a maize hybrid labelled at two weeks after anthesis

Stress treatment	
S	NS
66,18	57,51
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was significant (Table 4.61). There was a significant negative linear effect which indicates that the SR of the whole plant declined steadily from 2 WAA to PM. The general decline in the SR of the whole plant from 2 WAA to PM reflects the increase in the dry mass of the whole plant particularly as a result of the dry mass gain of the grain (Table 4.58 and Appendix 49). As the whole plant increased in dry mass

$^{12}\text{C}$  was assimilated and incorporated into the dry mass of the whole plant thus the  $^{14}\text{C}$  in the whole plant was diluted. The decline in the SR of the whole plant also reflects the general loss of  $^{14}\text{C}$  due to respiration.

Table 4.61 Specific radioactivity (dpm x  $10^{-3}$  g $^{-1}$ ) of whole plant meaned over water stress treatments from two weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at two weeks after anthesis

WAA			
2	4	6	8
77,62	68,10	51,48	50,18
LSD (0,05)	12,86		
LSD (0,01)	17,85		

#### Labelling at 4 WAA

The main effect for stress treatment was significant (Table 4.62 and Appendix 4.63). The SR of the whole plant under stress conditions was significantly ( $p = 0,05$ ) less than that under non-stress conditions. When the plants were labelled at 4 WAA the stressed plants had already undergone four consecutive stress cycles. This resulted in the stressed plants assimilating less  $^{14}\text{C}$  than the non-stressed plants thus recording significantly ( $p = 0,01$ ) lower TR of the whole plant averaged over 4 WAA to PM than the non-stressed plants (Section 4.3.7.2). Although the stressed plants had averaged over 4 WAA to PM lower whole plant dry mass than the non-stressed plants (Table 4.58 and Appendix

49), the low whole plant TR recorded for the stressed plants resulted in a lower SR for the stressed plants.

Table 4.62 Effect of water stress (S) and lack of water stress (NS) on whole plant specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) meaned over three growth periods during grain fill for a maize hybrid labelled at four weeks after anthesis

Stress treatment	
S	NS
25,26	30,93
LSD (0,05)	4,93
LSD (0,01)	7,01

The main effect for WAA was non-significant. However, there was a significant positive quadratic effect which indicates that the whole plant SR declined from 4 to 6 WAA and then increased from 6 WAA to PM (Table 4.63). The increase in SR from 6 WAA to PM is partly due to the decline in whole plant dry mass (Table 4.58 and Appendix 49) from 6 WAA to PM, but is largely due to the higher whole plant TR recorded at PM than at 6 WAA (Section 4.3.7.2). As mentioned earlier the grain of the stressed, and particularly the non-stressed, plants sampled from replication one at PM after being labelled at 4 WAA recorded high SR. This resulted in the SR and TR of the whole plant at PM being non-significantly higher than at 6 WAA. If the data from replication one were ignored then the general trend would have been one of an overall decline in the SR of the whole plant from 4 WAA to PM.

The general decline in the SR of the whole plant from 4 WAA to PM reflects the increase in the dry mass of the whole plant, particularly the grain, as  $^{12}\text{C}$  was assimilated and incorporated into the dry mass of the whole plant thus diluting the  $^{14}\text{C}$  in the whole plant. The decline in the SR of the whole plant also reflects the general loss of  $^{14}\text{C}$  due to respiration.

Table 4.63 Specific radioactivity (dpm  $\times 10^{-3} \text{ g}^{-1}$ ) of whole plant meaned over water stress treatments from four weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at four weeks after anthesis

	WAA		
	4	6	8
	31,28	24,22	28,78
LSD (0,05)		6,04	
LSD (0,01)		8,59	

#### Labelling at 6 WAA

The main effect for stress treatment was non-significant (Table 4.64 and Appendix 41.4). The SR of the whole plant under stress conditions was non-significantly lower than that under non-stress conditions. Although the stressed plants recorded lower whole plant dry mass from 6 WAA to PM (Table 4.58 and Appendix 49), the lower amount of  $^{14}\text{C}$  assimilated by the stressed plants, as indicated by the lower TR of the whole plant under stress

conditions (Section 4.3.7.2), resulted in the stressed plants recording a lower SR of the whole plant.

Table 4.64 Effect of water stress (S) and lack of water stress (NS) on whole plant specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) meaned over two growth periods during grain fill for a maize hybrid labelled at six weeks after anthesis

Stress treatment	
S	NS
7,71	8,39
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was just non-significant (Table 4.65). The SR of the whole plant at PM was non-significantly less than

Table 4.65 Specific radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of whole plant meaned over water stress treatments from six weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at six weeks after anthesis

WAA	
6	8
8,91	7,18
LSD (0,05)	NS
LSD (0,01)	NS

that at 6 WAA. Although the TR of the whole plant declined from 6 WAA to PM (Section 4.3.7.2), the whole plant dry mass averaged over stressed and non-stressed plants increased slightly from 6 WAA to PM as the rate of dry mass gain by the grain declined (Table 4.8 and Appendix 46). This resulted in a slight decline in the SR of the whole plant from 6 WAA to PM.

#### First order interactions for labelling at A, 2 WAA, 4 WAA and 6 WAA

Each first order interaction of stress treatment with WAA for labelling at A, 2 WAA, 4 WAA and 6 WAA was non-significant (Figure 4.25). There were no significant components of each interaction either. However, the apparent trends of these first order interactions are discussed.

The stressed and non-stressed plants labelled at A maintained a higher SR of the whole plant on all sampling occasions than plants labelled at 4 WAA and 6 WAA (Figure 4.25). However, the stressed plants labelled at A only had a higher SR of the whole plant when sampled at A and 2 WAA than the stressed plants labelled at 2 WAA. The non-stressed plants labelled at A had a higher SR of the whole plant when sampled at A, 2 WAA and 6 WAA when compared to stressed plants labelled at 2 WAA. The SR of the whole plant of stressed and non-stressed plants at A was 123 472 and 114 890 dpm g<sup>-1</sup>, respectively. This declined to 101 044 and 104 638 dpm g<sup>-1</sup> at 2 WAA and then declined further and sharply to 63 971 and 61 081 dpm g<sup>-1</sup> at 4 WAA in stressed and non-stressed plants, respectively. At 6 WAA the SR of the whole

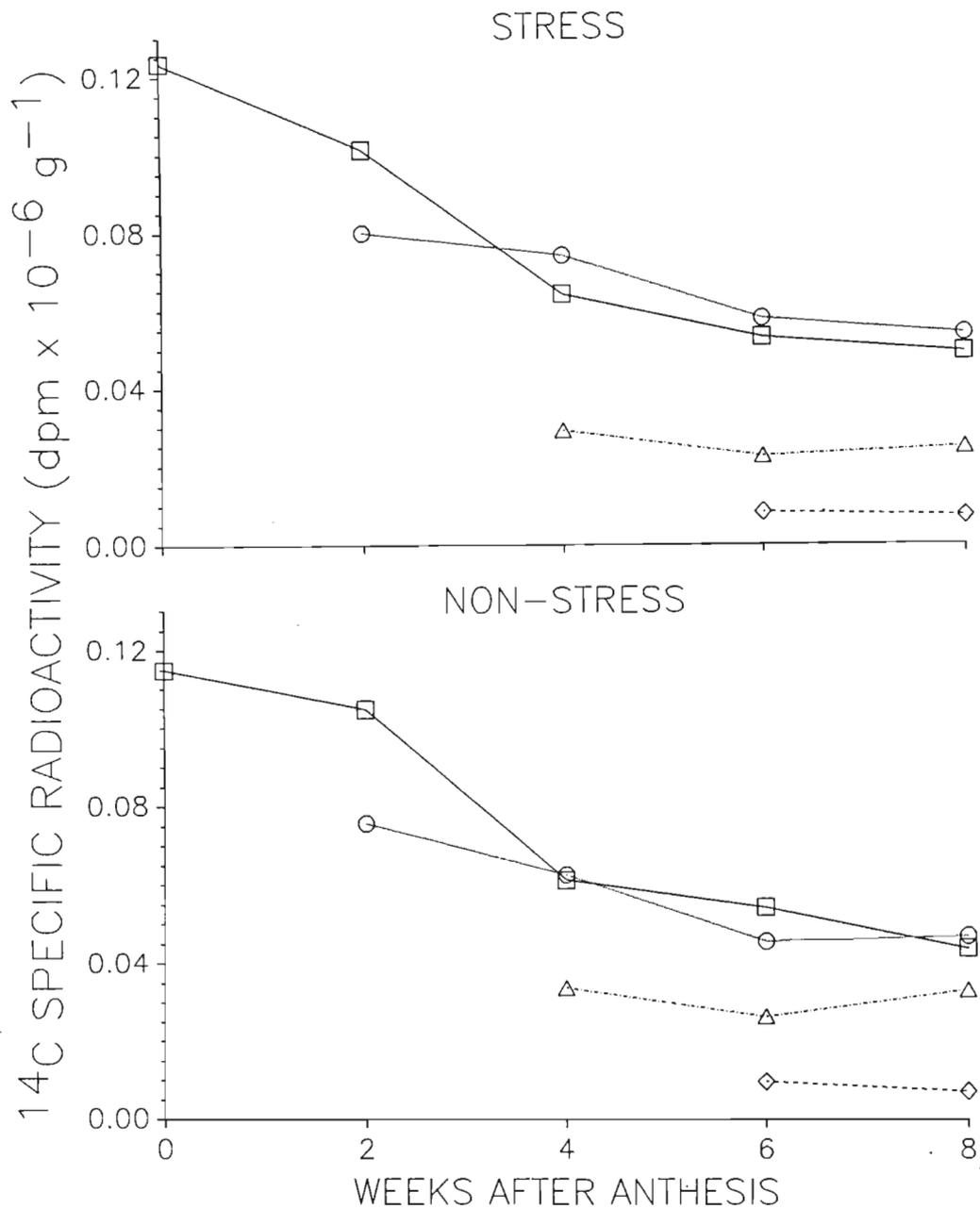


Figure 4.25 Effect of water stress during grain fill on specific radioactivity of the whole plant sampled at fortnightly intervals from a maize hybrid labelled at anthesis ( $\square-\square$ ), 2 ( $\circ-\circ$ ), 4 ( $\triangle-\triangle$ ) and 6 ( $\diamond-\diamond$ ) weeks after anthesis

plant had declined to 52 761 and 54 038 dpm g<sup>-1</sup> and then declined further to 48 867 and 43 531 dpm g<sup>-1</sup> at PM in stressed and non-stressed plants, respectively. The overall decline in the SR of the whole plant from A to PM reflects the decline in the TR of the whole plant as <sup>14</sup>C was lost from the whole plant through respiration. It also reflects the incorporation of new non-radioactive photosynthate into the dry mass of the whole plant particularly by the grain. The marked decline in the SR of the whole plant from 2 to 4 WAA reflects the rapid incorporation of non-radioactive photosynthate into the grain as the grain became established as a major sink for photosynthate. It also possibly reflects the increased respiration losses as a result of the greater energy requirements to rapidly translocate photosynthate to the grain. The SR of the whole plant of the stressed plants was generally higher than that of the non-stressed plants on all sampling occasions. This reflects the decreased incorporation of non-radioactive photosynthate into the dry mass of the whole plant under stress conditions as judged by the lower whole plant dry mass under stress conditions (Table 4.58 and Appendix 49).

When plants were labelled at 2 WAA the SR of the whole plant on all sampling occasions was higher than that of plants labelled at 4 WAA and 6 WAA (Figure 4.25). The SR of the whole plant of plants labelled at 2 WAA relative to plants labelled at A has been discussed above. The SR of the whole plant of stressed and non-stressed plants at 2 WAA was 79 712 and 75 528 dpm g<sup>-1</sup>, respectively. This declined to 73 855 and 62 353 dpm g<sup>-1</sup> at 4 WAA; 57 488 and 45 465 dpm g<sup>-1</sup> at 6 WAA and 53 654 and 46 698 dpm g<sup>-1</sup> at PM in stressed and non-stressed plants,

respectively. The overall decline in the SR of the whole plant reflects the loss of  $^{14}\text{C}$  from the plants through respiration. It also reflects the incorporation of  $^{12}\text{C}$  into the dry mass of the whole plant particularly by the grain thus diluting the  $^{14}\text{C}$  in the whole plant. The SR of the whole plant of stressed plants was higher on all sampling occasions than that of non-stressed plants. This reflects the higher TR of the whole plant of the stressed plants on all sampling occasions (Section 4.3.7.2) and the decreased incorporation of  $^{12}\text{C}$  into the dry mass of the whole plant under stress conditions as judged by the lower whole plant dry mass under stress conditions (Table 4.58 and Appendix 49).

When plants were labelled at 4 WAA, the SR of the whole plant of stressed and non-stressed plants on all sampling occasions was less than that of plants labelled at A and 2 WAA, but greater than that of plants labelled at 6 WAA (Figure 4.25). The SR of the whole plant of stressed and non-stressed plants at 4 WAA was 28 977 and 33 587 dpm  $\text{g}^{-1}$ , respectively. This declined to 22 283 and 26 160 dpm  $\text{g}^{-1}$  at 6 WAA and then increased to 24 514 and 33 043 dpm  $\text{g}^{-1}$  at PM in stressed and non-stressed plants, respectively. The overall decline in the SR of the whole plant reflects the loss of  $^{14}\text{C}$  from the plants through respiration. It also reflects the incorporation of  $^{12}\text{C}$  into the dry mass of the whole plant particularly by the grain. The increase in the SR of the whole plant from 6 WAA to PM, particularly in the non-stressed plants, was due to the high SR recorded for the grain of plants sampled from replication one. The SR of the whole plant of non-stressed plants was higher on all sampling occasions than that of stressed plants. This reflects the higher TR of the

whole plant of the non-stressed plants on all sampling occasions (Section 4.3.7.2) even though the non-stressed plants incorporated more  $^{12}\text{C}$  into the dry mass of the whole plant as judged by the higher whole plant dry mass under non-stress conditions (Table 4.58 and Appendix 49).

When plants were labelled at 6 WAA, the SR of the whole plant of stressed and non-stressed plants on all sampling occasions was less than that of plants labelled on the other three occasions (Figure 4.25). The SR of the whole plant at 6 WAA was 12 845 and 15 457 dpm  $\text{g}^{-1}$ , which declined to 6 350 and 7 765 dpm  $\text{g}^{-1}$  at PM in stressed and non-stressed plants, respectively. The overall decline in the SR of the whole plant reflects the loss of  $^{14}\text{C}$  from the plants through respiration. It also reflects the incorporation of  $^{12}\text{C}$  into the dry mass of the whole plant particularly by the grain. The SR of the whole plant of non-stressed plants was higher than that of stressed plants on all sampling occasions. This reflects the higher TR of the whole plant of non-stressed plants on all sampling occasions even though non-stressed plants incorporated more  $^{12}\text{C}$  into the dry mass of the whole plant as judged by the higher whole plant dry mass under non-stress conditions (Table 4.58 and Appendix 49).

#### 4.3.7.2 Total radioactivity

##### Labelling at A

The main effect for stress treatment was non-significant (Table 4.66 and Appendix 42.1). The TR of the whole plant under stress conditions was non-significantly lower than that under non-stress conditions. Imposition of water deficits for the stressed plants occurred after the plants were labelled at A. Theoretically then, the stressed and non-stressed plants should have assimilated the same amount of  $^{14}\text{C}$  at A. In fact data from the non-significant interaction of stress treatment with WAA indicates that whole plant TR was higher in stressed plants than non-stressed plants 48 h after labelling at A. It would be expected that the stressed plants would respire less than the non-stressed plants. However, since the  $^{14}\text{C}$  assimilated at A would be in the plants for the entire grain filling period eventually the stressed plants would respire a substantial amount

Table 4.66 Effect of water stress (S) and lack of water stress (NS) on whole plant total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over five growth periods during grain fill for a maize hybrid labelled at anthesis

Stress treatment	
S	NS
14 290	15 534
LSD (0,05)	NS
LSD (0,01)	NS

of the  $^{14}\text{C}$ , as previously assimilated C would have to be utilized for respiration requirements, because the assimilation of new C would be reduced as a result of stress (Section 4.3.7.2). Averaged over the grain filling period the stressed plants had less  $^{14}\text{C}$  in the whole plant than the non-stressed plants indicating that more of the  $^{14}\text{C}$  assimilated at A was respired in the stressed plants than the non-stressed plants.

The main effect for WAA was significant (Table 4.67). There was a significant negative linear effect superimposed with a significant deviation from linear, quadratic and cubic effects. This indicates that TR of the whole plant fluctuated somewhat as it declined from A to PM. The TR of the whole plant at 2 WAA was non-significantly higher than at A. The TR of the whole plant at 6 WAA was non-significantly higher than at 4 WAA. These fluctuations in the TR of the whole plant can only be attributed to sampling error, for the amount of  $^{14}\text{C}$  in the plants labelled at A should generally have declined from A to PM as a result of respiration losses. Averaged over stressed and non-stressed plants the TR of the whole plant at PM was 76,0 % of that at A, which means that 24,0 % of the  $^{14}\text{C}$  assimilated at A was respired during the entire grain filling period on a whole plant basis. Averaged over the stressed and non-stressed plants labelled at A, 71,1 % of the  $^{14}\text{C}$  recovered in the whole plant at PM occurred in the whole shoot. This means that the shoot was the major sink for  $^{14}\text{C}$  assimilated at A. It would be expected that the  $^{14}\text{C}$  located in the shoot would be respired to a greater extent than  $^{14}\text{C}$  located in the grain.

Table 4.67 Total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) of whole plant meaned over water stress treatments from anthesis to eight weeks after anthesis (WAA) for a maize hybrid labelled at anthesis

WAA				
0	2	4	6	8
17 082	17 459	13 230	13 811	12 977
LSD (0,05)	1 979			
LSD (0,01)	2 727			

#### Labelling at 2 WAA

The main effect for stress treatment was non-significant (Table 4.68 and Appendix 42.2). The TR of the whole plant under stress conditions was non-significantly higher than that under non-stress conditions. When plants were labelled at 2 WAA the stressed plants had already undergone two consecutive stress

Table 4.68 Effect of water stress (S) and lack of water stress (NS) on whole plant total radioactivity (dpm x 10<sup>-3</sup> g<sup>-1</sup>) meaned over four growth periods during grain fill for a maize hybrid labelled at two weeks after anthesis

Stress treatment	
S	NS
14 784	13 591
LSD (0,05)	NS
LSD (0,01)	NS

cycles. However, they apparently recovered sufficiently to assimilate more  $^{14}\text{C}$  at 2 WAA than the non-stressed plants and to record on average from 2 WAA to PM a higher whole plant TR than the non-stressed plants.

The main effect for WAA was non-significant. There were no significant components of the main effect either (Table 4.69). The TR of the whole plant increased slightly from 2 to 4 WAA which can only be ascribed to sampling error. From 4 WAA to PM TR of the whole plant declined. Averaged over the stressed and non-stressed plants the TR of the whole plant at PM was 91,7 % of that at 2 WAA, which means that 8,3 % of the  $^{14}\text{C}$  assimilated at 2 WAA was respired from 2 WAA to PM. Averaged over the stressed and non-stressed plants labelled at 4 WAA only 14,0 % of the  $^{14}\text{C}$  recovered in the whole plant at PM occurred in the whole shoot. It is clear then that the grain was the major sink for the  $^{14}\text{C}$  assimilated at 2 WAA. This would mean that the

Table 4.69 Total radioactivity (dpm x  $10^{-3}$  g $^{-1}$ ) of whole plant meaned over water stress treatments from two weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at two weeks after anthesis

WAA			
2	4	6	8
14 555	15 354	13 487	13 353
LSD (0,05)	NS		
LSD (0,01)	NS		

overall loss of  $^{14}\text{C}$  due to respiration on a whole plant basis would be low.

#### Labelling at 4 WAA

The main effect for stress treatment was significant (Table 4.70 and Appendix 42.3). The TR of the whole plant under stress conditions was significantly ( $p = 0,01$ ) less than that under non-stress conditions. When the plants were labelled at 4 WAA the stressed plants had already undergone four consecutive stress cycles. This resulted in the stressed plants assimilating less  $^{14}\text{C}$  than the non-stressed plants at 4 WAA.

Table 4.70 Effect of water stress (S) and lack of water stress (NS) on whole plant total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over three growth periods during grain fill for a maize hybrid labelled at four weeks after anthesis

	Stress treatment	
	S	NS
	6 257	8 332
LSD (0,05)	1 359	
LSD (0,01)	1 933	

The main effect for WAA was non-significant. There were no significant components of the main effect either (Table 4.71). Whole plant TR declined from 4 to 6 WAA and then increased from 6 WAA to PM. In fact whole plant TR at PM was marginally higher than at 4 WAA due to sampling error. Averaged over the stressed

and non-stressed plants labelled at 4 WAA 20,0 % of the  $^{14}\text{C}$  recovered in the whole plant at PM occurred in the whole shoot (Section 4.3.6.3). Clearly the grain was the major sink for  $^{14}\text{C}$  assimilated at 4 WAA. However, since the percentage of the  $^{14}\text{C}$  located in the grain at PM was not as high as was the case with plants labelled at 2 WAA it may be expected that the plants labelled at 4 WAA would have respired slightly more than the 8,3 % recorded for plants labelled at 2 WAA.

Table 4.71 Total radioactivity (dpm x  $10^{-3}$  g $^{-1}$ ) of whole plant meaned over water stress treatments from four weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at four weeks after anthesis

WAA		
4	6	8
7 640	6 575	7 668
LSD (0,05)	NS	
LSD (0,01)	NS	

#### Labelling at 6 WAA

The main effect for stress treatment was non-significant (Table 4.72 and Appendix 42.4). The TR of the whole plant under stress conditions was non-significantly lower than that under non-stress conditions. The TR of the whole plant at 6 WAA was less than that at A, 2 WAA and 4 WAA which indicates that whole plant photosynthetic activity was greatly reduced by 6 WAA. So,

although the stressed plants would assimilate less  $^{14}\text{C}$  at 6 WAA as a result of the effects of stress, the non-stressed plants assimilated only marginally more than the stressed plants as a result of the reduced demand for photosynthate by the grain and a decline in photosynthetic capacity due to leaf senescence. Of the  $^{14}\text{C}$  assimilated by the stressed whole plant at 6 WAA only 55,2 % remained in the shoot 48 h after labelling in comparison to 58,4 % for the non-stressed plants (Section 4.3.6.3). Thus the stressed plants translocated a greater proportion of the  $^{14}\text{C}$  assimilated at 6 WAA directly to the grain. It is therefore likely that since much of the  $^{14}\text{C}$  assimilated at 6 WAA was located in the grain of the stressed plants the stressed plants would respire less  $^{14}\text{C}$  on a whole plant basis than the non-stressed plants. These effects resulted in the TR of the whole plant under non-stress conditions being only marginally higher than that under stress conditions averaged over 6 WAA to PM.

Table 4.72 Effect of water stress (S) and lack of water stress (NS) on whole plant total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) meaned over two growth periods during grain fill for a maize hybrid labelled at six weeks after anthesis

Stress treatment	
S	NS
1 913	2 399
LSD (0,05)	NS
LSD (0,01)	NS

The main effect for WAA was just non-significant (Table 4.73). The TR of the whole plant at PM was non-significantly less than that at 6 WAA. Averaged over stressed and non-stressed plants the percentage of  $^{14}\text{C}$  recovered from the whole plant at PM, located in the shoot, was 32,7 %. This was a greater percentage of  $^{14}\text{C}$  remaining in the shoot at PM in comparison to plants labelled at 2 WAA and 4 WAA. However, this means that most of the  $^{14}\text{C}$  at PM, 67,3 % in fact, was located in the grain (Section 4.3.4.3). Averaged over the stressed and non-stressed plants the TR of the whole plant at PM was 79,6 % of that at 6 WAA, which means that 20,4 % of the  $^{14}\text{C}$  assimilated at 6 WAA was respired from 6 WAA to PM.

Table 4.73 Total radioactivity ( $\text{dpm} \times 10^{-3} \text{g}^{-1}$ ) of whole plant meaned over water stress treatments from six weeks after anthesis (WAA) to eight weeks after anthesis for a maize hybrid labelled at six weeks after anthesis

WAA	
6	8
2 402	1 911
LSD (0,05)	NS
LSD (0,01)	NS

First order interactions for labelling at A, 2 WAA, 4 WAA and 6 WAA

Each first order interaction of stress treatment with WAA for labelling at A, 2 WAA, 4 WAA and 6 WAA was non-significant (Figure 4.26). There were no significant components of each interaction either. However, the apparent trends of these first order interactions are discussed.

The stressed and non-stressed plants labelled at A maintained a higher TR of the whole plant on all sampling occasions than plants labelled at 4 WAA and 6 WAA (Figure 4.26). However, the stressed plants labelled at A only had a higher TR of the whole plant when sampled at A and 2 WAA than stressed plants labelled at 2 WAA. Stressed plants labelled at 2 WAA when sampled at 4 WAA did, however, have a higher TR of the whole plant than stressed plants labelled at A when sampled at 2 WAA. Non-stressed plants had a higher TR of the whole plant when sampled at A, 2 WAA and 6 WAA compared to non-stressed plants labelled at 2 WAA. The TR of the whole plant 48 h after labelling at A was 17 347 474 and 16 816 792 dpm plant<sup>-1</sup> in stressed and non-stressed plants, respectively. This declined to 15 971 044 dpm plant<sup>-1</sup> and increased to 18 947 951 dpm plant<sup>-1</sup> at 2 WAA and then decreased to 12 758 625 and 13 701 840 dpm plant<sup>-1</sup> at 4 WAA in stressed and non-stressed plants, respectively. At 6 WAA the TR of the whole plant had decreased slightly to 12 540 703 dpm plant<sup>-1</sup> in stressed plants and increased to 15 081 864 dpm plant<sup>-1</sup> in non-stressed plants. At PM the TR of the whole plant had increased to 12 831 044 dpm plant<sup>-1</sup> in

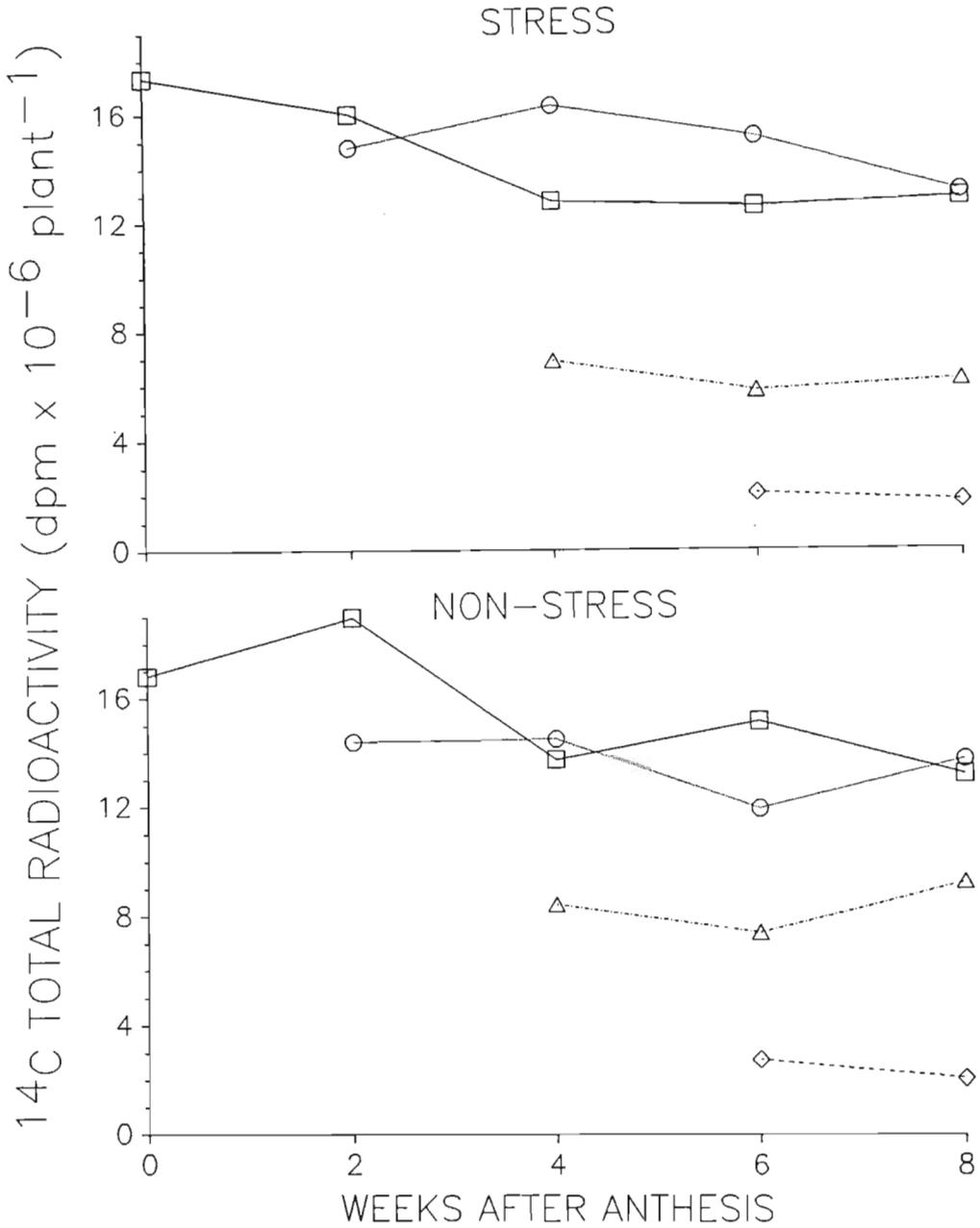


Figure 4.26 Effect of water stress during grain fill on total radioactivity of the whole plant sampled at fortnightly intervals from a maize hybrid labelled at anthesis (□—□), 2 (○—○), 4 (△—△) and 6 (◇—◇) weeks after anthesis

stressed plants and decreased to 13 122 208 dpm plant<sup>-1</sup> in the non-stressed plants. Thus the TR of the whole plant fluctuated somewhat from A to PM, particularly in the non-stressed plants. The increase in the TR of the whole plant of non-stressed plants from A to 2 WAA and from 4 to 6 WAA was due to sampling error. The TR of the whole plant of stressed plants at A was higher than that of non-stressed plants. It will be recalled that water deficits were imposed on the plants after labelling was completed at A so theoretically the stressed and non-stressed plants should have assimilated the same amount of <sup>14</sup>C at A. From 2 WAA to PM the TR of the whole plant of stressed plants was less than that of non-stressed plants. This may indicate that the stressed plants were forced to utilize more of the <sup>14</sup>C assimilated at A for respiration requirements particularly from 2 to 4 WAA as the primary grain became established as the major sink for photosynthate and the energy requirements to translocate photosynthate to the primary grain were high. The overall decline in the TR of stressed and non-stressed plants reflects the loss of <sup>14</sup>C from the whole plant due to respiration. The TR of the whole plant declined sharply from 2 to 4 WAA in both stressed and non-stressed plants which may indicate an increase in respiration to provide the energy required for the more direct and rapid translocation of photosynthate to the primary grain which had become established as the major sink for photosynthate at this stage. It is of interest to determine the respiration losses of <sup>14</sup>C assimilated at A during grain fill. From A to PM the TR of the whole plant of stressed and non-stressed plants declined by 4 516 430 and 3 694 584 dpm plant<sup>-1</sup>, respectively. This means that 26,0 and 22,0 % of the <sup>14</sup>C assimilated at A was

lost through respiration in stressed and non-stressed plants respectively.

When plants were labelled at 2 WAA the TR of the whole plant on all sampling occasions was greater than that of plants labelled at 4 WAA and 6 WAA (Figure 4.26). The TR of the whole plant of plants labelled at 2 WAA relative to plants labelled at A has been discussed above. The TR of the whole plant of stressed and non-stressed plants at 2 WAA was 14 749 517 and 14 361 047 dpm plant<sup>-1</sup>, respectively. This increased to 16 247 735 and 14 460 497 dpm plant<sup>-1</sup> at 4 WAA; decreased to 15 094 872 and 11 879 678 dpm plant<sup>-1</sup> at 6 WAA and then decreased to 13 045 213 dpm plant<sup>-1</sup> and increased to 13 660 899 dpm plant<sup>-1</sup> at PM in stressed and non-stressed plants, respectively. Thus the TR of the whole plant fluctuated from 2 WAA to PM particularly in the non-stressed plants. The increase in the TR of the whole plant of stressed and non-stressed plants from 2 to 4 WAA and in the non-stressed plants from 6 WAA to PM was due to sampling error. The TR of the whole plant of stressed plants was higher than that of non-stressed plants from 2 to 6 WAA. Only at PM was the TR of the whole plant of the stressed plants less than that of the non-stressed plants. When plants were labelled at 2 WAA, the stressed plants had already been subjected to two consecutive stress cycles. However, at 2 WAA the stressed plants were watered in the morning of the day on which labelling took place. Thus it appears that the stressed plants recovered sufficiently to assimilate slightly more <sup>14</sup>C than the non-stressed plants. However, in contrast to plants labelled at A the <sup>14</sup>C assimilated at 2 WAA was translocated to a greater

extent to the grain. The stressed plants in particular had mobilized 59,0 % of the  $^{14}\text{C}$  in the whole plant 48 h after labelling at 2 WAA to the grain as opposed to 51,8 % for the non-stressed plants. Assuming that the respiration losses of the grain are lower than those of the organs of the shoot (Palmer et al., 1973), it is possible that since the non-stressed plants translocated a smaller proportion of  $^{14}\text{C}$  to the grain and retained more in the whole shoot, more  $^{14}\text{C}$  was lost from the non-stressed plants through respiration of the shoot soon after labelling than was the case for the stressed plants. The overall decline in the TR of the whole plant of stressed and non-stressed plants reflects the loss of  $^{14}\text{C}$  from the whole plant due to respiration. It is of interest to determine the respiration losses of  $^{14}\text{C}$  assimilated at 2 WAA from 2 WAA to PM. From 2 WAA to PM the TR of the whole plant of the stressed and non-stressed plants declined by 1 704 304 and 700 148 dpm plant<sup>-1</sup>, respectively. This means that 11,6 and 4,9 % of the  $^{14}\text{C}$  recorded in the stressed and non-stressed plants, respectively at 2 WAA was lost through respiration. Thus it is clear that the stressed plants respired a greater amount and proportion of whole plant  $^{14}\text{C}$  from 2 WAA to PM compared to non-stressed plants.

When plants were labelled at 4 WAA the TR of the whole plant of stressed and non-stressed plants on all sampling occasions was less than that of plants labelled at A and 2 WAA but greater than that of plants labelled at 6 WAA (Figure 4.26). The TR of the whole plant of stressed and non-stressed plants at 4 WAA was 6 870 564 and 8 410 327 dpm plant<sup>-1</sup>, respectively. This declined to 5 766 073 and 7 383 929 dpm plant<sup>-1</sup> at 6 WAA and then increased

to 6 135 745 and 9 200 375 dpm plant<sup>-1</sup> at PM in stressed and non-stressed plants, respectively. The increase in the TR of the whole plant from 6 WAA to PM particularly in the non-stressed plants was due to the high SR for the grain recorded for plants sampled from replication one. The TR of the whole plant of non-stressed plants was higher on all sampling occasions than that of the stressed plants. When plants were labelled at 4 WAA the stressed plants had already undergone four consecutive stress cycles. Thus it appears that the photosynthetic capacity of the stressed plants had been reduced relative to that of the non-stressed plants since the TR of the whole plant of the stressed plants 48 h after labelling at 4 WAA was 81,7 % of the non-stressed plants. The overall decline in the TR of the whole plant reflects the loss of <sup>14</sup>C from the plants through respiration. It is of interest to determine the respiration losses of <sup>14</sup>C assimilated at 4 WAA from 4 WAA to PM. From 4 WAA to PM the TR of the whole plant of stressed and non-stressed plants declined by 734 819 and 889 697 dpm plant<sup>-1</sup>, respectively. For the non-stressed plants the TR of the whole plant at PM was calculated from the average of values for replications two and three. This means that 10,7 and 10,6 % of the <sup>14</sup>C recorded in the whole plant of stressed and non-stressed plants, respectively at 4 WAA was lost through respiration.

When plants were labelled at 6 WAA, the TR of the whole plant of stressed and non-stressed plants on all sampling occasions was less than that of plants labelled on the other three occasions (Figure 4.26). The TR of the whole plant at 6 WAA was 2 063 377 and 2 740 269 dpm plant<sup>-1</sup>, which declined to 1 763 592 and

2 057 907 dpm plant<sup>-1</sup> at PM in stressed and non-stressed plants, respectively. The TR of the whole plant of non-stressed plants was higher on all sampling occasions than that of stressed plants. When plants were labelled at 6 WAA the stressed plants had already undergone six consecutive stress cycles. Thus it appears that the photosynthetic capacity of stressed plants had been reduced relative to that of non-stressed plants since the TR of the whole plant of the stressed plants 48 h after labelling at 6 WAA was 75,3 % of the non-stressed plants. The overall decline in the TR of the whole plant reflects the loss of <sup>14</sup>C from the plants through respiration. It is of interest to determine the respiration losses of <sup>14</sup>C assimilated at 6 WAA from 6 WAA to PM. From 6 WAA to PM the TR of the whole plant of stressed and non-stressed plants declined by 299 785 and 682 362 dpm plant<sup>-1</sup>, respectively. This means that 14,5 and 24,9 % of the <sup>14</sup>C recorded in the whole plant of stressed and non-stressed plants respectively at 6 WAA was lost through respiration.

On each labelling occasion batches of 12 plants were exposed to  $720 \times 10^6$  dpm released from Na<sub>2</sub>CO<sub>3</sub>, assuming the complete evolution of all the <sup>14</sup>CO<sub>2</sub>. It is of interest to calculate what proportion of the  $60 \times 10^6$  dpm that each plant was exposed to on each labelling occasion was assimilated into the stressed and non-stressed plants 48 h after labelling on each occasion. The TR of the whole plant of stressed and non-stressed plants 48 h after labelling at A was 17 347 474 and 16 816 792 dpm plant<sup>-1</sup>, respectively. This represents an assimilation of 28,9 and 28,0 % of the  $60 \times 10^6$  dpm available to each plant for the stressed and non-stressed plants, respectively. The TR of the whole plant of

stressed and non-stressed plants 48 h after labelling at 2 WAA was 14 749 517 and 14 361 047 dpm plant<sup>-1</sup>, respectively. This represents an assimilation of 24,6 and 23,9 % of the  $60 \times 10^6$  dpm available to each plant for the stressed and non-stressed plants, respectively. The TR of the whole plant of stressed and non-stressed plants 48 h after labelling at 4 WAA was 6 870 564 and 8 410 327 dpm plant<sup>-1</sup>, respectively. This represents an assimilation of 11,4 and 14,0 % of the  $60 \times 10^6$  dpm available to each plant for the stressed and non-stressed plants, respectively. The TR of the whole plant of stressed and non-stressed plants 48 h after labelling at 6 WAA was 2 063 377 and 2 740 269 dpm plant<sup>-1</sup>, respectively. This represents an assimilation of 3,4 and 4,6 % of the  $60 \times 10^6$  dpm available to each plant for the stressed and non-stressed plants, respectively.

From the above data it is apparent that the photosynthetic activity of the plants declined from anthesis to physiological maturity. The stressed plants assimilated a greater proportion of the available <sup>14</sup>C than the non-stressed plants at A and 2 WAA. However, the non-stressed plants assimilated a greater proportion of the available <sup>14</sup>C than the stressed plants at 4 and 6 WAA.

#### 4.3.8 Radioactivity associated with total sugars and starch

The data presented in Tables 4.74 to 4.77 are largely self explanatory thus only some of the points of interest will be discussed.

##### Labelling at A

When plants were labelled at A, 7,5 and 5,0 % of the whole plant  $^{14}\text{C}$  at A occurred in the grain of the stressed and non-stressed plants respectively and at PM this had increased to 31,0 and 26,9 %, respectively, of the whole plant  $^{14}\text{C}$  (Section 4.3.4.3). Thus plants labelled at A retained the highest percentage of whole plant  $^{14}\text{C}$  in the shoot compared to plants labelled on each of the three subsequent occasions. This tends to indicate that a large proportion of the  $^{14}\text{C}$  assimilated at A was used for the final structural growth of the whole shoot with little  $^{14}\text{C}$  left as labile organic compounds that could be mobilized to the grain. The grain became established as the major sink for photosynthate 10 to 14 d after the plants were first labelled at A.

The SR of the TS of the A1 and B1 plant parts of the stressed plants at 48 h after labelling at A was lower than that of the non-stressed plants 48 h after labelling at A (Table 4.74). However, the SR of the TS of the cob and grain of the stressed plants at 48 h after labelling at A was higher than that of the non-stressed plants at 48 h after labelling, while the SR of the shank of stressed plants was marginally higher than that of non-

Table 4.74 Component non-structural carbohydrate  $^{14}\text{C}$  radioactivity in selected plant parts sampled at 48h and at physiological maturity (PM) from a maize hybrid subjected to water stress (stress) and lack of water stress (non-stress) during grain fill and labelled at anthesis

**LABELLING AT ANTHESIS - STRESS**

Sampling at	Plant part	Specific radioactivity (dpm x $10^{-3}$ g $^{-1}$ )			Total radioactivity (dpm x $10^{-3}$ (plant part) $^{-1}$ )				Radioactivity per plant part (%)			Radioactivity per whole plant (%)		
		Total sugars	Starch	TNC	Total sugars	Starch	TNC	Residual	Total sugars	Starch	TNC	Total sugars	Starch	TNC
48h	A1	446,6	135,6	338,4	331,6	53,7	385,3	232,4	53,7	8,7	62,4	1,91	0,31	2,22
	B1	356,0	109,8	284,8	530,1	66,6	596,7	353,9	55,8	7,1	62,8	3,06	0,38	3,44
	Shank	294,2	621,9	367,8	118,9	72,7	191,5	465,6	18,1	11,1	29,2	0,69	0,42	1,10
	Cob	867,3	604,9	721,0	439,3	386,2	825,5	673,6	29,3	25,8	55,1	2,53	2,23	4,76
	Grain	710,7	540,0	632,8	407,1	259,9	667,0	610,2	31,9	20,4	52,2	2,35	1,50	3,85
PM	A1	47,4	86,2	55,7	43,5	21,6	65,1	180,5	17,7	8,8	26,5	0,34	0,17	0,51
	B1	67,2	64,1	66,4	113,1	35,6	148,7	219,9	30,7	9,6	40,4	0,88	0,28	1,16
	Shank	64,7	217,2	89,3	39,0	25,2	64,2	336,9	9,7	6,2	16,0	0,30	0,20	0,50
	Cob	155,5	76,8	104,2	179,2	165,8	344,9	1 789,2	8,4	7,7	16,2	1,40	1,29	2,69
	Grain	121,6	27,0	29,7	294,2	2 148,3	2 442,4	1 457,7	7,5	55,0	62,6	2,29	16,74	19,04

**LABELLING AT ANTHESIS - NON-STRESS**

48h	A1	473,5	108,9	352,2	369,3	42,3	411,6	127,9	68,5	7,8	76,3	2,20	0,25	2,45
	B1	435,2	81,8	324,4	640,2	55,0	695,2	283,2	65,4	5,6	71,1	3,81	0,33	4,13
	Shank	288,5	614,3	360,3	108,0	65,0	173,1	265,6	24,6	14,8	39,4	0,64	0,39	1,03
	Cob	512,2	326,0	432,1	482,7	231,7	714,4	681,0	34,6	16,6	51,2	2,87	1,38	4,25
	Grain	638,8	553,5	602,9	366,3	231,2	597,4	291,4	41,2	26,0	67,2	2,18	1,37	3,55
PM	A1	39,8	97,7	50,2	56,5	30,4	86,8	277,8	15,5	8,4	23,8	0,43	0,23	0,66
	B1	48,1	59,2	50,7	118,7	45,8	164,5	366,7	22,3	8,7	31,0	0,90	0,35	1,25
	Shank	36,2	79,4	44,8	29,6	16,3	46,0	304,2	8,5	4,7	13,1	0,23	0,12	0,35
	Cob	44,5	41,8	42,7	70,8	122,7	193,5	1 932,4	3,3	5,8	9,1	0,54	0,93	1,47
	Grain	127,2	20,7	23,6	355,0	2 042,3	2 397,3	1 160,3	10,0	57,5	67,4	2,71	15,56	18,27

stressed plants. The SR of the starch of the A1 and B1 plant parts and particularly the cob of the stressed plants at 48 h after labelling at A was higher, while that of the shank was marginally higher, than that of the non-stressed plants 48 h after labelling at A. This indicates that within 48 h of labelling at A the stressed plants had converted less  $^{14}\text{C}$  into TS per unit mass in the A1 and B1 plant parts than did the non-stressed plants. However, the stressed plants converted more  $^{14}\text{C}$  into TS per unit mass in the shank, cob and grain than did the non-stressed plants within 48 h of labelling at A. Also, the stressed plants converted more  $^{14}\text{C}$  into starch per unit mass in the A1, B1, shank and cob plant parts than did the non-stressed plants within 48 h after labelling at A. The non-stressed plants did convert more  $^{14}\text{C}$  per unit mass into starch in the grain than did the stressed plants within 48 h after labelling. The physiological significance of the greater utilization of  $^{14}\text{C}$  for starch synthesis in the A1, B1, shank and cob plant parts of the stressed plants within 48 h of labelling at A is not certain. In particular the SR of the TS and starch in the cob of stressed plants was substantially higher than that of non-stressed plants. At A the grain was not yet established as the major sink for photosynthate and during the first 10 to 14 d after fertilization the cob and husks underwent large increases in dry mass (Table 4.8 and Appendix 46). Thus within 48 h of labelling at A stressed plants had translocated more  $^{14}\text{C}$  directly to the cob than non-stressed plants resulting in a greater concentration of  $^{14}\text{C}$  per unit mass of TS and per unit mass of starch in the cob. The lower SR of the TS of the A1 and B1 plant parts in conjunction with the higher SR of the shank of stressed plants in comparison

to non-stressed plants is indicative of the more direct and rapid translocation of  $^{14}\text{C}$  from the leaves through the stem to the shank and cob and eventually to the grain under stress conditions. It is noteworthy that 48 h after labelling at A, only in the shank of stressed and non-stressed plants did the SR of the starch exceed the SR of the TS. This may indicate the rapid formation of starch in the shank soon after labelling resulting in more  $^{14}\text{C}$  per unit mass being utilized. At PM the SR of the TS of the A1, B1, shank and cob plant parts of the stressed plants was higher than that of the non-stressed plants, while the SR of the TS of the grain of the stressed plants was lower than that of the non-stressed plants. The SR of the starch of the B1, shank, cob and grain plant parts of stressed plants at PM was higher than that of non-stressed plants. Only the SR of the starch in the A1 plant part of non-stressed plants at PM was higher than that of the A1 plant part of stressed plants. It appears therefore that since the stressed plants assimilated less  $^{12}\text{C}$  from A to PM in comparison to the non-stressed plants (as judged by the lower whole plant dry mass under stress conditions, Table 4.58 and Appendix 49) stressed plants generally maintained a higher concentration of  $^{14}\text{C}$  in the TS and starch at PM than did non-stressed plants. In particular the SR of the TS and starch of the shank and cob of stressed plants at PM was higher than that of the shank and cob of non-stressed plants at PM. This may indicate the more direct and rapid mobilization of  $^{14}\text{C}$  to the primary ear under stress conditions with the result that more  $^{14}\text{C}$  was used per unit mass to synthesize TS and starch in the shank and cob under stress conditions. It may also indicate that less  $^{12}\text{C}$  was used later to synthesize these non-structural carbohydrate

components in the stressed plants. It may also indicate that stressed plants mobilized more  $^{14}\text{C}$  to the grain during grain fill and that as the rate of dry mass gain by the grain ceased at PM, more  $^{14}\text{C}$  accumulated in these plant parts in the form of TS and starch compared to non-stressed plants. The higher SR of the starch in the grain of stressed plants at PM is indicative of the more direct translocation of the  $^{14}\text{C}$  assimilated at A to the grain under stress conditions. The general decline in the SR of the TS and starch in the five plant parts in stressed and non-stressed plants from A to PM reflects the utilization of these components for respiration and it also reflects the incorporation of  $^{12}\text{C}$  into TS and starch.

The TR of the TS and starch in the five organs provides a different picture to the SR of these non-structural carbohydrates. Forty-eight hours after labelling at A the TS in all five plant parts of both stressed and non-stressed plants recorded a higher TR than did the starch. The difference between the TR of the TS and starch was greatest in the A1 and B1 plant parts of both stressed and non-stressed plants. This indicates that the predominant non-structural carbohydrates in these stem segments are TS. The TR of the TS in the A1, B1 and cob plant parts of stressed plants was less than that of non-stressed plants 48 h after labelling at A. The TR of the starch of stressed plants in all five plant parts at 48 h was greater than that of non-stressed plants. This would seem to indicate that the stressed plants tended to utilize more  $^{14}\text{C}$  for the synthesis of starch in these plant parts. The higher TR of the starch in the grain of stressed plants at 48 h is probably due to the more

direct and rapid translocation of  $^{14}\text{C}$  to the grain under stress conditions. However, the physiological significance of the greater utilization of  $^{14}\text{C}$  to synthesize starch in the A1, B1, shank and cob plant parts under stress conditions is not certain. However, when the TR of the TS and starch are viewed in combination i.e. as TNC, the TR of TNC in the A1 and B1 plant parts of stressed plants was less than that of the non-stressed plants, while the TR of the TNC in the shank, cob and grain of the stressed plants was higher than that of the non-stressed plants. Thus it would seem that the stressed plants mobilized more  $^{14}\text{C}$  to the grain within 48 h of labelling with the result that the TR of the TNC in the grain and in the plant parts in closest proximity to the grain i.e. the cob and shank was higher than that of the non-stressed plants. The non-stressed plants, on the other hand, retained more  $^{14}\text{C}$  in the A1 and B1 stem segments with the result that the TR of the TNC in these plant parts was higher than that of the stressed plants. At PM the TR of the TS in the A1, B1, shank and cob plant parts of stressed plants was still higher than that of the TR of the starch, while the TR of the starch in the grain was higher than that of the TS. In the non-stressed plants at PM the TR of the TS in the A1, B1 and shank plant parts was higher than the TR of the starch, while the TR of the starch in the cob and grain was higher than the TR of the TS. It is clear therefore that at PM most of the  $^{14}\text{C}$  in the grain of stressed and non-stressed plants was converted to starch whereas at A the  $^{14}\text{C}$  in the grain was still predominantly in the form of TS as the process of starch deposition had not become fully operational. At PM more of the  $^{14}\text{C}$  in the A1, B1 and shank plant parts was in the form of TS than starch in both

stressed and non-stressed plants. However, in contrast to the non-stressed plants more of the  $^{14}\text{C}$  in the cob of the stressed plants was in the form of TS than starch. The physiological significance of this is not certain but it does indicate the greater accumulation of  $^{14}\text{C}$  in the cob as TS under stress conditions. From A to PM the TR of the TNC in the A1, B1, shank and cob plant parts declined while the TR of the TNC in the grain increased substantially in both stressed and non-stressed plants. The decline in the TR of the TNC in the A1, B1, shank and cob plant parts is indicative of the mobilization of the  $^{14}\text{C}$  in these plant parts to the grain in the form of the main translocatory sugar, sucrose. It is also indicative of the loss of  $^{14}\text{C}$  through respiration. The increase in the TR of the TNC in the grain was due to the translocation of  $^{14}\text{C}$  from the shoot to the grain. As mentioned the high TR of the TNC in the grain was due largely to  $^{14}\text{C}$  in the form of starch. It is noteworthy that the TR of the TNC in the A1 and B1 plant parts in the non-stressed plants was higher than that in the stressed plants, while the TR of the TNC in the shank, cob and grain in the non-stressed plants was less than that in the stressed plants. Thus it would appear that during grain fill the stressed plants mobilized more  $^{14}\text{C}$  out of the shoot, specifically the A1 and B1 stem segments, to the grain and to the plant parts in close proximity to the grain, viz the shank and cob, than did the non-stressed plants.

At 48 h the TR of the TNC as a percentage of the TR of each plant part was lower in the A1, B1, shank and grain plant parts of the stressed plants than the non-stressed plants. Why a smaller proportion of the TR of these plant parts was in the form of TNC

under stress conditions is not certain. It is also not clear why a higher proportion of the TR of the cob was in the form of TNC under stress conditions than under non-stress conditions. Ignoring data for the shank for the moment, the proportion of plant part TR in the form of TNC at 48 h ranged from 52,2 % in the grain of the stressed plants to 76,3 % in the A1 plant part of the non-stressed plants. Except for the shank, at 48 h more than half of the radioactivity in each plant part was in the form of TNC with the remaining proportion in the form of residual components. Nonetheless the proportion in the form of residual components in each plant part represents a higher proportion 48 h after labelling at A than the proportions that occurred in each plant part 48 h after labelling at each of the three subsequent occasions. The markedly low proportion of shank radioactivity in the form of TNC, namely 29,2 and 39,4 % for stressed and non-stressed plants respectively, indicates that much of the  $^{14}\text{C}$  in the shank occurred in the form of residual components. This may indicate the synthesis of structural compounds, proteins and lipids since it will be recalled that the shank almost doubled in dry mass from A to 2 WAA (Table 4.8 and Appendix 46). The shank may synthesize much protein which may be involved in translocating the photosynthate arriving in it from the rest of the plant to the grain. Ignoring data for the grain for the moment, at PM the proportion of the TR of each plant part in the form of TNC had declined substantially and ranged from 9,1 % in the cob of non-stressed plants to 40,4 % in the B1 plant part of stressed plants. Except for the grain, at PM more than half of the radioactivity in each plant part was in the form of residual components. In stressed plants the decline in the proportion of

TR in the form of TNC in the A1, B1 and shank plant parts was due to a larger decline in the amount of  $^{14}\text{C}$  in the form of TNC than in the form of residual components. On the other hand, the decline in the proportion of the cob TR in the form of TNC was due to a decline in the amount of  $^{14}\text{C}$  in the form of TNC as well as a substantial increase in the amount of  $^{14}\text{C}$  in the form of residual components as judged by the increase in the TR of the residual components. It appears that the A1, B1 and shank plant parts lost more  $^{14}\text{C}$  in the form of TNC than  $^{14}\text{C}$  in the form of residual components from A to PM in stressed plants. The cob, on the other hand, appeared to lose  $^{14}\text{C}$  in the form of TNC from A to PM while converting  $^{14}\text{C}$  to residual components. The conversion of  $^{14}\text{C}$  to residual components probably occurred during the increase in the dry mass that the cob underwent from A to approximately 2 WAA and it is likely that the  $^{14}\text{C}$  was converted to structural material. In the stressed plants the proportion of grain TR in the form of TNC increased as a result of an increase in the amount of  $^{14}\text{C}$  in the form of TNC. However, the amount of  $^{14}\text{C}$  in the form of residual components also increased as judged by the increase in the TR of the residual components. In the non-stressed plants the decline in the proportion of the TR of the A1, B1 and shank plant parts in the form of TNC was due to a substantial decline in the amount of  $^{14}\text{C}$  in the form of TNC while the amount of  $^{14}\text{C}$  in the form of residual components increased slightly. On the other hand, the decline in the proportion of the cob TR in the form of TNC was due to a decline in the amount of  $^{14}\text{C}$  in the form of TNC as well as a substantial increase in the amount of  $^{14}\text{C}$  in the form of residual components. In contrast to the stressed plants, it appears that the A1, B1

and shank plant parts of the non-stressed plants lost  $^{14}\text{C}$  in the form of TNC while converting some  $^{14}\text{C}$  to residual components from A to PM. The cob, on the other hand, appeared to lose  $^{14}\text{C}$  in the form of TNC from A to PM while converting  $^{14}\text{C}$  to residual components. The conversion of  $^{14}\text{C}$  to residual components probably occurred during the increase in the dry mass that the cob underwent from A to approximately 2 WAA, and it is likely that the  $^{14}\text{C}$  was converted largely to structural material. In the non-stressed plants the proportion of grain TR in the form of TNC increased as a result of an increase in the amount of  $^{14}\text{C}$  in the form of TNC. However, the amount of  $^{14}\text{C}$  in the form of the residual components also increased as judged by the increase in the TR of the residual components.

It is interesting to note that at PM as much as 40,4 % of the radioactivity in the B1 plant part of the stressed plants was in the form of TNC with the majority (30,7 %) of this in the form of TS. It appears that not all of the  $^{14}\text{C}$  assimilated at A which occurred as labile organic compounds in the shoot particularly as TNC had been mobilized to the grain when physiological maturity was attained. However, this need not necessarily be interpreted as indicating that the  $^{14}\text{C}$  had been in the form of TNC from A to PM since there may be continual interconversions of sugars to amino acids, proteins and lipids and vice versa. It is noteworthy that at PM the stressed plants had a higher proportion of the TR of the A1, B1, shank and cob plant parts in the form of TNC in comparison to the non-stressed plants. This may indicate that less  $^{14}\text{C}$  was converted to residual components in these plant parts under stress conditions. As expected more

than half of the radioactivity in the grain at PM was in the form of TNC as starch.

It is of interest to note that at A, 3,85 and 3,55 % of the whole plant radioactivity occurred in the form of TNC in the grain of stressed and non-stressed plants, respectively. At PM this proportion had increased to 19,04 and 18,27 % in stressed and non-stressed plants, respectively. It appears that the stressed plants converted a greater proportion of whole plant  $^{14}\text{C}$  to TNC in the grain than did the non-stressed plants. It is also of interest to note that at A and at PM the non-stressed plants had a higher proportion of whole plant  $^{14}\text{C}$  in the form of TNC in the A1 and B1 plant parts than did the stressed plants, while the stressed plants had a higher proportion of whole plant  $^{14}\text{C}$  in the shank and cob. This may once again indicate that the stressed plants mobilized more  $^{14}\text{C}$  out of the shoot, specifically the A1 and B1 stem segments to the primary ear with the result that a greater proportion of whole plant  $^{14}\text{C}$  occurred as TNC in the cob and shank.

#### Labelling at 2 WAA

When plants were labelled at 2 WAA, 59,0 and 51,8 % of the whole plant  $^{14}\text{C}$  at 2 WAA occurred in the grain of stressed and non-stressed plants, respectively. This increased to 84,2 and 87,9 % in stressed and non-stressed plants respectively at PM (Section 4.3.4.3). Thus it is clear that  $^{14}\text{C}$  assimilated at 2 WAA was rapidly mobilized to the grain and by PM only a small proportion

remained in the whole shoot. Thus at 2 WAA the primary grain was established as a major sink for photosynthate.

At 48 h after labelling the SR of the TS of all five plant parts in both stressed and non-stressed plants was higher than the SR of the starch (Table 4.75). This would seem to indicate that less  $^{14}\text{C}$  per unit mass was utilized to synthesize starch 48 h after labelling. At 48 h the SR of the TS of all five plant parts was less in stressed plants than non-stressed plants. The SR of the starch in the A1, B1, shank and cob plant parts of stressed plants was substantially lower than that of the non-stressed plants. However, the SR of the starch in the grain of stressed plants was higher than that of non-stressed plants. Also the SR of the TNC in the grain of stressed plants was higher than that of non-stressed plants. It appears that within 48 h less  $^{14}\text{C}$  occurred in the form of TS and starch in the A1, B1, shank and cob plant parts in the stressed plants with more  $^{14}\text{C}$  being utilized for the synthesis of TNC per unit mass in the grain. At PM the SR of the TS in the A1, B1, cob and grain plant parts of stressed plants was higher than that of non-stressed plants, while the SR of the starch in the B1, shank and grain plant parts of stressed plants was higher than that of non-stressed plants. However, the SR of the TNC in only the B1 and grain plant parts of stressed plants was higher at PM than that of non-stressed plants. This would seem to indicate that stressed plants utilized more  $^{14}\text{C}$  per unit mass to synthesize the TNC in the grain with the result that the SR of the TNC in the grain at PM under stress conditions was higher than that under non-stress conditions. However, why the SR of the TNC in the B1

Table 4.75 Component non-structural carbohydrate <sup>14</sup>C radioactivity in selected plant parts sampled at 48h and at physiological maturity (PM) from a maize hybrid subjected to water stress (stress) and lack of water stress (non-stress) during grain fill and labelled at two weeks after anthesis

**LABELLING 2 WEEKS AFTER ANTHESIS - STRESS**

Sampling at	Plant part	Specific radioactivity (dpm x 10 <sup>-3</sup> g <sup>-1</sup> )			Total radioactivity (dpm x 10 <sup>-3</sup> (plant part) <sup>-1</sup> )				Radioactivity per plant part (%)			Radioactivity per whole plant (%)		
		Total sugars	Starch	TNC	Total sugars	Starch	TNC	Residual	Total sugars	Starch	TNC	Total sugars	Starch	TNC
48h	A1	253,8	38,2	184,5	211,1	15,1	226,2	30,6	82,2	5,9	88,1	1,43	0,10	1,53
	B1	207,9	59,6	159,5	249,7	34,7	284,4	29,8	79,5	11,0	90,5	1,69	0,24	1,93
	Shank	313,3	134,1	287,5	256,6	18,5	275,1	18,3	87,5	6,3	93,8	1,74	0,13	1,86
	Cob	321,9	130,6	253,3	819,3	185,7	1 005,0	467,7	55,6	12,6	68,2	5,55	1,26	6,81
	Grain	822,0	271,5	303,2	1 138,3	6 140,9	7 279,2	1 421,7	13,1	70,6	83,7	7,72	41,63	49,35
PM	A1	12,5	25,5	14,8	11,9	5,3	17,2	29,5	25,5	11,3	36,8	0,09	0,04	0,13
	B1	18,4	29,3	20,5	30,7	11,7	42,5	24,9	45,6	17,4	63,1	0,24	0,09	0,33
	Shank	26,9	51,9	31,7	13,9	6,3	20,2	42,5	22,2	10,1	32,3	0,11	0,05	0,16
	Cob	89,0	18,7	43,8	101,4	38,6	140,0	897,3	9,8	3,7	13,5	0,78	0,30	1,07
	Grain	545,9	109,1	118,4	931,8	8 534,0	9 465,8	1 552,9	8,5	77,5	85,9	7,14	65,42	72,56

**LABELLING 2 WEEKS AFTER ANTHESIS - NON-STRESS**

48h	A1	295,0	106,2	245,6	220,3	28,1	248,3	58,7	71,8	9,1	80,9	1,53	0,20	1,73
	B1	319,8	114,0	240,0	284,7	64,3	348,9	91,8	64,6	14,6	79,2	1,98	0,45	2,43
	Shank	387,5	286,1	371,3	279,2	39,3	318,5	26,7	80,9	11,4	92,3	1,94	0,27	2,22
	Cob	428,6	146,9	322,6	1 267,6	262,1	1 529,6	54,2	80,0	16,6	96,6	8,83	1,82	10,65
	Grain	850,6	212,8	242,8	1 019,4	5 153,6	6 172,9	1 199,1	13,8	69,9	83,7	7,10	35,89	42,98
PM	A1	10,9	33,4	15,3	10,8	7,9	18,7	23,1	25,8	19,0	44,8	0,08	0,06	0,14
	B1	18,2	21,6	18,9	32,3	10,8	43,1	22,4	49,4	16,5	65,8	0,24	0,08	0,32
	Shank	34,5	49,8	37,0	24,1	6,6	30,7	20,7	47,0	12,8	59,8	0,18	0,05	0,22
	Cob	72,4	53,8	61,0	100,5	119,4	219,9	571,0	12,7	15,1	27,8	0,74	0,87	1,61
	Grain	292,9	88,2	93,3	663,8	7 879,0	8 542,8	3441,1	5,5	65,8	71,3	4,86	57,68	62,53

plant part under stress conditions was higher than that under non-stress conditions is not certain.

At 48 h after labelling the TR of the TS in the A1, B1, shank and cob plant parts of both stressed and non-stressed plants was higher than the TR of the starch. However, the TR of the starch in the grain of both stressed and non-stressed plants was substantially higher than the TR of the TS. In fact, the difference in TR between the TS and starch was greatest in the grain of both stressed and non-stressed plants. The higher TR of the TS in the A1, B1, shank and cob plant parts compared to that of starch indicates that the predominant non-structural carbohydrates in these plant parts at 48 h are TS. The TR of both the TS and the starch in the A1, B1, shank and cob plant parts of stressed plants was less than that of non-stressed plants, while the TR of the TS and the starch in the grain of the stressed plants was higher than that of the non-stressed plants. It would appear that within 48 h after labelling less  $^{14}\text{C}$  remained in the A1, B1, shank and cob plant parts of the stressed plants with more  $^{14}\text{C}$  rapidly translocated to the grain under stress conditions than non-stress conditions. The radioactivity associated with the TS in the grain is indicative of  $^{14}\text{C}$  arriving at the grain from the rest of the plant as sucrose and then being converted to glucose and fructose prior to uptake from the apoplast by the basal endosperm cells (Shannon et al., 1986). Once inside the symplast of the endosperm cells glucose and fructose are converted to sucrose whereupon sucrose is converted back to glucose and fructose which are then used for the synthesis of starch (Shannon, 1968). The radioactivity

associated with the TS in the grain is also indicative of these sugars being utilized for various metabolic processes such as respiration and amino acid and lipid synthesis within the kernels. At PM the TR of the TS in the A1, B1, shank and cob plant parts of stressed plants was still higher than the TR of the starch. In non-stressed plants at PM the TR of the TS in the A1, B1 and shank plant parts was still higher than the TR of the starch. However, the TR of the starch in the cob was higher than the TR of the TS. The physiological significance of the higher TR of the starch in the cob of the non-stressed plants at PM than the TR of the TS is uncertain. It may, however, indicate the mobilization of  $^{14}\text{C}$  to the primary ear in the latter phase of grain fill with the sucrose in excess to grain requirements being converted to starch in the cob. From 2 WAA to PM the TR of the TS and the starch in the A1, B1, shank and cob plant parts declined, while in the grain the TR of the TS declined and the TR of the starch increased in both stressed and non-stressed plants. The overall decline in the TR of the TS and the starch in the A1, B1, shank and cob plant parts is indicative of the mobilization of the  $^{14}\text{C}$  in these plant parts to the grain in the form of the main translocatory sugar, sucrose. It is also indicative of the loss of  $^{14}\text{C}$  through respiration. The overall increase in the TR of the TNC in the grain was due to the translocation of  $^{14}\text{C}$  from the shoot to the grain. As mentioned, the TR of the TS in the grain declined from A to PM so that the increase in the TR of the TNC in the grain was due to the increase in the TR of the starch in the grain. At PM the TR of the TNC in the A1, B1, shank and cob plant parts was higher in non-stressed plants than stressed plants, while the TR of the TNC

in the grain of stressed plants was higher than that of non-stressed plants. Thus it would appear that from 2 WAA to PM stressed plants retained less  $^{14}\text{C}$  in the A1, B1, shank and cob plant parts in the form of TNC while mobilizing more  $^{14}\text{C}$  to the grain and converting more  $^{14}\text{C}$  into TNC specifically starch than did the non-stressed plants. This is indicative of the more direct translocation of  $^{14}\text{C}$  assimilated at 2 WAA to the grain and the greater mobilization of  $^{14}\text{C}$  to the grain from the shoot under stress conditions.

At 48 h the proportion of the radioactivity in the plant parts in the form of TNC ranged from 68,2 % in the cob to 93,8 % in the shank of the stressed plants. In the non-stressed plants the proportion of plant part TR in the form of TNC ranged from 79,2 % in the B1 plant part to 96,6 % in the cob. The proportion of plant part TR in the form of TNC at 48 h was higher in the A1, B1 and shank plant parts of stressed plants than non-stressed plants. The proportion of plant part TR in the form of TNC in the cob of non-stressed plants was, however, higher than that of stressed plants. The stressed and non-stressed plants had, however, the same proportion of the grain TR in the form of TNC. It would appear that in contrast to the plants labelled at A, stressed plants at 48 h after labelling at 2 WAA had a higher proportion of the TR of the A1, B1 and shank plant parts in the form of TNC than the non-stressed plants while non-stressed plants had a greater proportion of the  $^{14}\text{C}$  in these plant parts in the form of residual components particularly in the B1 plant part. On the other hand, the proportion of cob TR in the form of TNC in the stressed plants was substantially less than that

of the non-stressed plants. It appears that a greater proportion (31,8 %) of the  $^{14}\text{C}$  in the cob was in the form of residual components. Since 93,8 % of the shank TR was in the form of TNC it appears that as carbohydrate arrived in the cob from the shank it was converted to residual components which are likely to be labile components such as amino acids and proteins. The physiological significance of this is uncertain, however, it may indicate altered patterns in N metabolism under stress conditions (Hsiao, 1973; Stewart and Larher, 1980). The high proportion of the shank TR in the form of TNC is once again indicative of its rôle as a conduit for photosynthate being translocated from the shoot to the grain. The stressed plants had a higher proportion of the shank TR in the form of TS than did the non-stressed plants, while the non-stressed plants had a higher proportion of shank TR in the form of starch. This is indicative of the more direct and rapid mobilization of  $^{14}\text{C}$  to the primary ear under stress conditions with a greater proportion of  $^{14}\text{C}$  occurring in the form of TS in the shank. At PM the proportion of the TR of each plant part (except for the grain of the stressed plants) in the form of TNC had declined substantially. Conversely, a greater proportion of the  $^{14}\text{C}$  in the plant parts at PM (except for the grain of the stressed plants) occurred in the form of residual components than at 48 h. Ignoring data for the grain for the moment, the proportion of plant part TR in the form of TNC ranged from 13,5 % in the cob of stressed plants to 65,8 % in the B1 plant part of non-stressed plants. In the stressed plants the decline in the proportion of the TR of the A1 and B1 plant parts in the form of TNC was due to a larger decline in the amount of  $^{14}\text{C}$  in the form of TNC than the decline in the amount

of  $^{14}\text{C}$  in the form of residual components. On the other hand, the decline in the proportion of the shank and cob TR in the form of TNC was due to a decline in the amount of  $^{14}\text{C}$  in the form of TNC as well as an increase in the amount of  $^{14}\text{C}$  in the form of residual components. The decline in the TR of the TNC in the cob was particularly marked. It appears that the A1 and B1 plant parts lost more  $^{14}\text{C}$  in the form of TNC than  $^{14}\text{C}$  in the form of residual components from 2 WAA to PM in stressed plants. The shank and cob appeared to lose  $^{14}\text{C}$  in the form of TNC from 2 WAA to PM while converting  $^{14}\text{C}$  to residual components. The physiological significance of the increase in the amount of  $^{14}\text{C}$  in the form of residual components in the shank and cob from 2 WAA to PM is uncertain. In the stressed plants the proportion of grain TR in the form of TNC increased slightly from 2 WAA to PM as a result of an increase in the amount of  $^{14}\text{C}$  in the form of TNC. However, the amount of  $^{14}\text{C}$  in the form of residual components also increased slightly in the grain as judged by the increase in the TR of the residual components. In the non-stressed plants the decline in the proportion of the TR of the A1, B1 and shank plant parts in the form of TNC was due to a more substantial decline in the amount of  $^{14}\text{C}$  in the form of TNC compared to the decline in the amount of  $^{14}\text{C}$  in the form of residual components. On the other hand, the marked decline in the proportion of the cob TR in the form of TNC was due to a substantial decline in the amount of  $^{14}\text{C}$  in the form of TNC as well as an increase in the amount of  $^{14}\text{C}$  in the form of residual components. Thus in both stressed and non-stressed plants the A1 and B1 plant parts lost  $^{14}\text{C}$  in the form of TNC and residual components. However, the shank of the stressed plants in

contrast to that of the non-stressed plants declined in the amount of  $^{14}\text{C}$  in the form of TNC while increasing in the amount of  $^{14}\text{C}$  in the form of residual components. In contrast to the stressed plants the proportion of grain TR in the form of TNC declined from 2 WAA to PM in non-stressed plants. Although the amount of  $^{14}\text{C}$  in the form of TNC increased in the grain during this period, the amount of  $^{14}\text{C}$  in the form of residual components increased substantially and by a greater proportion. The physiological significance of the greater proportion of grain TR in the form of residual components under non-stress conditions is uncertain. However, it may indicate that the non-stressed plants were able to afford the conversion of  $^{14}\text{C}$  assimilated at 2 WAA to organic compounds other than TNC in the grain as they assimilated more additional C after labelling than did the stressed plants.

It is noteworthy that the proportion of the shank TR in the form of TNC in the stressed plants declined to a greater extent than that in the non-stressed plants. This may indicate that the non-stressed plants continued to mobilize  $^{14}\text{C}$  through the shank in the form of TNC as late as at PM.

It is interesting to note that the B1 plant part of both stressed and non-stressed plants maintained a high proportion of its TR in the form of TNC at PM, namely 63,1 and 65,8 % in stressed and non-stressed plants, respectively. It appears that not all the  $^{14}\text{C}$  which occurred as TNC was mobilized to the grain by the time physiological maturity was attained. However, this need not necessarily be interpreted as indicating that the  $^{14}\text{C}$  had been in

the form of TNC from 2 WAA to PM in the B1 plant part. There may have been continual interconversions of sugars to amino acids, proteins and lipids within the B1 plant part. Also additional  $^{14}\text{C}$  may have been translocated into the B1 plant part from the leaves and lower stem internodes right up to physiological maturity.

It is noteworthy that at PM the non-stressed plants had a higher proportion of the TR of the A1, B1, shank and cob plant parts in the form of TNC than the stressed plants. This may indicate that the non-stressed plants mobilized  $^{14}\text{C}$  in the shoot into the form of TNC later into grain fill than the stressed plants.

It is of interest to note that at 2 WAA 49,35 and 42,98 % of the whole plant radioactivity occurred in the form of TNC in the grain of stressed and non-stressed plants, respectively. At PM this proportion had increased to 72,56 and 62,53 % in stressed and non-stressed plants, respectively. It appears that the stressed plants converted a greater proportion of whole plant  $^{14}\text{C}$  to TNC in the grain than did the non-stressed plants.

#### Labelling at 4 WAA

When plants were labelled at 4 WAA, 56,2 and 54,6 % of the whole plant  $^{14}\text{C}$  at 4 WAA occurred in the grain of stressed and non-stressed plants, respectively. This increased to 79,7 and 80,3 % in stressed and non-stressed plants respectively at PM (Section 4.3.4.3). Thus it is clear that  $^{14}\text{C}$  assimilated at 4 WAA was rapidly mobilized to the grain and at PM only a small proportion

remained in the whole shoot. Thus at 4 WAA the primary grain was still established as the major sink for photosynthate.

At 48 h after labelling the SR of the TS in the A1, B1, cob and grain plant parts of stressed plants and all five plant parts of non-stressed plants was higher than the SR of the starch (Table 4.76). This would seem to indicate that less  $^{14}\text{C}$  per unit mass was utilized to synthesize starch at 2 WAA. The reason for the higher SR of the starch in the shank of stressed plants than the SR of the TS is, however, not certain. At 48 h the SR of the TS of all five plant parts was less in stressed plants than non-stressed plants. The SR of the starch in the A1, B1, shank and cob plant parts of stressed plants was lower than that of the non-stressed plants. However, the SR of the starch in the grain of stressed plants was higher than that of non-stressed plants. But the SR of the TNC in the grain of the stressed plants was less than that of the non-stressed plants. Generally the lower SR of the TNC for all five plant parts of the stressed plants compared to the non-stressed plants reflects the lower whole plant TR recorded in the stressed plants at 48 h after labelling at 4 WAA (Section 4.3.7.2). Nonetheless the stressed plants still managed to rapidly convert more  $^{14}\text{C}$  per unit mass into starch in the grain than the non-stressed plants. It is noteworthy that at 48 h the SR of the starch in the shank was highest of all plant parts for both stressed and non-stressed plants. This may indicate that  $^{14}\text{C}$  was so rapidly mobilized to the primary ear resulting in more  $^{14}\text{C}$  per unit mass being utilized for starch synthesis in the shank. The exact rôle of starch in the shank once again comes into debate. Why the plants rapidly

Table 4.76 Component non-structural carbohydrate <sup>14</sup>C radioactivity in selected plant parts sampled at 48h and at physiological maturity (PM) from a maize hybrid subjected to water stress (stress) and lack of water stress (non-stress) during grain fill and labelled at four weeks after anthesis

**LABELLING AT 4 WEEKS AFTER ANTHESIS - STRESS**

Sampling at	Plant part	Specific radioactivity (dpm x 10 <sup>-3</sup> g <sup>-1</sup> )			Total radioactivity (dpm x 10 <sup>-3</sup> (plant part) <sup>-1</sup> )				Radioactivity per plant part (%)			Radioactivity per whole plant (%)		
		Total sugars	Starch	TNC	Total sugars	Starch	TNC	Residual	Total sugars	Starch	TNC	Total sugars	Starch	TNC
48h	A1	94,3	42,5	82,5	119,1	15,8	134,9	28,4	72,9	9,7	82,6	1,73	0,23	1,96
	B1	156,8	37,6	120,9	203,6	21,0	224,6	4,8	88,7	9,2	97,9	2,96	0,31	3,27
	Shank	141,8	143,9	142,0	149,6	21,4	171,0	27,5	75,4	10,8	86,1	2,18	0,31	2,49
	Cob	161,9	37,4	81,5	279,6	118,0	397,5	83,1	58,2	24,6	82,7	4,07	1,72	5,79
	Grain	346,7	43,2	53,1	756,6	2 784,7	3 541,3	382,2	19,3	71,0	90,3	11,01	40,53	51,54
PM	A1	29,3	30,0	29,5	25,3	7,5	32,8	13,3	55,0	16,2	71,2	0,41	0,12	0,53
	B1	40,6	32,5	38,2	67,5	22,0	89,5	29,3	56,8	18,6	75,4	1,10	0,36	1,46
	Shank	27,5	64,4	32,8	15,4	6,1	21,5	50,2	21,5	8,5	30,0	0,25	0,10	0,35
	Cob	76,1	32,0	52,0	83,7	42,2	125,9	90,5	38,7	19,5	58,2	1,36	0,69	2,05
	Grain	355,4	49,7	57,2	692,1	3 836,4	4 528,5	345,3	14,2	78,7	92,9	11,28	62,53	73,81

**LABELLING 4 WEEKS AFTER ANTHESIS - NON-STRESS**

48h	A1	163,2	93,3	148,6	135,0	20,5	155,5	45,0	67,3	10,2	77,6	1,61	0,24	1,85
	B1	278,9	126,3	244,7	283,6	37,1	320,7	18,9	83,5	10,9	94,4	3,37	0,44	3,81
	Shank	187,2	167,9	184,3	223,0	35,3	258,3	7,7	83,8	13,3	97,1	2,65	0,42	3,07
	Cob	320,1	52,9	177,9	612,3	115,1	727,3	24,9	81,4	15,3	96,7	7,28	1,37	8,65
	Grain	543,9	35,3	56,2	1 696,0	2 562,5	4 258,5	311,3	37,1	56,1	93,2	20,17	30,47	50,63
PM	A1	34,7	36,4	35,1	49,1	12,4	61,5	21,8	59,0	14,9	73,9	0,53	0,14	0,67
	B1	44,3	23,7	38,4	96,3	20,6	116,9	63,6	53,3	11,4	64,7	1,05	0,22	1,27
	Shank	35,5	68,1	40,5	19,4	6,8	26,2	41,7	28,6	10,0	38,5	0,21	0,07	0,28
	Cob	169,5	47,8	100,3	181,8	67,6	249,4	13,8	69,1	25,7	94,8	1,98	0,74	2,71
	Grain	306,2	57,2	63,1	743,1	5 670,6	6 413,7	1020,2	10,0	76,3	86,3	8,08	61,63	69,71

convert the assimilated  $^{14}\text{C}$  into starch in the shank is a matter for further research. Perhaps the C assimilated is so rapidly translocated to the primary ear that a backlog develops as the rate of starch deposition in the grain lags behind the rate at which C is translocated to the grain. This may lead to the excess C being temporarily converted to starch in the shank. It is theorised that the turgor pressure of sink cells may serve as a feedback inhibitor or promoter of the translocation pathway (Lucas and Madore, 1988). By removing sucrose from the solution in the cytosol of the shank cells and converting it to starch, the continued translocation of sucrose to the primary ear may be facilitated. The starch in the shank may also serve as an emergency buffer supply of photosynthate to the grain should the production of current photosynthate be reduced. At PM the SR of the TS in the A1 and grain plant parts of stressed plants was higher than that of non-stressed plants. The SR of the starch in only the B1 plant part of stressed plants was higher than that of non-stressed plants. However, the SR of the TNC at PM in all five plant parts of stressed plants was less than that of non-stressed plants. The SR of the TNC in the B1 plant part of stressed plants was, however, just less than that of non-stressed plants. This is once again indicative of the lower amount of  $^{14}\text{C}$  assimilated by the stressed plants at 4 WAA.

At 48 h after labelling the TR of the TS in the A1, B1, shank and cob plant parts of both stressed and non-stressed plants was higher than the TR of the starch. However, the TR of the starch in the grain of both stressed and non-stressed plants was substantially higher than the TR of the TS particularly in the

stressed plants. The higher TR of the TS in the A1, B1, shank and cob plant parts compared to that of starch indicates that the predominant non-structural carbohydrates in these plant parts at 48 h are TS. The TR of the TS in all five plant parts of stressed plants was less than that of non-stressed plants. However, while the TR of the starch in the A1, B1 and shank plant parts of stressed plants was less than that of non-stressed plants, the TR of the starch in the cob and grain of stressed plants was just higher than that of non-stressed plants. The higher TR of the starch in the grain of the stressed plants at 48 h is indicative of the more direct and rapid conversion of  $^{14}\text{C}$  assimilated at 4 WAA to starch under stress conditions. The higher TR of the starch in the cob of the stressed plants at 48 h is of uncertain physiological significance. Generally, however, the TR of the TNC of all five plant parts of the stressed plants was less than that of the non-stressed plants at 48 h. This reflects the lower whole plant TR of the stressed plants at 4 WAA. The lower TR of the TNC in the A1, B1, shank and cob plant parts of stressed plants at 48 h compared to non-stressed plants does, however, also indicate the greater mobilization of the  $^{14}\text{C}$  assimilated at 4 WAA to the grain. The radioactivity associated with the TS in the grain of both stressed and non-stressed plants is indicative of the processes involved in the translocation of C to the grain and the deposition of starch in the endosperm cells which were discussed earlier. It is noteworthy, however, that the TR of the TS in the grain of non-stressed plants was substantially higher than that of stressed plants. This may indicate that stressed plants translocated the bulk of the  $^{14}\text{C}$  to the grain within 48 h after labelling where it

was assimilated into starch, whereas the translocation of  $^{14}\text{C}$  to the grain in the non-stressed plants peaked later. At PM the TR of the TS in the A1, B1, shank and cob plant parts of both stressed and non-stressed plants was still higher than the TR of the starch. As is expected the TR of the starch in the grain of stressed and non-stressed plants was also still higher than the TR of the TS. It is noteworthy, however, that the TR of the starch in the cob at 48 h and at PM of both stressed and non-stressed plants was higher than that of the A1, B1 and shank plant parts. This may indicate that  $^{14}\text{C}$  mobilized to the grain in the form of sucrose in excess of grain requirements accumulated in the cob as starch and the accumulation of  $^{14}\text{C}$  in the cob as starch occurred even at PM although to a lesser extent than was the case at 48 h. At PM the TR of the TS in all five plant parts of the stressed plants was less than that of the non-stressed plants. Only in the B1 plant part was the TR of the starch of the stressed plants greater than that of the non-stressed plants. The physiological significance of the higher TR of the starch in the B1 plant part of the stressed plants is, however, uncertain. Overall, however, the TR of the TNC in all five plant parts of the stressed plants was less than that of the non-stressed plants. This again reflects the lower whole plant TR of the stressed plants recorded at 48 h and at PM. From 4 WAA to PM the TR of the TS and the starch in the A1, B1, shank and cob plant parts declined, while in the grain the TR of the TS declined and the TR of the starch increased in both stressed and non-stressed plants. The increase in the TR of the starch in the grain of non-stressed plants was substantial. However, this may have been exaggerated by the high SR recorded for the grain of

plants sampled from replication one. The overall decline in the TR of the TS and starch in the A1, B1, shank and cob plant parts is indicative of the mobilization of the  $^{14}\text{C}$  in these plant parts to the grain in the form of the main translocatory sugar, sucrose. It was also indicative of the loss of  $^{14}\text{C}$  through respiration. The overall increase in the TR of the TNC in the grain was due to the translocation of  $^{14}\text{C}$  from the shoot to the grain. As mentioned the TR of the TS in the grain declined from 4 WAA to PM so that the increase in the TR of the TNC in the grain was due to the increase in the TR of the starch.

At 48 h the proportion of the TR in the plant parts in the form of TNC ranged from 82,6 % in the A1 plant part to 97,9 % in the B1 plant part of the stressed plants. In the non-stressed plants the proportion of plant part TR in the form of TNC ranged from 77,6 % in the A1 plant part to 97,1 % in the shank. The proportion of plant part TR in the form of TNC at 48 h was higher in the A1 and B1 plant parts of the stressed plants than the non-stressed plants. However, the non-stressed plants had a higher proportion of the TR of the shank, cob and grain in the form of TNC. The physiological significance of the lower proportion of the TR in the form of TNC in the shank, cob and grain at 48 h in the stressed plants compared to the non-stressed plants is uncertain. The non-stressed plants also had a higher proportion of the grain TR in the form of TNC than did the stressed plants. It appears that the stressed plants converted more  $^{14}\text{C}$  to residual components in the shank, cob and grain than the non-stressed plants 48 h after labelling at 4 WAA. This may once again hint at altered patterns in N metabolism in these plant parts under stress

conditions. In contrast to plants labelled at 2 WAA the stressed plants did not have a higher proportion of the shank TR in the form of TS than the non-stressed plants. Except for the grain of the stressed plants, at PM the proportion of the TR of each plant part in the form of TNC had declined substantially in both stressed and non-stressed plants. Conversely, at PM a greater proportion of the  $^{14}\text{C}$  in the plant parts, except for the grain of the stressed plants, occurred in the form of residual components than at 48 h. Ignoring data for the grain for the moment, the proportion of plant part TR in the form of TNC at PM in stressed plants ranged from 30,0 % in the shank to 75,4 % in the B1 plant part. In the non-stressed plants the proportion ranged from 38,5 % in the shank to 94,8 % in the cob. In the stressed plants the decline in the proportion of the TR in the A1 plant part in the form of TNC was due to a larger decline in the amount of  $^{14}\text{C}$  in the form of TNC than the decline in the amount of  $^{14}\text{C}$  in the form of residual components. On the other hand, the decline in the proportion of the B1, shank and cob plant parts TR in the form of TNC was due to a decline in the amount of  $^{14}\text{C}$  in the form of TNC as well as due to the increase in the amount of  $^{14}\text{C}$  in the form of residual components. The decline in the proportion of shank TR in the form of TNC was particularly marked. It appears that the A1 plant part lost more  $^{14}\text{C}$  in the form of TNC from 4 WAA to PM than  $^{14}\text{C}$  in the form of residual components. The B1, shank and cob plant parts appeared to lose  $^{14}\text{C}$  in the form of TNC from 4 WAA to PM while converting some  $^{14}\text{C}$  to residual components. The physiological significance of the increase in the amount of  $^{14}\text{C}$  in the form of residual components in the B1, shank and cob plant parts from 4 WAA to PM under stress conditions is uncertain. In

the stressed plants the proportion of grain TR in the form of TNC increased slightly from 4 WAA to PM as a result of an increase in the amount of  $^{14}\text{C}$  in the form of TNC. However, the amount of  $^{14}\text{C}$  in the form of the residual components decreased slightly in the grain as judged by the decrease in the TR of the residual components. In the non-stressed plants the decline in the proportion of the TR of the A1 and cob plant parts in the form of TNC from 4 WAA to PM was due to a larger decline in the amount of  $^{14}\text{C}$  in the form of TNC compared to the decline in the amount of  $^{14}\text{C}$  in the form of residual components. On the other hand, the decline in the proportion of the TR of the B1 and shank plant parts in the form of TNC from 4 WAA to PM was due to a decline in the amount of  $^{14}\text{C}$  in the form of TNC as well as due to an increase in the amount of  $^{14}\text{C}$  in the form of residual components. Thus in both the stressed and non-stressed plants the A1 plant part lost  $^{14}\text{C}$  in the form of TNC and residual components. However, in contrast to the stressed plants the cob of the non-stressed plants also lost  $^{14}\text{C}$  in the form of TNC and residual components. The B1 and shank plant parts of both stressed and non-stressed plants lost  $^{14}\text{C}$  in the form of TNC while converting some  $^{14}\text{C}$  to residual components. As with the stressed plants the decline in the proportion of shank TR in the form of TNC was marked in the non-stressed plants. This was largely indicative of the substantial decline in the amount of  $^{14}\text{C}$  in the form of TNC in the shank although the TR of the residual components in the shank did increase substantially from 4 WAA to PM. The increase in the amount of  $^{14}\text{C}$  at 4 WAA in the shank in the form of residual components is of uncertain physiological significance. A large decline in the proportion of shank TR in the form of TNC from

2 WAA to PM in stressed plants labelled at 2 WAA was also observed. In contrast to the stressed plants the proportion of grain TR in the form of TNC declined from 4 WAA to PM in non-stressed plants. Although the amount of  $^{14}\text{C}$  in the form of TNC increased in the grain during this period, the amount of  $^{14}\text{C}$  in the form of residual components increased substantially and by a greater proportion. The physiological significance of the increase in the proportion of grain TR in the form of residual components under non-stress conditions is uncertain. However, it may indicate that the non-stressed plants could afford the conversion of  $^{14}\text{C}$  assimilated at 4 WAA to organic compounds other than TNC in the grain as they assimilated more additional C after labelling than did the stressed plants.

It is noteworthy that the proportion of cob TR in the form of TNC in the stressed plants declined to a greater extent than that in the non-stressed plants. The physiological significance of the greater proportion of cob TR in the form of residual components, under stress conditions is uncertain. However, it will be recalled that the amount of  $^{14}\text{C}$  in the cob in the form of TNC declined while the amount of  $^{14}\text{C}$  in the form of residual components increased from 4 WAA to PM in the stressed plants. This may indicate altered N metabolism under stress conditions.

Of special importance is that generally in the stressed and non-stressed plants the proportion of the TR of the A1, B1, shank and cob plant parts in the form of TNC was higher at PM than when plants were labelled at A and 2 WAA. This indicates that of the  $^{14}\text{C}$  not mobilized out of these plant parts to the grain or lost

through respiration a greater proportion remained in the form of TNC at PM. In fact, except for the shank, more than half of the TR in these plant parts was in the form of TNC at PM.

It is of interest to note that at 4 WAA, 51,54 and 50,63 % of the whole plant radioactivity occurred in the form of TNC in the grain of the stressed and non-stressed plants, respectively. At PM this proportion had increased to 73,81 and 69,71 % in stressed and non-stressed plants, respectively. It appears that by PM the stressed plants converted a greater proportion of whole plant  $^{14}\text{C}$  to TNC in the grain than did the non-stressed plants. Except for the A1 plant part the stressed plants at 4 WAA had a lower proportion of whole plant  $^{14}\text{C}$  in the form of TNC in the B1, shank and cob plant parts than the non-stressed plants. However, at PM the proportion of whole plant  $^{14}\text{C}$  in the form of TNC in the B1 and shank plant parts of the stressed plants was higher than that of non-stressed plants.

#### Labelling at 6 WAA

When plants were labelled at 6 WAA, 44,8 and 41,6 % of the whole plant  $^{14}\text{C}$  at 6 WAA occurred in the grain of stressed and non-stressed plants, respectively. This increased to 67,6 and 67,0 % in stressed and non-stressed plants, respectively, at PM. Thus it is clear that  $^{14}\text{C}$  assimilated at 4 WAA was rapidly mobilized to the grain and by PM 32,4 and 33,0 % of the whole plant  $^{14}\text{C}$  remained in the whole shoot of the stressed and non-stressed plants respectively (Section 4.3.4.3). Thus at 6 WAA the primary grain was still established as the major sink for photosynthate

but to a lesser extent than was the case when plants were labelled at 2 WAA and 4 WAA.

At 48 h the SR of the TS and starch of all five plant parts of the stressed and non-stressed plants was generally less than at 48 h after plants were labelled at A, 2 WAA and 4 WAA (Table 4.77). This reflects the fact that the TR of the whole plant of stressed and non-stressed plants labelled at 6 WAA was the lowest of all four labelling occasions. At 48 h after labelling the SR of the TS of all five plant parts in both stressed and non-stressed plants was higher than the SR of the starch. This would seem to indicate that less  $^{14}\text{C}$  per unit mass was utilized to synthesize starch at 6 WAA. At 48 h the SR of the TS of all five plant parts was less in stressed plants than non-stressed plants. However, only the SR of the starch in the B1 plant part of the stressed plants was higher than that of the non-stressed plants. The physiological significance of this is, however, uncertain. The SR of the TNC in all five plant parts of the stressed plants was less than that of the non-stressed plants at 48 h. Generally the lower SR of the TNC for all five plant parts of the stressed plants compared to the non-stressed plants reflects the lower whole plant TR recorded for stressed plants at 48 h after labelling at 6 WAA. At PM the SR of the TS in the A1, B1, shank and cob plant parts of stressed plants was higher than that of non-stressed plants. The SR of the starch in the A1, cob and grain plant parts of stressed plants was higher than that of non-stressed plants. However, in complete contrast to the pattern at 48 h, the SR of the TNC in all five plant parts of the stressed plants at PM was higher than that of the non-stressed

Table 4.77 Component non-structural carbohydrate <sup>14</sup>C radioactivity in selected plant parts sampled at 48h and at physiological maturity (PM) from a maize hybrid subjected to water stress (stress) and lack of water stress (non-stress) during grain fill and labelled at six weeks after anthesis

**LABELLING AT 6 WEEKS AFTER ANTHESIS - STRESS**

Sampling at	Plant part	Specific radioactivity (dpm x 10 <sup>-3</sup> g <sup>-1</sup> )			Total radioactivity (dpm x 10 <sup>3</sup> (plant part) <sup>-1</sup> )				Radioactivity per plant part (%)			Radioactivity per whole plant (%)		
		Total sugars	Starch	TNC	Total sugars	Starch	TNC	Residual	Total sugars	Starch	TNC	Total sugars	Starch	TNC
48h	A1	62,9	12,7	49,4	65,7	4,9	70,5	1,0	91,9	6,8	98,6	3,18	0,24	3,42
	B1	60,4	18,1	49,0	118,3	13,2	131,5	1,6	88,9	9,9	98,8	5,73	0,64	6,38
	Shank	42,0	25,1	38,9	40,6	5,5	46,1	14,8	66,7	9,0	75,7	1,97	0,27	2,23
	Cob	83,9	14,2	45,3	142,0	29,9	171,9	7,1	79,3	16,7	96,0	6,88	1,45	8,33
	Grain	153,8	7,1	10,9	317,7	552,6	870,3	52,2	34,4	59,9	94,3	15,40	26,78	42,18
PM	A1	26,0	19,7	24,7	20,9	4,0	25,0	2,1	77,2	14,9	92,1	1,19	0,23	1,42
	B1	40,5	13,1	32,2	49,6	7,0	56,6	0,9	86,2	12,2	98,4	2,81	0,40	3,21
	Shank	35,0	20,7	32,9	20,8	2,2	23,0	0,8	87,7	9,1	96,9	1,18	0,12	1,30
	Cob	68,2	9,4	32,0	74,1	16,3	90,5	1,7	80,4	17,7	98,1	4,20	0,93	5,13
	Grain	92,5	11,6	13,3	153,5	904,3	1 057,8	133,6	12,9	75,9	88,8	8,71	51,28	59,98

**LABELLING 6 WEEKS AFTER ANTHESIS - NON-STRESS**

48h	A1	70,2	19,1	59,3	78,3	5,8	84,1	2,4	90,6	6,7	97,3	2,86	0,21	3,07
	B1	67,4	15,9	53,3	136,7	12,2	148,9	9,4	86,3	7,7	94,0	4,99	0,45	5,43
	Shank	54,5	47,9	53,6	64,2	8,8	73,0	1,1	86,6	11,8	98,5	2,34	0,32	2,66
	Cob	97,4	14,7	52,0	191,2	35,1	226,3	11,1	80,6	14,8	95,3	6,98	1,28	8,26
	Grain	159,9	6,9	11,2	421,9	632,4	1 054,3	83,1	37,1	55,6	92,7	15,39	23,08	38,47
PM	A1	23,6	15,8	22,1	28,6	4,6	33,2	1,9	81,6	13,2	94,8	1,39	0,23	1,62
	B1	31,0	14,0	26,9	61,5	9,0	70,5	4,0	82,6	12,1	94,6	2,99	0,44	3,43
	Shank	29,6	23,4	28,7	24,1	3,2	27,3	0,8	85,7	11,3	97,0	1,17	0,15	1,33
	Cob	48,5	9,2	25,9	63,6	16,3	79,9	5,9	74,1	19,0	93,0	3,09	0,79	3,88
	Grain	106,2	10,3	12,4	250,8	1 054,7	1 305,5	69,6	18,2	76,7	94,9	12,19	51,25	63,44

plants. It would appear that from 6 WAA to PM the stressed plants incorporated less  $^{12}\text{C}$  into the molecules of TS and starch than the non-stressed plants. It will also be recalled that the respiration losses of the non-stressed plants from 6 WAA to PM were higher than those of the stressed plants (Section 4.3.7.2). Thus the amount of  $^{14}\text{C}$  in the TNC of the five plant parts of the stressed plants remained more concentrated. It is of interest to note that the SR of the TNC in the grain of both stressed and non-stressed plants at 48 h and at PM was lower than that of the other four plant parts. This would appear to indicate that the amount of  $^{14}\text{C}$  assimilated at 6 WAA was not enough to provide a high concentration of  $^{14}\text{C}$  per unit mass when incorporated into the TNC in the grain. It is also interesting to note that the SR of the TNC in the grain of stressed and non-stressed plants increased slightly from 48 h to PM. This indicates that the rate of incorporation of  $^{14}\text{C}$  into the TNC in the grain per unit mass slightly exceeded the rate of incorporation of  $^{12}\text{C}$  into the TNC in the grain.

At 48 h after labelling the TR of the TS in the A1, B1, shank and cob plant parts of both stressed and non-stressed plants was higher than the TR of the starch. However, the TR of the starch in the grain of both stressed and non-stressed plants was substantially higher than the TR of the TS. The higher TR of the TS in the A1, B1, shank and cob plant parts compared to that of the starch indicates that the predominant non-structural carbohydrates in these plant parts at 48 h are TS. At 48 h after labelling the TR of the TS in all five plant parts of the stressed plants was less than that of the non-stressed plants.

Only in the B1 plant part was the TR of the starch in the stressed plants greater than that of the non-stressed plants. Overall, however, the TR of the TNC in all five plant parts of the stressed plants was less than that of the non-stressed plants. This generally reflects the lower TR of the whole plant recorded for the stressed plants at 48 h after labelling at 6 WAA. The radioactivity associated with the TS in the grain of both stressed and non-stressed plants is indicative of processes involved in the translocation of C to the grain and the deposition of starch in endosperm cells which were discussed earlier. At PM the TR of the TS in the A1, B1, shank and cob plant parts of both stressed and non-stressed plants was still higher than the TR of the starch. As is expected the TR of the starch in the grain of stressed and non-stressed plants was also still higher than the TR of the TS. It is noteworthy that the TR of the TS and starch in the cob at 48 h and at PM of both stressed and non-stressed plants was higher than that of the A1, B1 and shank plant parts. This reflects the rôle of the cob in serving as a conduit for photosynthate being translocated to the grain from the whole shoot. The high TR of the starch in the cob may indicate that  $^{14}\text{C}$  mobilized to the grain in the form of sucrose in excess to grain requirements accumulated in the cob in the form of starch. This accumulation of  $^{14}\text{C}$  in the cob in the form of starch occurred even at PM although to a lesser extent than was the case at 48 h. At PM the TR of the TS in the A1, B1, shank and grain plant parts of stressed plants was less than that of non-stressed plants. However, the TR of the TS in the cob of the stressed plants was higher than that of the non-stressed plants. At PM the TR of the starch in the A1, B1, shank and

grain plant parts of the stressed plants was less than that of the non-stressed plants. However, the TR of the TS in the cob of the stressed and non-stressed plants was similar. Overall the TR of the TNC in the A1, B1, shank and grain plant parts of the stressed plants was less than that of the non-stressed plants but the TR of the TNC in the cob of the stressed plants was higher than that of the non-stressed plants. The physiological significance of the higher TR of the TNC in the cob of the stressed plants at PM is uncertain. However, it may indicate that  $^{14}\text{C}$  mobilized to the grain accumulated in the cob at PM to a greater extent under stress conditions. This may be due to a reduction in the rate of starch deposition in the endosperm cells of the kernels under stress conditions (Section 4.3.3.6). The lower TR of the TNC in the A1, B1, shank and grain plant parts of the stressed plants does, however, reflect the lower TR of the whole plant of the stressed plants at PM. From 6 WAA to PM the TR of the TS and starch in the A1, B1, shank and cob plant parts declined, while in the grain the TR of the TS declined as the TR of the starch increased in both stressed and non-stressed plants, respectively. The overall decline in the TR of the TS and starch in the A1, B1, shank and cob plant parts is indicative of the mobilization of the  $^{14}\text{C}$  in these plant parts to the grain in the form of the main translocatory sugar, sucrose. It is also indicative of the loss of  $^{14}\text{C}$  through respiration. The overall increase in the TR of the TNC in the grain was due to the translocation of  $^{14}\text{C}$  from the shoot to the grain. As mentioned the TR of the TS in the grain declined from 6 WAA to PM so that the increase in the TR of the TNC in the grain was due to the increase in the TR of the starch in the grain.

At 48 h the proportion of the TR in the plant parts in the form of TNC ranged from 75,7 % in the shank to 98,8 % in the B1 plant part of the stressed plants. In the non-stressed plants the proportion of plant part TR in the form of TNC ranged from 92,7 % in the grain to 94,0 % in the B1 plant part. Except for the shank the proportion of plant part TR in the form of TNC at 48 h was higher in the plant parts of the stressed plants than the non-stressed plants. The higher proportion of the TR of the A1, B1, cob and grain plant parts in the form of TNC of the stressed plants would seem to indicate that less of the  $^{14}\text{C}$  assimilated at 6 WAA was converted to residual components within 48 h after labelling under stress conditions. On the other hand, the lower proportion of the TR of the shank in the form of TNC in the stressed plants is of uncertain physiological significance. At PM the proportion of the shank and cob TR in the form of TNC had increased while that in the A1, B1 and grain plant parts had declined in stressed plants. In the non-stressed plants the proportion of A1, shank and cob plant parts TR in the form of TNC declined while that of the B1 and grain plant parts increased. At PM the proportion of plant part TR in the form of TNC ranged from 88,8 % in the grain to 98,4 % in the B1 plant part of the stressed plants. In the non-stressed plants the proportion ranged from 93,0 % in the cob to 97,0 % in the shank. In the stressed plants the decline in the proportion of the TR of the A1 plant part in the form of TNC from 6 WAA to PM was due to a decline in the amount of  $^{14}\text{C}$  in the form of TNC as well as due to an increase in the amount of  $^{14}\text{C}$  in the form of residual components. In the B1 plant part the small decline in the proportion of the TR in the form of TNC was due to a larger

decline in the amount of  $^{14}\text{C}$  in the form of TNC than the decline in the amount of  $^{14}\text{C}$  in the form of residual components. The decline in the proportion of the grain TR in the form of TNC was due to the greater proportional increase in the amount of  $^{14}\text{C}$  in the form of residual components than the increase in the amount of  $^{14}\text{C}$  in the form of TNC. The increase in the proportion of the shank and cob TR in the form of TNC was due to the greater proportional decline in the amount of  $^{14}\text{C}$  in the form of residual components than the decline in the amount of  $^{14}\text{C}$  in the form of TNC. In the non-stressed plants the decline in the proportion of the TR of the A1, shank and cob plant parts in the form of TNC was due to a greater proportional decline in the amount of  $^{14}\text{C}$  in the form of TNC than the decline in the amount of  $^{14}\text{C}$  in the form of residual components. In the B1 plant part of non-stressed plants the increase in the proportion of the TR in the form of TNC was due to the marginally greater proportional decline in the amount of  $^{14}\text{C}$  in the form of residual components than the decline in the amount of  $^{14}\text{C}$  in the form of TNC. In contrast to stressed plants the increase in the proportion of grain TR in the form of TNC in non-stressed plants was due to an increase in the amount of  $^{14}\text{C}$  in the form of TNC while the amount of  $^{14}\text{C}$  in the form of residual components declined. The physiological significance of the increase in the proportion of the residual components in the grain of the stressed plants from 4 WAA to PM is not certain since this was the only labelling occasion in which this phenomenon was recorded for the stressed plants. The physiological significance for the lower proportion of shank TR in the form of TNC in stressed plants at 48 h compared to non-stressed plants, which then increased substantially at PM, is

also uncertain. Most noteworthy is that generally in the stressed and non-stressed plants the proportion of the TR of the A1, B1, shank and cob plant parts in the form of TNC was higher at PM than when plants were labelled on the other three occasions and sampled at PM. This indicates that of the  $^{14}\text{C}$  not mobilized out of these plant parts to the grain or lost through respiration, a greater proportion of the plant part TR remained in the form of TNC. In fact, averaged over the stressed and non-stressed plants the average proportion of the TR in these plant parts remaining in the form of residual components at PM was 4,4 %.

It is of interest to point out that although stressed plants at 48 h recorded a lower TR of the TNC in the grain than non-stressed plants this represented a higher proportion of the whole plant  $^{14}\text{C}$  in the form of TNC in the grain of the stressed plants namely 42,18 % compared to 38,47 % in the non-stressed plants. However, at PM this proportion had increased to a greater extent in non-stressed plants and was 59,98 % in stressed plants and 63,44 % in non-stressed plants. It appears that the stressed plants converted a greater proportion of the whole plant  $^{14}\text{C}$  assimilated at 6 WAA to TNC in the grain within 48 h of labelling than did the non-stressed plants. However, as leaf senescence decreased the photosynthetic capacity of the non-stressed plants, the proportion of whole plant  $^{14}\text{C}$  mobilized to the grain of the non-stressed plants increased and in fact exceeded that of the stressed plants at PM. At 48 h the stressed plants had a higher proportion of whole plant  $^{14}\text{C}$  in the form of TNC in the A1, B1 and cob plant parts than the stressed plants. However, at PM the

proportion of whole plant  $^{14}\text{C}$  in the form of TNC in the A1, B1 and shank plant parts was less than that of the non-stressed plants, but the proportion was higher in the cob of the stressed plants than the non-stressed plants.

#### 4.3.9 Radioactivity associated with glucose, fructose and sucrose

In the previous section (Section 4.3.8) the radioactivity associated with the TS in selected plant parts was discussed. The purpose of this section is to examine the radioactivity associated with the components of TS, viz glucose, fructose and sucrose, determined using thin layer chromatography. Only a few plant parts had enough radioactivity above background associated with glucose, fructose and sucrose to provide reliable counts.

The higher SR of sucrose in the shank of the stressed plants 48 h after labelling at A is indicative of the more direct and rapid translocation of assimilated  $^{14}\text{C}$  in the form of sucrose through the shank to the primary ear under stress conditions (Table 4.78). The physiological significance of the shank of the stressed plants having a higher SR of fructose than the non-stressed plants, and the shank of the non-stressed plants having a higher SR of glucose than the stressed plants is not certain. However, these differences in the SR of glucose and fructose of stressed and non-stressed plants are marginal and may be due to experimental error. Interestingly, both stressed and non-stressed plants incorporated more  $^{14}\text{C}$  per unit mass into glucose and fructose than into sucrose. This probably reflects the

Table 4.78 Effect of water stress (S) or lack of water stress (NS) during grain fill on radioactivity associated with glucose (G), fructose (F) and sucrose (S) in selected plant parts sampled from a maize hybrid labelled at anthesis (A), two and four weeks after anthesis (WAA)

Stress treatment	Labeling at	Sampling at	Plant part	Specific radioactivity (dpm x 10 <sup>-3</sup> g <sup>-1</sup> )			Total radioactivity (dpm x 10 <sup>-3</sup> (plant part) <sup>-1</sup> )		
				G	F	S	G	F	S
S	A	48h	shank	315,7	267,5	238,2	47,3	40,1	26,2
NS			shank	345,0	228,2	161,7	56,9	37,7	6,5
S	2 WAA	48h	A1	181,2	107,5	276,3	15,4	9,1	185,1
S			shank	241,6	186,8	332,3	18,1	14,0	222,5
S			cob	235,4	206,2	366,2	99,9	87,6	618,9
NS			A1	229,5	193,6	317,7	24,1	20,3	171,5
NS			shank	283,1	244,1	435,2	32,6	28,1	213,2
NS			cob	556,2	530,8	357,3	236,4	225,6	753,8
S	4 WAA	48h	shank	145,4	118,2	139,7	26,2	21,3	97,8
NS		48h	shank	151,0	141,8	202,1	30,2	28,7	159,7

greater amount of RS that occurred in the shank at A compared to sucrose in both stressed and non-stressed plants (Section 4.3.3.4, Table 4.4), and may be indicative of the greater utilization of <sup>14</sup>C assimilated at A for metabolic processes and structural growth within the shank itself. At this stage the primary grain was not established as the major sink for photosynthate. The TR of glucose, fructose and sucrose in the shank of stressed and non-stressed plants mirrors the SR recorded for these sugars. The TR of sucrose in the shank of stressed plants was four times that of sucrose in the shank of non-stressed plants. This is once again indicative of the more

direct and rapid mobilization of assimilated  $^{14}\text{C}$  in the form of sucrose to the primary ear under stress conditions. The observation that the non-stressed plants had much higher TR of glucose and fructose than sucrose in the shank may indicate that the non-stressed plants converted sucrose, translocated to the shank, into glucose and fructose for utilization within the shank for metabolic processes and structural growth. The smaller amounts of  $^{14}\text{C}$  translocated directly to the primary ear under non-stress conditions resulted in a much lower TR of sucrose in the non-stressed plants compared to stressed plants.

Forty-eight hours after plants were labelled at 2 WAA stressed plants maintained less  $^{14}\text{C}$  per unit mass of glucose and fructose in the A1, shank and particularly, the cob plant parts compared to non-stressed plants (Table 4.78). The stressed plants also maintained less  $^{14}\text{C}$  per unit mass of sucrose in the A1 and shank plant parts, but maintained marginally more  $^{14}\text{C}$  per unit mass of sucrose in the cob compared to non-stressed plants. It will be recalled (Section 4.3.8, Table 4.75) that 48 h after labelling at 2 WAA stressed plants recorded a higher SR of the TNC in the grain than did non-stressed plants. Thus it would appear that within 48 h of labelling the stressed plants maintained less  $^{14}\text{C}$  per unit mass in glucose, fructose and sucrose in the A1 and shank plant parts, and in glucose and fructose in the cob compared to non-stressed plants with more  $^{14}\text{C}$  being utilized for the synthesis of TNC per unit mass in the grain. The physiological significance of the marginally higher SR of sucrose in the cob of stressed than non-stressed plants is not certain. However, it may indicate the greater translocation of  $^{14}\text{C}$  per unit

mass of sucrose through the cob to the grain under stress conditions. In contrast to the shank of plants 48 h after being labelled at A, 48 h after plants were labelled at 2 WAA the A1, shank and cob plant parts of stressed plants and the A1 and shank plant parts of non-stressed plants incorporated more  $^{14}\text{C}$  per unit mass into sucrose than into glucose and fructose. This probably reflects the greater amount of sucrose that occurred in these plant parts at 2 WAA compared to RS in both stressed and non-stressed plants (Section 4.3.3.4, Table 4.4). Interestingly, even though the ratio of sucrose content to RS content in the cob of non-stressed plants was 2,47, the non-stressed plants still incorporated less  $^{14}\text{C}$  per unit mass into sucrose in the cob than into glucose and fructose. This may indicate the greater utilization of  $^{14}\text{C}$  assimilated at 2 WAA for metabolic processes and structural growth within the cob itself under non-stress conditions. The TR of glucose, fructose and sucrose in the A1, shank and cob plant parts generally mirrored the SR recorded for these sugars. However, it must be noted that the TR of sucrose in the cob of stressed plants was lower than that of the non-stressed plants and the TR of sucrose in the shank of the stressed plants was marginally higher than that of the non-stressed plants. It will be recalled (Section 4.3.8, Table 4.75) that 48 h after labelling at 2 WAA stressed plants had lower TR of the TS and starch in the A1, B1, shank and cob plant parts but had higher TR of the TS and starch in the grain compared to non-stressed plants. It appears that within 48 h of labelling at 2 WAA, the stressed plants mobilized more  $^{14}\text{C}$  on an absolute basis to the grain. The stressed plants thus maintained less  $^{14}\text{C}$  in the form of glucose, fructose and sucrose in the A1 and cob plant

parts, and glucose and fructose in the shank compared to non-stressed plants. The higher TR of sucrose in the shank of stressed plants may indicate the greater mobilization of  $^{14}\text{C}$  in the form of sucrose on an absolute basis through the shank to the grain under stress conditions. However, it would be expected that this would occur in conjunction with more  $^{14}\text{C}$  moving through the cob to the grain under stress conditions. The higher TR of sucrose in the cob of non-stressed plants was largely associated with the greater mass of the cob under non-stress conditions, since on a unit mass basis stressed plants did have more  $^{14}\text{C}$  in the form of sucrose in the cob than did the non-stressed plants.

Forty-eight hours after plants were labelled at 4 WAA stressed whole plants assimilated 75,3 % of the  $^{14}\text{C}$  assimilated by non-stressed whole plants (Section 4.3.7.2). The lower whole plant  $^{14}\text{C}$  assimilated by stressed plants is reflected in the lower SR and TR recorded for glucose, fructose and sucrose in the shank at 48 h after labelling at 4 WAA compared to non-stressed plants (Table 4.78). Both stressed and non-stressed plants incorporated more  $^{14}\text{C}$  per unit mass into sucrose than into glucose and fructose. This probably reflects the greater amount of sucrose that occurred in the shank at 4 WAA compared to RS in both stressed and non-stressed plants (Section 4.3.3.4, Table 4.4). It is also indicative of the greater mobilization of  $^{14}\text{C}$  in the form of sucrose to the primary grain which was established as the major sink for photosynthate. Both stressed and non-stressed plants assimilated less  $^{14}\text{C}$  on a whole plant basis when labelled at 4 WAA compared to plants labelled at A and 2 WAA (Section 4.3.7.2). Nonetheless, the TR of sucrose in the shank of

stressed and non-stressed plants at 48 h after labelling at 4 WAA was higher than the TR of sucrose in the shank of stressed and non-stressed plants at 48 h after labelling at A. This is indicative of the observation that at 4 WAA the primary grain was established as the major sink for photosynthate with much of the  $^{14}\text{C}$  being mobilized through the shank to the grain in the form of sucrose. However, at A the primary grain was not established as the major sink for photosynthate, thus the bulk of the  $^{14}\text{C}$  assimilated at A remained in the whole shoot. On the other hand, at 2 WAA the primary grain was established as the major sink for photosynthate, with the bulk of the  $^{14}\text{C}$  assimilated at 2 WAA mobilized to the grain through the shank in the form of sucrose. The higher whole plant TR recorded for stressed and non-stressed plants labelled at 2 WAA, compared to plants labelled at 4 WAA, resulted in a higher TR being recorded for sucrose in the shank of stressed and non-stressed plants at 2 WAA compared to plants at 4 WAA.

#### 4.3.10 Yield and yield components

##### Grain yield

The 13,6 % reduction in final grain yield in B254W x M162W from 161,2 g plant<sup>-1</sup> under non-stress conditions to 139,3 g plant<sup>-1</sup> under stress conditions was significant ( $p = 0,05$ ) (Figure 4.27 and Appendix 43).

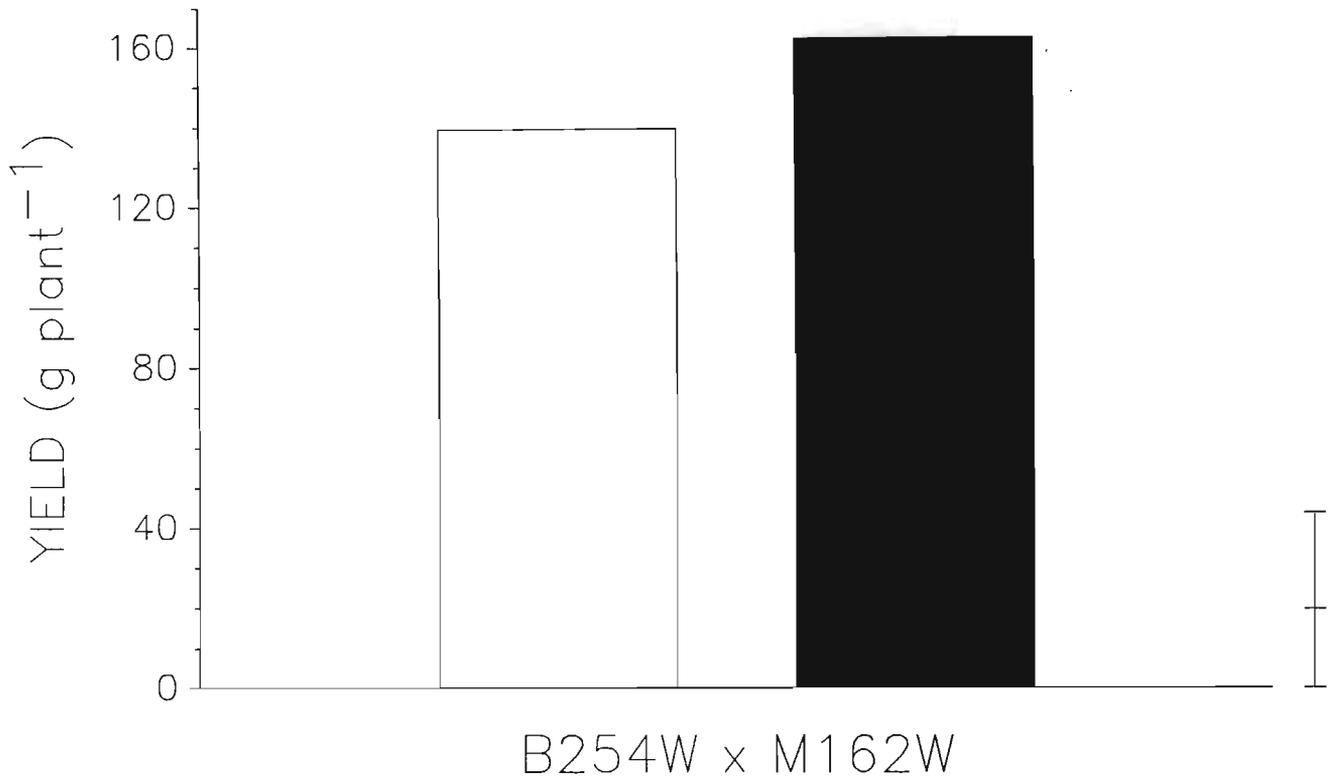


Figure 4.27 Effect of water stress (□) and lack of water stress (■) from anthesis to physiological maturity on grain yield (primary plus secondary ears) at harvest maturity of the maize hybrid B254W x M162W

Primary ear yield components, primary cob production and 2° ear yield

Although the plants were deliberately grown in a high humidity environment in order to reduce the rate at which stressed plants depleted the available water in the pots it appears that the development of stress occurred rapidly enough to result in a non-significant decline in kernels ear<sup>-1</sup> (Table 4.79 and Appendix 44.1). Interestingly, however, water stress resulted in a significant ( $p = 0,05$ ) decline in kernels row<sup>-1</sup> (Table 4.79 and Appendix 44.2). It was expected that water stress throughout grain fill would have reduced the supply of photosynthate to the grain resulting in a reduction in mass kernel<sup>-1</sup>. Although this did occur, water stress resulted in only a marginal and non-significant reduction in the mass kernel<sup>-1</sup> of the stressed plants (Table 4.79 and Appendix 44.4). Water stress also resulted in

Table 4.79 Primary ear yield components, primary cob production and 2° ear grain yield for the hybrid B254W x M162W subjected to water stress (S) and lack of water stress (NS)

Stress treatment	Kernels ear <sup>-1</sup>	Kernels row <sup>-1</sup>	Rows ear <sup>-1</sup>	Mass kernel <sup>-1</sup> (g)	Cob production (g plant) <sup>-1</sup>	2° ear grain yield (g plant) <sup>-1</sup>
S	449,1	30,7	14,7	0,309	16,0	0,613
NS	514,1	37,7	13,7	0,313	19,1	0,880

F values

Stress treatment	11,308 <sup>NS</sup>	24,266*	0,750 <sup>NS</sup>	1,316 <sup>NS</sup>	2,085 <sup>NS</sup>	4,030 <sup>NS</sup>
------------------	----------------------	---------	---------------------	---------------------	---------------------	---------------------

\* Significant at the 0,05 probability level. NS = non-significant

a non-significant reduction in cob production and 2° ear grain yield (Table 4.79 and Appendices 44.5 and 45, respectively).

Although the stressed plants generally had depleted the available water in the pots after 3 to 4 d without water and showed visible symptoms of severe water stress at the end of each stress cycle, it is apparent from the yield reduction of 13,6 % that the stressed plants were still able to produce a considerable amount of current photosynthate to meet grain fill requirements. The question which needs to be raised here is what environmental factor inhibits yield production more, low leaf  $\Psi_w$  (water stress) or high ambient temperatures (heat stress)? Obviously under field conditions it is difficult to separate the effects of reduced availability of water from temperature or heat stress. It was pointed out earlier (Section 4.3.1) that the high humidity within the growth tunnel coupled with the forced removal of air by the fan ducts may have enabled the stressed plants to maintain leaf temperatures low enough to continue metabolic processes, in particular photosynthesis, even though there was no water available in the pots to transpire and thereby keep the temperature of the leaves low enough for metabolic processes through the evaporative cooling effect of transpiration.

## CHAPTER 5

### REVIEW OF RESULTS AND FINAL CONCLUSIONS

From research reports in the literature and the results of this study it is apparent that the stem of the maize plant may serve as a temporary reservoir for photosynthate produced in the leaves. This photosynthate may then be utilized for cell growth and maintenance requirements of the plant and in particular for grain requirements during grain fill. Thus it is important to emphasize that pools of photosynthate in stem tissue are in a state of dynamic flux, regularly being added to by current photosynthate and utilized by the various sinks in the plant. If the rate at which photosynthate pools in stem tissue are utilized is equalled by the rate at which they are added to, levels of photosynthate pools in stem tissue will remain constant. However, should the capacity of the source to maintain levels of photosynthate pools in the stem be exceeded by sink utilization, levels of photosynthate pools in stem tissue will decline. Thus for a specific genotype x environment interaction, the levels of photosynthate pools in the stem (particularly during the reproductive phase) may be regarded as indicators of the balance that exists between source supply of photosynthate and sink utilization of photosynthate. It is, however, important to emphasize that whether or not the stem actively demands photosynthate and serves as an alternative sink for photosynthate in excess to grain and general plant cell maintenance and growth requirements is dependent on genotype. Unfavourable environmental conditions, specifically water stress, may alter

source-sink relations in the maize plant. Water stress results in a decline in whole plant photosynthesis as a result of a reduction in photosynthetic activity per unit leaf area and as a result of decreased leaf area due to enhanced leaf senescence. Thus the total photosynthate production of the plant is decreased and it would be expected that source capacity would limit yield production. However, the photosynthate requirements of the grain may also be reduced if water deficits occur early enough in the reproductive phase to cause abortion of developing kernels. Thus the decline in source supply could be counter-balanced by the decline in sink demand. It is even possible for severe water deficits to cause such a marked decline in kernels ear<sup>-1</sup> that, even under conditions of continued water deficits, the photosynthetic capacity of the source exceeds the sink capacity of the grain. Under these circumstances the stem may serve as an alternative sink for photosynthate and may in fact accumulate significant levels of photosynthate.

From research reports in the literature and the results of this study it is possible to provide a general overview of the rôle of the stem in supplying photosynthate to the developing grain. Under favourable environmental conditions the two limitations to grain yield, viz a sink limitation and a source limitation as reflected in the gains or losses of stem dry mass and stem non-structural carbohydrate content, are respectively shown in the idealized diagrams Figure 5.1a and b. Specific interactions of genotype with environmental factors may lead to the generalized patterns of stem dry mass and stem non-structural carbohydrate accumulation shown in Figure 5.1a. During vegetative development

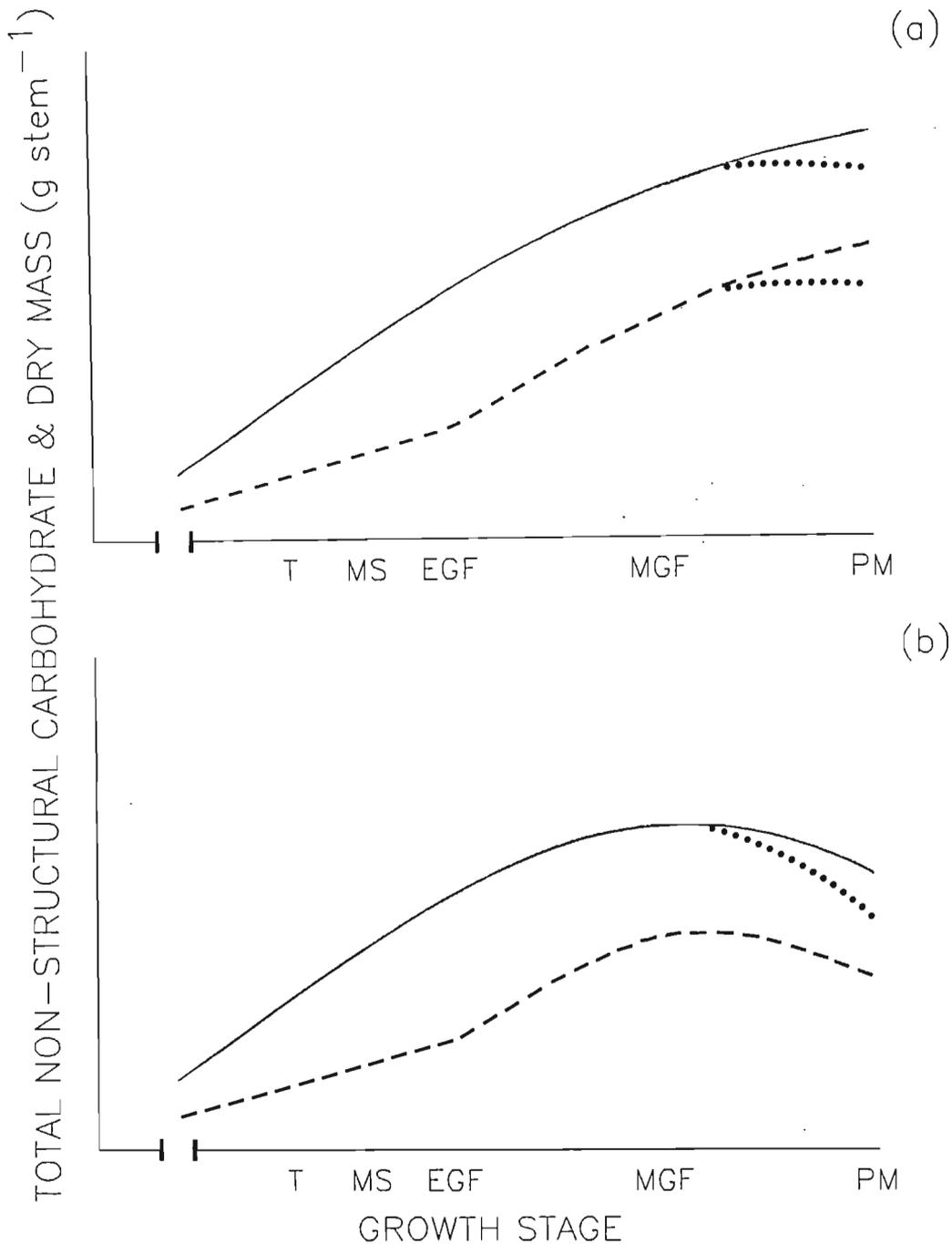


Figure 5.1 Idealized diagrams representing (a) a SINK limitation to final grain yield as inferred by increases in stem total non-structural carbohydrate content (---) and stem dry mass (—), and (b) a SOURCE limitation to final grain yield as inferred by losses in stem total non-structural carbohydrate content and stem dry mass during the grain filling period. The dotted line(s) (.....) in (a) indicate possible losses in stem dry mass and total non-structural carbohydrate content due to reduced photosynthetic capacity and/or microbial decomposition; and in (b) indicates losses in stem dry mass due to a decline in the residual content of the stem in addition to a decline in total non-structural carbohydrate content.  
 T = Tasseling, MS = Mid-silking, EGF = Early grain fill, MGF = Mid-grain fill, PM = Physiological maturity

up until early grain fill (EGF), TNC levels remain low whereas during the same period a rapid increase in stem dry mass continues to occur. This indicates that TNC are being rapidly converted to structural material in the stem. During the same period there is a rapid increase in leaf dry mass which would result in carbohydrate not being translocated out of the leaves but instead being used for the production of leaf structural material. After EGF the stem dry mass continues to increase but at a slower rate. Increases in stem girth and height cease during this period, and thus TNC begins to accumulate in the stem as they are not being rapidly converted into stem structural material. Additionally, during the transition from the lag phase to the linear phase of grain fill the photosynthetic capacity of the leaves may exceed the demand for photosynthate by the grain, allowing for the accumulation of photosynthate in the stem to occur. Thus increases in stem dry mass during this phase are in the main as a result of the accumulation of TNC in the stem. During the same period leaf dry mass declines indicating that structural growth of the leaves has ceased and that more carbohydrate is now available for translocation out of the leaves. The dotted lines indicate that during late grain fill a decline in stem dry mass and TNC may occur as a result of photosynthetic capacity of the leaves declining due to senescence and as a result of microbial action.

Specific interactions of genotype with environmental factors may lead to the generalized patterns of an initial accumulation of stem dry mass and TNC during the first half of grain fill with a decline occurring during the second half of grain fill as shown

in Figure 5.1b. From the late vegetative phase to EGF stem dry mass increases as a result of structural growth while TNC levels remain low as they are rapidly converted to structural material. In the initial phase following EGF stem growth ceases but stem dry mass continues to increase as a result of an accumulation of TNC in the stem. However, a decline in the photosynthetic capacity of the plant during grain fill results in the translocation of carbohydrate out of the stem (with a parallel decline in stem dry mass) to meet grain fill requirements. The TNC content may decline to pre-anthesis levels or lower. A larger decrease in stem dry mass may occur (shown by dotted lines) which cannot be accounted for by losses in TNC content. This means that metabolites other than TNC are mobilized out of the stem, namely amino acids, protein and lipids. It is important to bear in mind that should environmental conditions limit the production of current photosynthate during the period from mid-silking to EGF, the accumulation of photosynthate in the stem will be reduced which will in turn reduce the amount of photosynthate that could be remobilized out of the stem to the grain at a later stage.

The stay green hybrids such as the one tested by Swank *et al.* (1982) may show continued accumulation of TNC in the stem even after the grain has ceased mass accumulation due to photosynthetic activity of the plant outlasting the duration of grain fill. Many genotypes which may show the patterns of stem dry mass and TNC accumulation shown in Figure 5.1a are those with either (i) genetically based extended duration of photosynthetic activity - stay green genotypes; or (ii) genetically based

tolerance to environmental limitations to photosynthesis such as light, temperature and water. Genotypes with genetically based early senescence or genotypes exposed to environmental conditions that limit photosynthesis, such as those grown by Daynard et al. (1969) in Canada, may exhibit the patterns shown in Figure 5.1b.

The data for the 1985/86 maize hybrid rain grown trial show that the temperate environmental conditions combined with the water stress conditions that prevailed from MGF to PM, resulted in whole stem TNC content levels being lower at PM than at A in all hybrids except SR 52. SR 52 was bred in the tropical to sub-tropical environment of S. Rhodesia (now Zimbabwe) and is photoperiod sensitive. With the planting of this trial on 5 December 1985 reproductive development of SR 52 was retarded such that the stem served as an alternative sink to the grain, accumulating TNC from A to PM. Total non-structural carbohydrate content in the whole stem of PNR 6427, CG 4602 and PNR 473 declined from A to PM indicating a general source limitation to yield during grain fill. In contrast TNC content in the whole stem of SA 60 and HL 1 declined from A to MGF and then increased substantially in SA 60 and marginally in HL 1 from MGF to PM. Thus there was a general source limitation from A to MGF in these two hybrids. However, as grain fill declined after MGF and ceased at PM, excess photosynthate accumulated in the stem indicating a sink limitation to yield in these two hybrids, particularly in SA 60, during the last half of grain fill. HL 1 recorded the highest grain yield out of the six hybrids. The good performance of HL 1 under the environmental conditions that prevailed during this trial can possibly be attributed to a number of factors, namely:

(i) it recorded the highest LAI at peak canopy; (ii) it exhibited 'stay green' characteristics in that it retained green leaf and stem tissue at PM; (iii) averaged over grain fill HL 1 had the smallest differences in TNC content between the shank and the A1 and B1 stem segments which may infer that there was a good balance between production of photosynthate and utilization by the developing grain; (iv) although HL 1 recorded the second lowest TNC content levels in the whole stem at A it showed a tendency to deplete available TNC pools to supplement the supply of current photosynthate to the grain at peak or mid-grain fill; and (v) as the rate of grain fill declined after MGF and ceased at PM, TNC content increased marginally in the stem indicating that photosynthetic activity extended beyond grain fill. It is noteworthy that HL 1 recorded the second lowest TNC content levels in the whole stem at A. It has been reported from farmers who grew HL 1 that this hybrid is very sensitive to drought occurring at flowering which results in large final grain yield reductions (Gevers, 1991; personal communication). This sensitivity to drought during flowering may be explained by the low levels of TNC in the stem available to supplement the reduced supply of current photosynthate for utilization by the processes that determine grain sink potential. Since water stress conditions only developed from MGF onward in this trial (Appendix 4), it is likely that the processes which determine kernel sink potential occurred under relatively favourable environmental conditions and that the supply of current photosynthate was adequate.

PNR 473 recorded the second highest grain yield but in contrast

to HL 1 this was achieved by markedly depleting available TNC in the stem to supplement the supply of current photosynthate to the grain. At PM PNR 473 recorded the lowest TNC content levels in the whole stem compared to the other hybrids. Thus the poor standability rating for PNR 473 mentioned earlier (Section 2.1) appears to be due to this tendency to deplete non-structural carbohydrates at the expense of stem structural strength and resistance to microbial infection of stem tissue. SA 60, as with HL 1, showed stay green characteristics. However, grain capacity apparently limited yield production in SA 60 as TNC content levels in the whole stem increased markedly from MGF to PM, and since SA 60 had the highest cob production of the six hybrids it appears that photosynthate in excess to grain requirements was partitioned to the cob. In fact, SA 60 serves as an example of a genotype in which the stay green characteristic may not result in high grain yields unless the grain sink capacity can utilize the available photosynthate production capacity. Leaf senescence in PNR 6427, and particularly in CG 4602, preceded the attainment of physiological maturity. Both hybrids depleted TNC pools in the stem throughout grain fill but more markedly so from A to MGF than from MGF to PM. The smaller depletion of TNC pools in the stem in the second half of grain fill than in the first half may indicate that the biochemical processes involved in the conversion of sucrose to starch in the grain may have become less efficient resulting in a termination of grain fill before available photosynthate was maximally utilized (Jenner, 1986). Chevalier and Lingle (1983) have shown that the activity of many of the enzymes involved in the conversion of sucrose to starch declines as the grain of wheat and barley approaches maturity.

In terms of the distribution of non-structural carbohydrates in the stem segments of the six hybrids, the larger by dry mass basal stem segments, in particular the B3 stem segment, generally recorded the highest contents of the component non-structural carbohydrates. On the other hand, the shank generally recorded the highest compositions of the component non-structural carbohydrates compared to the other stem segments. It is not possible to determine with certainty the relative contributions of available accumulated TNC by the stem segments to grain fill requirements, since levels of non-structural carbohydrates fluctuated in all the stem segments during grain fill. However, since the A1, B1, shank and cob segments serve as conduits for photosynthate destined for the primary grain it is clear that large amounts of non-structural carbohydrates would be translocated through these segments when integrated over the entire grain filling period.

Interpretation of the data from the 1985/86 maize hybrid rain grown trial was hindered by the fact that the hybrids were not grown under water stress and non-stress conditions. Nonetheless, the data obtained from this trial indicate that commercially grown maize hybrids in South Africa exhibit considerable variation in amounts of stem carbohydrates accumulated and/or utilized during grain fill. Additionally, monitoring the fluctuation in TNC in the stem of maize genotypes during grain fill, may provide an indication of the balance that exists between source production of photosynthate and sink (primarily grain) utilization of photosynthate as influenced by the prevailing environmental conditions. Whole plant photosynthesis

is difficult to measure and leaf  $\Psi_w$  data in isolation is inconclusive in terms of explaining plant responses to water stress. Thus quantitative analysis of non-structural carbohydrates in the maize stem may provide a more complete and convenient assessment of whether a source or sink limitation determines final grain yield in a particular maize genotype.

The peak TNC content levels which occurred in the whole stem of PNR 6427, SA 60, CG 4602, PNR 473 and HL 1 at A amounted to 10,4, 17,1, 15,1, 12,8 and 12,9 g stem<sup>-1</sup>, respectively. In SR 52 TNC content levels peaked at PM, amounting to 25,1 g stem<sup>-1</sup>. If the photosynthetic capacity of the hybrids is completely inhibited when TNC levels in the stem are at a maximum and if the hybrids were able to mobilize all the TNC in the stem to the grain this would contribute only 16,0, 20,3, 16,1, 11,2 and 9,4 % of the final grain yield attained in this trial in PNR 6427, SA 60, CG 4602, PNR 473 and HL 1, respectively. In SR 52 peak TNC content levels in the stem at PM were 166,2 % of that of the final grain yield. Thus it is apparent that, apart from SR 52, peak amounts of TNC in the stem amount to only a small proportion of the final grain yield which is realized if the production and mobilization of current photosynthate to the grain are not completely inhibited. It is clear that should the supply of current photosynthate to the grain be completely inhibited as a result of unfavourable environmental conditions, non-structural carbohydrates in the stem may only serve as a temporary buffer supply of carbohydrate to the grain until the production of current photosynthate is adequately resumed. Nonetheless, the mobilization of non-structural carbohydrates in the stem to the

grain may allow the processes that determine grain sink potential to occur, or, allow continued linear grain fill to occur for brief periods when the supply of current photosynthate does not meet demand.

Non-structural carbohydrate in the stem of the maize plant at PM may represent a significant source of energy which may be harvested in the production of silage or utilized in maize stover fed to livestock after grain harvesting. The TNC which remained in the stem at PM amounted to 0,27, 0,56, 0,31, 1,26, 0,08 and 0,23 t ha<sup>-1</sup> in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. It is once again evident that SR 52 accumulated the greatest amount of TNC in the whole stem with PNR 473 retaining the lowest amounts of TNC in the whole stem compared to the other hybrids at PM.

In the 1986/87 maize single cross hybrid rain-out shelter trial SA 6 and K78Y x I137TN showed a similar difference between the stressed and non-stressed A1 and B1 stem segments in TNC content, residual content and dry mass. This remarkably similar response to water deficits should be viewed against the background of very different patterns in the partitioning of TNC for sink requirements. SA 6 exhibited the early senescing characteristic while K78Y x I137TN exhibited the stay green, or late senescing, characteristic. SA 6 generally showed a greater increase in the component non-structural carbohydrates (composition and content) in the A1 and B1 segments from 1 to between 3 to 4 WAA under stress and non-stress conditions compared to K78Y x I137TN. However, from between 3 to 4 WAA until PM the composition and

content of the component non-structural carbohydrates declined more markedly and to lower final levels at PM in the A1 and B1 segments of SA 6 under stress and non-stress conditions compared to K78Y x I137TN. It is possible that the early leaf senescence characteristic exhibited by SA 6 is also linked to a tendency to accumulate TNC in the stem during EGF. The accumulated TNC is then depleted to supplement the supply of current photosynthate to the grain which declines as a result of greater leaf senescence during late grain fill. Thus the overall greater leaf senescence in SA 6 from 3 WAA to PM, under stress and non-stress conditions, resulted in a greater depletion of TNC pools in the stem to lower levels at PM in order to supplement the declining supply of current photosynthate to the grain in comparison to K78Y x I137TN. The higher grain yield production of K78Y x I137TN under the stress and non-stress conditions that prevailed in this trial compared to SA 6 may be attributed to a number of factors, namely: (i) K78Y x I137TN recorded a higher LAI throughout grain fill under stress and non-stress conditions compared to SA 6; (ii) it did not partition as much non-structural carbohydrate to the stem during the first three weeks of grain fill as did SA 6 and did not markedly deplete stem non-structural carbohydrate pools to the same extent as did SA 6 under stress and non-stress conditions; and (iii) in the last week of grain fill as the leaf  $\Psi_w$  of K78Y x I137TN increased sharply under stress conditions, it exhibited an ability to deplete stem non-structural carbohydrates to supplement the supply of current photosynthate to the grain. Thus the less marked increases and decreases in stem non-structural carbohydrates in K78Y x I137TN under stress and non-stress

conditions compared to SA 6 may indicate that photosynthetic capacity of the leaves was evenly matched by grain sink capacity and demand. This meant that there was less excess photosynthate available to accumulate in the stem, rather than the grain, and the extended photosynthetic activity of the leaves allowed the photosynthate requirements of the grain to be met by current photosynthate, with available stem carbohydrate pools being depleted to supplement current photosynthate supply to the grain in the final week of grain fill in K78Y x I137TN. It is noteworthy that K78Y x I137TN did partition more photosynthate to cob dry mass production under stress and non-stress conditions in comparison to SA 6. This may indicate that the grain sink capacity was somewhat limiting in K78Y x I137TN even though it out-yielded SA 6 in grain production.

A noteworthy feature of the response of the two hybrids to water stress was that the patterns in the changes in the content of each component non-structural carbohydrate under stress conditions generally paralleled that under non-stress conditions, but at lower overall content levels. In other words, water stress caused a step-like suppression in the amount of non-structural carbohydrates that accumulated in the stem but the overall rates of increase or decline (the patterns in the changes) in the content of the non-structural carbohydrates remained similar under stress and non-stress conditions for each hybrid. A similar situation occurred with LAI where there was an immediate step-like decline in LAI in the stressed plants from 1 WAA to 2 WAA compared to non-stressed plants, but thereafter the changes in LAI of the stressed plants generally paralleled

that of the non-stressed plants until PM (Figure 3.2). This may indicate that the hybrids were initially sensitive to water deficits immediately after imposition of water stress, but then the stressed plants developed a degree of stress hardening and continued ontogenetical development at similar rates as the non-stressed plants but with reduced 'amounts' of anatomical and biochemical components. Although K78Y x I137TN retained a higher LAI at PM under stress and non-stress conditions compared to SA 6 under stress and non-stress conditions, the rate at which LAI declined in K78Y x I137TN due to leaf senescence was greater than that for SA 6 from 5 WAA to PM. This may be explained by the observation that K78Y x I137TN did not decline in LAI as rapidly as did SA 6 from 1 to 5 WAA and recorded a higher LAI during this period. The greater leaf area may therefore have exposed K78Y x I137TN to greater transpirational water loss and therefore greater utilization of soil water. Thus the more marked decline in the leaf  $\Psi_w$  of the K78Y x I137TN stressed plants from 6 WAA to PM compared to SA 6 stressed plants may have been in response to the smaller amounts of soil water available to the K78Y x I137TN stressed plants. Another noteworthy feature of the data of the 1986/87 rain-out shelter trial was the remarkably smooth patterns in the changes in the non-structural carbohydrates during grain fill. The use of single cross hybrids has clearly contributed to reducing the plant to plant variability which bedevils destructive sampling procedures in detailed physiological studies.

The topography of the site at which the rain-out shelter is situated is not ideal for the induction of stress. The rain-out

shelter is situated on a slope with a gradient of 1:20, and is situated below the Department of Agricultural Development's maize breeding trial plots which are regularly sprinkler irrigated during the season. It is hypothesised that the impervious layer of Ecca shale, 500 to 1000 mm below the soil surface, would permit the lateral and down-slope movement of the irrigation water through the rain-out shelter site. The maize breeding plots were planted earlier than this trial and irrigation of the maize breeding plots terminated approximately three weeks before the plants in the rain-out shelter trial attained physiological maturity. Consequently, there was a sharp decline in leaf  $\Psi_w$  in the last week of grain fill in SA 6 and in the final two weeks of grain fill in K78Y x I137TN which supports this hypothesis. Further on up-slope from the rain-out shelter trial a small hill runs across the land which increases the run-off and subsurface movement of rain water down-slope into the rain-out shelter trial site. It is proposed that the imposition of water stress conditions could be more effectively controlled if sunken walls constructed of sheets of fibreglass were placed around each plot at the rain-out shelter trial site. Thus each plot would be effectively isolated from the other preventing the lateral movement of water from within and without the site. Obviously irrigation water applied to an isolated plot would have to be drained away using for instance french drains.

A feature common to the non-structural carbohydrate data of all three trials presented in this thesis is that during the first week or two of grain fill the amount of RS in the stem segments exceeded the amount of sucrose. This may indicate that during

the lag phase of grain fill, before the grain becomes established as the major sink for photosynthate, photosynthate produced in the leaves is utilized within the stem for final structural growth with RS predominating over sucrose. However, as the grain becomes established as the major sink for photosynthate and the metabolic activity associated with structural growth of the stem ceases, sucrose predominates over RS as photosynthate produced in the leaves is mobilized through the stem to the grain, primarily as sucrose.

In the 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial the maize single cross hybrid B254W x M162W was used. This hybrid exhibited the stay green characteristic of the one inbred parent M162W as well as exhibiting the tendency to utilize stem non-structural carbohydrates under water stress conditions during the latter phase of grain fill which is characteristic of the other inbred parent B254W (Section 4.3.3). Non-structural carbohydrate data showed that the content of the component non-structural carbohydrates generally declined in the A1, B1, shank and cob plant parts of B254W x M162W under stress conditions from 4 to 6 WAA until PM. On the other hand, under non-stress conditions the content of the component non-structural carbohydrates in the same plant parts generally increased from 4 to 6 WAA until PM. In the grain the content of the component non-structural carbohydrates was generally lower during grain fill under stress conditions than under non-stress conditions. In particular, the sucrose content of the grain of the non-stressed plants continued to increase throughout grain fill, whereas the sucrose content in the grain of stressed plants peaked at lower levels at 6 WAA

before remaining constant until PM. At PM the TNC content in the grain of stressed plants was 75,8 % of that in the grain of non-stressed plants; and the dry mass of the grain of stressed plants at PM was 78,3 % of that of non-stressed plants. It is apparent from the non-structural carbohydrate data that the stay green characteristic allowed the non-stressed B254W x M162W plants to continually produce current photosynthate throughout grain fill, as judged by the continual increase in whole plant dry mass throughout grain fill (Table 4.58). In fact, non-stressed plants produced photosynthate in excess to grain requirements which accumulated as TNC and residual components in the stem segments and cob (Figures 4.11 and 4.12). Stressed plants continued to produce current photosynthate during grain fill until 6 WAA as judged by the increase in whole plant dry mass during this period (Table 4.58). However, from 6 WAA to PM current photosynthate production virtually ceased as judged by the constant whole plant dry mass during this period (Table 4.58). Stressed plants apparently supplemented the reduced supply of photosynthate to the grain during the latter phase of grain fill by depleting TNC and residual components in the stem segments and cob. Thus it would appear that under the non-stress conditions which prevailed inside the growth tunnel, grain sink capacity limited yield in this single cross hybrid B254W x M162W. Compared to the 1986/87 maize single cross hybrid rain-out shelter trial, the component non-structural carbohydrates fluctuated to a greater extent in the B254W x M162W A1 and B1 stem segments under stress and non-stress conditions. The reason(s) for this is not certain, however, it may be due to the combined effects of the plants being grown in pots inside a growth tunnel.

Exposure of water stressed and non-stressed B254W x M162W plants to  $^{14}\text{CO}_2$  on four consecutive occasions during grain fill revealed, at first glance, subtle differences between stressed and non-stressed plants in the partitioning of  $^{14}\text{C}$  among organs and component non-structural carbohydrates. That the partitioning patterns of  $^{14}\text{C}$  were slightly different between stressed and non-stressed plants was as a consequence of the water stress conditions attained (Section 4.3.1) and the plants were exposed to  $^{14}\text{C}$  for a short period of 15 min. However, water stress did consistently alter the partitioning patterns of  $^{14}\text{C}$  on all four labelling occasions. Forty-eight hours after each labelling occasion the stressed plants had partitioned a higher proportion of the whole plant  $^{14}\text{C}$  to the grain than the non-stressed plants. However, at PM the non-stressed plants had partitioned an equal or greater proportion of the whole plant  $^{14}\text{C}$  recovered at PM to the grain compared to the stressed plants for plants labelled on all occasions except at A. Thus it appears that water stress initially resulted in a more direct and rapid translocation of  $^{14}\text{C}$ -labelled photosynthate to the grain.

Associated with the similarities between labelling dates there were also major differences in the partitioning patterns of  $^{14}\text{C}$  assimilated on each labelling occasion. It is apparent from the whole plant TR data (Section 4.3.7.2, Figure 4.26) that the plants assimilated less  $^{14}\text{C}$  on each subsequent labelling occasion during grain fill, with plants labelled at A assimilating the most  $^{14}\text{C}$  and plants labelled at 6 WAA assimilating the least. In fact, the amount of  $^{14}\text{C}$  assimilated at 6 WAA was only 12,1 and 16,3 % of that assimilated at A in stressed and non-stressed

plants, respectively. Although it was not possible to measure photosynthetic activity per unit leaf area in this study it is clear that, based on the amount of  $^{14}\text{C}$  assimilated on each labelling occasion, the photosynthetic activity of the whole plant declined in this maize hybrid from A to PM. Thus it may be concluded that photosynthetic activity per unit leaf area does not increase during grain fill in order to compensate for a decline in whole plant photosynthetic activity through leaf senescence. It is possible, however, that whole plant photosynthetic activity may have increased during the two week period between labelling at A and at 2 WAA.

It is also apparent from the whole shoot TR data expressed as a percentage of whole plant TR (Section 4.3.6.3, Figure 4.22) that stressed and non-stressed plants labelled at A translocated a smaller proportion of assimilated  $^{14}\text{C}$  to the grain during grain fill. Consequently, stressed and non-stressed plants labelled at A recorded the highest proportion of whole plant  $^{14}\text{C}$  recovered in the whole shoot at PM compared to plants labelled on any of the other occasions. At A the primary ear was not yet established as the major sink for photosynthate and much of the  $^{14}\text{C}$  assimilated at A was utilized for final structural growth of the whole shoot including the cob and husks of the primary ear. This tendency coupled with the higher amount of  $^{14}\text{C}$  assimilated at A explains why the segments of the whole shoot of stressed and non-stressed plants labelled at A generally had a higher SR (Section 4.3.4.1) and TR (Section 4.3.4.2) on all sampling occasions than did segments of the whole shoot when plants were labelled at 2 WAA, 4 WAA and 6 WAA. It is of interest to note

that 48 h after labelling at A, the husks of the primary ear followed by the laminae of both stressed and non-stressed plants recorded the highest TR of all segments. This is in direct contrast to plants labelled at 2 WAA, 4 WAA and 6 WAA in which the grain recorded the highest TR 48 h after labelling. It appears that  $^{14}\text{C}$  was not as rapidly translocated out of the leaves within 48 h after labelling at A, as was the case when plants were labelled at 2 WAA, 4 WAA and 6 WAA. The higher TR recorded for the husks 48 h after labelling at A compared to the laminae may indicate that the husks have a higher photosynthetic activity per unit leaf area soon after A than the laminae. However, it would be necessary to determine how much of the photosynthate in the husks is produced from own photosynthesis and how much is translocate from the rest of the plant, to establish whether or not this is true. Stressed and non-stressed plants labelled at 2 WAA translocated the greatest proportion of assimilated  $^{14}\text{C}$  to the grain during grain fill and consequently recorded the lowest proportion of whole plant  $^{14}\text{C}$  recovered in the whole shoot at PM compared to plants labelled on the other occasions. This indicates that at 2 WAA the primary ear was established as the major sink for photosynthate, with most of the  $^{14}\text{C}$  assimilated by the plants at 2 WAA translocated to the grain. Thus the lower amount of  $^{14}\text{C}$  assimilated by the whole plant at 2 WAA compared to that assimilated at A, coupled with the tendency to translocate most of the assimilated  $^{14}\text{C}$  to the grain, resulted in the SR and TR of the segments of the whole shoot of plants labelled at 2 WAA being generally less on all sampling occasions, in comparison to the SR and TR of the segments of the whole shoot of plants labelled at A. The SR of the grain at 48 h after labelling at

A was higher than the SR of the grain 48 h after labelling at 2 WAA. This was due to the lower dry mass of the grain at A in comparison to that at 2 WAA. However, the greater amount of  $^{14}\text{C}$  assimilated at 2 WAA partitioned to the grain, resulted in the grain of plants labelled at 2 WAA recording the highest TR on all sampling occasions, in comparison to the grain of plants labelled at A, 4 WAA and 6 WAA. When plants were labelled at 4 WAA, the proportion of whole plant  $^{14}\text{C}$  recovered in the whole shoot at PM was greater than that for plants labelled at 2 WAA but less than for plants labelled at A. Thus it is clear that although the primary grain was established as the major sink for photosynthate at 4 WAA, this was to a lesser extent than was the case at 2 WAA. The lower amount of  $^{14}\text{C}$  assimilated by the whole plant at 4 WAA compared to that at A and 2 WAA coupled with the tendency to translocate much of the assimilated  $^{14}\text{C}$  to the grain, resulted in the SR of the segments of the whole shoot being less on all sampling occasions in comparison to segments of the whole shoot of plants labelled at A and 2 WAA. The SR of the grain of plants labelled at 4 WAA was lower on all sampling occasions than the SR of the grain of plants labelled at 2 WAA on all sampling occasions. The grain of non-stressed plants labelled at 4 WAA had a higher SR at 4, 6 and 8 WAA than the grain of non-stressed plants labelled at A and sampled at 4, 6 and 8 WAA. The grain of stressed plants labelled at 4 WAA had a higher SR only at 8 WAA than the grain of stressed plants labelled at A and sampled at 8 WAA. On the other hand, the TR of the segments of the whole shoot of plants labelled at 4 WAA was less on all sampling occasions in comparison to segments of the whole shoot of plants labelled at A. However, the observation that the plants labelled

at 4 WAA had a greater proportion of the whole plant  $^{14}\text{C}$  in the shoot at PM, in comparison to plants labelled at 2 WAA, has resulted in the TR of some of the segments of the shoot on each of the sampling occasions exceeding that of the segments of the shoot of plants labelled at 2 WAA. The grain of plants labelled at 4 WAA had a higher TR on all sampling occasions than the grain of plants labelled at A. However, the grain of plants labelled at 2 WAA had a higher TR on all sampling occasions than the grain of plants labelled at 4 WAA. When plants were labelled at 6 WAA, the proportion of whole plant  $^{14}\text{C}$  recovered in the whole shoot at PM was greater than that for plants labelled at 2 WAA and 4 WAA but less than that for plants labelled at A. It is apparent that although the primary grain was still established as the major sink for photosynthate at 6 WAA, this was to a lesser extent than was the case for plants labelled at 2 WAA and 4 WAA. The considerably lower amount of  $^{14}\text{C}$  assimilated by the whole plant at 6 WAA, coupled with the tendency to translocate a large proportion of the assimilated  $^{14}\text{C}$  to the grain, resulted in the SR and TR of the whole shoot segments being generally less on all sampling occasions in comparison to segments of the whole shoot of plants labelled at A, 2 WAA and 4 WAA. The grain too, as a result of the low amount of  $^{14}\text{C}$  assimilated at 6 WAA, had a lower TR on all sampling occasions compared to the grain sampled on all occasions from plants labelled at A, 2 WAA and 4 WAA.

In addition, it is apparent from the whole plant TR data (Section 4.3.7.2, Figure 4.26) that the difference between stressed and non-stressed plants in the amount of  $^{14}\text{C}$  assimilated varied greatly on each labelling occasion. When plants were labelled

at A, the imposition of water deficits commenced after labelling. Thus there was, theoretically, no difference in the photosynthetic capacity of the plants when they were labelled at A. In fact, 48 h after labelling at A, the whole plant TR of plants to be stressed was 530 682 dpm plant<sup>-1</sup> higher than that of non-stressed plants. However, at PM the whole plant TR of stressed plants was 291 164 dpm less than that of non-stressed plants. Thus on an absolute and on a proportional basis the stressed plants respired more of the <sup>14</sup>C assimilated at A than the non-stressed plants from A to PM (Section 4.3.7.2). When plants were labelled at 2 WAA, the stressed plants had already undergone two consecutive stress cycles. However, 48 h after labelling at 2 WAA whole plant TR of stressed plants was 388 470 dpm plant<sup>-1</sup> higher than that of non-stressed plants. At 2 WAA the leaf  $\Psi_w$  of the stressed plants was significantly ( $p = 0,05$ ) less by 475 kPa than that of non-stressed plants. However, it appears that the stressed plants recovered from the effects of the water deficits sufficiently enough after being rewatered at 2 WAA to assimilate marginally more <sup>14</sup>C than the non-stressed plants. At PM the whole plant TR of stressed plants was 615 686 dpm plant<sup>-1</sup> less than that of non-stressed plants. Thus on an absolute and on a proportional basis the stressed plants respired more of the <sup>14</sup>C assimilated at 2 WAA than the non-stressed plants from 2 WAA to PM (Section 4.3.7.2). When plants were labelled at 4 WAA, the stressed plants had already undergone four consecutive stress cycles, with leaf  $\Psi_w$  of stressed plants significantly ( $p = 0,05$ ) less by 593 kPa than that of non-stressed plants, and leaf area of stressed plants 0,089 m<sup>2</sup> plant<sup>-1</sup> less than that of non-stressed plants. Thus stressed plants did not have the same

photosynthetic capacity as the non-stressed plants and 48 h after labelling at 4 WAA the whole plant TR of stressed plants was 1 539 763 dpm plant<sup>-1</sup> less than that of non-stressed plants, i.e. the stressed plants assimilated 18,3 % less <sup>14</sup>C than the non-stressed plants at 4 WAA. At PM the whole plant TR of the stressed plants was 3 064 630 dpm plant<sup>-1</sup> less than that of the non-stressed plants, although this difference was exaggerated by the high TR recorded for the grain of non-stressed plants from replication one. Using the average whole plant TR from the other two replications at PM for non-stressed plants, stressed plants respired less <sup>14</sup>C on an absolute basis than non-stressed plants from 4 WAA to PM but respired marginally more than non-stressed plants on a proportional basis (Section 4.3.7.2). When plants were labelled at 6 WAA, the stressed plants had already undergone six consecutive stress cycles, with leaf  $\Psi_w$  of stressed plants significantly ( $p = 0,05$ ) less by 509 kPa than that of non-stressed plants, and leaf area of stressed plants 0,098 m<sup>2</sup> plant<sup>-1</sup> less than that of non-stressed plants. Thus stressed plants did not have the same photosynthetic capacity as the non-stressed plants and 48 h after labelling at 6 WAA, the whole plant TR of stressed plants was 676 892 dpm less than that of non-stressed plants, i.e. the stressed plants assimilated 24,7 % less <sup>14</sup>C than the non-stressed plants at 6 WAA. At PM the whole plant TR of the stressed plants was 294 315 dpm plant<sup>-1</sup> less than that of the non-stressed plants. On an absolute and on a proportional basis, the non-stressed plants respired more of the <sup>14</sup>C assimilated at 6 WAA than the stressed plants from 6 WAA to PM (Section 4.3.7.2).

A problem encountered with the whole plant  $^{14}\text{C}$  data was that when plants were labelled at A, 2 WAA and 4 WAA the TR of the whole plant did not consistently decline from labelling to PM as a result of respiration losses. Instead, the TR of the whole plant fluctuated from one sampling occasion to another. Although the hybrid used in this study was a single cross, and plants grown in the pots appeared remarkably uniform to the eye, environmental influences clearly induced enough plant to plant variation resulting in variable rates of  $\text{CO}_2$  assimilation among similarly treated plants. With only two plants being sampled per plot and there being only three replications, slight differences between plants may result in bias of calculated means. A good example of this is the high TR recorded for the grain of non-stressed plants from replication one labelled at 4 WAA and sampled at PM which resulted in a higher whole plant TR being recorded at PM than 48 h after labelling at 4 WAA. Additionally, with the technique of labelling batches of 12 plants it is difficult to obtain uniform distribution of  $^{14}\text{C}$  throughout the chamber even with the assistance of fans, as the plants themselves impede the even flow and distribution of released  $^{14}\text{CO}_2$  throughout the chamber. Labelling of plants on each occasion commenced at 11h00 in the morning and was completed after 12h00. Clearly, during the course of a labelling session the sun's azimuthal orientation, incident solar radiation and ambient temperatures will change, and so the environmental conditions prevailing during the labelling of each batch of plants will not be identical. Unfortunately there are few solutions to these problems if plants are to be placed inside labelling chambers and exposed to  $^{14}\text{CO}_2$  under 'field' conditions. On the other hand, if

large controlled environmental chambers are available it may be possible to conduct  $^{14}\text{C}$ -labelling experiments under controlled conditions thereby reducing the environmental influence on the  $^{14}\text{C}$  assimilation rates.

An interesting partitioning pattern revealed by the data is that the TR of the 2° ear and the proportion of whole plant  $^{14}\text{C}$  in the 2° ear peaked 48 h after labelling at A, but then declined until 4 WAA before increasing to PM. A similar pattern was shown for plants labelled at 2 WAA and 4 WAA, where the TR of the 2° ear and the proportion of whole plant  $^{14}\text{C}$  in the 2° ear peaked 48 h after labelling on these occasions, but declined until 6 WAA before increasing to PM. The TR of the 2° ear and the proportion of whole plant  $^{14}\text{C}$  in the 2° ear also peaked 48 h after labelling at 6 WAA but then declined until PM. It appears that some  $^{14}\text{C}$  assimilated at A, 2 WAA and 4 WAA was initially partitioned to the 2° ear but then, judging by the decline in the TR of the 2° ear,  $^{14}\text{C}$  was mobilized back out of the 2° ear into the rest of the plant with presumably much of the  $^{14}\text{C}$  then translocated to the primary grain. In the last one to two weeks of grain fill, as the rate of grain dry mass gain by the primary grain slowed and then ceased at PM,  $^{14}\text{C}$  was once again mobilized back into the 2° ear judging by the increase in the TR of the 2° ear and the proportion of whole plant  $^{14}\text{C}$  in the 2° ear. On the other hand, some of the  $^{14}\text{C}$  assimilated at 6 WAA was initially partitioned to the 2° ear 48 h after labelling but thereafter  $^{14}\text{C}$  was mobilized out of the 2° ear, judging by the decline in the TR of the 2° ear and the proportion of whole plant  $^{14}\text{C}$  in the 2° ear. On all four labelling occasions the TR of the 2° ear and the proportion of

whole plant  $^{14}\text{C}$  in the 2° ear was highest in the non-stressed plants on all sampling occasions. This clearly indicates that more  $^{14}\text{C}$  was available to be partitioned to the 2° ear under non-stress conditions than under stress conditions. In fact, 48 h after labelling at A the non-stressed plants recorded a higher TR of the 2° ear and proportion of whole plant  $^{14}\text{C}$  in the 2° ear than for the primary grain.

A significant feature of the  $^{14}\text{C}$  data is the rapid rate at which  $^{14}\text{C}$  assimilated by the leaves on each labelling occasion was mobilized out of the leaves and into the rest of the plant and then subsequently translocated to the primary grain. Of the final amount of  $^{14}\text{C}$  which occurred in the grain at PM for plants labelled at A, 32,7 and 25,0 % occurred in the grain of stressed and non-stressed plants 48 h after labelling. However, for plants labelled at A, once the primary grain was established as the major sink for photosynthate at 2 WAA, 75,3 and 76,6 % of the final amount of  $^{14}\text{C}$  which occurred in the grain at PM occurred in the grain of stressed and non-stressed plants at 4 WAA. When plants were labelled at 2 WAA, 4 WAA and 6 WAA the primary grain was established as the major sink for photosynthate and therefore  $^{14}\text{C}$  was rapidly mobilized to the primary grain. For plants labelled at 2 WAA, 79,0 and 61,5 % of the final amount of  $^{14}\text{C}$  which occurred in the grain at PM occurred in the grain of stressed and non-stressed plants respectively, 48 h after labelling. For plants labelled at 4 WAA, 80,5 and 76,3 % (data for replication two and three used) of the final amount of  $^{14}\text{C}$  which occurred in the grain at PM occurred in the grain of stressed and non-stressed plants respectively, 48 h after

labelling. For plants labelled at 6 WAA, 77,4 and 82,7 % of the final amount of  $^{14}\text{C}$  which occurred in the grain at PM, occurred in the grain of stressed and non-stressed plants respectively, 48 h after labelling.

On the other hand, the above data also indicates that not all the  $^{14}\text{C}$  which accumulated in the grain was immediately translocated to it following labelling. In fact, the TR of the grain of stressed and non-stressed plants generally continued to increase in the weeks following each labelling occasion. This may be interpreted as indicating that the  $^{14}\text{C}$  assimilated on each labelling occasion was used to synthesize labile organic compounds which accumulated in the vegetative organs of the plant and could therefore be mobilized to the grain at a later stage. The radioactivity associated with one of the components of the labile organic compounds, namely the non-structural carbohydrates, was determined using ion-exchange column chromatography (Section 4.3.8). The ion-exchange column chromatography procedure provided detailed information on the radioactivity associated with TS and starch and therefore it is not an easy task to provide a shortened discussion of the data. Generally, however, the TR of the TNC in the A1, B1, shank and cob plant parts peaked 48 h after labelling at A, 2 WAA, 4 WAA and 6 WAA and then declined at PM as  $^{14}\text{C}$  was mobilized out of these plant parts into the grain. Consequently the TR of the TNC in the grain increased from 48 h after labelling on each of the four occasions to PM as  $^{14}\text{C}$  was translocated into the grain from the rest of the plant. At PM the  $^{14}\text{C}$  in the form of starch in the grain represented 55,0 and 57,5 % of the total grain  $^{14}\text{C}$  in

stressed and non-stressed plants labelled at A; 77,5 and 65,8 % in stressed and non-stressed plants labelled at 2 WAA; 78,7 and 76,3 % in stressed and non-stressed plants labelled at 4 WAA; and 75,9 and 76,7 % in stressed and non-stressed plants labelled at 6 WAA. It is apparent from these data that the proportion of  $^{14}\text{C}$  in the form of starch in the grain at PM for  $^{14}\text{C}$  assimilated at A was less than that compared to  $^{14}\text{C}$  assimilated at 2 WAA, 4 WAA and 6 WAA. This indicates that a considerable proportion of the  $^{14}\text{C}$  assimilated at A and translocated to the grain was converted to residual components, viz protein, lipids and also structural components of the kernel cells.

Forty-eight hours after labelling on each of the four occasions the TR of the TS exceeded the TR of the starch in the A1, B1, shank and cob plant parts, and except for the cob of non-stressed plants labelled at A and 2 WAA, this was still the case at PM. The proportion of  $^{14}\text{C}$  in the form of TS in these plant parts was consequently also higher than the proportion of  $^{14}\text{C}$  in the form of starch. Thus it is apparent that the  $^{14}\text{C}$  assimilated on each of the labelling occasions was in terms of non-structural carbohydrates predominantly converted to TS rather than starch in the A1, B1, shank and cob plant parts. Forty-eight hours after labelling at A the TR of the TS in the grain of stressed and non-stressed plants exceeded that of the TR of the starch. However, at PM this situation was reversed with the TR of the starch in the grain exceeding the TR of the TS. In contrast 48 h after plants were labelled at 2 WAA, 4 WAA and 6 WAA the TR of the starch in the grain exceeded the TR of the TS and this situation still pertained at PM. Thus 48 h after plants were

labelled at A, the  $^{14}\text{C}$  translocated to the grain was not as rapidly converted from sucrose into starch as was the case 48 h after plants were labelled at 2 WAA, 4 WAA and 6 WAA. In terms of the effects of water stress on the distribution of  $^{14}\text{C}$  among the non-structural carbohydrate components, stressed plants labelled at A maintained a lower TR of the TNC in the A1 and B1 plant parts, but a higher TR of the TNC in the shank, cob and grain compared to non-stressed plants at 48 h and at PM. Stressed plants only maintained a higher TR of the TNC in the grain compared to non-stressed plants at 48 h and at PM, when labelled at 2 WAA. Due to the lower whole plant TR recorded for stressed plants labelled at 4 WAA and 6 WAA, the TR of the TNC in all five plant parts was lower in the stressed plants compared to non-stressed plants at 48 h and at PM. Stressed plants labelled at A had a higher proportion of the TR of the A1, B1, shank and cob plant parts in the form of TNC at PM in comparison to non-stressed plants. This may indicate that less  $^{14}\text{C}$  was converted to residual components in these plant parts under stress conditions. Stressed plants labelled at 2 WAA had a lower proportion of the TR of the A1, B1, shank and cob plant parts in the form of TNC at PM in comparison to non-stressed plants. This indicates that a greater proportion of  $^{14}\text{C}$  assimilated at 2 WAA occurred in the form of TNC in these plant parts later into grain fill in the non-stressed plants, than the stressed plants. Except for the B1 plant part, stressed plants labelled at 4 WAA had a lower proportion of the TR of the A1, shank and cob plant parts in the form of TNC at PM in comparison to non-stressed plants. As with plants labelled at 2 WAA, this indicates that a greater proportion of the  $^{14}\text{C}$  in these plant parts occurred as

TNC later into grain fill in non-stressed plants than stressed plants. The physiological significance of the higher proportion of the TR in the form of TNC in the B1 plant part of non-stressed plants is uncertain. Stressed plants labelled at 6 WAA had a higher proportion of the TR of the B1 and cob plant parts and a marginally lower proportion of the TR of the A1 and shank plant parts in the form of TNC at PM, in comparison to non-stressed plants. The physiological significance of these variable patterns is, however, uncertain.

As pointed out earlier, the continued increase in the TR of the grain throughout grain fill after being labelled on each of the four occasions indicates that assimilated  $^{14}\text{C}$  occurred as labile organic compounds in the vegetative plant parts which could be mobilized to the grain at a later stage. The ion-exchange column chromatography data confirms this assertion. By way of examples, at PM as much as 40,4 % of the radioactivity in the B1 segment of the stressed plants labelled at A was in the form of TNC with the majority (30,7 %) of this in the form of TS. At PM as much as 65,8 % of the radioactivity in the B1 segment of the non-stressed plants labelled at 2 WAA was in the form of TNC with the majority (49,4 %) of this in the form of TS. At PM as much as 75,4 % of the radioactivity in the B1 segment of stressed plants labelled at 4 WAA was in the form of TNC with the majority (56,8 %) of this in the form of TS. At PM as much as 98,4 % of the radioactivity in the B1 segment of stressed plants labelled at 6 WAA was in the form of TNC with the majority (86,2 %) of this in the form of TS. However, these data should not necessarily be interpreted as indicating that the  $^{14}\text{C}$  had been in the form of TNC from the time

of labelling to PM since there may be continual interconversions of sugars to amino acids, proteins and lipids, and vice versa. These data indicate another important trend and that is that generally in the stressed and non-stressed plants the proportion of the TR of the A1, B1, shank and cob plant parts in the form of TNC at PM increased from labelling at A to labelling at 6 WAA. This indicates that the later  $^{14}\text{C}$  was assimilated during grain fill and not mobilized to the grain from the vegetative plant parts, or lost through respiration, the greater was the tendency for the  $^{14}\text{C}$  to remain in the form of TNC in these plant parts and not be converted to residual components. In fact, for plants labelled at 6 WAA and averaged over stressed and non-stressed plants, the average proportion of TR in the A1, B1, shank and cob plant parts in the form of residual components at PM, was only 4,4 % compared to 78,0 % for plants labelled at A.

It was pointed out in the main discussion of ion-exchange column chromatography data (Section 4.3.8) that the proportion of the cob TR in the form of TNC in stressed plants 48 h after labelling at 2 WAA was 68,2 % which was markedly less than the 96,6 % recorded for the non-stressed plants. Thus a greater proportion (31,8 %) of the  $^{14}\text{C}$  in the cob was in the form of residual components. Since 93,8 % of the shank TR of the stressed plants was in the form of TNC it appears that as carbohydrate arrived in the cob through the shank it was converted to residual components which are likely to be labile components, such as amino acids and proteins. It was suggested that this may indicate altered patterns in nitrogen metabolism under stress conditions (Stewart and Larher, 1980). This may warrant further

research in order to determine whether water stress results in a greater accumulation of  $^{14}\text{C}$  in the cob in the form of amino acids, such as proline, asparagine or glutamine which may indicate some form of physiological adaptation to drought.

It is also apparent from ion-exchange column chromatography data that within the 48 h after  $^{14}\text{CO}_2$  was assimilated on each of the labelling occasions,  $^{14}\text{C}$  was rapidly converted to non-structural carbohydrate and residual components. The objective of a future research project could possibly attempt to examine the distribution of  $^{14}\text{C}$  among the non-structural carbohydrates and residual components during those first 48 h after labelling. Sampling of plants could be carried out as often as is logistically possible.

The ion-exchange column chromatography procedure used in this study proved to be a reliable technique in removing water soluble amino acids and organic acids from 80 % ethanol extracted tissue samples. Nonetheless, careful technique is required throughout the procedure in order to reduce losses due to accidental spillage or splashing and during the evaporating off of ethanol. The slow rate at which samples have to be eluted through the columns does make the procedure rather laborious. If many samples are to be eluted through the columns it is advisable to test the columns regularly using ninhydrin for the retention of amino acids.

It was initially intended to determine the radioactivity associated with glucose, fructose and sucrose using thin layer

chromatography. Unfortunately, only a few plant parts from plants labelled at A, 2 WAA and 4 WAA had a high enough SR to provide radioactivity counts above background. Even for these plant parts that had a high SR the TS had to be spotted on the prepared plates at 400  $\mu$ g per spot. The high loading of each spot resulted in bearding and tailing of the glucose, fructose and sucrose spots after separating out. Despite all these shortcomings the data obtained from the few samples analyzed by thin layer chromatography provided interesting patterns of the distribution of  $^{14}\text{C}$  among glucose, fructose and sucrose. Forty-eight hours after plants were labelled at A, the SR and TR of glucose and fructose in the shank was higher than the SR and TR of sucrose. This probably reflects the greater amount of RS that occurred in the shank at A compared to sucrose in both stressed and non-stressed plants (Section 4.3.3, Table 4.4), and may be indicative of the greater utilization of  $^{14}\text{C}$  assimilated at A for metabolic processes and structural growth within the shank itself. At this stage the primary grain was not yet established as the major sink for photosynthate. The SR and TR of sucrose in the shank of stressed plants 48 h after labelling at A were higher than that of the shank of non-stressed plants which is indicative of the more direct and rapid mobilization of assimilated  $^{14}\text{C}$  in the form of sucrose to the primary ear under stress conditions. In contrast to the shank of plants labelled at A, the A1, shank and cob plant parts of plants labelled at 2 WAA (except for the cob of non-stressed plants) and the shank of plants labelled at 4 WAA recorded a substantially higher SR and TR of sucrose than glucose and fructose. This probably reflects the greater amount of sucrose that occurred in these

plant parts at 2 WAA and 4 WAA compared to RS in both stressed and non-stressed plants (Section 4.3.3, Table 4.4). When plants were labelled at 2 WAA and 4 WAA the primary grain was established as the major sink for photosynthate. Thus photosynthate was predominantly mobilized through the vegetative plant parts in the form of sucrose to be translocated into the grain. Apart from specific exceptions discussed in Section 4.3.9, the stressed plants labelled at 2 WAA and 4 WAA recorded lower SR and TR of glucose, fructose and sucrose in the particular plant parts analyzed compared to non-stressed plants. With respect to plants labelled at 2 WAA this reflects the greater synthesis of TNC per unit mass in the grain under stress conditions, whereas with respect to plants labelled at 4 WAA this reflects the more direct and rapid mobilization of  $^{14}\text{C}$  to the grain under stress conditions as well as the lower whole plant TR recorded for stressed plants compared to non-stressed plants 48 h after labelling at 4 WAA.

The water stress conditions that prevailed in the  $^{14}\text{C}$ -labelling study resulted in a 13,6 % reduction in final grain yield in B254W x M162W. Non-structural carbohydrate analysis data revealed that B254W x M162W continued to produce enough current photosynthate to meet grain requirements until the last two weeks of grain fill under stress conditions. In the last two weeks of grain fill, judging by the decline in stem non-structural carbohydrates, the production of current photosynthate was inadequate for grain requirements and stem carbohydrate pools were depleted to supplement the supply of current photosynthate to the grain. The stay green characteristic imparted to

B254W x M162W by the one parent M162W enabled this hybrid to continue accumulating non-structural carbohydrates in the vegetative organs until PM under non-stress conditions. The data from the  $^{14}\text{C}$ -labelling experiment revealed that stressed plants initially partitioned a greater proportion of the assimilated whole plant  $^{14}\text{C}$  to the grain than the non-stressed plants. However, in the later stages of grain fill the proportion of whole plant  $^{14}\text{C}$  in the grain of the non-stressed plants was similar to that of the stressed plants.

The statistical analysis procedure used for all three studies in this thesis namely analysis of variance as a split-plot in time coupled with the Greenhouse-Geisser epsilon factor was adequate for the specific objectives. The Greenhouse-Geisser epsilon factor provides the user with a measure of confidence in declaring statistically significant interactions to be due to real treatment effects as opposed to being due to heteroscedasticity of the data. However, analysis of variance does have shortcomings for analyzing data from repeated measures designs, namely: (i) there are no legitimate tests for comparing the effects of sampling dates since sampling dates cannot be randomized; (ii) when the number of splits in the split-plot design is greater than two the number of plots required is large and the analysis of data becomes cumbersome and inefficient; (iii) important physiological trends may be overlooked if only data of significant interactions are presented and discussed; and (iv) where data has a wide range, subtle treatment responses may be masked in tests of significance. One alternative approach for data where the number of sampling occasions exceeds five, is to

develop polynomial regression curves for each experimental unit describing the quantitative variate as a function of sampling occasion (time). The regression coefficients from the fitted models may then be used as data in a multivariate analysis of variance to test for coincident and parallel growth curves (Eskridge and Stevens, 1987). A statistical procedure which has recently become available on the Genstat 5.0 statistical package (PC version) is the Antorder Macro developed by Ridout and Payne (1990) which tests the degree of ante-dependence of a set of variates observed at successive times. In collaboration with staff members of the Department of Statistics and Biometry, University of Natal these alternative statistical procedures may be used to analyze the data of the studies presented in this thesis for purposes of further testing these procedures.

Drought conditions are notoriously difficult to simulate experimentally and are also difficult to repeat over seasons and at different geographical locations. In addition, it is extremely difficult to subject the plant species under study to a specific controlled level or degree of water stress, a problem which also affected the results obtained from the experiments presented in this thesis. The procedure often reported in the literature of watering stressed plants with less water than non-stressed plants in order to maintain leaf  $\Psi_w$  at a certain level is, from a theoretical basis, flawed since the soil profile of the stress treatment will still be watered to field capacity but to a shallower depth than the soil water profile of the non-stress treatment. This determines that the roots of stressed plants are still able to take up water from the upper soil layer

at a similar soil  $\Psi_w$  as the non-stressed plants. The problem of exposing plants to a root environment where the available water is held at a controlled specific  $\Psi_w$  has led to some bizarre experiments, for example growing plants in a saline solution at a specific osmotic potential. The effects of water stress would clearly be confounded with the effects of the high levels of Na on the metabolism of the plants. Another problem which frustrates workers in the field of water stress physiology is that the effects of water stress are usually confounded with the effects of heat stress. Obviously much research and innovative thinking is required in order to overcome these problems before definitive results can be obtained relating specific and controlled levels of water stress to the growth and development of plants.

In final conclusion; the stay green characteristic evident in certain genotypes is apparently an advantageous characteristic under favourable environmental conditions in that the maize plant is able to meet the photosynthate requirements of the grain largely with current photosynthate until physiological maturity is reached. Under unfavourable environmental conditions, specifically water stress, the stay green characteristic may only be an advantageous one if it is coupled to a photosynthesis machinery that is tolerant to low leaf  $\Psi_w$  and low soil  $\Psi_w$ . A future research programme could be directed towards identifying genotypes with the stay green characteristic coupled with a water stress tolerant photosynthetic machinery. On the other hand, the stay green characteristic does not preclude the advantages of the capacity to accumulate photosynthate in the vegetative organs

during favourable environmental conditions and then mobilize the accumulated photosynthate to the grain under environmental conditions that limit the production of current photosynthate. This is because it is possible that environmental conditions may completely inhibit the production of current photosynthate and stay green genotypes that do not also accumulate surplus photosynthate in the vegetative organs are likely to have the processes of grain fill severely disrupted. As mentioned previously, should water stress conditions not occur, non-structural carbohydrates which remain in the stem may be regarded as wasted grain yield. However, this should be weighed against the risk of large yield losses being incurred should hybrids be grown without built in insurance in regions with a high drought risk. In addition, maize genotypes which photosynthesize late into the season or that have some non-structural carbohydrates stored in the stem after photosynthesis ceases, may be able to delay structural degeneration by microorganisms which often leads to lodging. As mentioned earlier, high sugar levels in the stem pith tissue of the maize plant apparently results in greater structural strength of the stem and provides the maize plant with greater resistance to *D. zea* stem rot. In addition, carbohydrates remaining in the stem after grain harvest may be fed to livestock as stover in the field. However, utilization by microorganisms of the carbohydrates remaining in the stover after grain harvest may result in substantial energy losses. Future research projects may attempt to quantify these energy losses. Efforts could also be made to determine whether maize genotypes exhibit differential susceptibility to microbial decomposition of carbohydrates remaining in the stover.

## REFERENCES

- Ackerson, R.C., 1983. Comparative physiology and water relations of two corn hybrids during water stress. Crop Sci. 23, 278-283.
- Akazawa, T. and Okamoto, K., 1980. Biosynthesis and metabolism of sucrose. In Priess, J. (ed.). The biochemistry of plants. Vol 3. Carbohydrates: structure and function. Academic Press, New York. Pp. 100-220.
- Aldrich, S.R., Scott, W.O. and Leng, E.R., 1975. Modern corn production, 2nd ed. A & L Publications, Illinois. Pp. 1-18.
- Allison, J.C.S., 1969. Effect of plant population on the production and distribution of dry matter in maize. Ann. Appl. Biol. 63, 135-144.
- Allison, J.C.S. and Watson, D.J. 1966. The production and distribution of dry matter in maize after flowering. Ann. Bot. 30, 365-381.
- Allison, J.C.S. and Weinmann, H., 1970. Effect of absence of developing grain on carbohydrate content and senescence of maize leaves. Plant Physiol. 46, 435-436.
- Allison, J.C.S., Wilson, J.H.H. and Williams, J.H., 1975. Effect of defoliation after flowering on changes in stem and grain mass of closely and widely spaced maize. Rhod. J. agric. Res. 13, 145-147.
- Anon, 1985. Irrigation in developing countries. S.A. Water Bulletin, May, 1-2.
- Anon, 1986. Management of the water resources of the Republic of South Africa, Department of Water Affairs, 1986. CTP Book Printers, Cape Town. Pp. 1.3-2.7.
- Anon, 1989a. Agriculture in South Africa. Chris van Rensburg Publication, Johannesburg. Pp. 83-97.
- Anon, 1989b. Abstracts of agricultural statistics. Directorate Agricultural Economic Trends, Pretoria. Pp. 1-9.
- Anon, 1989c. Maize Board annual report. Published by the maize board, Pretoria. Pp. 1-25.
- ap Rees, T., 1980. Integration of pathways of synthesis and degradation of hexose phosphates. In Priess, J. (ed.). The biochemistry of plants. Vol. 3. Carbohydrates: structure and function. Academic Press, New York. Pp. 1-42.
- ap Rees, T., 1984. Sucrose metabolism. In Lewis, D.H. (ed.). Storage carbohydrates in vascular plants. Distribution, physiology and metabolism. Cambridge University Press, Cambridge. Pp. 53-74.

- ap Rees, T., 1985. The organisation of glycolysis and the oxidative pentose phosphate pathway in plants. In Douce, R. and Day, D.A. (eds). Encyclopedia of plant physiology. Vol. 18. Springer-Verlag, Berlin. Pp. 391-417.
- ap Rees, T., 1988. Hexose phosphate metabolism. In Preiss, J. (ed.). The biochemistry of plants. Vol. 14. Carbohydrates. Academic Press, Inc., San Diego. Pp. 1-33.
- Austin, R.B., Edrich, J.A., Ford, M.A. and Blackwell, R.D., 1977. The fate of the dry matter, carbohydrates and <sup>14</sup>C lost from the leaves and stems of wheat during grain fill. Ann. Bot. 41, 1309-1321.
- Balasko, J.A. and Smith, D., 1973. Carbohydrates in grasses: V. Incorporation of <sup>14</sup>C into plant parts and nonstructural carbohydrates of timothy (Phleum pratense L.) at three developmental stages. Crop Sci. 13, 19-22.
- Banks, W. and Greenwood, C.T., 1975. Starch and its components. Edinburgh : Edinburgh University Press.
- Barr, C.G., 1939. Polysaccharides of the vegetative tissue of maize. Plant Physiol. 14, 737-753.
- Bassham, J.A., 1979. The reductive pentose phosphate cycle and its regulation. In Gibbs, M. and Latzko, E. (eds). Encyclopedia of plant physiology. Vol. 6. Springer-Verlag, Berlin. Pp. 9-30.
- Baxter, E.D. and Duffus, C.M., 1971. Starch synthetase in developing barley amyloplasts. Phytochemistry 10, 2641-2644.
- Below, F.E., Christensen, L.E., Reed, A.J. and Hageman, R.H., 1981. Availability of reduced N and carbohydrate for ear development of maize. Plant Physiol. 68 : 1186-1190.
- Bidinger, F., Musgrave, R.B., and Fischer, R.A., 1977. Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. Nature 270, 431-433.
- Block, R.J., Durrum, E.L. and Zweig, G., 1955. A manual of paper chromatography and paper electrophoresis. Academic Press Inc., Publishers, New York. Pp. 127-156.
- Box, G.E.P., 1950. Problems in the analysis of growth and wear curves. Biometrics 6, 362-389.
- Boyer, J.S., 1970a. Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. Plant Physiol. 46, 233-235.
- Boyer, J.S., 1970b. Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybean. Plant Physiol. 46, 236-239.

- Boyer, J.S., 1973. Response of metabolism to low water potentials in plants. Phytopathology. 63, 466-472.
- Boyer, J.S., and McPherson, H.G., 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27, 1-23.
- Boyer, C.D., and Shannon, C.D., 1987. Carbohydrates of the kernel. In Watson, S.A. and Ramstad, P.E. (eds). Corn: chemistry and technology. American Association of cereal chemists, Inc. St Paul, Minnesota, U.S.A. Pp. 253-272.
- Brooking, I.R. and Kirby, E.J.M., 1981. Interrelationships between stem and ear development in winter wheat: the effects of a Norin 10 dwarfing gene, Gai/Rht 2. J. Agric. Sci. Cambridge. 97, 373-381.
- Bull, T.A., 1971. The C4 pathway related to growth rates in sugarcane. In Hatch, M.D. Osmond, C.B. and Slatyer R.O. (eds). Photosynthesis and photorespiration. Wiley, New York. Pp. 68-75.
- Campbell, C.M., 1964. Influence of seed formation of corn on accumulation of vegetative dry matter and stalk strength. Crop Sci. 4 : 31-34.
- Causton, D.R. and Venus, J.C., 1981. The biometry of plant growth. Edward Arnold Ltd., London. Pp. 133-143.
- Chevalier, P. and Lingle, S.E., 1983. Sugar metabolism in developing kernels of wheat and barley. Crop Sci. 23, 272-277.
- Christensen, L.E., Below, F.E. and Hageman, R.H., 1981. The effects of ear removal on senescence and metabolism of maize. Plant Physiol. 68, 1180-1185.
- Claassen, M. and Shaw, R.H., 1970. Water deficit effect on corn. II Grain components. Agron. J. 62, 652-655.
- Clarke, G.P.Y., 1988. Personal communication. Department of Statistics and Biometry, University of Natal, Pietermaritzburg.
- Clarke, J.M. and Townley-Smith, T.F., 1984. Screening and selection techniques for improving drought resistance. In Vose, P.B. and Blixt, S.G. (eds). Crop breeding: a contemporary basis. Pergamon Press. Pp. 137-162.
- Cole, J.W.L. and Grizzle, J.E., 1966. Applications of multivariate analysis of variance to repeated measurements experiments. Biometrics 22, 810-828.
- Conrad, J.P., 1937. The carbohydrate composition of corn and sorghum roots. J. Amer. Soc. Agron. 29, 1014-1021.
- Constable, G.A. and Hearn, A.B., 1978. Agronomic and physiological responses of soybean and sorghum crops to

- water deficits. I. Growth, development and yield. Aust. J. Plant Physiol. 5, 159-167.
- Craig, J. and Hooker, A.L., 1961. Relation of sugar trends and pith density to *Diplodia* stalk rot in dent corn. Phytopathology 51, 376-382.
- Czaja, A.T., 1978. Structure of starch grains and the classification of vascular plant families. Taxon. 27, 463-470.
- Daie, J., 1985. Carbohydrate partitioning and metabolism in crops. Hort. Reviews 7, 69-108.
- Darbyshire, B., 1971. The effect of water stress on activity of indolacetic acid oxidase in pea plants. Plant Physiol. 47, 65-67.
- Davies, D.R., 1974. Some aspects of sucrose metabolism. In Pridham, J.B. (ed.). Plant Carbohydrate Biochemistry. Academic Press, London. Pp. 61-82.
- Daynard, T.B. and Duncan, E.G., 1969. The black layer and grain maturity in corn. Crop Sci. 9, 473-476.
- Daynard, T.B., Tanner, J.W. and Hume, D.J., 1969. Contribution of stalk soluble carbohydrates to grain yield in corn (*Zea mays* L) Crop Sci. 9, 831-834.
- Deinum, B. and Struik, P.C., 1986. Improving the nutritive value of forage maize. In Dolstra, O and Miedema, P. (eds). Breeding of silage maize. Proc. 13th Cong. Maize and Sorghum Section of Eucarpia. Pudoc, Wageningen. Pp. 77-90.
- Dickson, R.E., 1979. Analytical procedures for the sequential extraction of <sup>14</sup>C-labeled constituents from leaves, bark and wood of cottonwood plants. Physiol. Plant. 45, 480-488.
- Donald, C.M., 1962. In search of yield. J. Austral. Inst. Agr. Sci. 28, 171-178.
- Dubois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.A. and Smith, F., 1956. Colorimetric method for determination of sugars and related substances. Anal. Chem. 28, 350-356.
- Duffus, C.M. and Duffus, J.H., 1984. Carbohydrate metabolism in plants. Longman, London.
- Duncan, W.G. and Hesketh, J.D., 1968. Net photosynthetic rates, relative growth rates and leaf numbers of 22 races of maize grown at eight temperatures. Crop Sci. 8, 670-674.
- Dunstone, R.L., Gifford, R.M. and Evans, L.T., 1973. Photosynthetic characteristics of modern and primitive wheat species in relation to ontogeny and adaption to light. Aust. J. Biol. Sci. 26, 295-307.

- Early, E.B., McIlrath, W.O., Seif, R.D. and Hageman, R.H., 1967. Effect of shade applied at different stages of plant development on corn (Zea mays L.) production. Crop Sci. 7, 151-156.
- Eastin, J.A., 1970. C-14 labeled photosynthate export from fully expanded corn (Zea mays L.) leaf blades. Crop Sci. 10, 415-418.
- Edwards, G. and Walker, D., 1983. C<sub>3</sub>, C<sub>4</sub>: mechanisms, and cellular and environmental regulation, of photosynthesis. Blackwell Scientific Publications, Oxford.
- Egharevba, P.N., Horrocks, R.D. and Zuber, M.S., 1976. Dry matter accumulation in maize in response to defoliation. Agron. J. 68, 40-43.
- Erwee, M.G. and Goodwin, P.B., 1985. Symplast domains in extrastelar tissues of Egeria densa Planch. Planta. 163, 9-19.
- Esau, K., 1977. Anatomy of seed plants. John Wiley and Sons, New York. Pp. 157-171.
- Eskridge, K.M and Stevens, E.J., 1987. Growth curve analysis of temperature-dependent phenology models. Agron. J. 79, 291-297
- Evert, R.F., Eschrich, W. and Heyser, W., 1977. Distribution and structure of the plasmodesmata in mesophyll and bundle sheath cells of Zea mays L. Planta. 136, 77-89.
- Evert, R.F., Eschrich, W. and Heyser, W., 1978. Leaf structure in relation to solute transport and phloem loading in Zea mays L. Planta. 138, 279-294.
- Evert, R.F. and Mierzwa, R.J., 1986. Pathways of assimilate movement from mesophyll cells to sieve tubes in the Beta vulgaris leaf. In Cronshaw, J., Lucas, W.J. and Giaquinta, R.T. (eds). Phloem Transport, Allan R. Liss, New York. Pp. 419-432.
- Fairey, N.A. and Daynard, T.B., 1978. Quantitative distributions of assimilates in component organs of maize during reproductive growth. Can. J. Plant Sci. 58, 709-717.
- Feingold, D.S. and Avigad, G., 1980. Sugar nucleotide transformations in plant. In Preiss, J. (ed.). The biochemistry of plants. Vol. 3. Carbohydrates: structure and function. Academic Press, New York. Pp. 101-170.
- Fisher, D.B., 1978. The estimation of sugar concentration in individual sieve-tube elements by negative staining. Planta. 139, 19-24.
- Fondy, B.R. and Geiger, D.R., 1982. Diurnal pattern of translocation and carbohydrate metabolism in source leaves of Beta vulgaris L. Plant Physiol. 70, 671-676.

- Franceschi, V.R., 1986. Temporary storage and its role in partitioning among sinks. In Cronshaw, J.C., Lucas, W.J. and Giaquinta, R.T. (eds). Phloem transport. Alan, R. Liss, Inc., New York. Pp. 399-409.
- Freeman, J.E., Bocan, B.J. and Zobel, H.F., 1972. Starch: variation associated with location in corn and sorghum plants. Crop Sci. 12, 122-124.
- Frey, N.M., 1981. Dry matter accumulation in kernels of maize. Crop Sci. 21, 118-122.
- Gevers, H.O., 1986 & 1991. Personal communication. Maize breeder, Department of Agricultural Development, summer grains sub-centre, Cedara.
- Giaquinta, R.T., 1983. Phloem loading of sucrose. Ann. Rev. Plant Physiol. 34, 347-387.
- Gifford, R.M. and Evans, L.T., 1981. Photosynthesis, carbon partitioning, and yield. Ann. Rev. Plant Physiol. 32, 485-509.
- Gill, J.L., 1978. Design and analysis of experiments in animal and medical sciences. Vol. 2. Iowa State University Press, Ames IA.
- Glasziou, K.T., 1961. Accumulation and transformation of sugars in stalks of sugar cane. Origin of glucose and fructose in the inner space. Plant Physiol. 36, 175-179.
- Glasziou, K.T. and Gayler, K.R., 1972. Storage of sugars in stalks of sugar cane. Bot. Rev. 38, 471-490.
- Green, G.C., 1984. A green look at irrigation. S.A. Water Bulletin, May, 31-33.
- Green, G.C., 1991. Personal communication. Water Research Commission, P.O. Box 824, Pretoria.
- Greenfield, P.L., Noble, A.D. and Jarvie, J.A., 1987. Morphological characteristics related to drought tolerance in maize (incorporating a study of leaf epidermal structure potentially associated with stress tolerance). Proc. 7th S. Afr. Maize Breeding Symp., Potchefstroom, 1986. Dept. Agric. and Water supply, Repub. S. Afr. Tech. commun. No. 212, 84-89.
- Greenhouse, S.W. and Geisser, S., 1959. On methods in the analysis of profile data. Psychometrika 24, 95-112.
- Hall, D.D. and Rao, K.K., 1987. Photosynthesis. New series in biology, 4th edition. Edward Arnold, London. Pp. 75-76.
- Hanway, J.J., 1962. Corn growth and composition in relation to soil fertility. I. Growth of different plant parts and relation between leaf weight and grain yield. Agron. J. 54, 145-148.

- Hanway, J.J. and Russell, W.A., 1969. Dry matter accumulation in corn (Zea mays L.) plants: Comparisons among single-cross hybrids. Agron. J. 61, 947-951.
- Heinze, P.H. and Murneek, A.E., 1940. Comparative accuracy and efficiency in determination of carbohydrates in plant material. Missouri Agric. Exp. Sta. Res. Bull. 314.
- Herold, A., 1984. Biochemistry and physiology of synthesis of starch in leaves: autotrophic and heterotrophic chloroplasts. In Lewis, D.H. (ed.). Storage carbohydrates in vascular plants: Distribution, physiology and metabolism. Cambridge University Press, Cambridge. Pp. 181-229.
- Herrero, M.P. and Johnson, R.R., 1981. Drought stress and its effects on maize reproductive systems. Crop Sci 21, 105-110.
- Hesketh, J.D. and Musgrave, R.B., 1962. Photosynthesis under field conditions. IV. Light studies with individual corn leaves. Crop Sci. 2, 311-315.
- Heslop-Harrison, J., 1961. Experimental control of sexuality and inflorescence structure in Zea mays L. Proc. Linn. Soc. Lond. 172, 108-123.
- Hilliard, J.H. and Daynard, T.B., 1974. Starch content, test weight and other quality parameters of corn produced in different maturity areas of Ontario. Crop Sci. 14, 546-548.
- Ho, L.C., 1986. Metabolism and compartmentation of translocates in sink organs. In Cronshaw, J., Lucas, W.J. and Giaquinta, R.J. (eds). Phloem transport. Alan R. Liss, Inc., New York. Pp. 197-209.
- Ho, L.C., 1988. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength, Ann. Rev. Plant Physiol. 39, 355-378.
- Hofstra, G. and Nelson, C.D., 1969. The translocation of photosynthetically assimilated <sup>14</sup>C in corn. Can. J. Bot. 47, 1435-1442.
- Hsiao, T.C., 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24, 519-570.
- Hsiao, T.C. and Acevedo, E., 1974. Plant responses to water deficits, water-use efficiency, and drought resistance. Agric. Meteorol. 14, 59-84.
- Huber, S.C., 1986. Fructose 2,6-bisphosphate as a regulatory metabolite in plants. Ann. Rev. Plant Physiol. 37, 233-246.
- Human Sciences Research Council, 1991. Personal communication. HSRC Building 134, Pretoria.

- Hume, D.J. and Campbell, D.K., 1972. Accumulation and translocation of soluble solids in corn stalks. Can. J. Plant. Sci. 52, 363-368.
- Husain, I. and Aspinall, D., 1970. Water stress and apical morphogenesis in barley. Ann. Bot. 34, 393-408.
- Jenner, C.F., 1970. Relationship between levels of soluble carbohydrate and starch synthesis in detached ears of wheat. Aust. J. Biol. Sci. 23, 991-1003.
- Jenner, C.F., 1982. Storage of starch. In Loewus, F.A. and Tanner, W. (eds). Encyclopedia of plant physiology. Vol. 13A. Springer-Verlag, Berlin. Pp. 700-747.
- Jenner, C.F., 1986. End product storage in cereals. In Cronshaw, J., Lucas, W.J. and Giaquinta, R.T. (eds). Phloem transport. Alan R. Liss, Inc., New York. Pp. 561-572
- Johnson, D.R. and Tanner, J.W., 1972. Calculation of the rate and duration of grain filling in corn (Zea mays L.) Crop Sci. 12, 485-486.
- Jones, R.J., Roessler, J. and Ouattar, S., 1985. Thermal environment during endosperm cell division in maize. Effect on number of endosperm cells and starch granules. Crop Sci. 25, 830-831.
- Jones, R.J. and Simmons, S.R., 1983. Effect of altered source sink ratio on growth of maize kernels. Crop Sci. 23, 129-134.
- Jurgens, S.K., Johnson, R.R. and Boyer, J.S., 1978. Dry matter production and translocation in maize subjected to drought during grain fill. Agron. J. 70, 678-682.
- Kainuma, K., 1988. Structure and chemistry of the starch granule. In Preiss, J. (ed.). The biochemistry of plants. Vol 14. Carbohydrates. Academic Press, Inc., San Diego. Pp. 141-180.
- Kaiser, W.M., Paul, J.S. and Bassham, J.A., 1979. Release of photosynthates from mesophyll cells in vitro and in vivo. Plant Physiol. 94, 377-385.
- Kalt-Torres, W., Kerr, P.S., Usuda, H. and Huber, S.C., 1987. Diurnal changes in maize leaf photosynthesis. I. Carbon exchange rate, assimilate, export rate, and enzyme activities. Plant Physiol. 83, 283-288.
- Kemp, W.B. and Henson, P.R., 1934. The effect of type of endosperm upon carbohydrate distribution in the mature corn plant. J. Amer. Soc. Agron. 26, 519-524.
- Kiesselbach, T.A., 1948. Endosperm type as a physiologic factor in corn yields. J. Am. Soc. Agron. 40, 216-236.

- Lenton, J.R., 1984. Are plant growth substances involved in the partitioning of assimilate to reproductive sinks? Plant Growth Regulation 2, 267-276.
- Leopold, A.C., 1961. Senescence in plant development. Science 134, 1727-1732.
- Lewis, D.H., 1984. Occurrence and distribution of storage carbohydrates in vascular plants. In Lewis, D.H. (ed.). Storage carbohydrates in vascular plants. Distribution, physiology and metabolism. Cambridge University Press, Cambridge. Pp. 1-52
- Lewis, B.A. and Smith, F., 1969. Sugars and derivatives. In Stahl, E. (ed.). Thin-layer chromatography. A laboratory manual. Sixth printing of the second edition, 1990. Springer-Verlag, Berlin. Pp. 807-837.
- Lucas, E.O., 1981. Remobilization of stem assimilates in maize varieties grown under tropical conditions. Maydica. 26, 287-292.
- Lucas, W.J. and Madore, M.A., 1988. Recent advances in sugar transport. In Lucas, W.J. and Madore, M.A. (eds). The biochemistry of plants. Vol 14. Carbohydrates. Academic Press, Inc., San Diego. Pp. 35-84.
- Ludlow, M.M. and Ng. T.T., 1976. Effect of water deficit on carbon dioxide exchange and leaf elongation rate of Panicum maximum var. trichoglume. Aust. J. Plant Physiol. 3, 401-413.
- Lush, W.M. and Evans, L.T., 1974. Longitudinal translocation of <sup>14</sup>C labelled assimilates in leaf blades of Lolium temulentum. Aust. J. Plant Physiol. 1, 433-443.
- Madore, M.A. and Lucas, W.J., 1986. Characterisation of the source leaf symplast by means of Lucifer Yellow CH. In Cronshaw, J.C., Lucas, W.J. and Giaquinta, R.T., (eds). Phloem transport. Pp. 129-134.
- Madore, M.A. and Webb, J.A., 1981. Leaf free space analysis and vein loading in Cucurbita pepo. Can. J. Bot. 59, 2550-2557.
- Maynard, J.W. and Lucas, W.J., 1982. Sucrose and glucose uptake into Beta vulgaris leaf tissues. A case for general (apoplastic) retrieval systems. Plant Physiol. 70, 1436-1443.
- McCree, K.J., 1974. Changes in the stomatal response characteristics produced by water stress during growth. Crop Sci. 14, 273-278.
- McGill, A.E.J., 1988. Future uses of maize grain. Proc. 8th S. Afr. Maize breeding Symp., Potchefstroom, 1988. Department of Agriculture and Water Supply, Repub. S. Afr. Tech Commun. No. 222, 60-62.

- McPherson, H.G. and Boyer, J.S., 1977. Regulation of grain yield by photosynthesis in maize subjected to a water deficiency. Agron. J. 69, 714-718.
- Meyer, R.F. and Boyer, J.S., 1981. Osmoregulation, solute distribution, and growth in soybean seedlings having low water potentials. Planta 151, 482-489.
- Milthorpe, F.L. and Moorby, J., 1969. Vascular transport and its significance in plant growth. Ann. Rev. Plant Physiol. 20, 117-138.
- Morgan, J.M., 1984. Osmoregulation and water stress in higher plants. Ann. Rev. Plant Physiol. 35, 299-348.
- Mortimore, C.G. and Ward, C.M., 1964. Root and stalk rot of corn in southwestern Ontario. III. Sugar levels as a measure of plant vigor and resistance. Can. J. Plant Sci. 44, 451-457.
- Moss, D.N., 1962. Photosynthesis and barrenness. Crop Sci. 2, 366-367.
- Moss, G.I. and Downey, L.A., 1971. Influence of drought stress on female gametophyte development in corn (Zea mays L.) and subsequent grain yield. Crop Sci. 11, 368-372.
- Muchow, R.C. and Wilson, G.L., 1976. Photosynthetic and storage limitations to yield in Sorghum bicolor (L. Moench). Aust. J. Agric. Res. 27, 478-500.
- Mühling, H.G., 1963. Substance formation and its storage in maize. Z. Acker-Pflanzenbau. 116, 129-153.
- Munns, R., Brady, C.J. and Barlow, E.W., 1979. Solute accumulation in the apex and leaves of wheat during water stress. Aust. J. Plant Physiol. 6, 379-389.
- Murata, Y. and Matsushima, 1975. Rice. In Evans, L.T. (ed). Crop physiology some case histories. Cambridge University Press, Cambridge, England. Pp. 73-99.
- Nishikawa, H. and Kudo, M., 1973. Explicational studies on the sterile ear as appeared on mechanized cultivation of the corn plant (Zea mays L.). (In Japanese, English summary). Tohoku Agricultural Experiment Station Research report. 44, 51-95.
- Ouattar, S., Jones, R.J. and Crookston, R.K., 1987a. Effect of water deficit during grain filling on the pattern of maize kernel growth and development. Crop Sci. 27, 726-730.
- Ouattar, S., Jones, R.J., Crookston, R.K. and Kajeiou, M., 1987b. Effect of drought on water relations of developing maize kernels. Crop Sci. 27, 730-735.
- Palmer, A.F.E., Heichel, G.H. and Musgrave, R.B., 1973. Patterns of translocation, respiration loss, and redistribution of

- $^{14}\text{C}$  in maize labelled after flowering. Crop Sci 13, 371-376.
- Passioura, J.B., 1986. Resistance to drought and salinity : avenues for improvement. Aust. J. Plant Physiol. 13, 191-201.
- Patrick, J.W., 1982. Hormonal control of assimilate transport. In Wareing, P.F. (ed.). Plant growth substances. Academic Press, New York. Pp. 669-678.
- Patrick, J.W., 1988. Assimilate partitioning in relation to crop production. Hort. Sci. 23, 33-40.
- Payne, R.W. and Dixon, T.J., 1984. MACRO-REPMEAS. Testing homogeneity and compound symmetry of covariance matrices from repeated measures designs. Genstat 4.04 Macro Library Manual.
- Pioneer Seed Company Catalogue, 1985. Pioneer Seed Company (PTY) LTD. Head office, Greytown, Natal, RSA.
- Potter, J.R. and Jones, J.W., 1977. Leaf area partitioning as an important factor in growth. Plant Physiol. 59. 10-14.
- Priess, J., 1982. Biosynthesis of starch and its regulation. In Loewus, F.A. and Tanner, W. (eds). Encyclopedia of plant physiology. Vol. 13A. Springer-Verlag, Berlin. Pp. 397-417.
- Preiss, J. and Levi, C., 1979. Metabolism of starch in leaves. In Gibbs, M. and Latzko, E. (eds). Encyclopedia of plant physiology. Vol. 6. Springer-Verlag, Berlin. Pp. 282-312.
- Quarrie, S.A., 1980. Genotypic differences in leaf water potential, abscisic acid and proline concentration in spring wheat during drought stress. Ann. Bot. 46, 383-394.
- Reed, A.J., Singletary, G.W., Schussler, J.R., Williamson, D.R. and Christy, A.L., 1988. Shading effects on dry matter and nitrogen partitioning, kernel number, and yield of maize. Crop Sci. 28, 819-825.
- Reinhold, L. and Kaplan, A., 1984. Membrane transport of sugars and amino acids. Ann. Rev. Plant Physiol. 35, 45-83.
- Rench, W.E. and Shaw, R.H., 1971. Black layer development in corn. Agron. J. 63, 303-305.
- Ridout, M.S. and Payne, R.W., 1990. MACRO-ANTORDER. Procedure to assess the order of ante-dependence for repeated measures data. Genstat 5.0 Macro Library Manual
- Robbroeck, T.P.C., 1983. Irrigation water resources, planning for the 90's. Keynote address : Irrigation workshop, Nov. 1983. Water Research Commission, Pretoria.

- Salvador, R.J. and Pearce, R.B., 1988. Husk removal and its effect on maize grain yield. Crop Sci. 28, 961-964.
- Schulze, E.D., 1986. Whole plant responses to drought. Aust. J. Plant Physiol. 13, 127-141.
- Setter, T.L. and Flannigan, B.A., 1986. Sugar and starch redistribution in maize in response to shade and ear temperature treatment. Crop Sci. 26, 575-579.
- Shannon, J.C., 1968. Carbon-14 distribution in carbohydrates of immature Zea mays kernels following  $^{14}\text{CO}_2$  treatment of intact plants. Plant Physiol. 43, 1215-1220.
- Shannon, J.C., Porter, G.A. and Knievel, D.P., 1986. Phloem unloading and transfer of sugars into developing corn endosperm. In Cronshaw, J., Lucas, W.J. and Giaquinta, R.T. (eds). Phloem transport. Alan R. Liss, Inc., New York. Pp. 265-277
- Sharp, R.E. and Davies, W.J., 1979. Solute regulation and growth by roots and shoots of water stressed maize plants. Planta. 147, 43-49.
- Simmons, S.R. and Jones, R.J., 1985. Contributions of pre-silking assimilate to grain yield in maize. Crop Sci. 25, 1004-1006.
- Smith, D., 1981. Removing and analyzing total non-structural carbohydrates from plant tissue. Wisconsin Agric. Exp. Stn. Res. Rep. R2107.
- Snyder, F.W. and Carlson, G.E., 1984. Selecting for partitioning of photosynthetic products in crops. Adv. Agron. 37, 47-72.
- Stanhill, G., 1986. Water use efficiency. Adv. Agron. 39, 53-85.
- Steup, M., 1988. Starch degradation. In Priess, J. (ed.). The biochemistry of plants. Vol. 14. Carbohydrates. Academic Press, Inc., San Diego. Pp. 255-296.
- Stewart, G.R. and Larher, F., 1980. Accumulation of amino acids and related compounds in relation to environmental stress. In Mifflin, B.J. (ed). The biochemistry of plants. Vol. 5. Amino acids and derivatives. Academic Press, Inc., New York. Pp. 609-635
- Stielau, K., 1990. Personal communication. Department of Statistics and Biometry, University of Natal, Pietermaritzburg.
- Stitt, M. 1984. Degradation of starch in chloroplasts: a buffer to sucrose metabolism. In Lewis, D.H. (ed.). Storage carbohydrates in vascular plants: distribution, physiology and metabolism. Cambridge University Press, Cambridge. Pp. 205-229.

- Stitt, N., 1986. Regulation of photosynthetic sucrose synthesis: integration, adaptation and limits. In Cronshaw, J., Lucas, W.J. and Giaquinta, R.T. (eds). Phloem transport. Alan R. Liss, Inc., New York. Pp. 331-347.
- Stitt, M. and Steup, M., 1985. Starch and sucrose degradation. In Douce, R. and Day, D.A. (eds). Encyclopedia of plant physiology. Vol 18. Springer-Verlag, Berlin. Pp. 347-390.
- Stoskopf, N.C., 1981. Understanding crop production. Reston Publishing Company, Inc., Reston. Pp. 92-03.
- Stoy, V., 1965. Photosynthesis, respiration and carbohydrate accumulation in spring wheat in relation to yield. Physiol. Plant. Suppl. 4, 1-125.
- Sullivan, C.Y. and Eastin, J.D., 1974. Plant physiological responses to water stress. Agric. Meteorol. 14 : 113-127.
- Swank, J.C., Below, F.E., Lambert, R.J. and Hageman, R.H., 1982. Interaction of carbon and nitrogen metabolism in the productivity of maize. Plant Physiol. 70, 1185-1190.
- Thorne, J.H., 1982. Characterization of the active sucrose transport system of immature soybean embryo's. Plant Physiol. 70, 953-958.
- Thorne, J.H., 1986. Sieve tube unloading. In Cronshaw, J.C. Lucas, W.J. and Giaquinta, R.T. (eds). Phloem transport. Alan R. Liss, Inc., New York. Pp. 211-224.
- Thorne, J.H., and Giaquinta, R.T., 1984. Carbohydrate translocation. In Lewis, D.H. (ed.). Storage carbohydrates in vascular plants. Cambridge University Press, Cambridge. Pp. 75-96.
- Tollenaar, M., 1977. Sink-source relationships during reproductive development in maize. Maydica. 22, 49-75.
- Tollenaar, M., 1989. Response to dry matter accumulation in maize to temperature. I. Dry matter partitioning. Crop Sci. 29, 1239-1246.
- Tollenaar, M. and Daynard, T.B., 1978a. Dry matter, soluble sugar content, and starch content of maize kernels during the early postsilking period. Can. J. Plant Sci. 58, 199-206.
- Tollenaar, M. and Daynard, T.B., 1978b. Effect of defoliation on kernel development in maize. Can. J. Plant Sci. 58. 207-212.
- Turgeon, R., 1989. The sink-source transition in leaves. Ann. Rev. Plant Physiol. 40, 119-138.
- Turner, N.C., 1986a. Adaptation to water deficits : a changing perspective. Aust. J. Plant Physiol. 13, 175-190.

- Turner, N.C., 1986b. Crop water deficits : a decade of progress. Adv. Agron. 39, 1-51.
- Turner, N.C. and Begg, J.E., 1978. Responses of pasture plants to water deficits. In Wilson, J.R. (ed.). Plant relations in pastures. CSIRO, Melbourne. Pp. 50-66.
- Turner, N.C. and Begg, J.E., 1981. Plant-water relations and adaption to stress. Plant and Soil. 58, 97-131.
- Tsai, C.Y., Huber, D.M. and Warren, H.L., 1978. Relationship of the kernel sink for N to maize productivity. Crop Sci. 18, 399-404.
- Tsai, C.Y., Salamini, F. and Nelson, O.E., 1970. Enzymes of carbohydrate metabolism in the developing endosperm of maize. Plant Physiol. 46, 299-306.
- Van Reen, R. and Singleton, W.R., 1952. Sucrose content in the stalks of maize inbreds. Agron. J. 44, 610-614.
- Vomhof, D.W. and Tucker, T.C., 1965. The separation of simple sugars by cellulose thin-layer chromatography. J. Chromatogr. 17, 300-306.
- Walker, A.J., Ho, L.C. and Baker, D.A., 1978. Carbon translocation in the tomato: Pathways of carbon metabolism in the fruit. Ann. Bot. 43, 437-448.
- Wallsgrave, R.M., Keys, A.J., Lea, P.J. and Mifflin, B.J., 1983. Photosynthesis, photorespiration and nitrogen metabolism. Plant, cell and environ. 6, 301-309.
- Wardlaw, I.F., 1968. The control and pattern of movement of carbohydrates in plants. Bot. Review. 34, 79-105.
- Wardlaw, I.F. and Monuir, L., 1976. Source, sink and hormonal control of translocation in wheat. Planta. 128, 93-100.
- Weinmann, H., 1947. Determination of total available carbohydrates in plants. Plant Physiol. 22, 279-290.
- Welton, F.A., Morris, V.H. and Hartzler, A.J., 1930. Distribution of moisture, dry matter, and sugars in the maturing corn stem. Plant Physiol. 5, 555-564.
- Westgate, M.E. and Boyer, J.S., 1985a. Carbohydrate reserves and reproductive development at low leaf water potentials in maize. Crop Sci. 25, 762-769.
- Westgate, M.E. and Boyer, J.S., 1985b. Osmotic adjustment and the inhibition of leaf, root, stem, and silk growth at low water potentials in maize. Planta. 164, 540-549.
- Westgate, M.E. and Boyer, J.S., 1986a. Silk and pollen water potentials in maize. Crop Sci 26, 947-951.

- Westgate, M.E. and Boyer, J.S., 1986b. Reproduction at low silk and pollen water potentials in maize. Crop Sci. 26, 951-956.
- Westgate, M.E. and Boyer, J.S., 1986c. Water status of the developing grain of maize. Agron. J. 78, 714-719.
- Wilhelm, W.W. and Nelson, C.J., 1978. Irradiance response of tall fescue genotypes with contrasting levels of photosynthesis and yield. Crop Sci. 18, 405-408.
- Wilson, C., Oross, J.W. and Lucas, W.J., 1985. Sugar uptake into Allium cepa leaf tissue: an integrated approach. Planta. 164, 227-240.
- Wolthers, W., 1988. The future of the maize industry in the Republic of South Africa. Proc. 8th S. Afr. Maize breeding Symp. Potchefstroom, 1988. Department of Agriculture and Water Supply, Repub. S. Afr. Tech. Commun. No. 222, 3-5.
- Wyse, R.E., 1986. Sinks as determinants of assimilate partitioning: possible sites for regulation. In Cronshaw, J., Lucas, W.J. and Giaquinta, R.T. (eds). Phloem transport. Alan R. Liss, Inc., New York. Pp. 197-209.
- Yoshida, S., 1972. Physiological aspects of grain yield. Ann. Rev. Plant Physiol. 23, 437-464.

## INDEX OF APPENDICES

	List of abbreviations used in the analysis of variance tables	778
1	Site description for Faculty of Agriculture - site of 1985/86 maize hybrid rain grown trial	779
2	Site description for Ukulinga - site of 1986/87 maize single cross hybrid rain-out shelter trial	780
3	Site description for Faculty of Agriculture growth tunnel - site of 1988/89 maize single cross hybrid <sup>14</sup> C-labelling study	781
4	CERES-maize simulation of stress-day factors CSD1 and CSD2 for the 1985/86 maize hybrid rain grown trial, Faculty of Agriculture	783
5	Daily maximum and minimum temperatures (°C) for November 1985 to May 1986, maize hybrid rain grown trial, Faculty of Agriculture	789
6	Rainfall figures (mm) for November 1985 to May 1986, maize hybrid rain grown trial, Faculty of Agriculture	790
7	Daily maximum and minimum temperatures (°C) for November 1986 to May 1987, maize single cross hybrid rain-out shelter trial, Ukulinga	791
8	Rainfall figures (mm) for November 1986 to May 1987, maize single cross hybrid rain-out shelter trial, Ukulinga	792
9	Daily maximum and minimum temperatures (°C) for December 1988 to May 1989, maize single cross hybrid <sup>14</sup> C-labelling study, Faculty of Agriculture	793
10	Rainfall figures (mm) for December 1988 to May 1989, maize single cross hybrid <sup>14</sup> C-labelling study, Faculty of Agriculture	794
11	Selected chemical properties of soil samples taken from the Faculty of Agriculture site	795
12	Selected chemical properties of soil samples taken from the Ukulinga rain-out shelter site	795
13	Selected chemical properties of soil samples taken from the commercially supplied Baynesvlei form Baynesvlei series soil used in the 1988/89 maize single cross hybrid <sup>14</sup> C-labelling study conducted in the growth tunnel at the Faculty of Agriculture	795
14	Field plan for 1985/86 maize hybrid rain grown trial, Faculty of Agriculture	796
15	Field plan for 1986/87 maize single cross hybrid	

	rain-out shelter trial, Ukulinga	797
16	Field plan for 1988/89 maize single cross hybrid <sup>14</sup> C-labelling study, Faculty of Agriculture growth tunnel	798
17	Characterisation of component total non-structural carbohydrates using high pressure liquid chromatography	799
18	Analyses of variance : non-structural carbohydrate analyses of STEM SEGMENTS : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture	802
18.1	VARIATE: Reducing sugars composition (%) of stem segments	802
18.2	VARIATE: Reducing sugars content (g segment <sup>-1</sup> ) of stem segments	803
18.3	VARIATE: Sucrose composition (%) of stem segments	804
18.4	VARIATE: Sucrose content (g segment <sup>-1</sup> ) of stem segments	805
18.5	VARIATE: Starch composition (%) of stem segments	806
18.6	VARIATE: Starch content (g segment <sup>-1</sup> ) of stem segments	807
18.7	VARIATE: Total non-structural carbohydrate composition (%) of stem segments	808
18.8	VARIATE: Total non-structural carbohydrate content (g segment <sup>-1</sup> ) of stem segments	809
18.9	VARIATE: Residual content (g segment <sup>-1</sup> ) of stem segments	810
18.10	VARIATE: Dry mass (g segment <sup>-1</sup> ) of stem segments	811
19	Analyses of variance : carbohydrate analyses of WHOLE STEM : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture	812
19.1	VARIATE: Reducing sugars composition (%) of whole stem	812
19.2	VARIATE: Reducing sugars content (g stem <sup>-1</sup> ) of whole stem	813
19.3	VARIATE: Sucrose composition (%) of whole stem	814
19.4	VARIATE: Sucrose content (g stem <sup>-1</sup> ) of whole stem	815
19.5	VARIATE: Starch composition (%) of whole stem	816
19.6	VARIATE: Starch content (g stem <sup>-1</sup> ) of whole stem	817
19.7	VARIATE: Total non-structural carbohydrate	

	composition (%) of whole stem	818
19.8	VARIATE: Total non-structural carbohydrate content (g stem <sup>-1</sup> ) of whole stem	819
19.9	VARIATE: Residual content (g stem <sup>-1</sup> ) of whole stem	820
19.10	VARIATE: Dry mass (g stem <sup>-1</sup> ) of whole stem	821
20	Analyses of variance : carbohydrate analyses of COB : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture	822
20.1	VARIATE: Reducing sugars composition (%) of cob	822
20.2	VARIATE: Reducing sugars content (g cob <sup>-1</sup> ) of cob	823
20.3	VARIATE: Sucrose composition (%) of cob	824
20.4	VARIATE: Sucrose content (g cob <sup>-1</sup> ) of cob	825
20.5	VARIATE: Starch composition (%) of cob	826
20.6	VARIATE: Starch content (g cob <sup>-1</sup> ) of cob	827
20.7	VARIATE: Total non-structural carbohydrate composition (%) of cob	828
20.8	VARIATE: Total non-structural carbohydrate content (g cob <sup>-1</sup> ) of cob	829
20.9	VARIATE: Residual content (g cob <sup>-1</sup> ) of cob	830
20.10	VARIATE: Dry mass (g cob <sup>-1</sup> ) of cob	831
21	Analyses of variance : carbohydrate analyses of GRAIN : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture	832
21.1	VARIATE: Reducing sugars composition (%) of grain	832
21.2	VARIATE: Reducing sugars content (g grain <sup>-1</sup> ) of grain	833
21.3	VARIATE: Sucrose composition (%) of grain	834
21.4	VARIATE: Sucrose content (g grain <sup>-1</sup> ) of grain	835
21.5	VARIATE: Starch composition (%) of grain	836
21.6	VARIATE: Starch content (g grain <sup>-1</sup> ) of grain	837
21.7	VARIATE: Total non-structural carbohydrate composition (%) of grain	838
21.8	VARIATE: Total non-structural carbohydrate content (g grain <sup>-1</sup> ) of grain	839
21.9	VARIATE: Residual content (g grain <sup>-1</sup> ) of grain	840

21.10	VARIATE: Dry mass (g grain <sup>-1</sup> ) of grain	841
22	Analysis of variance : Leaf area index at peak canopy : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture	842
23	Analysis of variance : Grain yield (g m <sup>-2</sup> , primary plus secondary ears) at harvest maturity : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture	843
24	Analyses of variance : yield components (primary ear only) and cob production at harvest maturity : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture	844
24.1	VARIATE: Kernels ear <sup>-1</sup>	844
24.2	VARIATE: Kernels row <sup>-1</sup>	844
24.3	VARIATE: Rows ear <sup>-1</sup>	845
24.4	VARIATE: Mass kernel <sup>-1</sup> (g)	845
24.5	VARIATE: Cob production (g m <sup>-2</sup> )	846
25	Analyses of variance : Agronomic characteristics at harvest maturity : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture	847
25.1	VARIATE: Stand percentage	847
25.2	VARIATE: Percentage barren plants	847
25.3	VARIATE: Percentage runt primary ears	848
25.4	VARIATE: Percentage of final grain yield from primary ear	848
26	Analysis of variance : VARIATE : Leaf water potential (kPa) : 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga	849
27	Analysis of variance : VARIATE : Leaf area index: 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga	850
28	Analyses of variance : carbohydrate analyses of STEM SEGMENTS : 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga	851
28.1	VARIATE: Reducing sugars composition (%) of stem segments	851
28.2	VARIATE: Reducing sugars content (g segment <sup>-1</sup> ) of stem segments	852
28.3	VARIATE: Sucrose composition (%) of stem segments	853

28.4	VARIATE: Sucrose content (g segment <sup>-1</sup> ) of stem segments	854
28.5	VARIATE: Starch composition (%) of stem segments	855
28.6	VARIATE: Starch content (g segment <sup>-1</sup> ) of stem segments	856
28.7	VARIATE: Total non-structural carbohydrate composition (%) of stem segments	857
28.8	VARIATE: Total non-structural carbohydrate content (g segment <sup>-1</sup> ) of stem segments	858
28.9	VARIATE: Residual content (g segment <sup>-1</sup> ) of stem segments	859
28.10	VARIATE: Dry mass (g segment <sup>-1</sup> ) of stem segments	860
29	Analysis of variance : grain yield (g m <sup>2</sup> , primary ears only) at harvest maturity : 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga	861
30	Analyses of variance : Yield components and cob production at harvest maturity : 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga	862
30.1	VARIATE: Kernels ear <sup>-1</sup>	862
30.2	VARIATE: Kernels row <sup>-1</sup>	862
30.3	VARIATE: Rows ear <sup>-1</sup>	863
30.4	VARIATE: Mass kernel <sup>-1</sup> (g)	863
30.5	VARIATE: Cob production (g m <sup>2</sup> )	864
31	Analyses of variance : agronomic characteristics at harvest maturity : 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga	865
31.1	VARIATE: Percentage barren plants at harvest maturity	865
31.2	VARIATE: Percentage runt primary ears at harvest maturity	865
32	Development of techniques used in the determination of radioactivity associated with non-structural carbohydrates for the 1988/89 maize single cross hybrid <sup>14</sup> C-labelling study	866
32.1	Development of the thin layer chromatography procedure adopted for the determination of radioactivity associated with glucose, fructose and sucrose	866
32.2	A short research note on the problem of chemiluminescence encountered while determining the radioactivity associated with total sugars and starch	

	using ion-exchange column chromatography	871
32.3	Development of the ion exchange column procedure adopted for the determination of radioactivity associated with total sugars	876
33	Analysis of variance : VARIATE : Leaf water potential (kPa) of the maize hybrid B254W x M162W subjected to water stress and lack of water stress during grain fill : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	879
34	Analysis of variance : VARIATE : Leaf area (m <sup>2</sup> plant <sup>-1</sup> ) of the maize hybrid B254W x M162W subjected to water stress and lack of water stress during grain fill : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	880
35	Analyses of variance : Specific radioactivity of segments from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	881
35.1	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of segments from plants labelled at A	881
35.2	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of segments from plants labelled at 2 WAA	882
35.3	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of segments from plants labelled at 4 WAA	883
35.4	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of segments from plants labelled at 6 WAA	884
36	Analyses of variance : Total radioactivity of segments from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	885
36.1	VARIATE: Total radioactivity of segments (dpm segment <sup>-1</sup> ) from plants labelled at A	885
36.2	VARIATE: Total radioactivity of segments (dpm segment <sup>-1</sup> ) from plants labelled at 2 WAA	886
36.3	VARIATE: Total radioactivity of segments (dpm segment <sup>-1</sup> ) from plants labelled at 4 WAA	887
36.4	VARIATE: Total radioactivity of segments (dpm segment <sup>-1</sup> ) from plants labelled at 6 WAA	888
37	Analyses of variance : VARIATE : Specific radioactivity of the whole stem from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	889

37.1	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole stem of plants labelled at A	889
37.2	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole stem of plants labelled at 2 WAA	890
37.3	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole stem of plants labelled at 4 WAA	891
37.4	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole stem of plants labelled at 6 WAA	892
38	Analyses of variance : VARIATE : Total radioactivity of the whole stem from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	893
38.1	VARIATE: Total radioactivity of whole stem (dpm stem <sup>-1</sup> ) of plants labelled at anthesis	893
38.2	VARIATE: Total radioactivity of whole stem (dpm stem <sup>-1</sup> ) of plants labelled at 2 WAA	894
38.3	VARIATE: Total radioactivity of whole stem (dpm stem <sup>-1</sup> ) of plants labelled at 4 WAA	895
38.4	VARIATE: Total radioactivity of whole stem (dpm stem <sup>-1</sup> ) of plants labelled at 6 WAA	896
39	Analyses of variance : VARIATE : Specific radioactivity of the whole shoot from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	897
39.1	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole shoot of plants labelled at A	897
39.2	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole shoot of plants labelled at 2 WAA	898
39.3	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole shoot of plants labelled at 4 WAA	899
39.4	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole shoot of plants labelled at 6 WAA	900
40	Analyses of variance : VARIATE : Total radioactivity of the whole shoot from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	901
40.1	VARIATE: Total radioactivity of whole shoot (dpm shoot <sup>-1</sup> ) of plants labelled at A	901
40.2	VARIATE: Total radioactivity of whole shoot	

	(dpm shoot <sup>-1</sup> ) of plants labelled at 2 WAA	902
40.3	VARIATE: Total radioactivity of whole shoot (dpm shoot <sup>-1</sup> ) of plants labelled at 4 WAA	903
40.4	VARIATE: Total radioactivity of whole shoot (dpm shoot <sup>-1</sup> ) of plants labelled at 6 WAA	904
41	Analyses of variance : VARIATE : Specific radioactivity of the whole plant from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	905
41.1	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole plant of plants labelled at A	905
41.2	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole plant of plants labelled at 2 WAA	906
41.3	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole plant of plants labelled at 4 WAA	907
41.4	VARIATE: Specific radioactivity (dpm g <sup>-1</sup> ) of whole plant of plants labelled at 6 WAA	908
42	Analyses of variance : VARIATE : Total radioactivity of the whole plant from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	909
42.1	VARIATE: Total radioactivity of whole plant (dpm plant <sup>-1</sup> ) of plants labelled at A	909
42.2	VARIATE: Total radioactivity of whole plant (dpm plant <sup>-1</sup> ) of plants labelled at 2 WAA	910
42.3	VARIATE: Total radioactivity of whole plant (dpm plant <sup>-1</sup> ) of plants labelled at 4 WAA	911
42.4	VARIATE: Total radioactivity of whole plant (dpm plant <sup>-1</sup> ) of plants labelled at 6 WAA	912
43	Analysis of variance : Grain yield (g plant <sup>-1</sup> , primary plus secondary ears) at harvest maturity : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	913
44	Analyses of variance : yield components and cob production (primary ear only) at harvest maturity : 1988/89 maize single cross hybrid <sup>14</sup> C labelling trial, Faculty of Agriculture	914
44.1	VARIATE: Kernels ear <sup>-1</sup>	914
44.2	VARIATE: Kernels row <sup>-1</sup>	914

44.3	VARIATE: Rows ear <sup>-1</sup>	915
44.4	VARIATE: Mass kernel <sup>-1</sup> (g)	915
44.5	VARIATE: Cob production (g plant <sup>-1</sup> )	916
45	VARIATE: Secondary ear grain yield (g plant <sup>-1</sup> ) at harvest maturity : 1988/89 maize single cross hybrid <sup>14</sup> C labelling trial, Faculty of Agriculture	916
46	Segment dry mass (g segment <sup>-1</sup> ) on each sampling occasion of each labelling occasion : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	917
47	Whole stem dry mass (g stem <sup>-1</sup> ) on each sampling occasion of each labelling occasion : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	920
48	Whole shoot dry mass (g shoot <sup>-1</sup> ) on each sampling occasion of each labelling occasion : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	922
49	Whole plant dry mass (g plant <sup>-1</sup> ) on each sampling occasion of each labelling occasion : 1988/89 maize single cross hybrid <sup>14</sup> C-labelling trial, Faculty of Agriculture	924

LIST OF ABBREVIATIONS USED IN THE ANALYSIS OF VARIANCE TABLES

In order to facilitate the presentation of the analysis of variance tables the following abbreviations were used:

A - Anthesis

adj - adjusted

ERROR MS - ERROR MEAN SQUARE (OR RESIDUAL MEAN SQUARE)

SEG - SEGMENT

STAGE - GROWTH STAGE

STRESS - STRESS TREATMENT

SUBPL - SUB-PLOT

SUBSUBPL - SUBSUB-PLOT

WAA - WEEKS AFTER ANTHESIS

WHPL - WHOLE-PLOT

Appendix 1 Site description for Faculty of Agriculture - site of 1985/86 maize hybrid rain grown trial

Location : the Faculty of Agriculture is situated 29° 35' S and 30° 19' E, at an altitude of 684 m above sea level.

Bioclimatic zone: Coast hinterland which occurs at an altitude of 450 to 900 m (Phillips, 1973).

Climate: annual rainfall: 926 mm,  
number of ecologically dry months: 4 to 5,  
range of mean annual temperatures: 17,5 to 20°C,  
short term droughts occur occasionally.

This area is considered to be humid to sub-humid.

Natural vegetation: southern tall grassland.

Topography of site: the trial site was situated on flat ground.

Soil: the soil at the trial site was classified as a 'synthetic' Mispah form (MacVicar, de Villiers, Loxton, Verster, Lambrecht, Merryweather, le Roux, van Rooyen and von M. Harmse, 1977) since soil from many different locations has, over the years, been placed on top of the Ecca shale which originally lay at or near the surface. However, in certain areas of the trial site an original Griffin form, Fairhill/Zwagershoek series is evident. This soil form has three horizons: 0 to 800 mm - Orthic A (disturbed, weak indistinct structure, 65 % clay content); 800 to 900 mm - Yellow-brown apedal B (concretionary, associated cutans, structure indistinct, 70 % clay content); 900 mm+ Red apedal B (poorly formed, associated with extreme concretionary habit, 70 % clay content) (MacVicar et al., 1977). The soil depth of the trial site varies from 250 to 1000 mm deep. Soil analysis was conducted by Cedara Fertilizer Advisory Service (Appendix 11) and

soil fertilization was conducted in accordance with the resultant recommendations.

Climatological data: daily temperature and rainfall data for November 1986 to May 1987 are presented in Appendices 5 and 6.

Appendix 2 Site description for Ukulinga - site of 1986/87 maize single cross hybrid rain-out shelter trial

Location : Ukulinga is situated 29° 40' S and 30° 24' E, at an altitude of 726 m above sea level.

Bioclimatic zone: interface between Moist upland and Coast hinterland at altitudes of 900 to 1 400 m, and 450 to 900 m respectively (Phillips, 1973).

Climate: annual rainfall: 705,5 mm,  
number of ecologically dry months: 4 to 5,  
range of mean annual temperatures: 18 to 23°C,  
occurrence of summer droughts: frequent.

This area is considered to be mild subarid to subarid.

Natural vegetation: southern tall grassland, thicket and wooded savanna with patches of riverine bushveld.

Topography of site: the rain-out shelter trial site was situated on a slope with a gradient of 1:20.

Soil: the soil at the trial site was classified as a Mispah form, Mispah series (MacVicar et al., 1977). This may be described as a surface layer of predominantly mineral particles, intimately mixed with a portion of humified organic matter, overlying hard rock (Middle Ecca shale). The depth site for the class is 3 which incorporates soils 250 to 500 mm deep. Soil analysis was

conducted by Cedara Fertilizer Advisory Service (Appendix 12) and soil fertilization was conducted in accordance with the resultant recommendations.

Climatological data: daily rainfall and temperature data for November 1986 to May 1987 are presented in Appendices 7 and 8.

Appendix 3 Site description for Faculty of Agriculture growth tunnel - site of 1988/89 maize single cross hybrid <sup>14</sup>C-labelling study

Location, bioclimatic zone, climate, and natural vegetation are as for the 1985/86 maize hybrid rain grown trial (Appendix 1). Topography of site: the growth tunnel is situated on level ground.

Soil: the commercially supplied soil used in this pot trial was classified as a Bainsvlei form possible Bainsvlei series (MacVicar et al., 1977). This soil form has three horizons: Orthic A, Red apedal B and Soft plinthic B. However, the soil supplied had the three horizons mixed together. Soil analysis was conducted by Cedara Fertilizer Advisory Service (Appendix 13) and soil fertilization was conducted in accordance with the resultant recommendations.

Climatological data: daily rainfall and temperature data for December 1988 to May 1989 are presented in Appendices 9 and 10.

NOTE: plants were placed inside the growth tunnel approximately one week before tassel emergence on 6 February 1989. Details of the environmental modifications within the growth tunnel are given in Section 4.2.

## REFERENCES

MacVicar, C.M., de Villiers, J.M., Loxton, R.F., Verster, E., Lambrecht, J.J.N., Merryweather, F.R. le Roux, J., van Rooyen, T.H. and von M. Harmse, H.J., 1977. Soil classification : a binomial system for South Africa. The Department of Agricultural Technical Services, Republic of South Africa.

Phillips, J., 1973. The agricultural and related development of the Tugela basin and its influent surrounds. The town and regional planning commission, Pietermaritzburg.

#### Appendix 4 CERES-Maize: a computer simulation model of maize growth and development

The CERES-Maize computer programme is a mathematical model which, based on a series of inputs, attempts to simulate the growth and development of maize and predict, among other things, final grain yield (Jones, Ritchie, Kiniry and Godwin, 1986). The series of inputs required by the simulation model are: (i) meteorological data for example, daily rainfall, maximum and minimum temperatures and solar radiation; (ii) soil characteristics for example, soil albedo, soil evaporation coefficient, thickness of each layer in the profile, lower limit of plant-extractable water (cm/cm), drained upper limit (cm/cm), water content at saturation (cm/cm) and initial water content (cm/cm) (Table 1); and (iii) genetic coefficients for the maize hybrid plant for example, growing degree days from seedling emergence to the end of the juvenile phase, photoperiod sensitivity coefficient, growing degree days from silking to physiological maturity, potential kernel number (kernels plant<sup>-1</sup>), potential kernel growth

Table 1 Characteristics of the soil at the Faculty of Agriculture site. Data used to generate the CSD1 and CSD2 stress indices in the CERES-Maize simulation programme

Bulk density	1,533 g cm <sup>3</sup>
Porosity	42,2 %
Air filled porosity at field capacity	8,5 %
Field capacity	33,7 %
Wilting point	18,5 %

rate ( $\text{mg (kernel d)}^{-1}$ ), as well as measured 50 % silking date, physiological maturity date, kernel dry mass at maturity, grain number at maturity and peak leaf area index.

The simulation model also outputs two stress-day factors, namely CSD1 and CSD2 (Table 2). CSD1 is the less sensitive factor and provides an indication of the extent to which photosynthesis is inhibited by water stress, while CSD2 is the more sensitive factor and provides an indication of the extent to which cell turgor, and therefore cell expansion, is inhibited by water stress. If the values of CSD1 and CSD2 are zero then photosynthesis and cell expansion are minimally inhibited by water stress i.e. the supply and uptake of water is adequate, but if the values of CSD1 and CSD2 are one then photosynthesis and cell expansion are maximally inhibited by water stress. Since photosynthesis is reported to be less sensitive to water stress than cell expansion (Boyer, 1973) CSD1 is less than CSD2 unless severe water stress occurs and both CSD1 and CSD2 are equal to one.

It is beyond the scope of this brief summary of the CERES-Maize simulation model to detail all the mathematical computations carried out in the various subroutines of the computer programme. Instead, an extremely abridged account will be given here of how the stress-day factors CSD1 and CSD2 are calculated in the programme. The stress-day factors CSD1 and CSD2 are mathematically derived via the following formulae. A subroutine in CERES-Maize programme WATBAL calculates the water uptake from each soil layer in the soil profile (up to 10 soil layers (L) may

be defined by the user). The amount of water removed from the soil profile is determined by: (i) the total potential root uptake for all layers (RWU(L)); or (ii) the potential transpiration (EP1), whichever of the two is the smallest. Since the units of soil water uptake are cm and those of transpiration are mm, the value of transpiration (EP1) used for water extraction is calculated as:

$$EP1 = EP * 0,1. \quad (1)$$

The maximum rate of water uptake per unit root length (RWUMX) is defined in the programme as 0,03 ml/cm root. However, potential root water uptake per unit root length may be limited by soil water content and may therefore be less than RWUMX.

$$RWU(L) = 2,67E-3 * EXP(62. * (SW(L) - LL(L))) / (6,68 - ALOG(RLV(L))) \quad (2)$$

where SW(L) is the initial water content for a soil layer (cm/cm); LL(L) is the lower limit of plant-extractable water (cm/cm) for a soil layer; and RLV(L) is the root length density for a soil layer (cm root/ml soil).

If RWU(L) is greater than RWUMX, RWU(L) is set equal to RWUMX. RWU(L) is then converted to units of cm uptake/layer.

$$RWU(L) = RWU(L) * DLAYR(L) * RLV(L) \quad (3)$$

where DLAYR(L) is the layer thickness (cm).

Finally potential root water uptake from the entire soil profile (TRWU) is calculated by summing RWU(L) for all soil layers. If transpiration (EP1) is less than or equal to TRWU, the zero-to-unity water use factor (WUF) is calculated as:

$$WUF = EP1 / TRWU. \quad (4)$$

WUF is then used to reduce RWU(L) throughout the soil profile to the rate of transpiration as follows:

$$RWU(L) = RWU(L) * WUF. \quad (5)$$

This system allows either EP1 or the summation of all RWU(L) to limit transpiration. Actual soil water in each layer after the day's transpiration (SW(L)) is updated as follows:

$$SW(L) = SW(L) - RWU(L) / DLAYR(L). \quad (6)$$

The total soil in the profile (TSW) is calculated by summing (SW(L)\*DLAYR(L)) for all soil layers.

Total plant-extractable soil water (PESW) for the profile is the difference between TSW and the amount of water in the profile when all layers are at the lower limit of plant-extractable water (TLL).

Two zero-to-unity soil water factors are calculated. The less sensitive (SWDF1) is used to affect photosynthesis.

$$SWDF1 = TRWU / EP1 \quad (7)$$

The more sensitive factor (SWDF2) affects plant cell expansion and is less than 1,0 whenever TRWU/EP1 is less than 1,5, and is calculated as follows:

$$SWDF2 = 0,67 * TRWU / EP1. \quad (8)$$

Whenever EP1 is greater than TRWU, plant evaporation (expressed in mm) is set equal to TRWU, and total evapotranspiration (ET) is recalculated as:

$$ET = ES + EP. \quad (9)$$

Finally, stress-day factors used to evaluate stress during the various growth stages are calculated as:

$$CSD1 = CSD1 + 1,0 - SWDF1 \text{ (photosynthesis)} \quad (10)$$

$$CSD2 = CSD2 + 1,0 - SWDF2 \text{ (cell expansion)}. \quad (11)$$

Table 2 CERES-Maize model generated stress indices - CSD1 and CSD2, during the 1985/86 growing season for the maize hybrid PNR 6427 grown at the Faculty of Agriculture

Day	Month											
	Dec.		Jan.		Feb.		Mar.		Apr.		May	
	CSD1	CSD2	CSD1	CSD2	CSD1	CSD2	CSD1	CSD2	CSD1	CSD2	CSD1	CSD2
1			0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00		
2			0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00		
3			0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00		
4			0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00		
5	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00		
6	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00		
7	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,27	1,00	1,00		
8	0,00	0,00	0,00	0,00	0,00	0,00	0,28	0,51	1,00	1,00		
9	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,27	1,00	1,00		
10	0,00	0,00	0,00	0,00	0,00	0,00	0,66	0,77	1,00	1,00		
11	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00		
12	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00		
13	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00		
14	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00		
15	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00		
16	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00				
17	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00				
18	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00				
19	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00				
20	0,00	0,00	0,00	0,00	0,00	0,00	0,32	0,54				
21	0,00	0,00	0,00	0,00	0,00	0,00	0,72	0,81				
22	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00				
23	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00				
24	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00				
25	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00				
26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00				
27	0,00	0,00	0,00	0,00	0,00	0,00	0,52	0,68				
28	0,00	0,00	0,00	0,00	0,00	0,00	0,81	0,87				
29	0,00	0,00	0,00	0,00	0,00	0,00	0,83	0,88				
30	0,00	0,00	0,00	0,00	0,00	0,00	0,89	0,93				
31	0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00				

CSD1: photosynthesis stress index

CSD2: cell turgor stress index

Stations: Ukulinga Agriculture Research Station maximum and minimum temperature and rainfall data used;

Cedara Agriculture Research Station solar radiation data used.

Data supplied by South African Weather Bureau

## REFERENCES

- Boyer, J.S., 1973. Response of metabolism to low water potentials in plants. Phytopathology 63, 466-472.
- Jones, C.A., Ritchie, J.T., Kiniry, J.R. and Godwin, D.C., 1986. Subroutine structure. In Jones, C.A. and Kiniry, J.R. (eds). CERES-Maize. A simulation model of maize growth and development. Texas A&M University press, College Station. Pp. 49-66.

Appendix 5 Daily maximum and minimum temperatures (°C) for November 1985 to May 1986, maize hybrid rain grown trial, Faculty of Agriculture

Day	Month													
	Nov.		Dec.		Jan.		Feb.		Mar.		Apr.		May	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
1	17,5	12,5	26,0	13,0	21,0	17,0	20,4	18,0	27,0	16,0	33,3	8,8	29,7	13,5
2	22,6	14,0	30,0	13,3	25,5	16,0	19,0	14,6	35,0	16,0	26,7	14,0	30,3	14,5
3	25,8	14,0	31,0	18,9	28,0	17,5	36,0	13,9	36,5	14,5	26,0	13,7	27,0	13,5
4	22,0	11,0	25,7	17,0	23,0	17,0	27,7	17,9	34,5	16,4	27,7	10,7	16,0	13,5
5	28,0	13,7	25,7	17,9	23,5	14,0	29,5	15,0	29,0	17,4	33,0	16,8	23,0	7,7
6	31,9	15,2	28,9	19,0	27,2	17,5	23,3	16,5	36,0	17,3	28,0	16,0	25,4	5,5
7	20,0	14,4	19,2	17,0	25,6	17,3	22,7	15,9	27,2	18,0	34,8	11,9	21,7	9,5
8	30,0	19,5	31,0	16,0	25,5	18,9	27,0	17,5	32,5	19,5	30,9	18,9	17,0	9,5
9	22,0	11,5	33,0	17,3	31,1	16,3	22,5	17,5	25,5	18,5	33,7	16,5	28,9	7,0
10	19,5	12,5	28,2	16,6	29,9	17,0	32,0	16,7	35,2	18,4	31,4	16,5	26,0	9,5
11	23,5	12,5	26,6	15,2	25,5	17,0	32,0	16,0	29,5	17,5	28,3	18,2	27,5	14,5
12	22,3	13,3	21,5	13,5	29,0	16,4	27,3	15,4	26,5	16,4	16,0	14,0	28,7	7,0
13	28,5	10,6	23,3	14,7	30,7	18,0	32,0	16,5	24,0	15,6	24,0	14,5	29,7	12,4
14	35,2	17,9	22,0	18,0	38,1	19,3	23,0	16,5	32,3	20,2	28,3	18,5	28,7	8,7
15	27,3	18,7	19,0	13,5	28,6	20,0	27,5	16,0	32,0	18,5	26,5	16,9	25,7	10,7
16	26,5	18,0	24,1	13,5	20,0	16,0	26,5	18,5	28,0	20,0	23,5	17,5	28,2	8,0
17	27,5	17,5	37,2	13,4	34,9	16,8	30,3	16,5	33,3	17,2	26,0	12,5	20,9	8,5
18	29,0	15,0	26,2	19,0	22,5	17,5	30,5	14,9	23,5	15,0	31,0	17,0	22,4	9,5
19	27,0	16,5	23,7	17,4	23,5	17,0	32,0	15,0	31,0	20,0	18,1	16,5	30,0	12,5
20	25,5	14,3	28,0	15,5	32,7	16,7	34,2	16,5	27,8	17,0	20,5	15,5	29,7	8,5
21	29,0	17,3	22,5	16,0	23,3	14,4	36,5	19,7	27,0	14,5	28,2	14,4	31,0	5,5
22	29,5	18,6	16,0	12,5	20,5	11,7	32,0	20,5	35,0	20,0	19,5	13,4	29,0	7,5
23	27,5	17,0	25,0	13,5	24,0	15,4	26,5	18,0	35,0	20,5	23,0	14,0	29,7	7,0
24	30,5	17,0	24,0	14,5	30,0	16,7	24,5	15,0	35,5	18,0	31,2	15,4	22,5	10,0
25	32,5	16,4	24,5	15,5	28,5	16,0	21,5	13,5	20,0	11,0	25,7	15,9	22,5	12,0
26	31,0	19,4	24,5	15,0	30,5	19,0	28,7	16,0	20,8	8,5	24,5	14,0	24,5	12,5
27	29,7	19,0	26,5	15,0	30,5	16,7	24,7	15,0	23,3	13,3	26,5	12,5	29,0	8,5
28	25,0	18,0	27,0	18,0	31,5	20,2	26,3	12,7	31,5	14,0	28,5	11,0	29,4	9,5
29	27,0	16,9	29,5	16,0	34,0	18,3			25,0	15,5	25,2	12,2	27,5	8,0
30	23,0	15,5	20,0	16,0	27,0	17,0			32,5	17,2	27,6	15,0	30,5	9,2
31			24,0	16,0	25,5	17,2			21,5	12,5			28,6	13,0
Mon- thly mean	26,5	17,9	25,6	16,1	27,5	17,0	27,7	16,3	29,8	16,6	26,9	14,8	26,5	9,9

Station: Ukulinga Agricultural Research Station

Appendix 6 Rainfall figures (mm) for November 1985 to May 1986, maize hybrid rain grown trial, Faculty of Agriculture

Day	Month						
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
1	9,5			4,4			0,8
2							
3	0,4	3,8	31,2	3,0			
4	5,0	0,6	22,6	7,6			
5		0,2		1,2	1,0		
6	4,4	33,5	1,8		0,5		
7	17,3	11,2					
8	3,4	13,4		0,6	2,5		
9	5,2	5,5	2,0	14,5	1,0	10,4	
10	2,3	0,2	1,4	2,5		1,2	
11	1,0	0,7	4,5	2,3	2,4	10,0	
12		3,0			6,5		
13		5,0	0,1	5,5			
14		5,5	1,8	1,0	16,0	1,0	
15		3,5	7,6	1,0			
16		0,1	2,5		8,5		
17		1,9	4,5		2,5		
18		5,5	16,0				
19			2,2		4,0	1,5	
20		23,0	1,4			5,5	
21	3,0	7,5	10,2			6,5	
22		4,0		5,0			
23		7,5		14,5	16,0		
24		37,0			0,6	4,8	
25		13,0		0,1			
26	1,5	10,5					
27	1,0	1,0	3,0				
28	20,0	25,5	0,2				
29	11,5		11,4				
30		10,5	0,4		1,2	2,0	
31		1,8					
Monthly total	85,5	234,9	124,8	63,2	62,7	42,9	0,8
LTMM*	120,0	138,3	155,4	119,1	112,4	58,1	24,6

\* Long term monthly means. Station: Darville Purification Works

Source of data - Department of Agriculture and Water Supply  
 Department of Water Affairs  
 South African Weather Bureau

Data supplied by the Computer Centre for Water Research, University of Natal, Pietermaritzburg

Appendix 7 Daily maximum and minimum temperatures (°C) for November 1986 to May 1987, maize single cross hybrid rain-out shelter trial, Ukulinga

Day	Month													
	Nov.		Dec.		Jan.		Feb.		Mar.		Apr.		May	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
1	18,0	9,5	30,0	18,0	32,5	17,0	35,5	19,0	27,0	17,3	27,5	19,3	29,0	16,5
2	24,1	10,5	33,0	22,1	20,0	16,0	30,5	21,0	28,5	18,0	25,5	20,3	27,5	15,5
3	34,0	12,5	30,5	18,5	21,5	13,5	35,0	21,0	27,5	19,5	30,0	20,0	26,5	15,0
4	14,5	13,0	29,5	19,0	21,5	14,0	24,5	20,0	17,0	17,6	22,0	19,5	28,5	12,5
5	13,5	10,5	36,8	18,5	27,0	14,5	33,0	17,0	21,0	15,0	24,5	16,5	29,5	15,5
6	22,0	11,0	22,6	18,0	26,5	17,5	26,3	19,2	24,7	16,8	25,5	20,5	23,5	10,5
7	25,5	11,2	18,6	16,0	19,5	16,0	26,5	16,8	25,0	17,5	26,0	15,5	21,0	11,0
8	16,0	12,6	27,0	16,6	17,0	14,2	34,5	16,0	28,5	17,5	25,5	16,9	24,0	13,1
9	16,5	9,5	26,0	19,5	17,1	14,0	35,0	20,0	19,5	16,5	29,5	16,5	29,2	12,0
10	20,5	9,5	16,0	12,5	24,0	15,5	26,5	21,0	20,0	14,5	26,5	18,0	30,0	16,8
11	23,0	11,0	22,0	11,0	29,5	19,0	21,5	14,5	26,0	13,0	20,5	13,5	31,5	18,5
12	25,5	12,0	23,0	13,5	26,0	18,7	26,5	18,7	28,5	16,5	26,5	14,5	28,2	18,5
13	28,0	12,5	22,5	12,5	24,5	16,0	31,0	16,5	32,0	16,5	29,0	18,5	22,5	14,5
14	26,0	16,0	23,5	13,0	28,5	17,5	28,0	23,0	35,5	20,5	30,5	18,5	29,5	14,5
15	17,0	13,5	29,0	16,0	28,5	16,9	32,5	18,5	28,5	19,0	23,5	18,0	26,0	13,5
16	23,5	13,0	32,5	18,0	29,0	19,0	29,0	20,0	26,5	17,2	17,5	8,5	27,0	13,0
17	22,8	15,2	16,0	12,0	31,5	19,0	30,5	19,5	25,5	17,0	20,5	9,5	28,0	12,5
18	30,0	18,5	22,5	12,0	31,0	21,0	28,0	20,5	22,5	18,5	23,4	10,0	26,5	12,0
19	22,5	16,5	21,5	15,5	29,5	21,5	35,5	20,0	27,5	16,5	29,2	13,3	23,5	11,5
20	16,4	14,5	24,0	15,0	21,5	18,0	23,0	18,5	25,0	15,5	28,5	16,0	19,5	14,0
21	25,5	13,5	26,5	13,5	21,0	15,0	24,0	16,0	20,5	15,0	24,0	14,3	22,5	12,5
22	25,5	17,5	25,0	16,0	26,5	14,3	33,0	15,5	23,5	15,5	27,5	14,6	15,5	13,5
23	20,5	15,0	24,5	17,5	29,0	17,4	32,0	22,5	23,5	14,5	24,5	16,5	24,5	9,5
24	22,5	13,0	25,0	16,5	19,5	17,8	27,0	17,8	25,0	13,5	16,5	13,0	25,5	15,0
25	24,0	13,3	28,5	18,5	19,5	13,5	30,0	17,5	23,5	16,0	24,0	13,0	26,0	11,0
26	26,0	14,5	26,5	17,5	24,5	14,5	27,5	17,3	23,0	13,5	25,0	14,5	22,6	15,5
27	29,0	17,4	26,0	19,5	33,0	16,5	28,5	17,5	26,0	14,0	27,0	13,0	20,0	9,5
28	21,5	15,0	25,0	18,0	26,2	21,5	26,5	16,5	30,0	14,0	22,5	15,0	25,8	12,0
29	14,0	14,5	25,0	17,0	29,0	16,4			31,5	18,0	23,5	12,5	22,5	9,4
30	29,5	18,0	23,5	15,0	26,5	18,0			26,0	18,0	27,5	14,5	21,7	6,3
31			26,0	14,9	23,0	19,5			27,0	15,0			26,5	13,5
Mon- thly mean	22,6	13,5	25,4	16,2	25,3	16,9	29,3	16,5	25,7	16,4	25,1	15,5	25,3	13,6

Station: Ukulinga Agricultural Research Station

Appendix 8 Rainfall figures (mm) for November 1986 to May 1987, maize single cross hybrid rain-out shelter trial, Ukulinga

Day	Month						
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
1						0,3	
2		9,6		0,5			
3							
4	5,4	0,2		1,4	5,0	1,5	
5	9,0	2,2			10,3	0,8	
6	2,5	18,0	0,2	1,2	0,4		
7	0,8	19,0	4,1		1,3	0,4	
8	3,4	2,5	6,2		2,6	1,3	
9	0,5	6,6	3,4		5,9	9,7	
10		1,4		10,0		9,2	
11			0,6	2,2	0,2	1,7	
12			0,1	0,5			0,6
13	0,2		1,3	20,0			
14	2,6		3,0	4,2			
15	7,4			2,9	29,2	7,8	
16	0,3	6,0			1,8		
17	3,0	2,8					
18	1,5				7,5		
19	0,4		7,4	7,8	12,3		
20	2,8		31,6		0,4		
21	2,5			3,2	6,0	0,4	0,8
22	21,0				7,4		4,0
23			4,6	14,8	0,8		
24			0,8	0,6			
25		11,0	1,2	9,2	4,2		
26				8,6	0,1		2,0
27	1,2	1,6				0,7	
28	3,5						
29		16,5	2,6				
30		2,8	1,2		16,7		
31			1,8				
Monthly total	68,0	100,2	70,1	87,1	112,1	33,8	7,4
LTMM*	82,7	97,1	116,4	90,4	84,1	47,3	25,8

\* Long term monthly mean. Station: Ukulinga Agricultural Research Station

Source of data - Department of Agriculture and Water Supply  
 Department of Water Affairs  
 South African Weather Bureau

Data supplied by the Computer Centre for Water Research, University of Natal, Pietermaritzburg

Appendix 9 Daily maximum and minimum temperatures (°C) for December 1988 to May 1989, maize single cross hybrid <sup>14</sup>C-labelling study, Faculty of Agriculture

Day	Month											
	Dec.		Jan.		Feb.		Mar.		Apr.		May	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
1	20,5	12,5	27,4	15,0	33,0	20,0	29,5	16,5	23,3	9,0	23,0	8,7
2	27,5	16,5	27,0	15,0	37,0	20,0	31,5	17,4	29,5	9,2	22,7	8,5
3	25,6	15,0	28,5	17,0	23,5	15,0	21,8	12,0	29,5	10,5	27,0	8,6
4	26,8	16,5	27,0	16,0	19,8	13,8	27,0	15,3	28,4	11,2	28,9	10,3
5	26,0	13,5	23,0	13,0	28,7	15,4	31,3	15,5	33,8	11,5	28,0	8,8
6	20,0	11,0	28,0	19,0	27,5	12,0	31,8	12,8	27,5	12,8	26,8	12,2
7	20,7	11,0	23,5	18,5	23,5	15,0	30,0	15,0	32,6	13,5	25,8	10,5
8	21,5	13,4	22,1	16,8	21,5	12,0	28,0	16,0	27,0	15,8	26,5	10,5
9	19,0	14,0	20,5	15,1	26,5	16,0	27,4	16,0	28,7	13,0	24,5	10,2
10	30,2	15,3	25,7	14,5	24,0	17,5	27,5	18,2	29,5	14,0	27,0	10,0
11	30,0	15,3	31,0	17,4	25,9	15,7	25,4	18,9	30,2	14,5	27,7	9,5
12	29,5	14,7	26,6	17,1	25,8	17,5	34,8	17,7	30,5	14,0	30,2	9,5
13	26,0	15,5	26,0	15,9	25,5	16,0	34,5	17,5	32,0	13,5	14,5	10,7
14	28,7	15,0	29,5	14,5	27,5	17,0	31,5	15,0	33,0	13,5	17,2	9,4
15	28,5	17,3	28,0	17,6	23,0	16,0	27,0	16,0	21,4	13,3	33,2	9,4
16	21,0	15,4	31,0	15,0	18,0	14,5	25,5	15,5	17,6	13,3	26,0	8,5
17	22,4	15,5	27,0	17,0	21,5	15,0	28,0	17,0	31,6	12,0	22,0	8,5
18	25,5	12,4	24,0	16,0	31,1	15,6	31,3	11,7	21,5	10,2	24,2	8,5
19	27,5	11,5	17,0	16,0	27,7	17,9	30,3	14,1	22,0	5,4	30,5	8,5
20	31,0	17,0	28,0	18,0	30,5	16,5	33,0	13,5	28,2	6,6	28,0	7,0
21	25,0	14,0	28,2	17,1	30,5	16,5	29,0	18,0	30,5	10,0	29,0	9,5
22	28,0	19,0	35,7	19,3	29,5	17,5	23,5	17,5	29,0	15,7	30,5	8,5
23	31,0	13,0	35,0	17,0	26,0	17,0	28,5	15,5	25,0	10,6	21,5	9,0
24	31,7	19,6	19,0	13,0	23,5	17,0	26,2	17,3	19,7	8,2	22,0	9,0
25	31,1	19,2	27,0	16,0	24,5	18,5	26,0	16,0	25,0	5,9	30,5	8,2
26	22,0	16,6	24,0	13,0	28,0	16,8	27,2	11,8	22,5	10,1	22,5	8,2
27	19,7	14,9	27,0	18,0	30,0	16,7	28,0	13,9	27,8	10,0	13,8	10,1
28	31,0	13,0	30,6	17,9	29,2	17,6	29,0	12,5	17,8	12,9	19,4	4,4
29	26,0	16,0	31,7	17,7			28,0	14,0	17,9	12,0	21,5	3,2
30	27,0	17,0	34,0	16,0			29,5	16,5	21,1	8,0	23,5	3,5
31	23,5	15,6	33,0	19,0			34,6	14,5			24,6	4,4
Mon- thly mean	28,8	15,2	27,3	16,4	26,5	16,3	27,9	15,5	26,5	11,3	24,9	8,6

Station: Ukulinga Agricultural Research Station

Appendix 10 Rainfall figures (mm) for December 1988 to May 1989, maize single cross hybrid <sup>14</sup>C-labelling study, Faculty of Agriculture

Day	Month					
	Dec.	Jan.	Feb.	Mar.	Apr.	May
1	0,1			0,5		
2		1,0	40,5	7,7	1,8	
3		1,1	30,0	0,3		
4	13,7		5,2			1,2
5	1,5	0,3	39,0			
6		33,0	14,4	2,0		
7	0,2	7,5	0,2	0,2		
8	4,5	4,0	2,3			
9	0,1	1,6	1,0			
10			5,5	1,1		
11	2,0	26,7		1,0		
12	2,5	0,2	10,3	1,8		3,9
13	0,1		17,7	0,3		0,2
14	0,3	1,0	0,2			
15	5,5		10,7		18,1	1,0
16	32,0	1,5	8,0		0,6	
17	2,0		0,1			
18	0,2					
19	33,5		1,1			
20	29,0	3,6		12,8		
21		1,2	0,7	6,3		
22			0,1			
23	1,5	0,5	27,3		20,2	
24	49,2					
25	10,0	0,2				
26	6,1		0,1			13,7
27	0,9	0,2			1,7	0,2
28			0,1			
29	0,5				0,3	
30					0,1	
31						0,2
Monthly total	195,4	83,6	214,5	34,0	42,8	20,4
LTMM*	38,3	155,4	119,1	112,4	58,1	24,6

\* Long term monthly means. Station: Darville Purification Works

Source of data - Department of Agriculture and Water Supply  
 Department of Water Affairs  
 South African Weather Bureau

Data supplied by the Computer Centre for Water Research, University of Natal, Pietermaritzburg

Appendix 11 Selected chemical properties of soil samples taken from the Faculty of Agriculture site. Fertilization of the site for the 1985/86 maize hybrid rain grown trial was carried out in accordance with fertilizer recommendations based on these properties

pH (KCl)	Exch acidity cmol(+) $\ell^{-1}$	Ca	Mg	K	P	Zn	Acid sat (%)
		----- (mg $\ell^{-1}$ ) -----					
4,8	0,12	1 528	328	103	39	10,7	1

Data supplied by Cedara Fertilizer Advisory Service

Appendix 12 Selected chemical properties of soil samples taken from the Ukulinga rain-out shelter site. Fertilization of the site for the 1986/87 maize single cross hybrid rain-out shelter trial was carried out in accordance with fertilizer recommendations based on these properties

pH (KCl)	Exch acidity cmol(+) $\ell^{-1}$	Ca	Mg	K	P	Zn	Acid sat (%)
		----- (mg $\ell^{-1}$ ) -----					
4,6	0,09	1 143	315	53	9	2,8	1

Data supplied by Cedara Fertilizer Advisory Service

Appendix 13 Selected chemical properties of soil samples taken from the commercially supplied Baynesvlei form Baynesvlei series soil used in the 1988/89 maize single cross hybrid  $^{14}\text{C}$ -labelling study conducted in the growth tunnel at the Faculty of Agriculture. Fertilization of the soil used in this pot trial was carried out in accordance with fertilizer recommendations based on these properties

pH (KCl)	Exch acidity cmol(+) $\ell^{-1}$	Ca	Mg	K	P	Zn	Acid sat (%)
		----- (mg $\ell^{-1}$ ) -----					
4,52	0,13	1 264	389	220	11	8,2	1,3

Data supplied by Cedara Fertilizer Advisory Service

Appendix 14 Field plan for 1985/86 maize hybrid rain grown trial, Faculty of Agriculture : conducted to monitor the fluctuation in the non-structural carbohydrate composition and content in the stem, cob and grain during grain fill

←3,2m→								↑ 4,25m ↓
29 PNR 95	30 SA 4MS	31 HL 1	32 PNR 6427	33 CG 4602	34 PNR 473	35 SNK 2244	36 PNR 542	
								↑1,0m path
21 SNK 2244	22 PNR 6427	23 PNR 95	24 SA 4MS	25 SA 60	26 SR 52	27 SX 16	28 CG 4502	
								↑ Rows ↓
13 CG 4502	14 HL 1	15 SA 60	16 PNR 542	17 CG 4602	18 PNR 473	19 SX 16	20 SR 52	
5 SA 60	6 CG 4602	7 SR 52	8 PNR 473	9 HL 1	10 SX 16	11 CG 4502	12 PNR 95	
1 PNR 542	2 SA 4MS	3 SNK 2244	4 PNR 6427					

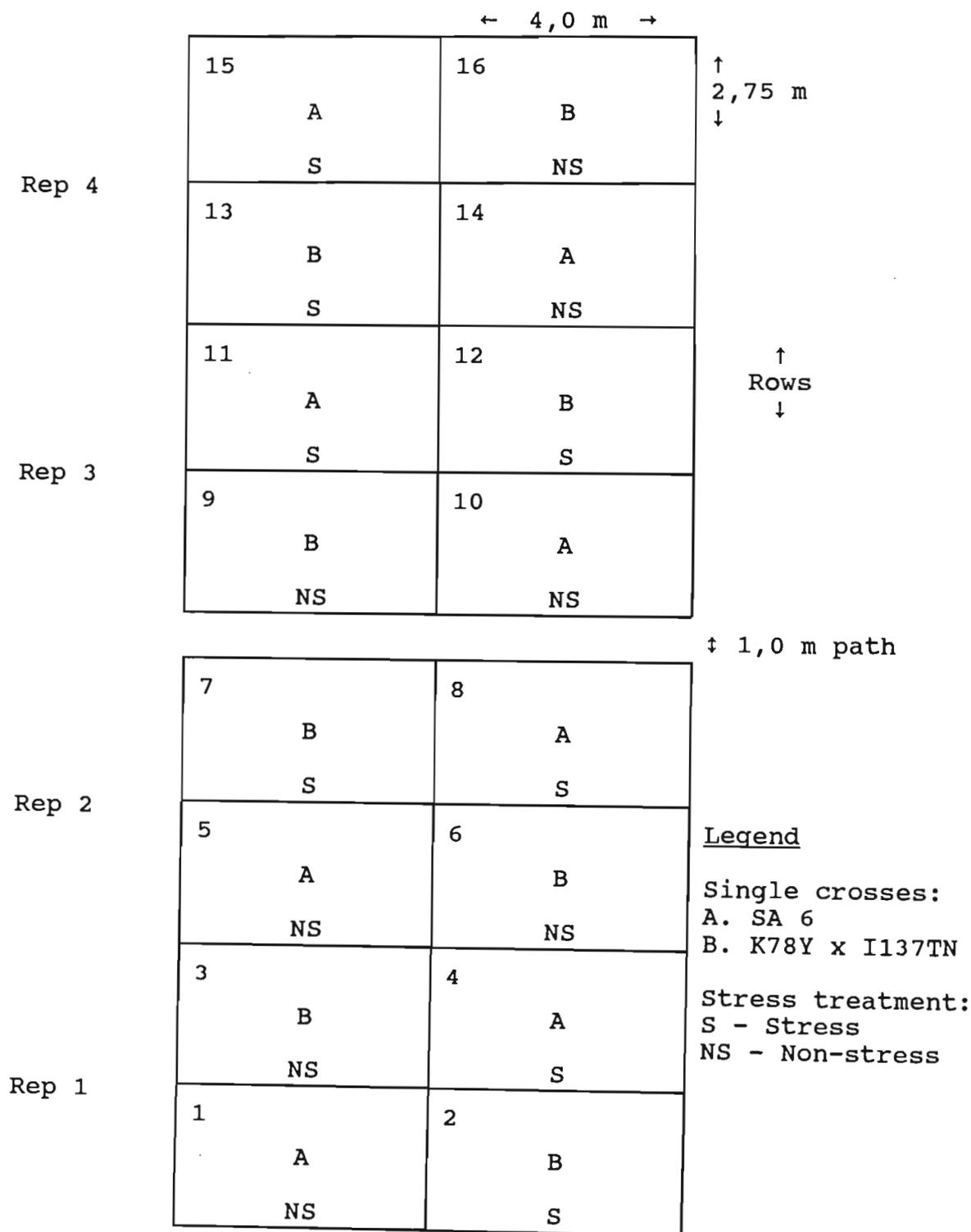
#### Growth tunnels

Two border rows planted around outer perimeter of trial

Gross plot size : 4 rows @ 0,8 m (3,2 m) x 17 plants @ 0,25 m (4,25 m) = 13,5 m<sup>2</sup>

Net plot size : 2 rows @ 0,8 m (1,6 m) x 17 plants @ 0,25 m (4,25 m) = 6,8 m<sup>2</sup>

Appendix 15 Field plan for 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga : conducted to determine the effect of water stress during grain fill on the non-structural carbohydrate composition and content of the stem



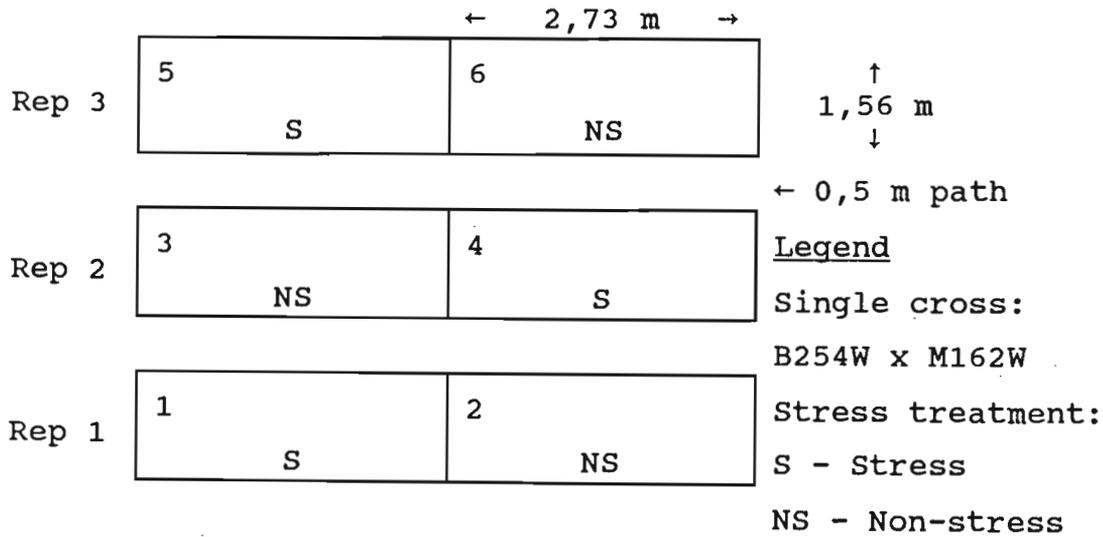
Range 5 ←

Range 4

Gross plot size : 5 rows @ 0,8 m (4,0 m) x 11 plants @ 0,25 m (2,75 m) = 11,0 m<sup>2</sup>

Net plot size : 4 rows @ 0,8 m (3,2 m) x 11 plants @ 0,25 m (2,75 m) = 8,8 m<sup>2</sup>

Appendix 16 Field plan for 1988/89 maize single cross hybrid <sup>14</sup>C-labelling study, Faculty of Agriculture growth tunnel : conducted to determine the effect of water stress during grain fill on the distribution of <sup>14</sup>C among non-structural carbohydrates and plant organs



Net plot size : 4 rows square spacing @ 0,39 m (1,56 m) x 7 plants @ 0,39 m (2,73 m) = 4,26 m

Appendix 17 Characterisation of component total non-structural carbohydrates using high pressure liquid chromatography. Selected stem segments sampled at mid-grain fill from the 1985/86 maize hybrid rain grown trial were analyzed

## Introduction

The modified Weinmann method described in the methods and materials in Chapter 2 provides values for TS classified into broad categories of reducing sugars and non-reducing sugars without providing an indication of which sugars constitute those categories. In order to determine the identity of the various sugars present in the plant sections, high pressure liquid chromatography was used on selected samples (A1, B1, B2 and shank) taken at MGF from the 1985/86 maize hybrid rain grown trial only.

## Methods and materials

Extraction of short chain sugars was carried out by mechanically shaking 200 mg of tissue sample for one hour with 50 ml of 80 % (v/v) ethanol in a stoppered 125 ml Erlenmeyer flask. The ethanol was then boiled off leaving the extracted sugars in approximately 10 ml of water. The water was removed by freeze drying overnight using a Xerotec 40 freeze dryer. The dried sample was taken up in 5 ml of water and  $1 \times 10^{-5}$  l was loaded directly onto a Waters Carbohydrate Analysis Column (4 x 250 mm) and eluted with distilled water (25 %) and acetonitrile (75 %). The sample was run at  $2 \text{ ml min}^{-1}$  flow rate, room temperature (27°C) on a Varian 5000 liquid chromatograph fitted with a Waters Differential Refractometer coupled to a Waters Differential

Refractometer Electronics unit. Peak areas were integrated electronically providing concentrations of the sugars in the 5 ml sample. Values were then expressed as a percentage of the original 200 mg sample.

### Results, discussion and conclusion

Analysis of selected samples by HPLC showed that sucrose was the only non-reducing sugar present in detectable quantities (Table 3). Non-reducing sugars are, therefore, referred to as sucrose throughout this thesis. Glucose and fructose were the primary reducing sugars present and occurred at similar concentrations in the stem segments analyzed at MGF.

Table 3 High pressure liquid chromatography determinations of fructose, glucose and sucrose composition (percent dry mass basis) of selected stem segments sampled at mid-grain fill from six maize hybrids. Each value is the mean of three replications  $\pm$  the standard error of the mean

Stem segment	PNR 6427			SA 60		
	Fructose (%)	Glucose (%)	Sucrose (%)	Fructose (%)	Glucose (%)	Sucrose (%)
A1	6,85 $\pm$ 0,39	5,15 $\pm$ 0,39	2,95 $\pm$ 0,54	2,04 $\pm$ 0,23	1,91 $\pm$ 0,12	0,81 $\pm$ 0,10
B1	3,15 $\pm$ 0,20	3,70 $\pm$ 0,25	2,85 $\pm$ 0,63	1,82 $\pm$ 0,20	2,02 $\pm$ 0,17	2,27 $\pm$ 0,19
B2	3,40 $\pm$ 0,31	4,35 $\pm$ 0,29	3,55 $\pm$ 0,81	2,56 $\pm$ 0,17	3,95 $\pm$ 0,06	0,93 $\pm$ 0,21
Shank	7,40 $\pm$ 0,48	8,00 $\pm$ 0,49	1,84 $\pm$ 0,32	3,75 $\pm$ 0,31	3,85 $\pm$ 0,42	1,26 $\pm$ 0,05

Stem segment	CG 4602			SR 52		
	Fructose (%)	Glucose (%)	Sucrose (%)	Fructose (%)	Glucose (%)	Sucrose (%)
A1	4,20 $\pm$ 0,92	3,91 $\pm$ 0,57	5,57 $\pm$ 0,08	9,50 $\pm$ 0,66	10,10 $\pm$ 0,78	2,82 $\pm$ 0,28
B1	5,35 $\pm$ 0,64	6,45 $\pm$ 0,72	2,99 $\pm$ 0,34	8,65 $\pm$ 0,42	9,25 $\pm$ 0,68	2,90 $\pm$ 0,71
B2	4,15 $\pm$ 0,41	5,15 $\pm$ 0,49	3,79 $\pm$ 0,83	8,80 $\pm$ 0,88	8,85 $\pm$ 0,89	1,87 $\pm$ 0,41
Shank	6,20 $\pm$ 0,15	6,76 $\pm$ 0,68	3,76 $\pm$ 0,34	8,95 $\pm$ 0,05	9,75 $\pm$ 0,95	2,04 $\pm$ 0,13

Stem segment	PNR 473			HL 1		
	Fructose (%)	Glucose (%)	Sucrose (%)	Fructose (%)	Glucose (%)	Sucrose (%)
A1	2,03 $\pm$ 0,50	2,90 $\pm$ 0,20	0,48 $\pm$ 0,04	2,25 $\pm$ 0,72	2,04 $\pm$ 0,37	0,64 $\pm$ 0,11
B1	1,36 $\pm$ 0,46	1,99 $\pm$ 0,24	1,95 $\pm$ 0,10	2,25 $\pm$ 0,16	2,66 $\pm$ 0,64	0,27 $\pm$ 0,12
B2	1,36 $\pm$ 0,08	1,53 $\pm$ 0,03	1,67 $\pm$ 0,11	2,14 $\pm$ 0,41	2,05 $\pm$ 0,41	1,53 $\pm$ 0,34
Shank	1,57 $\pm$ 0,03	1,85 $\pm$ 0,04	0,48 $\pm$ 0,09	4,20 $\pm$ 0,60	5,80 $\pm$ 0,41	0,90 $\pm$ 0,27

Appendix 18 Analyses of variance : non-structural carbohydrate analyses of STEM SEGMENTS : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture

Appendix 18.1 VARIATE: Reducing sugars composition (%) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	879.692	439.846			
REPS.WHPL STRATUM						
HYBRID	5	2575.470	515.094	5.789	<.001	
STAGE	2	1021.413	510.707	5.740	0.007	0.025>p>0.01
LIN	1	1021.002	1021.002	11.475	0.002	0.025>p>0.01
QUAD	1	0.412	0.412	0.005	0.946	
HYBRID.STAGE	10	667.116	66.712	0.750	0.674	
DEV.LIN	5	267.914	53.583	0.602	0.699	
DEV.QUAD	5	399.203	79.841	0.897	0.494	
RESIDUAL	34	3025.299	88.979			
TOTAL	51	7289.299	142.927			
REPS.WHPL.SUBPL STRATUM						
SEG	6	213.039	35.507	4.675	<.001	0.01>p>0.005
HYBRID.SEG	30	338.683	11.289	1.486	0.057	
STAGE.SEG	12	479.392	39.949	5.260	<.001	p<0.001
LIN.DEV	6	40.045	6.674	0.879	0.511	
QUAD.DEV	6	439.347	73.225	9.641	<.001	p<0.001
HYBRID.STAGE.SEG	60	495.877	8.265	1.088	0.326	
DEV.LIN.DEV	30	242.055	8.069	1.062	0.386	
DEV.QUAD.DEV	30	253.822	8.461	1.114	0.321	
RESIDUAL	216	1640.580	7.595			
TOTAL	324	3167.571	9.776			
GRAND TOTAL	377	11336.563				
GRAND MEAN		7.10				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.868	26.3
REPS.WHPL	34	3.565	50.2
REPS.WHPL.SUBPL	216	2.756	38.8

<sup>†</sup>Epsilon factor Error MS Stage = 0.7648

<sup>†</sup>Epsilon factor Error MS Segment = 0.4011

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 18.2 VARIATE: Reducing sugars content (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	2.6665	1.3333			
REPS.WHPL STRATUM						
HYBRID	5	60.0548	12.0110	7.357	<.001	
STAGE	2	2.5949	1.2975	0.795	0.460	
LIN	1	2.0641	2.0641	1.264	0.269	
QUAD	1	0.5308	0.5308	0.325	0.572	
HYBRID.STAGE	10	19.8759	1.9876	1.217	0.315	
DEV.LIN	5	15.8940	3.1788	1.947	0.112	
DEV.QUAD	5	3.9819	0.7964	0.488	0.783	
RESIDUAL	34	55.5063	1.6325			
TOTAL	51	138.0319	2.7065			
REPS.WHPL.SUBPL STRATUM						
SEG	6	53.4292	8.9049	36.142	<.001	p<0.001
HYBRID.SEG	30	36.7886	1.2263	4.977	<.001	p<0.001
STAGE.SEG	12	8.4623	0.7052	2.862	0.001	0.05>p>0.025
LIN.DEV	6	4.2548	0.7091	2.878	0.010	0.1>p>0.05
QUAD.DEV	6	4.2076	0.7013	2.846	0.011	0.1>p>0.05
HYBRID.STAGE.SEG	60	19.3710	0.3229	1.310	0.084	
DEV.LIN.DEV	30	14.5967	0.4866	1.975	0.003	0.05>p>0.025
DEV.QUAD.DEV	30	4.7743	0.1591	0.646	0.923	
RESIDUAL	216	53.2199	0.2464			
TOTAL	324	171.2711	0.5286			
GRAND TOTAL	377	311.9695				
GRAND MEAN		0.698				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.1029	14.7
REPS.WHPL	34	0.4829	69.2
REPS.WHPL.SUBPL	216	0.4964	71.1

<sup>†</sup>Epsilon factor Error MS Stage = 0.7281

<sup>†</sup>Epsilon factor Error MS Segment = 0.3815

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 18.3 VARIATE: Sucrose composition (%) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	323.237	161.619			
REPS.WHPL STRATUM						
HYBRID	5	325.789	65.158	2.767	0.033	
STAGE	2	5235.149	2617.575	111.158	<.001	p<0.001
LIN	1	2444.870	2444.870	103.824	<.001	p<0.001
QUAD	1	2790.279	2790.279	118.492	<.001	p<0.001
HYBRID.STAGE	10	546.369	54.637	2.320	0.033	0.05>p>0.025
DEV.LIN	5	349.084	69.817	2.965	0.025	0.05>p>0.025
DEV.QUAD	5	197.284	39.457	1.676	0.167	
RESIDUAL	34	800.643	23.548			
TOTAL	51	6907.950	135.450			
REPS.WHPL.SUBPL STRATUM						
SEG	6	419.626	69.938	13.446	<.001	p<0.001
HYBRID.SEG	30	242.572	8.086	1.555	0.040	0.1>p>0.05
STAGE.SEG	12	354.300	29.525	5.676	<.001	p<0.001
LIN.DEV	6	165.710	27.618	5.310	<.001	p<0.005
QUAD.DEV	6	188.590	31.432	6.043	<.001	0.005>p>0.001
HYBRID.STAGE.SEG	60	308.760	5.146	0.989	0.505	
DEV.LIN.DEV	30	216.192	7.206	1.385	0.097	
DEV.QUAD.DEV	30	92.568	3.086	0.593	0.955	
RESIDUAL	216	1123.512	5.201			
TOTAL	324	2448.769	7.558			
GRAND TOTAL	377	9679.956				
GRAND MEAN		5.44				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.133	20.8
REPS.WHPL	34	1.834	33.7
REPS.WHPL.SUBPL	216	2.281	41.9

<sup>†</sup>Epsilon factor Error MS Stage = 0.8085

<sup>†</sup>Epsilon factor Error MS Segment = 0.6013

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 18.4 VARIATE: Sucrose content (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	0.99716	0.49858			
REPS.WHPL STRATUM						
HYBRID	5	9.19134	1.83827	2.715	0.084	
RESIDUAL	10	6.77098	0.67710			
TOTAL	15	15.96232	1.06415			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	32.10279	16.05140	32.284	<.001	p<0.001
LIN	1	9.98116	9.98116	20.075	<.001	p<0.001
QUAD	1	22.12163	22.12163	44.493	<.001	p<0.001
HYBRID.STAGE	10	13.46356	1.34636	2.708	0.022	0.05>p>0.025
DEV.LIN	5	9.23433	1.84687	3.715	0.012	0.025>p>0.01
DEV.QUAD	5	4.22922	0.84584	1.701	0.173	
RESIDUAL	24	11.93275	0.49720			
TOTAL	36	57.49911	1.59720			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEG	6	18.39034	3.06506	34.968	<.001	p<0.001
HYBRID.SEG	30	7.13208	0.23774	2.712	<.001	0.01>p>0.005
STAGE.SEG	12	8.25734	0.68811	7.850	<.001	p<0.001
LIN.DEV	6	3.49592	0.58265	6.647	<.001	p<0.005
QUAD.DEV	6	4.76142	0.79357	9.053	<.001	p<0.001
HYBRID.STAGE.SEG	60	8.18410	0.13640	1.556	0.012	0.1>p>0.05
DEV.LIN.DEV	30	4.72608	0.15754	1.797	0.009	0.1>p>0.05
DEV.QUAD.DEV	30	3.45801	0.11527	1.315	0.137	
RESIDUAL	216	18.93331	0.08765			
TOTAL	324	60.89717	0.18795			
GRAND TOTAL	377	135.35576				
GRAND MEAN		0.483				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.0629	13.0
REPS.WHPL	10	0.1796	37.2
REPS.WHPL.SUBPL	24	0.2665	55.1
REPS.WHPL.SUBPL.SUBSUBPL	216	0.2961	61.3

<sup>†</sup>Epsilon factor Error MS Stage = 0.7953

<sup>†</sup>Epsilon factor Error MS Segment = 0.3968

Appendix 18.5 VARIATE: Starch composition (%) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	10.486	5.243					
REPS.WHPL STRATUM								
HYBRID	5	127.584	25.517	3.564	0.011			
STAGE	2	257.683	128.842	17.995	<.001	p<0.001		
LIN	1	257.631	257.631	35.983	<.001	p<0.001		
QUAD	1	0.052	0.052	0.007	0.933			
HYBRID.STAGE	10	72.329	7.233	1.010	0.455			
DEV.LIN	5	58.596	11.719	1.637	0.177			
DEV.QUAD	5	13.733	2.747	0.384	0.856			
RESIDUAL	34	243.430	7.160					
TOTAL	51	701.027	13.746					
REPS.WHPL.SUBPL STRATUM								
SEG	6	195.531	32.589	14.360	<.001	p<0.001		
HYBRID.SEG	30	166.803	5.560	2.450	<.001	p<0.005		
STAGE.SEG	12	39.588	3.299	1.454	0.144			
LIN.DEV	6	22.363	3.727	1.642	0.137			
QUAD.DEV	6	17.225	2.871	1.265	0.275			
HYBRID.STAGE.SEG	60	231.037	3.851	1.697	0.003	p<0.005		
DEV.LIN.DEV	30	107.937	3.598	1.585	0.033	0.05>p>0.025		
DEV.QUAD.DEV	30	123.099	4.103	1.808	0.009	0.025>p>0.01		
RESIDUAL	216	490.204	2.269					
TOTAL	324	1123.163	3.467					
GRAND TOTAL	377	1834.676						
GRAND MEAN		3.134						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.2040	6.5
REPS.WHPL	34	1.0113	32.3
REPS.WHPL.SUBPL	216	1.5065	48.1

<sup>†</sup>Epsilon factor Error MS Stage = 0.8338

<sup>†</sup>Epsilon factor Error MS Segment = 0.6764

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 18.6 VARIATE: Starch content (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	0.05341	0.02671			
REPS.WHPL STRATUM						
HYBRID	5	2.81250	0.56250	6.072	<.001	
STAGE	2	0.86131	0.43065	4.649	0.016	0.05>p>0.025
LIN	1	0.86121	0.86121	9.297	0.004	0.01>p>0.005
QUAD	1	0.00000	0.00000	0.000		
HYBRID.STAGE	10	1.47014	0.14701	1.587	0.153	
DEV.LIN	5	1.08934	0.21787	2.352	0.062	
DEV.QUAD	5	0.38080	0.07616	0.822	0.543	
RESIDUAL	34	3.14956	0.09263			
TOTAL	51	8.29350	0.16262			
REPS.WHPL.SUBPL STRATUM						
SEG	6	3.22563	0.53760	16.717	<.001	p<0.001
HYBRID.SEG	30	2.19798	0.07327	2.278	<.001	0.01>p>0.005
STAGE.SEG	12	0.73395	0.06116	1.902	0.035	0.1>p>0.05
LIN.DEV	6	0.42498	0.07083	2.203	0.044	0.1>p>0.05
QUAD.DEV	6	0.30897	0.05149	1.601	0.148	
HYBRID.STAGE.SEG	60	2.57615	0.04294	1.335	0.070	
DEV.LIN.DEV	30	1.38672	0.04622	1.437	0.075	
DEV.QUAD.DEV	30	1.18943	0.03965	1.233	0.198	
RESIDUAL	216	6.94629	0.03216			
TOTAL	324	15.68000	0.04840			
GRAND TOTAL	377	24.02691				
GRAND MEAN		0.2612				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.01456	5.6
REPS.WHPL	34	0.11504	44.0
REPS.WHPL.SUBPL	216	0.17933	68.7

<sup>†</sup>Epsilon factor Error MS Stage = 0.7956

<sup>†</sup>Epsilon factor Error MS Segment = 0.5067

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 18.7 VARIATE: Total non-structural carbohydrate composition (%) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	2555.06	1277.53			
REPS.WHPL STRATUM						
HYBRID	5	5515.63	1103.13	6.678	<.001	
STAGE	2	12379.34	6189.67	37.473	<.001	p<0.001
LIN	1	9496.43	9496.43	57.492	<.001	p<0.001
QUAD	1	2882.91	2882.91	17.453	<.001	p<0.001
HYBRID.STAGE	10	2034.81	203.48	1.232	0.307	
DEV.LIN	5	1464.43	292.89	1.773	0.145	
DEV.QUAD	5	570.38	114.08	0.691	0.634	
RESIDUAL	34	5616.02	165.18			
TOTAL	51	25545.81	500.90			
REPS.WHPL.SUBPL STRATUM						
SEG	6	1037.20	172.87	12.361	<.001	p<0.001
HYBRID.SEG	30	802.90	26.76	1.914	0.004	0.05>p>0.025
STAGE.SEG	12	276.83	23.07	1.650	0.080	
LIN.DEV	6	200.53	33.42	2.390	0.030	0.1>p>0.05
QUAD.DEV	6	76.30	12.72	0.909	0.489	
HYBRID.STAGE.SEG	60	1049.19	17.49	1.250	0.127	
DEV.LIN.DEV	30	536.57	17.89	1.279	0.162	
DEV.QUAD.DEV	30	512.62	17.09	1.222	0.208	
RESIDUAL	216	3020.65	13.98			
TOTAL	324	6186.77	19.09			
GRAND TOTAL	377	34287.64				
GRAND MEAN		15.68				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	3.184	20.3
REPS.WHPL	34	4.858	31.0
REPS.WHPL.SUBPL	216	3.740	23.8

<sup>†</sup>Epsilon factor Error MS Stage = 0.9113

<sup>†</sup>Epsilon factor Error MS Segment = 0.4760

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 18.8 VARIATE: Total non-structural carbohydrate content (g segment<sup>-1</sup>)  
of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	6.4537	3.2269					
REPS.WHPL STRATUM								
HYBRID	5	144.6903	28.9381	7.610	<.001			
STAGE	2	60.1273	30.0636	7.906	0.002		p<0.005	
LIN	1	30.5147	30.5147	8.024	0.008		0.01>p>0.005	
QUAD	1	29.6125	29.6125	7.787	0.009		0.01>p>0.005	
HYBRID.STAGE	10	70.0725	7.0072	1.843	0.090			
DEV.LIN	5	61.4938	12.2988	3.234	0.017		0.025>p>0.01	
DEV.QUAD	5	8.5787	1.7157	0.451	0.809			
RESIDUAL	34	129.2959	3.8028					
TOTAL	51	404.1859	7.9252					
REPS.WHPL.SUBPL STRATUM								
SEG	6	168.8219	28.1370	53.257	<.001		p<0.001	
HYBRID.SEG	30	87.9610	2.9320	5.550	<.001		p<0.001	
STAGE.SEG	12	32.9437	2.7453	5.196	<.001		p<0.001	
LIN.DEV	6	19.6662	3.2777	6.204	<.001		p<0.001	
QUAD.DEV	6	13.2775	2.2129	4.189	<.001		0.01>p>0.005	
HYBRID.STAGE.SEG	60	45.9792	0.7663	1.450	0.029		p>0.1	
DEV.LIN.DEV	30	37.4858	1.2495	2.365	<.001		0.005>p>0.001	
DEV.QUAD.DEV	30	8.4934	0.2831	0.536	0.978			
RESIDUAL	216	114.1190	0.5283					
TOTAL	324	449.8248	1.3883					
GRAND TOTAL	377	860.4645						
GRAND MEAN		1.443						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.1600	11.1
REPS.WHPL	34	0.7371	51.1
REPS.WHPL.SUBPL	216	0.7269	50.4

<sup>†</sup>Epsilon factor Error MS Stage = 0.7988

<sup>†</sup>Epsilon factor Error MS Segment = 0.4557

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 18.9 VARIATE: Residual content (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	402.574	201.287			
REPS.WHPL STRATUM						
HYBRID	5	344.065	68.813	1.583	0.251	
RESIDUAL	10	434.662	43.466			
TOTAL	15	778.727	51.915			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	286.097	143.049	18.117	<.001	p<0.001
LIN	1	254.764	254.764	32.266	<.001	p<0.001
QUAD	1	31.334	31.334	3.968	0.058	
HYBRID.STAGE	10	298.533	29.853	3.781	0.004	p=0.004
DEV.LIN	5	194.742	38.948	4.933	0.003	p=0.003
DEV.QUAD	5	103.791	20.758	2.629	0.049	p=0.05
RESIDUAL	24	189.499	7.896			
TOTAL	36	774.129	21.504			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEG	6	5102.608	850.435	246.179	<.001	p<0.001
HYBRID.SEG	30	255.102	8.503	2.462	<.001	0.025>p>0.01
STAGE.SEG	12	185.437	15.453	4.473	<.001	p<0.001
LIN.DEV	6	176.093	29.349	8.496	<.001	p<0.001
QUAD.DEV	6	9.344	1.557	0.451	0.844	
HYBRID.STAGE.SEG	60	238.306	3.972	1.150	0.235	
DEV.LIN.DEV	30	182.095	6.070	1.757	0.012	0.1>p>0.05
DEV.QUAD.DEV	30	56.211	1.874	0.542	0.976	
RESIDUAL	216	746.179	3.455			
TOTAL	324	6527.632	20.147			
GRAND TOTAL	377	8483.061				
GRAND MEAN		7.911				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.2639	16.0
REPS.WHPL	10	1.4387	18.2
REPS.WHPL.SUBPL	24	1.0621	13.4
REPS.WHPL.SUBPL.SUBSUBPL	216	1.8586	23.5

<sup>†</sup>Epsilon factor Error MS Stage = 0.9924

<sup>†</sup>Epsilon factor Error MS Segment = 0.3505

Appendix 18.10 VARIATE: Dry mass (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	321.576	160.788			
REPS.WHPL STRATUM						
HYBRID	5	794.720	158.944	2.743	0.082	
RESIDUAL	10	579.461	57.946			
TOTAL	15	1374.180	91.612			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	108.962	54.481	4.777	0.018	0.025>p>0.01
LIN	1	108.937	108.937	9.552	0.005	0.01>p>0.005
QUAD	1	0.000	0.000	0.000		
HYBRID.STAGE	10	580.692	58.069	5.092	<.001	p<0.001
DEV.LIN	5	473.574	94.715	8.305	<.001	p<0.001
DEV.QUAD	5	107.117	21.423	1.878	0.136	
RESIDUAL	24	273.716	11.405			
TOTAL	36	963.369	26.760			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEG	6	7120.333	1186.722	257.283	<.001	p<0.001
HYBRID.SEG	30	561.962	18.732	4.061	<.001	p<0.001
STAGE.SEG	12	292.054	24.338	5.276	<.001	p<0.001
LIN.DEV	6	260.356	43.393	9.408	<.001	p<0.001
QUAD.DEV	6	31.697	5.283	1.145	0.337	
HYBRID.STAGE.SEG	60	410.652	6.844	1.484	0.022	0.1>p>0.05
DEV.LIN.DEV	30	342.756	11.425	2.477	<.001	p<0.01
DEV.QUAD.DEV	30	67.895	2.263	0.491	0.989	
RESIDUAL	216	996.302	4.613			
TOTAL	324	9381.303	28.955			
GRAND TOTAL	377	12040.428				
GRAND MEAN		9.35				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.130	12.1
REPS.WHPL	10	1.661	17.8
REPS.WHPL.SUBPL	24	1.276	13.6
REPS.WHPL.SUBPL.SUBSUBPL	216	2.148	23.0

<sup>†</sup>Epsilon factor Error MS Stage = 0.9055

<sup>†</sup>Epsilon factor Error MS Segment = 0.3852

Appendix 19 Analyses of variance : non-structural carbohydrate analyses of WHOLE  
STEM : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture

Appendix 19.1 VARIATE: Reducing sugars composition (%) of whole stem

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	120.45	60.23					
REPS.WHPL STRATUM								
HYBRID	5	461.07	92.21	5.667	<.001			
STAGE	2	146.52	73.26	4.502	0.018	0.05	>p>0.025	
LIN	1	143.77	143.77	8.835	0.005	0.01	>p>0.005	
QUAD	1	2.75	2.75	0.169	0.684			
HYBRID.STAGE	10	108.99	10.90	0.670	0.744			
DEV.LIN	5	45.55	9.11	0.560	0.730			
DEV.QUAD	5	63.44	12.69	0.780	0.571			
RESIDUAL	34	553.25	16.27					
TOTAL	51	1269.83	24.90					
GRAND TOTAL	53	1390.28						
GRAND MEAN		7.21						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.829	25.4
REPS.WHPL	34	4.034	55.9

<sup>†</sup>Epsilon factor Error MS Stage = 0.6635

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 19.2 VARIATE: Reducing sugars content (g stem<sup>-1</sup>) of whole stem

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	18.71	9.36					
REPS.WHPL STRATUM								
HYBRID	5	420.38	84.08	7.362	<.001			
STAGE	2	18.17	9.08	0.795	0.460			
LIN	1	14.47	14.47	1.267	0.268			
QUAD	1	3.70	3.70	0.324	0.573			
HYBRID.STAGE	10	139.08	13.91	1.218	0.315			
DEV.LIN	5	111.24	22.25	1.948	0.112			
DEV.QUAD	5	27.84	5.57	0.488	0.783			
RESIDUAL	34	388.31	11.42					
TOTAL	51	965.95	18.94					
GRAND TOTAL	53	984.66						
GRAND MEAN		4.89						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION

STRATUM	DF	SE	CV%
REPS	2	0.721	14.8
REPS.WHPL	34	3.379	69.2

<sup>†</sup>Epsilon factor Error MS Stage = 0.6416

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 19.3 VARIATE: Sucrose composition (%) of whole stem

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	53.603	26.802			
REPS.WHPL STRATUM						
HYBRID	5	54.393	10.879	2.737	0.082	
RESIDUAL	10	39.743	3.974			
TOTAL	15	94.135	6.276			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	633.393	316.696	87.039	<.001	p<0.001
LIN	1	304.069	304.069	83.568	<.001	p<0.001
QUAD	1	329.324	329.324	90.509	<.001	p<0.001
HYBRID.STAGE	10	75.569	7.557	2.077	0.069	
DEV.LIN	5	42.657	8.531	2.345	0.072	
DEV.QUAD	5	32.912	6.582	1.809	0.149	
RESIDUAL	24	87.326	3.639			
TOTAL	36	796.287	22.119			
GRAND TOTAL	53	944.026				
GRAND MEAN		5.15				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.220	23.7
REPS.WHPL	10	1.151	22.3
REPS.WHPL.SUBPL	24	1.908	37.0

<sup>†</sup>Epsilon factor Error MS Stage = 0.6652

Appendix 19.4 VARIATE: Sucrose content (g stem<sup>-1</sup>) of whole stem

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	6.998	3.499			
REPS.WHPL STRATUM						
HYBRID	5	64.319	12.864	2.714	0.084	
RESIDUAL	10	47.390	4.739			
TOTAL	15	111.709	7.447			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	224.639	112.319	32.290	<.001	p<0.001
LIN	1	69.862	69.862	20.084	<.001	p<0.001
QUAD	1	154.777	154.777	44.496	<.001	p<0.001
HYBRID.STAGE	10	94.187	9.419	2.708	0.022	0.05>p>0.025
DEV.LIN	5	64.562	12.912	3.712	0.012	0.05>p>0.025
DEV.QUAD	5	29.626	5.925	1.703	0.172	
RESIDUAL	24	83.483	3.478			
TOTAL	36	402.309	11.175			
GRAND TOTAL	53	521.016				
GRAND MEAN		3.38				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.441	13.0
REPS.WHPL	10	1.257	37.2
REPS.WHPL.SUBPL	24	1.865	55.1

<sup>†</sup>Epsilon factor Error MS Stage = 0.7073

Appendix 19.5 VARIATE: Starch composition (%) of whole stem

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	1.668	0.834			
REPS.WHPL STRATUM						
HYBRID	5	15.047	3.009	2.070	0.093	
STAGE	2	30.014	15.007	10.324	<.001	p<0.001
LIN	1	30.014	30.014	20.647	<.001	p<0.001
QUAD	1	0.000	0.000	0.000		
HYBRID.STAGE	10	11.816	1.182	0.813	0.618	
DEV.LIN	5	9.514	1.903	1.309	0.283	
DEV.QUAD	5	2.302	0.460	0.317	0.899	
RESIDUAL	34	49.424	1.454			
TOTAL	51	106.302	2.084			
GRAND TOTAL	53	107.970				
GRAND MEAN		2.81				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.215	7.7
REPS.WHPL	34	1.206	42.9

<sup>†</sup>Epsilon factor Error MS Stage = 0.7495

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 19.6 VARIATE: Starch content (g stem<sup>-1</sup>) of whole stem

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	0.3743	0.1872			
REPS.WHPL STRATUM						
HYBRID	5	19.7040	3.9408	6.082	<.001	
STAGE	2	6.0194	3.0097	4.645	0.016	0.025>p>0.01
LIN	1	6.0188	6.0188	9.288	0.004	0.01>p>0.005
QUAD	1	0.0000	0.0000	0.000		
HYBRID.STAGE	10	10.2561	1.0256	1.583	0.154	
DEV.LIN	5	7.5930	1.5186	2.344	0.062	
DEV.QUAD	5	2.6631	0.5326	0.822	0.543	
RESIDUAL	34	22.0317	0.6480			
TOTAL	51	58.0112	1.1375			
GRAND TOTAL	53	58.3855				
GRAND MEAN		1.83				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.102	5.6
REPS.WHPL	34	0.805	44.0

<sup>†</sup>Epsilon factor Error MS Stage = 0.7032

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 19.7 VARIATE: Total non-structural carbohydrate composition (%) of whole stem

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	377.95	188.98			
REPS.WHPL STRATUM						
HYBRID	5	931.87	186.37	6.359	<.001	
STAGE	2	1612.47	806.24	27.508	<.001	p<0.001
LIN	1	1219.03	1219.03	41.592	<.001	p<0.001
QUAD	1	393.44	393.44	13.424	<.001	p<0.001
HYBRID.STAGE	10	301.32	30.13	1.028	0.442	
DEV.LIN	5	214.52	42.90	1.464	0.227	
DEV.QUAD	5	86.80	17.36	0.592	0.706	
RESIDUAL	34	996.51	29.31			
TOTAL	51	3842.17	75.34			
GRAND TOTAL	53	4220.12				
GRAND MEAN		15.18				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	3.240	21.3
REPS.WHPL	34	5.414	35.7

<sup>†</sup>Epsilon factor Error MS Stage = 0.7737

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 19.8 VARIATE: Total non-structural carbohydrate content (g stem<sup>-1</sup>) of whole stem

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	45.20	22.60			
REPS.WHPL STRATUM						
HYBRID	5	1012.99	202.60	7.610	<.001	
STAGE	2	420.96	210.48	7.906	0.002	0.01>p>0.005
LIN	1	213.60	213.60	8.024	0.008	0.01>p>0.005
QUAD	1	207.36	207.36	7.789	0.009	0.01>p>0.005
HYBRID.STAGE	10	490.47	49.05	1.842	0.090	
DEV.LIN	5	430.49	86.10	3.234	0.017	0.05>p>0.025
DEV.QUAD	5	59.98	12.00	0.451	0.810	
RESIDUAL	34	905.13	26.62			
TOTAL	51	2829.55	55.48			
GRAND TOTAL	53	2874.75				
GRAND MEAN		10.10				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.121	11.1
REPS.WHPL	34	5.160	51.1

<sup>†</sup>Epsilon factor Error MS Stage = 0.7313

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 19.9 VARIATE: Residual content (g stem<sup>-1</sup>) of whole stem

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	2818.34	1409.17			
REPS.WHPL STRATUM						
HYBRID	5	2407.87	481.57	1.583	0.251	
RESIDUAL	10	3042.48	304.25			
TOTAL	15	5450.35	363.36			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	2002.79	1001.40	18.121	<.001	p<0.001
LIN	1	1783.37	1783.37	32.272	<.001	p<0.001
QUAD	1	219.42	219.42	3.971	0.058	
HYBRID.STAGE	10	2089.84	208.98	3.782	0.004	0.01>p>0.005
DEV.LIN	5	1363.21	272.64	4.934	0.003	0.005>p>0.003
DEV.QUAD	5	726.62	145.32	2.630	0.049	0.1>p>0.05
RESIDUAL	24	1326.25	55.26			
TOTAL	36	5418.88	150.52			
GRAND TOTAL	53	13687.57				
GRAND MEAN		55.4				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	8.85	16.0
REPS.WHPL	10	10.07	18.2
REPS.WHPL.SUBPL	24	7.43	13.4

<sup>†</sup>Epsilon factor Error MS Stage = 0.9324

Appendix 19.10 VARIATE: Dry mass (g stem<sup>-1</sup>) of whole stem

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	2251.08	1125.54			
REPS.WHPL STRATUM						
HYBRID	5	5562.95	1112.59	2.743	0.082	
RESIDUAL	10	4056.16	405.62			
TOTAL	15	9619.11	641.27			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	762.76	381.38	4.777	0.018	0.025>p>0.01
LIN	1	762.59	762.59	9.552	0.005	0.01>p>0.005
QUAD	1	0.00	0.00	0.000		
HYBRID.STAGE	10	4064.94	406.49	5.092	<.001	0.005>p>0.001
DEV.LIN	5	3315.15	663.03	8.305	<.001	0.005>p>0.001
DEV.QUAD	5	749.80	149.96	1.878	0.136	
RESIDUAL	24	1916.01	79.83			
TOTAL	36	6743.71	187.33			
GRAND TOTAL	53	18613.91				
GRAND MEAN		65.5				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	7.91	12.1
REPS.WHPL	10	11.63	17.8
REPS.WHPL.SUBPL	24	8.93	13.6

<sup>†</sup>Epsilon factor Error MS Stage = 0.8839

Appendix 20 Analyses of variance : non-structural carbohydrate analyses of COB :  
1985/86 maize hybrid rain grown trial, Faculty of Agriculture

Appendix 20.1 VARIATE: Reducing sugars composition (%) of cob

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>1</sup>
REPS STRATUM	2	39.54	19.77					
REPS.WHPL STRATUM								
HYBRID	5	115.55	23.11	2.080	0.092			
STAGE	2	781.65	390.83	35.173	<.001	p<0.001		
LIN	1	764.71	764.71	68.821	<.001	p<0.001		
QUAD	1	16.95	16.95	1.525	0.225			
HYBRID.STAGE	10	118.08	11.81	1.063	0.416			
DEV.LIN	5	19.67	3.93	0.354	0.876			
DEV.QUAD	5	98.41	19.68	1.771	0.145			
RESIDUAL	34	377.79	11.11					
TOTAL	51	1393.08	27.32					
GRAND TOTAL	53	1432.62						
GRAND MEAN		6.34						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.048	16.5
REPS.WHPL	34	3.333	52.6

<sup>1</sup>Epsilon factor Error MS Stage = 0.8517

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 20.2 VARIATE: Reducing sugars content (g cob<sup>-1</sup>) of cob

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	0.07311	0.03655			
REPS.WHPL STRATUM						
HYBRID	5	1.14757	0.22951	1.897	0.182	
RESIDUAL	10	1.20999	0.12100			
TOTAL	15	2.35756	0.15717			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	4.10220	2.05110	34.383	<.001	p<0.001
LIN	1	0.10307	0.10307	1.728	0.201	
QUAD	1	3.99913	3.99913	67.039	<.001	p<0.001
HYBRID.STAGE	10	2.39628	0.23963	4.017	0.003	0.01>p>0.005
DEV.LIN	5	0.47907	0.09581	1.606	0.197	
DEV.QUAD	5	1.91721	0.38344	6.428	<.001	0.005>p>0.001
RESIDUAL	24	1.43170	0.05965			
TOTAL	36	7.93019	0.22028			
GRAND TOTAL	53	10.36085				
GRAND MEAN		0.534				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.0451	8.4
REPS.WHPL	10	0.2008	37.6
REPS.WHPL.SUBPL	24	0.2442	45.8

<sup>†</sup>Epsilon factor Error MS Stage = 0.7175

Appendix 20.3 VARIATE: Sucrose composition (%) of cob

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	3.281	1.641			
REPS.WHPL STRATUM						
HYBRID	5	39.045	7.809	1.418	0.243	
STAGE	2	226.945	113.473	20.607	<.001	p<0.001
LIN	1	94.122	94.122	17.093	<.001	p<0.001
QUAD	1	132.823	132.823	24.122	<.001	p<0.001
HYBRID.STAGE	10	44.356	4.436	0.806	0.625	
DEV.LIN	5	36.327	7.265	1.319	0.279	
DEV.QUAD	5	8.029	1.606	0.292	0.914	
RESIDUAL	34	187.217	5.506			
TOTAL	51	497.563	9.756			
GRAND TOTAL	53	500.845				
GRAND MEAN		3.04				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.302	9.9
REPS.WHPL	34	2.347	77.2

<sup>†</sup>Epsilon factor Error MS Stage = 0.6495

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 20.4 VARIATE: Sucrose content (g cob<sup>-1</sup>) of cob

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	0.02467	0.01234			
REPS.WHPL STRATUM						
HYBRID	5	0.21166	0.04233	0.851	0.545	
RESIDUAL	10	0.49756	0.04976			
TOTAL	15	0.70922	0.04728			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	1.26169	0.63084	14.020	<.001	p<0.001
LIN	1	0.96741	0.96741	21.500	<.001	p<0.001
QUAD	1	0.29428	0.29428	6.540	0.017	0.025>p>0.01
HYBRID.STAGE	10	0.93740	0.09374	2.083	0.068	0.1>p>0.05
DEV.LIN	5	0.63697	0.12739	2.831	0.038	0.1>p>0.05
DEV.QUAD	5	0.30043	0.06009	1.335	0.283	
RESIDUAL	24	1.07990	0.04500			
TOTAL	36	3.27899	0.09108			
GRAND TOTAL	53	4.01288				
GRAND MEAN		0.248				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.0262	10.5
REPS.WHPL	10	0.1288	51.8
REPS.WHPL.SUBPL	24	0.2121	85.4

<sup>†</sup>Epsilon factor Error MS Stage = 0.8403

Appendix 20.5 VARIATE: Starch composition (%) of cob

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	78.160	39.080			
REPS.WHPL STRATUM						
HYBRID	5	43.751	8.750	0.878	0.506	
STAGE	2	533.819	266.910	26.786	<.001	p<0.001
LIN	1	409.624	409.624	41.108	<.001	p<0.001
QUAD	1	124.196	124.196	12.464	0.001	0.005>p>0.001
HYBRID.STAGE	10	139.936	13.994	1.404	0.220	
DEV.LIN	5	61.676	12.335	1.238	0.313	
DEV.QUAD	5	78.261	15.652	1.571	0.195	
RESIDUAL	34	338.794	9.965			
TOTAL	51	1056.301	20.712			
GRAND TOTAL	53	1134.460				
GRAND MEAN		6.43				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.473	22.9
REPS.WHPL	34	3.157	49.1

<sup>†</sup>Epsilon factor Error MS Stage = 0.6592

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 20.6 VARIATE: Starch content (g cob<sup>-1</sup>) of cob

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	0.61305	0.30652			
REPS.WHPL STRATUM						
HYBRID	5	0.70186	0.14037	0.923	0.505	
RESIDUAL	10	1.52031	0.15203			
TOTAL	15	2.22217	0.14814			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	2.86663	1.43332	15.929	<.001	p<0.001
LIN	1	2.53947	2.53947	28.222	<.001	p<0.001
QUAD	1	0.32717	0.32717	3.636	0.069	
HYBRID.STAGE	10	1.29091	0.12909	1.435	0.225	
DEV.LIN	5	0.45728	0.09146	1.016	0.430	
DEV.QUAD	5	0.83363	0.16673	1.853	0.140	
RESIDUAL	24	2.15955	0.08998			
TOTAL	36	6.31710	0.17547			
GRAND TOTAL	53	9.15232				
GRAND MEAN		0.625				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.1305	20.9
REPS.WHPL	10	0.2251	36.0
REPS.WHPL.SUBPL	24	0.3000	48.0

<sup>†</sup>Epsilon factor Error MS Stage = 0.9364

Appendix 20.7 VARIATE: Total non-structural carbohydrate composition (%) of cob

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	98.25	49.13				
REPS.WHPL STRATUM							
HYBRID	5	381.60	76.32	3.729	0.008		
STAGE	2	4034.56	2017.28	98.558	<.001	p<0.001	
LIN	1	3317.09	3317.09	162.063	<.001	p<0.001	
QUAD	1	717.47	717.47	35.054	<.001	p<0.001	
HYBRID.STAGE	10	367.02	36.70	1.793	0.100		
DEV.LIN	5	228.89	45.78	2.237	0.073		
DEV.QUAD	5	138.13	27.63	1.350	0.268		
RESIDUAL	34	695.91	20.47				
TOTAL	51	5479.09	107.43				
GRAND TOTAL	53	5577.34					
GRAND MEAN		15.81					

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.652	10.4
REPS.WHPL	34	4.524	28.6

<sup>†</sup>Epsilon factor Error MS Stage = 0.6386

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 20.8 VARIATE: Total non-structural carbohydrate content (g cob<sup>-1</sup>) of cob

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	0.6843	0.3422			
REPS.WHPL STRATUM						
HYBRID	5	3.8939	0.7788	1.468	0.282	
RESIDUAL	10	5.3033	0.5303			
TOTAL	15	9.1972	0.6131			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	12.5175	6.2588	26.747	<.001	p<0.001
LIN	1	8.3995	8.3995	35.896	<.001	p<0.001
QUAD	1	4.1180	4.1180	17.599	<.001	p<0.001
HYBRID.STAGE	10	6.5914	0.6591	2.817	0.018	0.025>p>0.01
DEV.LIN	5	3.6117	0.7223	3.087	0.027	0.05>p>0.025
DEV.QUAD	5	2.9797	0.5959	2.547	0.055	0.1>p>0.05
RESIDUAL	24	5.6159	0.2340			
TOTAL	36	24.7249	0.6868			
GRAND TOTAL	53	34.6064				
GRAND MEAN		1.407				

\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.1379	9.8
REPS.WHPL	10	0.4204	29.9
REPS.WHPL.SUBPL	24	0.4837	34.4

<sup>†</sup>Epsilon factor Error MS Stage = 0.9712

Appendix 20.9 VARIATE: Residual content (g cob<sup>-1</sup>) of cob

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	93.230	46.615			
REPS.WHPL STRATUM						
HYBRID	5	879.432	175.886	4.496	0.021	
RESIDUAL	10	391.176	39.118			
TOTAL	15	1270.608	84.707			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	3336.157	1668.078	176.998	<.001	p<0.001
LIN	1	2789.087	2789.087	295.947	<.001	p<0.001
QUAD	1	547.069	547.069	58.049	<.001	p<0.001
HYBRID.STAGE	10	323.889	32.389	3.437	0.006	0.025>p>0.01
DEV.LIN	5	141.547	28.309	3.004	0.030	0.05>p>0.025
DEV.QUAD	5	182.342	36.468	3.870	0.010	0.025>p>0.01
RESIDUAL	24	226.183	9.424			
TOTAL	36	3886.229	107.951			
GRAND TOTAL	53	5250.067				
GRAND MEAN		12.76				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.609	12.6
REPS.WHPL	10	3.611	28.3
REPS.WHPL.SUBPL	24	3.070	24.1

<sup>†</sup>Epsilon factor Error MS Stage = 0.7243

Appendix 20.10 VARIATE: Dry mass (g cob<sup>-1</sup>) of cob

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	109.89	54.94			
REPS.WHPL STRATUM						
HYBRID	5	939.25	187.85	3.984	0.030	
RESIDUAL	10	471.55	47.16			
TOTAL	15	1410.80	94.05			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	3749.72	1874.86	185.629	<.001	p<0.001
LIN	1	3103.60	3103.60	307.287	<.001	p<0.001
QUAD	1	646.12	646.12	63.972	<.001	p<0.001
HYBRID.STAGE	10	313.49	31.35	3.104	0.011	0.025>p>0.01
DEV.LIN	5	110.40	22.08	2.186	0.089	
DEV.QUAD	5	203.09	40.62	4.022	0.009	0.025>p>0.01
RESIDUAL	24	242.40	10.10			
TOTAL	36	4305.61	119.60			
GRAND TOTAL	53	5826.30				
GRAND MEAN		14.17				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.747	12.3
REPS.WHPL	10	3.965	28.0
REPS.WHPL.SUBPL	24	3.178	22.4

<sup>†</sup>Epsilon factor Error MS Stage = 0.7483

Appendix 21 Analyses of variance : non-structural carbohydrate analyses of  
GRAIN : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture

Appendix 21.1 VARIATE: Reducing sugars composition (%) of grain

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	41.762	20.881					
REPS.WHPL STRATUM								
HYBRID	5	55.822	11.164	1.645	0.175			
STAGE	2	395.648	197.824	29.149	<.001	p<0.001		
LIN	1	387.401	387.401	57.082	<.001	p<0.001		
QUAD	1	8.247	8.247	1.215	0.278			
HYBRID.STAGE	10	265.280	26.528	3.909	0.001	0.01>p>0.005		
DEV.LIN	5	118.090	23.618	3.480	0.012	0.05>p>0.025		
DEV.QUAD	5	147.191	29.438	4.338	0.004	0.025>p>0.01		
RESIDUAL	34	230.748	6.787					
TOTAL	51	947.498	18.578					
GRAND TOTAL	53	989.260						
GRAND MEAN		3.24						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.077	33.3
REPS.WHPL	34	2.605	80.5

<sup>†</sup>Epsilon factor Error MS Stage = 0.6689

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 21.2 VARIATE: Reducing sugars content (g grain<sup>-1</sup>) of grain

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	0.0768	0.0384			
REPS.WHPL STRATUM						
HYBRID	5	1.7089	0.3418	1.832	0.194	
RESIDUAL	10	1.8652	0.1865			
TOTAL	15	3.5741	0.2383			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	16.1570	8.0785	49.253	<.001	p<0.001
LIN	1	0.0434	0.0434	0.265	0.612	
QUAD	1	16.1136	16.1136	98.241	<.001	p<0.001
HYBRID.STAGE	10	2.6647	0.2665	1.625	0.159	
DEV.LIN	5	0.1765	0.0353	0.215	0.953	
DEV.QUAD	5	2.4882	0.4976	3.034	0.029	0.1>p>0.05
RESIDUAL	24	3.9365	0.1640			
TOTAL	36	22.7582	0.6322			
GRAND TOTAL	53	26.4090				
GRAND MEAN		0.570				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.0462	8.1
REPS.WHPL	10	0.2493	43.7
REPS.WHPL.SUBPL	24	0.4050	71.0

<sup>†</sup>Epsilon factor Error MS Stage = 0.5749

Appendix 21.3 VARIATE: Sucrose composition (%) of grain

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	54.89	27.44					
REPS.WHPL STRATUM								
HYBRID	5	45.81	9.16	0.905	0.489			
STAGE	2	149.02	74.51	7.359	0.002	0.025	>p>0.01	
LIN	1	97.21	97.21	9.601	0.004	0.01	>p>0.005	
QUAD	1	51.81	51.81	5.117	0.030	0.05	>p>0.025	
HYBRID.STAGE	10	96.38	9.64	0.952	0.501			
DEV.LIN	5	68.08	13.62	1.345	0.269			
DEV.QUAD	5	28.30	5.66	0.559	0.730			
RESIDUAL	34	344.26	10.13					
TOTAL	51	635.47	12.46					
GRAND TOTAL	53	690.36						
GRAND MEAN		1.88						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.235	65.5
REPS.WHPL	34	3.182	168.9

<sup>†</sup>Epsilon factor Error MS Stage = 0.5035

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 21.4 VARIATE: Sucrose content (g grain<sup>-1</sup>) of grain

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	0.17724	0.08862			
REPS.WHPL STRATUM						
HYBRID	5	2.29778	0.45956	4.453	0.021	
RESIDUAL	10	1.03198	0.10320			
TOTAL	15	3.32976	0.22198			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	7.62332	3.81166	46.242	<.001	p<0.001
LIN	1	7.16205	7.16205	86.888	<.001	p<0.001
QUAD	1	0.46127	0.46127	5.596	0.026	0.05>p>0.025
HYBRID.STAGE	10	1.95333	0.19533	2.370	0.041	0.1>p>0.05
DEV.LIN	5	1.51436	0.30287	3.674	0.013	0.05>p>0.025
DEV.QUAD	5	0.43897	0.08779	1.065	0.404	
RESIDUAL	24	1.97829	0.08243			
TOTAL	36	11.55494	0.32097			
GRAND TOTAL	53	15.06194				
GRAND MEAN		0.446				

\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.0702	15.7
REPS.WHPL	10	0.1855	41.6
REPS.WHPL.SUBPL	24	0.2871	64.4

<sup>†</sup>Epsilon Factor Error MS Stage = 0.5866

Appendix 21.5 VARIATE: Starch composition (%) of grain

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	149.22	74.61					
REPS.WHPL STRATUM								
HYBRID	5	2027.70	405.54	6.949	<.001			
STAGE	2	25586.56	12793.28	219.211	<.001	p<0.001		
LIN	1	25467.11	25467.11	436.376	<.001	p<0.001		
QUAD	1	119.46	119.46	2.047	0.162			
HYBRID.STAGE	10	2899.58	289.96	4.968	<.001	0.005	p>0.001	
DEV.LIN	5	706.97	141.39	2.423	0.056			
DEV.QUAD	5	2192.61	438.52	7.514	<.001	0.005	p>0.001	
RESIDUAL	34	1984.26	58.36					
TOTAL	51	32498.10	637.22					
GRAND TOTAL	53	32647.32						
GRAND MEAN		39.1						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	2.04	5.2
REPS.WHPL	34	7.64	19.5

<sup>†</sup>Epsilon factor Error MS Stage = 0.7606

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 21.6 VARIATE: Starch content (g grain<sup>-1</sup>) of grain

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	822.7	411.4			
REPS.WHPL STRATUM						
HYBRID	5	12515.7	2503.1	5.579	0.010	
RESIDUAL	10	4486.9	448.7			
TOTAL	15	17002.6	1133.5			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	35425.6	17712.8	89.792	<.001	p<0.001
LIN	1	35371.2	35371.2	179.309	<.001	p<0.001
QUAD	1	54.5	54.5	0.276	0.604	
HYBRID.STAGE	10	7332.1	733.2	3.717	0.004	0.01>p>0.005
DEV.LIN	5	7083.7	1416.7	7.182	<.001	0.005>p>0.001
DEV.QUAD	5	248.5	49.7	0.252	0.935	
RESIDUAL	24	4734.3	197.3			
TOTAL	36	47492.1	1319.2			
GRAND TOTAL	53	65317.4				
GRAND MEAN		32.3				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	4.78	14.8
REPS.WHPL	10	12.23	37.9
REPS.WHPL.SUBPL	24	14.05	43.5

<sup>†</sup>Epsilon factor Error MS Stage = 0.8804

Appendix 21.7 VARIATE: Total non-structural carbohydrate composition (%) of grain

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	110.52	55.26			
REPS.WHPL STRATUM						
HYBRID	5	2308.74	461.75	6.222	<.001	
STAGE	2	16911.70	8455.85	113.940	<.001	p<0.001
LIN	1	16910.96	16910.96	227.869	<.001	p<0.001
QUAD	1	0.74	0.74	0.010	0.921	
HYBRID.STAGE	10	2331.83	233.18	3.142	0.006	0.025>p>0.01
DEV.LIN	5	1117.83	223.57	3.012	0.023	0.05>p>0.025
DEV.QUAD	5	1214.00	242.80	3.272	0.016	0.05>p>0.025
RESIDUAL	34	2523.26	74.21			
TOTAL	51	24075.53	472.07			
GRAND TOTAL	53	24186.05				
GRAND MEAN		44.2				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1.75	4.0
REPS.WHPL	34	8.61	19.5

<sup>†</sup>Epsilon factor Error MS Stage = 0.8405

NOTE: Since Error MS Stage > Error MS Hybrid, Error MS Stage was pooled with Error MS Hybrid

Appendix 21.8 VARIATE: Total non-structural carbohydrate content (g grain<sup>-1</sup>) of grain

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	851.0	425.5					
REPS.WHPL STRATUM								
HYBRID	5	13029.5	2605.9	5.512	0.011			
RESIDUAL	10	4727.5	472.7					
TOTAL	15	17757.0	1183.8					
REPS.WHPL.SUBPL STRATUM								
STAGE	2	36579.3	18289.7	89.757	<.001	p<0.001		
LIN	1	36464.5	36464.5	178.951	<.001	p<0.001		
QUAD	1	114.8	114.8	0.563	0.460			
HYBRID.STAGE	10	7530.2	753.0	3.695	0.004	0.01>p>0.005		
DEV.LIN	5	7287.4	1457.5	7.153	<.001	0.005>p>0.001		
DEV.QUAD	5	242.8	48.6	0.238	0.942			
RESIDUAL	24	4890.4	203.8					
TOTAL	36	48999.9	1361.1					
GRAND TOTAL	53	67607.8						
GRAND MEAN		33.3						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	4.86	14.6
REPS.WHPL	10	12.55	37.7
REPS.WHPL.SUBPL	24	14.27	42.9

<sup>†</sup>Epsilon factor Error MS Stage = 0.8923

Appendix 21.9 VARIATE: Residual content (g grain<sup>-1</sup>) of grain

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	580.8	290.4			
REPS.WHPL STRATUM						
HYBRID	5	4782.0	956.4	5.945	0.008	
RESIDUAL	10	1608.8	160.9			
TOTAL	15	6390.8	426.1			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	13367.3	6683.7	65.788	<.001	p<0.001
LIN	1	9265.0	9265.0	91.196	<.001	p<0.001
QUAD	1	4102.4	4102.4	40.380	<.001	p<0.001
HYBRID.STAGE	10	3300.4	330.0	3.249	0.009	0.025>p>0.001
DEV.LIN	5	1555.5	311.1	3.062	0.028	0.05>p>0.025
DEV.QUAD	5	1744.9	349.0	3.435	0.018	0.025>p>0.01
RESIDUAL	24	2438.3	101.6			
TOTAL	36	19106.0	530.7			
GRAND TOTAL	53	26077.6				
GRAND MEAN		23.5				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	4.02	17.1
REPS.WHPL	10	7.32	31.2
REPS.WHPL.SUBPL	24	10.08	43.0

<sup>†</sup>Epsilon factor Error MS Stage = 0.9370

Appendix 21.10 VARIATE: Dry mass (g grain<sup>-1</sup>) of grain

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	2772.9	1386.5			
REPS.WHPL STRATUM						
HYBRID	5	32700.9	6540.2	5.722	0.010	
RESIDUAL	10	11430.8	1143.1			
TOTAL	15	44131.6	2942.1			
REPS.WHPL.SUBPL STRATUM						
STAGE	2	88080.2	44040.1	118.934	<.001	p<0.001
LIN	1	82490.5	82490.5	222.773	<.001	p<0.001
QUAD	1	5589.7	5589.7	15.095	<.001	p<0.001
HYBRID.STAGE	10	17708.3	1770.8	4.782	<.001	0.005>p>0.001
DEV.LIN	5	15015.4	3003.1	8.110	<.001	p<0.001
DEV.QUAD	5	2692.9	538.6	1.455	0.241	
RESIDUAL	24	8886.9	370.3			
TOTAL	36	114675.5	3185.4			
GRAND TOTAL	53	161580.0				
GRAND MEAN		56.8				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	8.78	15.5
REPS.WHPL	10	19.52	34.4
REPS.WHPL.SUBPL	24	19.24	33.9

<sup>†</sup>Epsilon factor Error MS Stage = 0.7466

Appendix 22 Analysis of variance : Leaf area index at peak canopy : 1985/86  
maize hybrid rain grown trial, Faculty of Agriculture

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	3.12080	1.56040		
REPS.PLOTS STRATUM					
HYBRID	5	0.80807	0.16161	4.403	0.022
RESIDUAL	10	0.36704	0.03670		
TOTAL	15	1.17511	0.07834		
GRAND TOTAL	17	4.29591			

GRAND MEAN 3.429

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.5100	14.9
REPS.PLOTS	10	0.1916	5.6

Appendix 23 Analysis of variance : Grain yield (g m<sup>-2</sup>, primary plus secondary ears) at harvest maturity : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	115128	57564		
REPS.PLOTS STRATUM					
HYBRID	5	673865	134773	4.025	0.029
RESIDUAL	10	334874	33487		
TOTAL	15	1008740	67249		
GRAND TOTAL	17	1123868			

GRAND MEAN                   425

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	97.9	23.1
REPS.PLOTS	10	183.0	43.1

Appendix 24 Analyses of variance : yield components (primary ear only) and cob production at harvest maturity : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture

Appendix 24.1 VARIATE: Kernels ear<sup>-1</sup>

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	67317	33658		
REPS.PLOTS STRATUM					
HYBRID	5	335698	67140	7.657	0.003
RESIDUAL	10	87680	8768		
TOTAL	15	423378	28225		
GRAND TOTAL	17	490695			
GRAND MEAN		306			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	74.9	24.5
REPS.PLOTS	10	93.6	30.6

Appendix 24.2 VARIATE: Kernels row<sup>-1</sup>

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	230.88	115.44		
REPS.PLOTS STRATUM					
HYBRID	5	1531.71	306.34	5.191	0.013
RESIDUAL	10	590.10	59.01		
TOTAL	15	2121.81	141.45		
GRAND TOTAL	17	2352.70			
GRAND MEAN		24.9			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	4.39	17.6
REPS.PLOTS	10	7.68	30.9

Appendix 24.3 VARIATE: Rows ear<sup>-1</sup>

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	11.723	5.862		
REPS.PLOTS STRATUM					
HYBRID	5	82.052	16.410	14.824	<.001
RESIDUAL	10	11.070	1.107		
TOTAL	15	93.122	6.208		
GRAND TOTAL	17	104.845			
GRAND MEAN		11.52			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.988	8.6
REPS.PLOTS	10	1.052	9.1

Appendix 24.4 VARIATE: Mass kernel<sup>-1</sup> (g)

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	0.011713	0.005856		
REPS.PLOTS STRATUM					
HYBRID	5	0.104602	0.020920	5.939	0.008
RESIDUAL	10	0.035224	0.003522		
TOTAL	15	0.139826	0.009322		
GRAND TOTAL	17	0.151539			
GRAND MEAN		0.323			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.0312	9.7
REPS.PLOTS	10	0.0593	18.3

Appendix 24.5 VARIATE: Cob production (g m<sup>-2</sup>)

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	250.01	125.00		
REPS.PLOTS STRATUM					
HYBRID	5	637.79	127.56	3.621	0.040
RESIDUAL	10	352.24	35.22		
TOTAL	15	990.04	66.00		
GRAND TOTAL	17	1240.05			
GRAND MEAN		20.7			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	4.56	22.1
REPS.PLOTS	10	5.93	28.7

Appendix 25 Analyses of variance : Agronomic characteristics at harvest maturity : 1985/86 maize hybrid rain grown trial, Faculty of Agriculture

Appendix 25.1 VARIATE: Stand percentage

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	8.65	4.33		
REPS.PLOTS STRATUM					
HYBRID	5	115.34	23.07	0.432	0.816
RESIDUAL	10	533.45	53.34		
TOTAL	15	648.79	43.25		
GRAND TOTAL	17	657.44			
GRAND MEAN		92.2			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.85	0.9
REPS.PLOTS	10	7.30	7.9

Appendix 25.2 VARIATE: Percentage barren plants

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	1.18	0.59		
REPS.PLOTS STRATUM					
HYBRID	5	90.54	18.11	0.642	0.674
RESIDUAL	10	282.20	28.22		
TOTAL	15	372.74	24.85		
GRAND TOTAL	17	373.92			
GRAND MEAN		2.2			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.31	14.2
REPS.PLOTS	10	5.31	240.0

Appendix 25.3 VARIATE: Percentage runt primary ears

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	2883.4	1441.7		
REPS.PLOTS STRATUM					
HYBRID	5	14162.1	2832.4	6.725	0.005
RESIDUAL	10	4211.8	421.2		
TOTAL	15	18373.9	1224.9		
GRAND TOTAL	17	21257.3			
GRAND MEAN		46.8			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	15.50	33.1
REPS.PLOTS	10	20.52	43.9

Appendix 25.4 VARIATE: Percentage of final grain yield from primary ear

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	11.303	5.651		
REPS.PLOTS STRATUM					
HYBRID	5	49.093	9.819	3.048	0.063
RESIDUAL	10	32.216	3.222		
TOTAL	15	81.310	5.421		
GRAND TOTAL	17	92.612			
GRAND MEAN		99.01			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.971	1.0
REPS.PLOTS	10	1.795	1.8

Appendix 26 Analysis of variance : VARIATE: Leaf water potential (kPA) : 1986/87  
maize single cross hybrid rain-out shelter trial, Ukulinga

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	1130826	376942			
REPS.WHPL STRATUM						
HYBRID	1	93100	93100	1.155	0.285	
STRESS	1	5579633	5579633	69.219	<.001	
WAA	7	6808357	972622	12.066	<.001	p<0.001
LIN	1	4797880	4797880	59.520	<.001	p<0.001
QUAD	1	386595	386595	4.796	0.031	0.05>p>0.025
CUB	1	1530059	1530059	18.981	<.001	p<0.001
DEVIATIONS	4	93823	23456	0.291	0.883	
HYBRID.STRESS	1	130841	130841	1.623	0.206	
HYBRID.WAA	7	196865	28124	0.349	0.929	
DEV.LIN	1	25868	25868	0.321	0.572	
DEV.QUAD	1	328	328	0.004	0.949	
DEV.CUB	1	6231	6231	0.077	0.782	
DEVIATIONS	4	164438	41110	0.510	0.729	
STRESS.WAA	7	4601564	657366	8.155	<.001	p<0.001
DEV.LIN	1	3531780	3531780	43.814	<.001	p<0.001
DEV.QUAD	1	458147	458147	5.684	0.019	0.025>p>0.01
DEV.CUB	1	332811	332811	4.129	0.045	0.05>p>0.025
DEVIATIONS	4	278826	69706	0.865	0.488	
HYBRID.STRESS.WAA	7	719880	102840	1.276	0.271	
DEV.DEV.LIN	1	178447	178447	2.214	0.140	
DEV.DEV.QUAD	1	75653	75653	0.939	0.335	
DEVIATIONS	5	465780	93156	1.156	0.337	
RESIDUAL	93	7496631	80609			
TOTAL	124	25626869	206668			
GRAND TOTAL	127	26757695				
GRAND MEAN	717					

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	108.5	15.1
REPS.WHPL	93	283.9	39.6

<sup>†</sup>Epsilon factor Error MS WAA = 0.4052

NOTE: Since Error MS WAA > Error MS Hybrid and Stress, Error MS WAA was pooled with Error MS Hybrid and Stress

Appendix 27 Analysis of variance : VARIATE: Leaf area index : 1986/87 maize  
single cross hybrid rain-out shelter trial, Ukulinga

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	0.58370	0.19457			
REPS.WHPL STRATUM						
HYBRID	1	1.86339	1.86339	69.333	<.001	
STRESS	1	4.16238	4.16238	154.873	<.001	
HYBRID.STRESS	1	0.00529	0.00529	0.197	0.668	
RESIDUAL	9	0.24188	0.02688			
TOTAL	12	6.27294	0.52275			
REPS.WHPL.SUBPL STRATUM						
WAA	7	38.87009	5.55287	213.393	<.001	p<0.001
LIN	1	35.65304	35.65304	1370.122	<.001	p<0.001
QUAD	1	3.16190	3.16190	121.510	<.001	p<0.001
CUB	1	0.00000	0.00000	0.000		
DEVIATIONS	4	0.05515	0.01379	0.530	0.714	
HYBRID.WAA	7	1.02914	0.14702	5.650	<.001	p<0.005
DEV.LIN	1	0.38775	0.38775	14.901	<.001	p<0.001
DEV.QUAD	1	0.28513	0.28513	10.957	0.001	p<0.005
DEV.CUB	1	0.23007	0.23007	8.841	0.004	p<0.005
DEVIATIONS	4	0.12620	0.03155	1.212	0.312	
STRESS.WAA	7	0.87719	0.12531	4.816	<.001	p<0.005
DEV.LIN	1	0.19394	0.19394	7.453	0.008	0.01>p>0.005
DEV.QUAD	1	0.03505	0.03505	1.347	0.249	
DEV.CUB	1	0.20650	0.20650	7.936	0.006	0.01>p>0.005
DEVIATIONS	4	0.44171	0.11043	4.244	0.004	0.01>p>0.005
HYBRID.STRESS.WAA	7	0.04355	0.00622	0.239	0.974	
DEV.DEV.LIN	1	0.00537	0.00537	0.206	0.651	
DEV.DEV.QUAD	1	0.00260	0.00260	0.100	0.753	
DEVIATIONS	5	0.03557	0.00711	0.273	0.926	
RESIDUAL	84	2.18583	0.02602			
TOTAL	112	43.00581	0.38398			
GRAND TOTAL	127	49.86245				
GRAND MEAN		1.559				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	0.0780	5.0
REPS.WHPL	9	0.0580	3.7
REPS.WHPL.SUBPL	84	0.1613	10.3

<sup>†</sup>Epsilon factor Error MS WAA = 0.7250

Appendix 28 Analyses of variance : carbohydrate analyses of STEM SEGMENTS : 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga

Appendix 28.1 VARIATE: Reducing sugars composition (%) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	56.571	18.857			
REPS.WHPL STRATUM						
HYBRID	1	96.527	96.527	3.485	0.095	
STRESS	1	74.351	74.351	2.684	0.136	
HYBRID.STRESS	1	15.710	15.710	0.567	0.471	
RESIDUAL	9	249.307	27.701			
TOTAL	12	435.894	36.325			
REPS.WHPL.SUBPL STRATUM						
WAA	7	2943.563	420.509	35.406	<.001	p<0.001
LIN	1	2489.994	2489.994	209.652	<.001	p<0.001
QUAD	1	234.738	234.738	19.764	<.001	p<0.001
CUB	1	63.702	63.702	5.364	0.023	0.05>p>0.025
DEVIATIONS	4	155.129	38.782	3.265	0.015	0.05>p>0.025
HYBRID.WAA	7	226.318	32.331	2.722	0.014	0.05>p>0.025
DEV.LIN	1	198.039	198.039	16.674	<.001	p<0.001
DEV.QUAD	1	0.103	0.103	0.009	0.926	
DEV.CUB	1	2.094	2.094	0.176	0.676	
DEVIATIONS	4	26.082	6.521	0.549	0.700	
STRESS.WAA	7	74.460	10.637	0.896	0.514	
DEV.LIN	1	53.046	53.046	4.466	0.038	0.05>p>0.025
DEV.QUAD	1	4.944	4.944	0.416	0.521	
DEV.CUB	1	2.145	2.145	0.181	0.672	
DEVIATIONS	4	14.326	3.581	0.302	0.876	
HYBRID.STRESS.WAA	7	63.289	9.041	0.761	0.621	
DEV.DEV.LIN	1	1.759	1.759	0.148	0.701	
DEV.DEV.QUAD	1	1.630	1.630	0.137	0.712	
DEVIATIONS	5	59.900	11.980	1.009	0.418	
RESIDUAL	84	997.652	11.877			
TOTAL	112	4305.282	38.440			

REPS.WHPL.SUBPL.SUBSUBPL STRATUM	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
SEG	1	27.081	27.081	13.768	<.001	
HYBRID.SEG	1	84.828	84.828	43.128	<.001	
STRESS.SEG	1	1.221	1.221	0.621	0.433	
WAA.SEG	7	21.264	3.038	1.544	0.162	
LIN.DEV	1	17.281	17.281	8.786	0.004	
QUAD.DEV	1	2.560	2.560	1.302	0.257	
CUB.DEV	1	0.000	0.000	0.000		
DEVIATIONS	4	1.423	0.356	0.181	0.948	
HYBRID.STRESS.SEG	1	2.851	2.851	1.450	0.232	
HYBRID.WAA.SEG	7	14.648	2.093	1.064	0.393	
DEV.LIN.DEV	1	4.182	4.182	2.126	0.148	
DEV.QUAD.DEV	1	3.500	3.500	1.780	0.185	
DEVIATIONS	5	6.966	1.393	0.708	0.619	
STRESS.WAA.SEG	7	18.420	2.631	1.338	0.241	
DEV.LIN.DEV	1	1.956	1.956	0.994	0.321	
DEV.QUAD.DEV	1	7.749	7.749	3.940	0.060	
DEVIATIONS	5	8.715	1.743	0.886	0.494	
HYBRID.STRESS.WAA.SEG	7	6.039	0.863	0.439	0.876	
DEV.DEV.LIN.DEV	1	2.274	2.274	1.156	0.285	
DEVIATIONS	6	3.766	0.628	0.319	0.926	
RESIDUAL	96	188.822	1.967			
TOTAL	128	365.175	2.853			

GRAND TOTAL 255 5162.922

GRAND MEAN 12.319

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	0.5428	4.4
REPS.WHPL	9	1.3158	10.7
REPS.WHPL.SUBPL	84	2.4369	19.8
REPS.WHPL.SUBPL.SUBSUBPL	96	1.4025	11.4

<sup>†</sup>Epsilon factor Error MS WAA = 0.5048

<sup>†</sup>Epsilon factor Error MS Segment = 1.0000

Appendix 28.2 VARIATE: Reducing sugars content (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	0.57882	0.19294			
REPS.WHPL STRATUM						
HYBRID	1	0.20108	0.20108	2.622	0.109	
STRESS	1	1.82999	1.82999	23.860	<.001	
WAA	7	17.17160	2.45309	31.984	<.001	p<0.001
LIN	1	13.31965	13.31965	173.664	<.001	p<0.001
QUAD	1	2.61437	2.61437	34.087	<.001	p<0.001
CUB	1	0.65041	0.65041	8.480	0.004	0.01>p>0.005
DEVIATIONS	4	0.58718	0.14679	1.914	0.115	
HYBRID.STRESS	1	0.09153	0.09153	1.193	0.277	
HYBRID.WAA	7	1.24090	0.17727	2.311	0.032	0.1>p>0.05
DEV.LIN	1	0.60924	0.60924	7.943	0.006	0.01>p>0.005
DEV.QUAD	1	0.03422	0.03422	0.446	0.506	
DEV.CUB	1	0.01245	0.01245	0.162	0.688	
DEVIATIONS	4	0.58500	0.14625	1.907	0.116	
STRESS.WAA	7	0.67245	0.09606	1.253	0.283	
DEV.LIN	1	0.42635	0.42635	5.559	0.020	0.05>p>0.025
DEV.QUAD	1	0.09241	0.09241	1.205	0.275	
DEV.CUB	1	0.00537	0.00537	0.070	0.792	
DEVIATIONS	4	0.14832	0.03708	0.483	0.748	
HYBRID.STRESS.WAA	7	0.30418	0.04345	0.567	0.781	
DEV.DEV.LIN	1	0.08491	0.08491	1.107	0.295	
DEV.DEV.QUAD	1	0.03238	0.03238	0.422	0.517	
DEVIATIONS	5	0.18689	0.03738	0.487	0.785	
RESIDUAL	93	7.13290	0.07670			
TOTAL	124	28.64462	0.23100			
REPS.WHPL.SUBSUBPL STRATUM						
SEG	1	6.15702	6.15702	260.994	<.001	
HYBRID.SEG	1	0.00716	0.00716	0.303	0.583	
STRESS.SEG	1	0.11222	0.11222	4.757	0.032	
WAA.SEG	7	1.78889	0.25556	10.833	<.001	
LIN.DEV	1	1.55852	1.55852	66.065	<.001	
QUAD.DEV	1	0.10326	0.10326	4.377	0.039	
CUB.DEV	1	0.12329	0.12329	5.226	0.024	
DEVIATIONS	4	0.00382	0.00096	0.040	0.997	
HYBRID.STRESS.SEG	1	0.01489	0.01489	0.631	0.429	
HYBRID.WAA.SEG	7	0.05665	0.00809	0.343	0.932	
DEV.LIN.DEV	1	0.00506	0.00506	0.215	0.644	
DEV.QUAD.DEV	1	0.00051	0.00051	0.021	0.884	
DEVIATIONS	5	0.05109	0.01022	0.433	0.824	
STRESS.WAA.SEG	7	0.10798	0.01543	0.654	0.710	
DEV.LIN.DEV	1	0.01685	0.01685	0.714	0.400	
DEV.QUAD.DEV	1	0.04865	0.04865	2.062	0.154	
DEVIATIONS	5	0.04249	0.00850	0.360	0.875	
HYBRID.STRESS.WAA.SEG	7	0.02024	0.00289	0.123	0.997	
DEV.DEV.LIN.DEV	1	0.00756	0.00756	0.320	0.573	
DEVIATIONS	6	0.01269	0.00211	0.090	0.997	
RESIDUAL	96	2.26470	0.02359			
TOTAL	128	10.52976	0.08226			
GRAND TOTAL	255	39.75320				
GRAND MEAN		0.7485				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	0.05491	7.3
REPS.WHPL	93	0.19583	26.2
REPS.WHPL.SUBSUBPL	96	0.15359	20.5

<sup>†</sup>Epsilon factor Error MS WAA = 0.5144

<sup>†</sup>Epsilon factor Error MS Segment = 1.0000

NOTE: Since Error MS WAA > Error MS Hybrid and Stress, Error MS WAA was pooled with Error MS Hybrid and Stress

Appendix 28.3 VARIATE: Sucrose composition (%) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	236.617	78.872			
REPS.WHPL STRATUM						
HYBRID	1	126.933	126.933	2.990	0.118	
STRESS	1	10.980	10.980	0.259	0.623	
HYBRID.STRESS	1	43.838	43.838	1.033	0.336	
RESIDUAL	9	382.063	42.451			
TOTAL	12	563.813	46.984			
REPS.WHPL.SUBPL STRATUM						
WAA	7	3679.619	525.660	23.644	<.001	p<0.001
LIN	1	642.685	642.685	28.908	<.001	p<0.001
QUAD	1	2502.311	2502.311	112.552	<.001	p<0.001
CUB	1	181.863	181.863	8.180	0.005	0.01>p>0.005
DEVIATIONS	4	352.759	88.190	3.967	0.005	0.025>p>0.05
HYBRID.WAA	7	1002.321	143.189	6.441	<.001	p<0.001
DEV.LIN	1	586.356	586.356	26.374	<.001	p<0.001
DEV.QUAD	1	57.910	57.910	2.605	0.110	
DEV.CUB	1	222.421	222.421	10.004	0.002	p<0.005
DEVIATIONS	4	135.634	33.909	1.525	0.202	
STRESS.WAA	7	247.217	35.317	1.589	0.150	
DEV.LIN	1	103.436	103.436	4.652	0.034	0.05>p>0.025
DEV.QUAD	1	66.785	66.785	3.004	0.087	
DEV.CUB	1	37.807	37.807	1.701	0.196	
DEVIATIONS	4	39.189	9.797	0.441	0.779	
HYBRID.STRESS.WAA	7	115.143	16.449	0.740	0.639	
DEV.DEV.LIN	1	6.492	6.492	0.292	0.590	
DEV.DEV.QUAD	1	9.812	9.812	0.441	0.508	
DEVIATIONS	5	98.839	19.768	0.889	0.492	
RESIDUAL	84	1867.527	22.232			
TOTAL	112	6911.826	61.713			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEG	1	21.185	21.185	4.169	0.044	
HYBRID.SEG	1	0.000	0.000	0.000		
STRESS.SEG	1	15.095	15.095	2.971	0.088	
WAA.SEG	7	8.577	1.225	0.241	0.974	
LIN.DEV	1	0.451	0.451	0.089	0.766	
QUAD.DEV	1	1.739	1.739	0.342	0.560	
CUB.DEV	1	3.267	3.267	0.643	0.425	
DEVIATIONS	4	3.119	0.780	0.153	0.961	
HYBRID.STRESS.SEG	1	3.766	3.766	0.741	0.391	
HYBRID.WAA.SEG	7	13.938	1.991	0.392	0.905	
DEV.LIN.DEV	1	1.827	1.827	0.360	0.550	
DEV.QUAD.DEV	1	0.000	0.000	0.000		
DEVIATIONS	5	12.111	2.422	0.477	0.793	
STRESS.WAA.SEG	7	36.128	5.161	1.016	0.425	
DEV.LIN.DEV	1	0.788	0.788	0.155	0.695	
DEV.QUAD.DEV	1	12.971	12.971	2.553	0.113	
DEVIATIONS	5	22.370	4.474	0.881	0.497	
HYBRID.STRESS.WAA.SEG	7	22.465	3.209	0.632	0.729	
DEV.DEV.LIN.DEV	1	1.286	1.286	0.253	0.616	
DEVIATIONS	6	21.179	3.530	0.695	0.654	
RESIDUAL	96	487.765	5.081			
TOTAL	128	608.919	4.757			
GRAND TOTAL	255	8321.175				
GRAND MEAN	11.52					
***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****						
STRATUM	DF	SE	CV%			
REPS	3	1.110	9.6			
REPS.WHPL	9	1.629	14.1			
REPS.WHPL.SUBPL	84	3.334	28.9			
REPS.WHPL.SUBPL.SUBSUBPL	96	2.254	19.6			

<sup>†</sup>Epsilon factor Error MS WAA = 0.6232

<sup>†</sup>Epsilon factor Error MS Segment = 1.0000

Appendix 28.4 VARIATE: Sucrose content (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	2.07060	0.69020			
REPS.WHPL STRATUM						
HYBRID	1	0.25572	0.25572	0.476	0.508	
STRESS	1	1.66259	1.66259	3.095	0.112	
HYBRID.STRESS	1	0.26214	0.26214	0.488	0.503	
RESIDUAL	9	4.83520	0.53724			
TOTAL	12	7.01564	0.58464			
REPS.WHPL.SUBPL STRATUM						
WAA	7	22.97551	3.28222	27.378	<.001	p<0.001
LIN	1	4.00573	4.00573	33.413	<.001	p<0.001
QUAD	1	14.12015	14.12015	117.779	<.001	p<0.001
CUB	1	1.25519	1.25519	10.470	0.002	p<0.005
DEVIATIONS	4	3.59444	0.89861	7.495	<.001	p<0.001
HYBRID.WAA	7	3.60126	0.51447	4.291	<.001	p<0.005
DEV.LIN	1	1.60694	1.60694	13.404	<.001	p<0.005
DEV.QUAD	1	0.15537	0.15537	1.296	0.258	
DEV.CUB	1	0.92397	0.92397	7.707	0.007	0.025>p>0.01
DEVIATIONS	4	0.91499	0.22875	1.908	0.117	
STRESS.WAA	7	0.96990	0.13856	1.156	0.337	
DEV.LIN	1	0.57125	0.57125	4.765	0.032	0.05>p>0.025
DEV.QUAD	1	0.00076	0.00076	0.006	0.937	
DEV.CUB	1	0.20109	0.20109	1.677	0.199	
DEVIATIONS	4	0.19680	0.04920	0.410	0.801	
HYBRID.STRESS.WAA	7	0.49583	0.07083	0.591	0.762	
DEV.DEV.LIN	1	0.00000	0.00000	0.000		
DEV.DEV.QUAD	1	0.04667	0.04667	0.389	0.534	
DEVIATIONS	5	0.44916	0.08983	0.749	0.589	
RESIDUAL	84	10.07050	0.11989			
TOTAL	112	38.11301	0.34029			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEG	1	3.08221	3.08221	76.541	<.001	
HYBRID.SEG	1	0.24687	0.24687	6.131	0.015	
STRESS.SEG	1	0.39845	0.39845	9.895	0.002	
WAA.SEG	7	0.65313	0.09330	2.317	0.032	
LIN.DEV	1	0.28145	0.28145	6.989	0.010	
QUAD.DEV	1	0.27049	0.27049	6.717	0.011	
CUB.DEV	1	0.05246	0.05246	1.303	0.257	
DEVIATIONS	4	0.04873	0.01218	0.303	0.876	
HYBRID.STRESS.SEG	1	0.01618	0.01618	0.402	0.528	
HYBRID.WAA.SEG	7	0.34027	0.04861	1.207	0.306	
DEV.LIN.DEV	1	0.02076	0.02076	0.516	0.474	
DEV.QUAD.DEV	1	0.13182	0.13182	3.273	0.074	
DEVIATIONS	5	0.18769	0.03754	0.932	0.464	
STRESS.WAA.SEG	7	0.27670	0.03953	0.982	0.449	
DEV.LIN.DEV	1	0.00000	0.00000	0.000		
DEV.QUAD.DEV	1	0.03710	0.03710	0.921	0.340	
DEVIATIONS	5	0.23961	0.04792	1.190	0.320	
HYBRID.STRESS.WAA.SEG	7	0.26066	0.03724	0.925	0.491	
DEV.DEV.LIN.DEV	1	0.01379	0.01379	0.342	0.560	
DEVIATIONS	6	0.24687	0.04115	1.022	0.416	
RESIDUAL	96	3.86579	0.04027			
TOTAL	128	9.14027	0.07141			
GRAND TOTAL	255	56.33952				
GRAND MEAN		0.714				
***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****						
STRATUM	DF	SE	CV%			
REPS	3	0.1038	14.5			
REPS.WHPL	9	0.1832	25.7			
REPS.WHPL.SUBPL	84	0.2448	34.3			
REPS.WHPL.SUBPL.SUBSUBPL	96	0.2007	28.1			

<sup>†</sup>Epsilon factor Error MS WAA = 0.6105

<sup>†</sup>Epsilon factor Error MS Segment = 1.0000

Appendix 28.5 VARIATE: Starch composition (%) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	3	12.3992	4.1331					
REPS.WHPL STRATUM								
HYBRID	1	7.6452	7.6452	5.494	0.044			
STRESS	1	0.1511	0.1511	0.109	0.749			
HYBRID.STRESS	1	0.2796	0.2796	0.201	0.665			
RESIDUAL	9	12.5242	1.3916					
TOTAL	12	20.6001	1.7167					
REPS.WHPL.SUBPL STRATUM								
WAA	7	303.5048	43.3578	40.347	<.001		p<0.001	
LIN	1	114.3508	114.3508	106.411	<.001		p<0.001	
QUAD	1	136.8587	136.8587	127.356	<.001		p<0.001	
CUB	1	33.8580	33.8580	31.507	<.001		p<0.001	
DEVIATIONS	4	18.4373	4.6093	4.289	0.003		0.025>p>0.05	
HYBRID.WAA	7	15.5226	2.2175	2.064	0.056		0.05>p>0.025	
DEV.LIN	1	5.4506	5.4506	5.072	0.027		0.05>p>0.025	
DEV.QUAD	1	0.7629	0.7629	0.710	0.402			
DEV.CUB	1	4.6004	4.6004	4.281	0.042		0.05>p	
DEVIATIONS	4	4.7087	1.1772	1.095	0.364			
STRESS.WAA	7	7.1532	1.0219	0.951	0.472			
DEV.LIN	1	0.0299	0.0299	0.028	0.868			
DEV.QUAD	1	0.0086	0.0086	0.008	0.929			
DEV.CUB	1	0.9597	0.9597	0.893	0.347			
DEVIATIONS	4	6.1551	1.5388	1.432	0.231			
HYBRID.STRESS.WAA	7	4.6768	0.6681	0.622	0.737			
DEV.DEV.LIN	1	0.0219	0.0219	0.020	0.887			
DEV.DEV.QUAD	1	1.5792	1.5792	1.470	0.229			
DEVIATIONS	5	3.0757	0.6151	0.572	0.721			
RESIDUAL	84	90.2677	1.0746					
TOTAL	112	421.1250	3.7600					
REPS.WHPL.SUBPL.SUBSUBPL STRATUM								
SEG	1	14.3925	14.3925	37.310	<.001			
HYBRID.SEG	1	0.0000	0.0000	0.000				
STRESS.SEG	1	0.4456	0.4456	1.155	0.285			
WAA.SEG	7	3.5524	0.5075	1.316	0.251			
LIN.DEV	1	0.0994	0.0994	0.258	0.613			
QUAD.DEV	1	0.4148	0.4148	1.075	0.302			
CUB.DEV	1	2.0700	2.0700	5.366	0.023			
DEVIATIONS	4	0.9682	0.2421	0.627	0.644			
HYBRID.STRESS.SEG	1	2.1247	2.1247	5.508	0.021			
HYBRID.WAA.SEG	7	2.2909	0.3273	0.848	0.550			
DEV.LIN.DEV	1	0.0000	0.0000	0.000				
DEV.QUAD.DEV	1	0.1767	0.1767	0.458	0.500			
DEVIATIONS	5	2.1142	0.4228	1.096	0.368			
STRESS.WAA.SEG	7	1.9513	0.2788	0.723	0.653			
DEV.LIN.DEV	1	0.0758	0.0758	0.196	0.659			
DEV.QUAD.DEV	1	0.0940	0.0940	0.244	0.623			
DEVIATIONS	5	1.7815	0.3563	0.924	0.469			
HYBRID.STRESS.WAA.SEG	7	2.9907	0.4272	1.108	0.365			
DEV.DEV.LIN.DEV	1	0.3462	0.3462	0.897	0.346			
DEVIATIONS	6	2.6445	0.4407	1.143	0.344			
RESIDUAL	96	37.0325	0.3858					
TOTAL	128	64.7805	0.5061					
GRAND TOTAL	255	518.9048						
GRAND MEAN		4.094						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	0.2541	6.2
REPS.WHPL	9	0.2949	7.2
REPS.WHPL.SUBPL	84	0.7330	17.9
REPS.WHPL.SUBPL.SUBSUBPL	96	0.6211	15.2

<sup>†</sup>Epsilon factor Error MS WAA = 0.5243

<sup>†</sup>Epsilon factor Error MS Segment = 1.0000

Appendix 28.6 VARIATE: Starch content (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	0.036134	0.012045			
REPS.WHPL STRATUM						
HYBRID	1	0.020203	0.020203	1.434	0.262	
STRESS	1	0.114178	0.114178	8.102	0.019	
HYBRID.STRESS	1	0.000166	0.000166	0.012	0.916	
RESIDUAL	9	0.126834	0.014093			
TOTAL	12	0.261382	0.021782			
REPS.WHPL.SUBPL STRATUM						
WAA	7	2.054269	0.293467	37.438	<.001	p<0.001
LIN	1	0.752505	0.752505	95.998	<.001	p<0.001
QUAD	1	0.963472	0.963472	122.911	<.001	p<0.001
CUB	1	0.238754	0.238754	30.458	<.001	p<0.001
DEVIATIONS	4	0.099539	0.024885	3.175	0.018	0.1>p>0.05
HYBRID.WAA	7	0.145168	0.020738	2.646	0.016	0.05>p>0.025
DEV.LIN	1	0.018870	0.018870	2.407	0.125	
DEV.QUAD	1	0.000669	0.000669	0.085	0.771	
DEV.CUB	1	0.025115	0.025115	3.204	0.077	
DEVIATIONS	4	0.100513	0.025128	3.206	0.017	0.1>p>0.05
STRESS.WAA	7	0.034917	0.004988	0.636	0.725	
DEV.LIN	1	0.008736	0.008736	1.115	0.294	
DEV.QUAD	1	0.019345	0.019345	2.468	0.120	
DEV.CUB	1	0.000187	0.000187	0.024	0.878	
DEVIATIONS	4	0.006649	0.001662	0.212	0.931	
HYBRID.STRESS.WAA	7	0.028880	0.004126	0.526	0.812	
DEV.DEV.LIN	1	0.001535	0.001535	0.196	0.659	
DEV.DEV.QUAD	1	0.008025	0.008025	1.024	0.315	
DEVIATIONS	5	0.019319	0.003864	0.493	0.781	
RESIDUAL	84	0.658458	0.007839			
TOTAL	112	2.921691	0.026087			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEG	1	0.227127	0.227127	89.870	<.001	
HYBRID.SEG	1	0.032202	0.032202	12.742	<.001	
STRESS.SEG	1	0.003721	0.003721	1.472	0.228	
WAA.SEG	7	0.138519	0.019788	7.830	<.001	
LIN.DEV	1	0.066470	0.066470	26.301	<.001	
QUAD.DEV	1	0.012154	0.012154	4.809	0.031	
CUB.DEV	1	0.054242	0.054242	21.463	<.001	
DEVIATIONS	4	0.005653	0.001413	0.559	0.693	
HYBRID.STRESS.SEG	1	0.001855	0.001855	0.734	0.394	
HYBRID.WAA.SEG	7	0.015987	0.002284	0.904	0.507	
DEV.LIN.DEV	1	0.001716	0.001716	0.679	0.412	
DEV.QUAD.DEV	1	0.002566	0.002566	1.015	0.316	
DEVIATIONS	5	0.011704	0.002341	0.926	0.468	
STRESS.WAA.SEG	7	0.014725	0.002104	0.832	0.563	
DEV.LIN.DEV	1	0.000160	0.000160	0.063	0.802	
DEV.QUAD.DEV	1	0.000000	0.000000	0.000		
DEVIATIONS	5	0.014565	0.002913	1.153	0.338	
HYBRID.STRESS.WAA.SEG	7	0.008771	0.001253	0.496	0.836	
DEV.DEV.LIN.DEV	1	0.004246	0.004246	1.680	0.198	
DEVIATIONS	6	0.004524	0.000754	0.298	0.936	
RESIDUAL	96	0.242619	0.002527			
TOTAL	128	0.685526	0.005356			
GRAND TOTAL	255	3.904733				
GRAND MEAN		0.2455				
***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****						
STRATUM	DF	SE	CV%			
REPS	3	0.01372	5.6			
REPS.WHPL	9	0.02968	12.1			
REPS.WHPL.SUBPL	84	0.06261	25.5			
REPS.WHPL.SUBPL.SUBSUBPL	96	0.05027	20.5			

<sup>†</sup>Epsilon factor Error MS WAA = 0.5103

<sup>†</sup>Epsilon factor Error MS Segment = 1.0000

Appendix 28.7 VARIATE: Total non-structural carbohydrate composition (%) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	447.771	149.257			
REPS.WHPL STRATUM						
HYBRID	1	569.121	569.121	11.235	0.008	
STRESS	1	151.906	151.906	2.999	0.117	
HYBRID.STRESS	1	10.152	10.152	0.200	0.665	
RESIDUAL	9	455.886	50.654			
TOTAL	12	1187.064	98.922			
REPS.WHPL.SUBPL STRATUM						
WAA	7	14298.128	2042.590	51.148	<.001	p<0.001
LIN	1	7386.469	7386.469	184.962	<.001	p<0.001
QUAD	1	5935.611	5935.611	148.632	<.001	p<0.001
CUB	1	744.515	744.515	18.643	<.001	p<0.001
DEVIATIONS	4	231.533	57.883	1.449	0.225	
HYBRID.WAA	7	2217.815	316.831	7.934	<.001	0.005>p>0.001
DEV.LIN	1	1650.153	1650.153	41.321	<.001	p<0.001
DEV.QUAD	1	77.506	77.506	1.941	0.167	
DEV.CUB	1	342.455	342.455	8.575	0.004	0.01>p>0.005
DEVIATIONS	4	147.701	36.925	0.925	0.454	
STRESS.WAA	7	549.986	78.569	1.967	0.069	
DEV.LIN	1	310.695	310.695	7.780	0.007	0.01>p>0.005
DEV.QUAD	1	110.000	110.000	2.754	0.101	
DEV.CUB	1	73.838	73.838	1.849	0.178	
DEVIATIONS	4	55.452	13.863	0.347	0.845	
HYBRID.STRESS.WAA	7	106.098	15.157	0.380	0.912	
DEV.DEV.LIN	1	1.876	1.876	0.047	0.829	
DEV.DEV.QUAD	1	32.101	32.101	0.804	0.373	
DEVIATIONS	5	72.121	14.424	0.361	0.874	
RESIDUAL	84	3354.541	39.935			
TOTAL	112	20526.567	183.273			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEG	1	10.192	10.192	1.796	0.183	
HYBRID.SEG	1	89.752	89.752	15.818	<.001	
STRESS.SEG	1	4.463	4.463	0.787	0.377	
WAA.SEG	7	18.799	2.686	0.473	0.852	
LIN.DEV	1	14.446	14.446	2.546	0.114	
QUAD.DEV	1	0.000	0.000	0.000		
CUB.DEV	1	0.000	0.000	0.000		
DEVIATIONS	4	4.353	1.088	0.192	0.942	
HYBRID.STRESS.SEG	1	25.718	25.718	4.533	0.036	
HYBRID.WAA.SEG	7	28.042	4.006	0.706	0.667	
DEV.LIN.DEV	1	11.490	11.490	2.025	0.158	
DEV.QUAD.DEV	1	5.162	5.162	0.910	0.343	
DEVIATIONS	5	11.390	2.278	0.401	0.847	
STRESS.WAA.SEG	7	5.385	0.769	0.136	0.995	
DEV.LIN.DEV	1	0.618	0.618	0.109	0.742	
DEV.QUAD.DEV	1	1.264	1.264	0.223	0.638	
DEVIATIONS	5	3.502	0.700	0.123	0.987	
HYBRID.STRESS.WAA.SEG	7	9.001	1.286	0.227	0.978	
DEV.DEV.LIN.DEV	1	0.000	0.000	0.000		
DEVIATIONS	6	9.001	1.500	0.264	0.952	
RESIDUAL	96	544.706	5.674			
TOTAL	128	736.057	5.750			
GRAND TOTAL	255	22897.459				
GRAND MEAN	27.94					
***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****						
STRATUM	DF	SE	CV%			
REPS	3	1.527	5.5			
REPS.WHPL	9	1.779	6.4			
REPS.WHPL.SUBPL	84	4.469	16.0			
REPS.WHPL.SUBPL.SUBSUBPL	96	2.382	8.5			

<sup>†</sup>Epsilon factor Error MS WAA = 0.4110

<sup>†</sup>Epsilon factor Error MS Segment = 1.0000

Appendix 28.8 VARIATE: Total non-structural carbohydrate content (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	5.05157	1.68386			
REPS.WHPL STRATUM						
HYBRID	1	1.20175	1.20175	1.355	0.274	
STRESS	1	8.88091	8.88091	10.016	0.011	
HYBRID.STRESS	1	0.04944	0.04944	0.056	0.819	
RESIDUAL	9	7.98044	0.88672			
TOTAL	12	18.11255	1.50938			
REPS.WHPL.SUBPL STRATUM						
WAA	7	95.26538	13.60934	41.319	<.001	p<0.001
LIN	1	42.49100	42.49100	129.007	<.001	p<0.001
QUAD	1	40.40057	40.40057	122.660	<.001	p<0.001
CUB	1	5.83442	5.83442	17.714	<.001	p<0.001
DEVIATIONS	4	6.53938	1.63484	4.964	0.001	0.025>p>0.01
HYBRID.WAA	7	9.78874	1.39839	4.246	<.001	0.005>p>0.001
DEV.LIN	1	4.77665	4.77665	14.502	<.001	p<0.001
DEV.QUAD	1	0.05526	0.05526	0.168	0.683	
DEV.CUB	1	1.51607	1.51607	4.603	0.035	0.05>p>0.025
DEVIATIONS	4	3.44077	0.86019	2.612	0.041	0.1>p>0.05
STRESS.WAA	7	3.02201	0.43172	1.311	0.255	
DEV.LIN	1	2.25671	2.25671	6.852	0.011	0.025>p>0.01
DEV.QUAD	1	0.17269	0.17269	0.524	0.471	
DEV.CUB	1	0.15120	0.15120	0.459	0.500	
DEVIATIONS	4	0.44141	0.11035	0.335	0.854	
HYBRID.STRESS.WAA	7	0.47398	0.06771	0.206	0.983	
DEV.DEV.LIN	1	0.11090	0.11090	0.337	0.563	
DEV.DEV.QUAD	1	0.23578	0.23578	0.716	0.400	
DEVIATIONS	5	0.12729	0.02546	0.077	0.996	
RESIDUAL	84	27.66708	0.32937			
TOTAL	112	136.21718	1.21622			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEG	1	22.21743	22.21743	224.746	<.001	
HYBRID.SEG	1	0.57897	0.57897	5.857	0.017	
STRESS.SEG	1	1.05519	1.05519	10.674	0.002	
WAA.SEG	7	5.80223	0.82889	8.385	<.001	
LIN.DEV	1	4.14832	4.14832	41.963	<.001	
QUAD.DEV	1	0.90567	0.90567	9.162	0.003	
CUB.DEV	1	0.66109	0.66109	6.687	0.011	
DEVIATIONS	4	0.08715	0.02179	0.220	0.926	
HYBRID.STRESS.SEG	1	0.00233	0.00233	0.024	0.878	
HYBRID.WAA.SEG	7	0.71318	0.10188	1.031	0.415	
DEV.LIN.DEV	1	0.06588	0.06588	0.666	0.416	
DEV.QUAD.DEV	1	0.15305	0.15305	1.548	0.216	
DEVIATIONS	5	0.49425	0.09885	1.000	0.422	
STRESS.WAA.SEG	7	0.38294	0.05471	0.553	0.792	
DEV.LIN.DEV	1	0.02531	0.02531	0.256	0.614	
DEV.QUAD.DEV	1	0.00000	0.00000	0.000		
DEVIATIONS	5	0.35764	0.07153	0.724	0.607	
HYBRID.STRESS.WAA.SEG	7	0.39589	0.05656	0.572	0.777	
DEV.DEV.LIN.DEV	1	0.07264	0.07264	0.735	0.393	
DEVIATIONS	6	0.32325	0.05388	0.545	0.773	
RESIDUAL	96	9.49016	0.09886			
TOTAL	128	40.63832	0.31749			
GRAND TOTAL	255	200.01961				
GRAND MEAN		1.708				
***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****						
STRATUM	DF	SE	CV%			
REPS	3	0.1622	9.5			
REPS.WHPL	9	0.2354	13.8			
REPS.WHPL.SUBPL	84	0.4058	23.8			
REPS.WHPL.SUBPL.SUBSUBPL	96	0.3144	18.4			

<sup>†</sup>Epsilon factor Error MS WAA = 0.6103

<sup>†</sup>Epsilon factor Error MS Segment = 1.0000

Appendix 28.9 VARIATE: Residual content (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	58.0320	19.3440			
REPS.WHPL STRATUM						
HYBRID	1	1.7939	1.7939	0.566	0.471	
STRESS	1	27.8313	27.8313	8.788	0.016	
HYBRID.STRESS	1	0.6630	0.6630	0.209	0.658	
RESIDUAL	9	28.5017	3.1669			
TOTAL	12	58.7899	4.8992			
REPS.WHPL.SUBPL STRATUM						
WAA	7	9.7418	1.3917	1.439	0.201	
LIN	1	0.7807	0.7807	0.807	0.371	
QUAD	1	0.8951	0.8951	0.926	0.339	
CUB	1	0.2173	0.2173	0.225	0.637	
DEVIATIONS	4	7.8487	1.9622	2.030	0.098	
HYBRID.WAA	7	10.4394	1.4913	1.543	0.164	
DEV.LIN	1	3.3031	3.3031	3.416	0.068	
DEV.QUAD	1	1.2014	1.2014	1.243	0.268	
DEV.CUB	1	0.0959	0.0959	0.099	0.754	
DEVIATIONS	4	5.8391	1.4598	1.510	0.207	
STRESS.WAA	7	7.9137	1.1305	1.169	0.329	
DEV.LIN	1	3.0412	3.0412	3.146	0.080	
DEV.QUAD	1	2.6430	2.6430	2.734	0.102	
DEV.CUB	1	0.7738	0.7738	0.800	0.374	
DEVIATIONS	4	1.4558	0.3639	0.376	0.825	
HYBRID.STRESS.WAA	7	1.8201	0.2600	0.269	0.964	
DEV.DEV.LIN	1	0.6025	0.6025	0.623	0.432	
DEV.DEV.QUAD	1	0.1201	0.1201	0.124	0.725	
DEVIATIONS	5	1.0975	0.2195	0.227	0.950	
RESIDUAL	84	81.2133	0.9668			
TOTAL	112	111.1283	0.9922			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEG	1	149.7157	149.7157	303.202	<.001	
HYBRID.SEG	1	21.0426	21.0426	42.615	<.001	
STRESS.SEG	1	2.7503	2.7503	5.570	0.020	
WAA.SEG	7	2.8113	0.4016	0.813	0.578	
LIN.DEV	1	2.3648	2.3648	4.789	0.031	
QUAD.DEV	1	0.0062	0.0062	0.013	0.911	
CUB.DEV	1	0.2898	0.2898	0.587	0.446	
DEVIATIONS	4	0.1505	0.0376	0.076	0.989	
HYBRID.STRESS.SEG	1	1.3459	1.3459	2.726	0.102	
HYBRID.WAA.SEG	7	2.0585	0.2941	0.596	0.758	
DEV.LIN.DEV	1	0.6169	0.6169	1.249	0.266	
DEV.QUAD.DEV	1	0.1420	0.1420	0.287	0.593	
DEVIATIONS	5	1.2997	0.2599	0.526	0.756	
STRESS.WAA.SEG	7	0.3829	0.0547	0.111	0.998	
DEV.LIN.DEV	1	0.0122	0.0122	0.025	0.875	
DEV.QUAD.DEV	1	0.0672	0.0672	0.136	0.713	
DEVIATIONS	5	0.3034	0.0607	0.123	0.987	
HYBRID.STRESS.WAA.SEG	7	1.1523	0.1646	0.333	0.937	
DEV.DEV.LIN.DEV	1	0.5944	0.5944	1.204	0.275	
DEVIATIONS	6	0.5579	0.0930	0.188	0.979	
RESIDUAL	96	47.4031	0.4938			
TOTAL	128	228.6627	1.7864			
GRAND TOTAL	255	456.6129				
GRAND MEAN		4.203				
***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****						
STRATUM	DF	SE	CV%			
REPS	3	0.5498	13.1			
REPS.WHPL	9	0.4449	10.6			
REPS.WHPL.SUBPL	84	0.6953	16.5			
REPS.WHPL.SUBPL.SUBSUBPL	96	0.7027	16.7			

<sup>†</sup>Epsilon factor Error MS WAA = 0.4808

<sup>†</sup>Epsilon factor Error MS Segment = 1.0000

Appendix 28.10 VARIATE: Dry mass (g segment<sup>-1</sup>) of stem segments

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	3	91.8876	30.6292			
REPS.WHPL STRATUM						
HYBRID	1	0.0591	0.0591	0.009	0.926	
STRESS	1	68.1553	68.1553	10.410	0.010	
HYBRID.STRESS	1	0.3503	0.3503	0.054	0.822	
RESIDUAL	9	58.9251	6.5472			
TOTAL	12	127.4899	10.6242			
REPS.WHPL.SUBPL STRATUM						
WAA	7	139.2244	19.8892	11.108	<.001	p<0.001
LIN	1	54.7909	54.7909	30.599	<.001	p<0.001
QUAD	1	53.3229	53.3229	29.779	<.001	p<0.001
CUB	1	3.7999	3.7999	2.122	0.149	
DEVIATIONS	4	27.3107	6.8277	3.813	0.007	0.05>p>0.025
HYBRID.WAA	7	18.7860	2.6837	1.499	0.179	
DEV.LIN	1	0.1355	0.1355	0.076	0.784	
DEV.QUAD	1	0.7413	0.7413	0.414	0.522	
DEV.CUB	1	0.8494	0.8494	0.474	0.493	
DEVIATIONS	4	17.0598	4.2649	2.382	0.058	
STRESS.WAA	7	16.7163	2.3880	1.334	0.245	
DEV.LIN	1	10.5373	10.5373	5.885	0.017	0.025>p>0.01
DEV.QUAD	1	4.1669	4.1669	2.327	0.131	
DEV.CUB	1	0.2409	0.2409	0.135	0.715	
DEVIATIONS	4	1.7712	0.4428	0.247	0.911	
HYBRID.STRESS.WAA	7	2.6363	0.3766	0.210	0.982	
DEV.DEV.LIN	1	1.2304	1.2304	0.687	0.409	
DEV.QUAD.DEV	1	0.6924	0.6924	0.387	0.536	
DEVIATIONS	5	0.7135	0.1427	0.080	0.995	
RESIDUAL	84	150.4097	1.7906			
TOTAL	112	327.7726	2.9265			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEG	1	287.2813	287.2813	333.538	<.001	
HYBRID.SEG	1	28.6024	28.6024	33.208	<.001	
STRESS.SEG	1	7.2126	7.2126	8.374	0.005	
WAA.SEG	7	15.9609	2.2801	2.647	0.015	
LIN.DEV	1	12.7774	12.7774	14.835	<.001	
QUAD.DEV	1	1.0623	1.0623	1.233	0.270	
CUB.DEV	1	1.8262	1.8262	2.120	0.149	
DEVIATIONS	4	0.2950	0.0737	0.086	0.987	
HYBRID.STRESS.SEG	1	1.2363	1.2363	1.435	0.234	
HYBRID.WAA.SEG	7	3.2252	0.4607	0.535	0.806	
DEV.LIN.DEV	1	0.2796	0.2796	0.325	0.570	
DEV.QUAD.DEV	1	0.5898	0.5898	0.685	0.410	
DEVIATIONS	5	2.3558	0.4712	0.547	0.740	
STRESS.WAA.SEG	7	1.2819	0.1831	0.213	0.982	
DEV.LIN.DEV	1	0.0727	0.0727	0.084	0.772	
DEV.QUAD.DEV	1	0.0861	0.0861	0.100	0.753	
DEVIATIONS	5	1.1232	0.2246	0.261	0.933	
HYBRID.STRESS.WAA.SEG	7	2.2186	0.3169	0.368	0.919	
DEV.DEV.LIN.DEV	1	1.0826	1.0826	1.257	0.265	
DEVIATIONS	6	1.1359	0.1893	0.220	0.970	
RESIDUAL	96	82.6862	0.8613			
TOTAL	128	429.7053	3.3571			
GRAND TOTAL	255	976.8555				
GRAND MEAN		5.911				
***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****						
STRATUM	DF	SE	CV%			
REPS	3	0.6918	11.7			
REPS.WHPL	9	0.6397	10.8			
REPS.WHPL.SUBPL	84	0.9462	16.0			
REPS.WHPL.SUBPL.SUBSUBPL	96	0.9281	15.7			

<sup>†</sup>Epsilon factor Error MS WAA = 0.4941

<sup>†</sup>Epsilon factor Error MS Segment = 1.0000

Appendix 29 Grain yield (g m<sup>-2</sup>, primary ears only) at harvest maturity :  
 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR
REPS STRATUM	3	21948	7316			
REPS.PLOTS STRATUM						
HYBRID	1	23839	23839	20.933	0.001	
STRESS	1	39564	39564	34.741	<.001	
HYBRID.STRESS	1	443	443	0.389	0.548	
RESIDUAL	9	10249	1139			
TOTAL	12	74095	6175			
GRAND TOTAL	15	96043				
GRAND MEAN		274.1				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	42.77	15.6
REPS.PLOTS	9	33.75	12.3

Appendix 30 Analyses of variance : Yield components and cob production at harvest maturity : 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga

Appendix 30.1 VARIATE: Kernels ear<sup>-1</sup>

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	3	2405	802		
REPS.PLOTS STRATUM					
HYBRID	1	1529	1529	0.785	0.399
STRESS	1	11342	11342	5.826	0.039
HYBRID.STRESS	1	3097	3097	1.591	0.239
RESIDUAL	9	17522	1947		
TOTAL	12	33490	2791		
GRAND TOTAL	15	35896			
GRAND MEAN		299			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	14.2	4.7
REPS.PLOTS	9	44.1	14.8

Appendix 30.2 VARIATE: Kernels row<sup>-1</sup>

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	3	15.032	5.011		
REPS.PLOTS STRATUM					
HYBRID	1	28.891	28.891	3.952	0.078
STRESS	1	54.391	54.391	7.440	0.023
HYBRID.STRESS	1	2.976	2.976	0.407	0.539
RESIDUAL	9	65.796	7.311		
TOTAL	12	152.052	12.671		
GRAND TOTAL	15	167.084			
GRAND MEAN		23.42			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	1.119	4.8
REPS.PLOTS	9	2.704	11.5

Appendix 30.3 VARIATE: Rows ear<sup>-1</sup>

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	3	2.1675	0.7225		
REPS.PLOTS STRATUM					
HYBRID	1	19.8025	19.8025	24.339	<.001
STRESS	1	0.1225	0.1225	0.151	0.707
HYBRID.STRESS	1	1.1025	1.1025	1.355	0.274
RESIDUAL	9	7.3225	0.8136		
TOTAL	12	28.3500	2.3625		
GRAND TOTAL	15	30.5175			
GRAND MEAN		12.79			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	0.425	3.3
REPS.PLOTS	9	0.902	7.1

Appendix 30.4 VARIATE: Mass kernel<sup>-1</sup> (g)

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	3	0.008874	0.002958		
REPS.PLOTS STRATUM					
HYBRID	1	0.017161	0.017161	14.839	0.004
STRESS	1	0.001849	0.001849	1.599	0.238
HYBRID.STRESS	1	0.000144	0.000144	0.125	0.732
RESIDUAL	9	0.010408	0.001156		
TOTAL	12	0.029562	0.002463		
GRAND TOTAL	15	0.038436			
GRAND MEAN		0.2265			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	0.02719	12.0
REPS.PLOTS	9	0.03401	15.0

Appendix 30.5 VARIATE: Cob production (g m<sup>-2</sup>)

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	3	11.293	3.764		
REPS.PLOTS STRATUM					
HYBRID	1	244.923	244.923	38.728	<.001
STRESS	1	18.923	18.923	2.992	0.118
HYBRID.STRESS	1	2.723	2.723	0.430	0.528
RESIDUAL	9	56.918	6.324		
TOTAL	12	323.485	26.957		
GRAND TOTAL	15	334.778			
GRAND MEAN		13.49			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	0.970	7.2
REPS.PLOTS	9	2.515	18.6

Appendix 31 Analyses of variance : agronomic characteristics at harvest maturity : 1986/87 maize single cross hybrid rain-out shelter trial, Ukulinga

Appendix 31.1 VARIATE: Percentage barren plants at harvest maturity

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	3	393.07	131.02		
REPS.PLOTS STRATUM					
HYBRID	1	1406.25	1406.25	33.019	<.001
STRESS	1	0.00	0.00	0.000	
HYBRID.STRESS	1	119.63	119.63	2.809	0.128
RESIDUAL	9	383.30	42.59		
TOTAL	12	1909.18	159.10		
GRAND TOTAL	15	2302.25			
GRAND MEAN	14.5				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	5.72	39.6
REPS.PLOTS	9	6.53	45.2

Appendix 31.2 VARIATE: Percentage runt primary ears at harvest maturity

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	3	795.9	265.3		
REPS.PLOTS STRATUM					
HYBRID	1	167.2	167.2	1.368	0.272
STRESS	1	1432.7	1432.7	11.723	0.008
HYBRID.STRESS	1	0.0	0.0	0.000	0.986
RESIDUAL	9	1099.9	122.2		
TOTAL	12	2699.9	225.0		
GRAND TOTAL	15	3495.9			
GRAND MEAN	34.8				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	3	8.14	23.4
REPS.PLOTS	9	11.06	31.8

Appendix 32 Development of techniques used in the determination of radioactivity associated with non-structural carbohydrates for the 1988/89 maize single cross hybrid <sup>14</sup>C-labelling study

Appendix 32.1 Development of the thin layer chromatography procedure adopted for the determination of radioactivity associated with glucose, fructose and sucrose

#### Preparation of plates

Initially it was intended to determine the radioactivity associated with glucose, fructose and sucrose by separating out the sugars on commercially prepared MN (Macherey, Nagel & Company) thin layer plates. These plates consist of 0,1 mm thick layers of cellulose adsorbent (stationary phase) on aluminium or polyester backed plates. However, the capacity of these plates is only 5-30 µg of each sugar per spot applied. Since many of the plant parts sampled from each labelling occasion did not have high enough <sup>14</sup>C-specific radioactivity, it was decided to opt for self-prepared cellulose layers on glass plates. The advantage of cellulose as an adsorbent over kieselguhr G and silica gel G inorganic adsorbents is the greater separation capacity of cellulose for simple sugars (Lewis and Smith, 1969). However, generally much longer development times are required on cellulose layers than on buffered silica gel G or kieselguhr G. Vomhof and Tucker (1965) prepared plates using 300 MN cellulose at 0,37 mm thick layer on glass plates. Using a solvent of formic acid:methyl ethyl ketone (butanone):tert-butanol:water (15:30:40:15 v/v) they maintained that mixtures containing 100 mg

or more of sucrose, glucose and fructose could be separated by developing the plates twice in the same direction. As MN 300 cellulose powder is not readily available in this country Whatman CC41 cellulose powder was used as an alternative. Whereas MN 300 cellulose powder is native, fibrous cellulose, Whatman CC41 is so-called 'microcrystalline cellulose'. Fibrous cellulose is high quality material prepared in the usual way in the cellulose or cotton industry and then reduced under mild conditions to a fibre grade suitable for TLC. The average degree of polymerisation of the native cellulose MN 300 is of the order of 400-500. The fibre length of MN 300 ranges from 2 to 20  $\mu\text{m}$ . Microcrystalline cellulose is prepared through hydrolysis of extremely pure cellulose, such as regenerated cellulose, cotton linters and cotton of high purity, by 15 min treatment with boiling 2,5 N hydrochloric acid solution. Cellulose crystallites with an average degree of polymerisation from 40 to 200 are obtained, depending on the nature of the starting material and the subsequent processing. As a result of its preparation process 'microcrystalline' cellulose powder is purer than untreated, native, fibrous cellulose powder (Wollenweber, 1969). According to Lewis and Smith (1969) excellent resolutions have been obtained on either cellulose MN 300 or microcrystalline cellulose with solvents previously used for paper chromatography. Additionally visualization on cellulose thin layer chromatograms can be done using reagents suitable for paper chromatography (Lewis and Smith, 1969). As detailed in Section 4.2 the plates eventually used in the experiment were self prepared 200 mm x 200 mm glass plates with a 1,0 mm thick layer of Whatman CC41 cellulose as the stationary phase.

## Solvent

Lewis and Smith (1969) list two solvents commonly used to separate out free sugars on Avirin or microcrystalline cellulose. Unfortunately neither of the solvents were listed as capable of separating out a mixture of glucose, fructose and sucrose. Lacking in a range of alternative solvents, it was decided to test the formic acid:butanone:tert-butanol:water (15:30:40:15) solvent highly recommended by Vomhof and Tucker (1965) which they had used with MN 300 cellulose powder. Once a visualization spray reagent was found which was non-destructive to the cellulose layer, it was found that this solvent provided excellent resolution of a mixture of glucose, fructose and sucrose standard with each sugar spotted on at 50  $\mu\text{g}$  and run twice in the same direction for a total time of approximately 4 h.

## Visualization reagent

Lewis and Smith (1969) provide a list of visualization reagents to detect sugars on the inorganic absorbants silica gel G and kieselguhr G. Unfortunately these reagents utilize sulphuric or phosphoric acid which are destructive to cellulose and cause colour reactions with the cellulose adsorbent making it difficult to specifically visualize the sugar spots. The visualization reagent employed by Vomhof and Tucker (1965) was 2-aminodiphenyl-oxalic acid dissolved in 85 % ethanol. However, the 2-aminodiphenyl is no longer commercially available because of its suspected carcinogenic properties. It was decided to seek an

alternative. Some 20 different visualization reagents were tested with each proving to have shortcomings in either being unable to provide unique colour reactions with glucose, fructose and sucrose or being too acidic and reacting with the cellulose adsorbent. Fortunately a non-destructive visualization reagent was found in a manual on paper chromatography written by Block, Durrum and Zweig (1955). The reagent, aniline oxalate, is prepared by adding to 100 ml of 0,1 N oxalic acid, 0,9 ml of aniline. The chromatogram is sprayed with the reagent and treated at 100-105°C for 10-20 min. The reducing sugars appear as brown spots. When the same chromatogram is sprayed with 1 % KMNO<sub>4</sub> solution containing 3 % H<sub>2</sub>SO<sub>4</sub>, and heated to 100°C for a few minutes fructose and sucrose appear as grey black spots. This technique distinguishes between ketoses and aldoses.

#### Recovery efficiency of the chromatographic procedure

Recovery from the plates using 3 000 dpm of <sup>14</sup>C-labelled sucrose was determined to be 99,9 % (Table 4).

Table 4 Recovery of radioactivity from 3 000 dpm <sup>14</sup>C-labelled sucrose spots developed on thin layer chromatograms relative to external 3 000 dpm <sup>14</sup>C-labelled sucrose standards

Vial	External sucrose standard	Developed sucrose spots
1	3 006,4	2 994,2
2	3 011,3	3 012,6
3	2 997,0	3 010,6
4	3 013,7	3 002,8
5	3 005,1	2 992,5
Mean	3 006,7±2,9	3 002,5±4,1

Recovery percentage = 99,9 %

## REFERENCES

- Block, R.J., Durrum, E.L. and Zweig, G., 1955. A manual of paper chromatography and paper electrophoresis. Academic Press Inc., Publishers, New York. Pp. 127-156.
- Lewis, B.A. and Smith, F., 1969. Sugars and derivatives. In Stahl, E. (ed.). Thin-layer chromatography. A laboratory manual. Sixth printing of the second edition, 1990. Springer-Verlag, Berlin. Pp. 807-837.
- Vomhof, D.W. and Tucker, T.C., 1965. The separation of simple sugars by cellulose thin-layer chromatography. J. Chromatoqr. 17, 300-306.
- Wollenweber, P., 1969. Organic absorbents. In Stahl, E. (ed.). Thin-layer chromatography. A laboratory manual. Sixth printing of the second edition, 1990. Springer-Verlag, Berlin. Pp. 32-41.

Appendix 32.2 A short research note on the problem of chemiluminescence encountered while determining the radioactivity associated with total sugars and starch using ion-exchange column chromatography

Chemiluminescence results from chemical reactions between the additives or agents and the components of the liquid scintillation cocktail (LSC). Chemiluminescence arises from the conversion of chemical energy into molecular electronic excitation energy which undergoes radiative decay with the emission of light. The conditions necessary for the emission of visible light are that the chemical reaction supplies an energy of at least 168 to 293 kJ mole<sup>-1</sup> and that a molecule capable of fluorescing is present. Although chemiluminescence gives rise to one photon events, the vast number of events generated in a chemiluminescent reaction allows the light pulses to trigger and pass the coincidence gate in the spectrometer within its resolving time (approximately  $20 \times 10^{-9}$  s) and thus be detected. Three agents which commonly cause chemiluminescence with xylene and toluene LSC's are quaternary ammonium hydroxide (commonly used in tissue solubilizers), KOH and H<sub>2</sub>O<sub>2</sub> (Long, 1976; Peng, 1977).

In the determination of radioactivity associated with total sugars and starch (Section 4.3.8), both the total sugars and starch solutions were often coloured resulting in the quenching of radioactivity. A common procedure used to decolorize solutions is to bleach them with between 30 to 100  $\mu$ l of 30 % H<sub>2</sub>O<sub>2</sub> and then to heat the solution to ca. 40°C to destroy excess

peroxide residues before adding the LSC. This procedure was followed on some of the samples. When the samples were placed in the scintillation counter to be counted, the read-out was given as a series of asterisks for each sample denoting out-of-range counts. The excessive counts recorded by the scintillation counter indicated that chemiluminescence had still occurred despite heat treatment to destroy excess peroxide. It was discovered that when  $H_2O_2$  on its own is boiled down to dryness in a beaker, an acrid smelling white residue remains in the beaker. Upon investigating the modern method of manufacturing  $H_2O_2$  it was found that an auto-oxidation process using substituted anthraquinones is utilized (Brown, 1974). 2-Butyl anthraquinone, for example, is reduced by hydrogen, in the presence of a palladium catalyst, to the corresponding anthraquinol. Blowing air through the solution of the anthraquinol produces  $H_2O_2$  and liberates the 2-Butyl anthraquinone for re-use (Brown, 1974). Quinones are also agents known to cause chemiluminescence in the presence of LSC's (Long, 1976). It is likely that the chemiluminescence which occurred after heat treatment to remove excess peroxide after bleaching with  $H_2O_2$ , was due to quinone contaminants from the manufacturing process. The decay of chemiluminescence is dependent on the rate of the chemical reaction and the lifetime of the fluorescing molecular species; in general it may initially be fast and then slow down and persist for many hours or even days to yield a count rate appreciably above the background (Peng, 1977). It is often suggested that chemiluminescence of samples may decay completely allowing normal counting to be achieved if affected samples are stored in the dark. The decay is also temperature dependent and

will proceed faster if samples are, in addition, stored at elevated temperatures (Peng, 1977). The efficacy of this suggestion was tested on standards. Into 10 scintillation vials was placed 2 ml of 80 % ethanol, 3000 dpm of radioactive sucrose and into 5 of these vials was pipetted 100  $\mu$ l of H<sub>2</sub>O<sub>2</sub>. The H<sub>2</sub>O<sub>2</sub> treated vials were placed in an incubator in the dark at 40°C overnight. The LSC Insta-Gel was added at 10 ml and all 10 vials were immediately placed into the scintillation counter. Extremely high counts were recorded for samples treated with H<sub>2</sub>O<sub>2</sub> compared to untreated samples (Table 5). All 10 vials were then

Table 5 The chemiluminescent effect of H<sub>2</sub>O<sub>2</sub> on the radioactivity counts (dpm) of spiked standard samples

Solution	Vial	Immediately	24 h	48 h	72 h	144 h
4 ml 80% EtOH + 3000 dpm sucrose + 100 $\mu$ l H <sub>2</sub> O <sub>2</sub> + 10 ml Insta-Gel	1	10 001,0	8 906,3	5 045,4	2 572,6	2 104,6
	2	11 497,5	9 437,1	6 117,3	2 809,3	2 375,2
	3	13 420,9	10 545,8	6 322,0	2 776,1	2 444,3
	4	10 755,3	9 108,4	5 421,6	2 659,9	2 251,8
	5	12 723,8	10 871,3	5 972,8	2 526,7	2 038,8
4 ml 80% EtOH + 3000 dpm sucrose + 10 ml Insta-Gel	6	2 987,4	3 012,9	3 031,3	3 066,4	3 008,1
	7	3 024,6	3 036,4	3 027,4	2 957,1	2 902,3
	8	3 068,2	3 005,0	2 981,9	3 013,3	3 020,9
	9	3 103,7	3 067,2	3 055,7	3 088,0	3 037,5
	10	3 046,1	2 994,2	3 019,5	2 093,7	2 895,0

placed in the incubator at 30°C for 24 h and then recounted. The counts recorded for samples treated with H<sub>2</sub>O<sub>2</sub> had declined but were still much higher than that for the untreated standards (Table 5). All 10 vials were again placed in the incubator at

30°C for a further 24 h and then recounted. The counts recorded for samples treated with H<sub>2</sub>O<sub>2</sub> had declined further but were still higher than that for the untreated standards (Table 5). All 10 vials were placed in the incubator at 30°C for a further 24 h and then recounted. The counts recorded for samples treated with H<sub>2</sub>O<sub>2</sub> had declined but were now lower than that recorded for the untreated standards (Table 5). The samples were left in a dark cupboard for a further 72 h and then recounted. Samples treated with H<sub>2</sub>O<sub>2</sub> recorded counts even lower than at 72 h earlier (Table 5). In addition, counts obtained for the five standards treated with H<sub>2</sub>O<sub>2</sub> were quite different to one another on each counting session. After consulting with Professor Verbeeck, Head of analytical chemistry, Department of Chemistry, University of Natal, it was decided that the residual quinone compounds were causing the chemiluminescence but in addition were degrading the Insta-Gel cocktail resulting in a lowering of counting efficiency with time. As the H<sub>2</sub>O<sub>2</sub> used was analytical reagent quality and there was no superior grade readily available in this country it was decided to use chlorine water as an alternative oxidizing agent to bleach coloured samples. The chlorine water was prepared by simply bubbling pure chlorine gas through demineralised water. The chlorine water is not as potent a bleaching agent as H<sub>2</sub>O<sub>2</sub> and consequently as much as 2 ml per sample is required to effectively decolorize samples. The great advantage of chlorine water is that excess chlorine gas is driven off at room temperature with no residues remaining which cause chemiluminescence. The driving off of excess chlorine gas may be accelerated if so desired by heating samples to 40°C. A word of caution, however, is that oxidising agents and heating samples

to drive off ethanol and excess chlorine may result in a loss of  $^{14}\text{C}$  from samples in the form of  $^{14}\text{CO}_2$ .

Peng (1977) has the last word on chemiluminescence 'sample preparation by combustion may be practised if all other means of eliminating chemiluminescence fail'.

#### REFERENCES

- Brown, G.I., 1974. Introduction to inorganic chemistry. Longman Group, Ltd., London. P. 259.
- Long, E.C., 1976. Selective aspects of sample handling in liquid scintillation counting. Beckman Biomedical Technical Report, 1042-NUC-76-55 T.
- Peng, C.T., 1977. Sample preparation in liquid scintillation counting. Review 17, The Radiochemical centre, Amersham, England. Pp. 26-28.

Appendix 32.3 Development of the ion exchange column procedure adopted for the determination of radioactivity associated with total sugars

#### Preparation of ion exchange columns

Dickson (1979) recommends the preparation of a tandem column, with the cation exchange column containing Amberlite<sup>(R)</sup> CG-120 (Rohm and Haas, USA) over the anion exchange column containing Amberlite CG-400. The cation exchange column would remove the amino acids from solution whilst the anion exchange column would remove the organic acids from solution leaving the total sugars to pass through the column. Amberlite CG-120 (200-400 mesh) and Amberlite CG-400 (200-400 mesh) as recommended by Dickson (1979) are not readily available in this country. Amberlite IR-120 (mesh size (BSS) 14-52) was tried as an alternative to Amberlite CG-120, and Amberlite IRA-400 (mesh size (BSS) 14-52) was tried as an alternative to Amberlite CG-400. Pyrex glass tubing (diameter 10 mm) with one end shaped to a narrow tip was used as column supports. The tip of each glass column was plugged with glass-fibre and the anion exchange beads (IRA-400) in 80 % ethanol were poured gently into the glass columns and packed to a volume of 5 ml. The cation exchange beads (IR-120) in 80 % ethanol were then poured directly on top of the packed anion exchange beads to a volume of 5 ml making a combined total of 10 ml of cation and anion exchange beads. To maintain a constant head of ethanol above the 10 ml of beads, surgical rubber tubing was connected to the tip of the glass column and looped up the outside of the glass column with the open end of the surgical

tubing approximately 15 mm above the top of the cation exchange beads. To facilitate collection of the sample solutions a small curved section of glass tubing was inserted into the open end of the surgical tubing thus directing the drops of solution into a beaker placed underneath. The column was washed to neutrality with vast quantities of 80 % ethanol. Neutrality of the columns was tested by comparing the electrical conductivity of distilled, demineralized and decarbonized water passed through the column with a standard amount of the same pure water.

Efficacy of the ion exchange column in removing amino acids and organic acids

In order to test the efficacy of the cation and anion exchange column as set up, 10 g each of aspartic acid, glutamic acid and leucine each in 20 ml of 80 % ethanol were separately poured through a test column and eluted with 80 ml of 80 % ethanol. Each solution collected was tested for the presence of amino acids using ninhydrin. If the amino acids were not effectively removed from solution by the cation exchange column then the ninhydrin would have formed a characteristic blue compound with the amino acids used. This did not occur, which indicated that the cation exchange beads had effectively removed the amino acids from solution. The test of 10 g of each amino acid was an extreme one as each solution passed through the columns would be an extraction from 200 mg of milled sample containing only a few milligrams of free amino acids. Since ascorbic acid is a representative organic acid and it reacts with ninhydrin (Krebs, Heusser and Wimmer, 1969), it was used to test the efficacy of

the anion exchange beads. Absorbic acid at 10 g in 20 ml of 80 % ethanol was poured onto the column and eluted with 80 ml of 80 % ethanol. The ninhydrin test proved negative.

#### Recovery efficiency of the ion exchange columns

Recovery efficiency of radioactivity associated with sugars in unknown samples eluted through each column was monitored by eluting a standard solution containing 3 000 dpm of radioactive sucrose (Amersham, UK) through a column followed separately by a batch of five unknown samples. If the recovery of the sucrose standard radioactivity was less than 98 %, the five unknown samples would be re-eluted through a column. Careful technique is necessary to establish a recovery of 98 % or higher.

#### REFERENCES

- Dickson, R.E., 1979. Analytical procedures for the sequential extraction of <sup>14</sup>C-labeled constituents from leaves, bark and wood of cottonwood plants. Physiol. Plant. 45, 480-488.
- Krebs, K.G., Heusser, D. and Wimmer, H., 1969. Spray reagents. In Stahl, E. (ed.). Thin layer chromatography. A laboratory manual. Sixth printing of the second edition, 1990. Spring-Verlag, Berlin. Pp. 854-909.

Appendix 33 Analysis of variance : VARIATE: Leaf water potential (kPa) of the maize hybrid B254W x M162W subjected to water stress and lack of water stress during grain fill : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	729236	364618					
REPS.WHPL STRATUM								
STRESS	1	3365007	3365007	26.632	0.036			
RESIDUAL	2	252706	126353					
TOTAL	3	3617714	1205905					
REPS.WHPL.SUBPL STRATUM								
WAA	8	3577017	447127	37.067	<.001	p<0.001		
LIN	1	3478051	3478051	288.330	<.001	p<0.001		
QUAD	1	6497	6497	0.539	0.468			
CUB	1	13082	13082	1.084	0.306			
DEVIATIONS	5	79388	15878	1.316	0.282			
STRESS.WAA	8	273059	34132	2.830	0.017	p>0.05		
DEV.LIN	1	185641	185641	15.390	<.001	0.005	p>0.001	
DEV.QUAD	1	8709	8709	0.722	0.402			
DEV.CUB	1	3601	3601	0.299	0.589			
DEVIATIONS	5	75109	15022	1.245	0.311			
RESIDUAL	32	386007	12063					
TOTAL	48	4236083	88252					
GRAND TOTAL	53	8583033						
GRAND MEAN		871						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	142.3	16.3
REPS.WHPL	2	118.5	13.6
REPS.WHPL.SUBPL	32	109.8	12.6

<sup>†</sup>Epsilon factor Error MS WAA = 0.4862

Appendix 34 Analysis of variance : VARIATE: Leaf area (m<sup>2</sup> plant<sup>-1</sup>) of the maize hybrid B254W x M162W subjected to water stress and lack of water stress during grain fill : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	0.085964	0.042982			
REPS.PLOT STRATUM						
STRESS	1	0.031282	0.031282	5.738	0.028	
WAA	4	0.977027	0.244257	44.805	<.001	p<0.001
LIN	1	0.841438	0.841438	154.349	<.001	p<0.001
QUAD	1	0.027886	0.027886	5.115	0.036	0.10>p>0.05
CUB	1	0.047143	0.047143	8.648	0.009	0.025>p>0.01
DEVIATIONS	1	0.060560	0.060560	11.109	0.004	0.025>p>0.01
STRESS.WAA	4	0.007169	0.001792	0.329	0.855	
DEV.LIN	1	0.003119	0.003119	0.572	0.459	
DEV.QUAD	1	0.003965	0.003965	0.727	0.405	
DEV.CUB	1	0.000067	0.000067	0.012	0.913	
DEVIATIONS	1	0.000017	0.000017	0.003	0.956	
RESIDUAL	18	0.098128	0.005452			
TOTAL	27	1.113605	0.041245			
GRAND TOTAL	29	1.199569				
GRAND MEAN		0.467				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.0656	14.0
REPS.PLOT	18	0.0738	15.8

<sup>†</sup>Epsilon factor Error MS WAA = 0.4638

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 35 Analyses of variance : Specific radioactivity of segments from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 35.1 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of segments from plants labelled at A

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	4.856E 10	2.428E 10				
REPS.WHPL STRATUM							
STRESS	1	1.123E 9	1.123E 9	0.262	0.615		
WAA	4	8.495E 11	2.124E 11	49.528	<.001		p<0.001
LIN	1	6.511E 11	6.511E 11	151.842	<.001		p<0.001
QUAD	1	1.882E 11	1.882E 11	43.899	<.001		p<0.001
CUB	1	8.882E 9	8.882E 9	2.071	0.167		
DEVIATIONS	1	1.291E 9	1.291E 9	0.301	0.590		
STRESS.WAA	4	1.412E 10	3.531E 9	0.823	0.527		
DEV.LIN	1	3.291E 9	3.291E 9	0.768	0.393		
DEV.QUAD	1	7.380E 9	7.380E 9	1.721	0.206		
DEV.CUB	1	1.386E 9	1.386E 9	0.323	0.577		
DEVIATIONS	1	2.065E 9	2.065E 9	0.482	0.497		
RESIDUAL	18	7.719E 10	4.288E 9				
TOTAL	27	9.420E 11	3.489E 10				
REPS.WHPL.SUBPL STRATUM							
SEGMENT	13	1.741E 12	1.340E 11	99.896	<.001		p<0.001
STRESS.SEGMENT	13	4.723E 10	3.633E 9	2.709	0.001		0.1>p>0.05
WAA.SEGMENT	52	9.763E 11	1.877E 10	14.000	<.001		p<0.001
LIN.DEV	13	5.638E 11	4.337E 10	32.343	<.001		p<0.001
QUAD.DEV	13	2.900E 11	2.231E 10	16.637	<.001		p<0.001
CUB.DEV	13	8.456E 10	6.504E 9	4.850	<.001		0.025>p>0.01
DEVIATIONS	13	3.785E 10	2.912E 9	2.171	0.011		p>0.1
STRESS.WAA.SEGMENT	52	5.872E 10	1.129E 9	0.842	0.769		
DEV.LIN.DEV	13	2.036E 10	1.566E 9	1.168	0.303		
DEV.QUAD.DEV	13	2.675E 10	2.058E 9	1.535	0.105		
DEVIATIONS	26	1.161E 10	4.465E 8	0.333	0.999		
RESIDUAL	260	3.487E 11	1.341E 9				
TOTAL	390	3.172E 12	8.134E 9				
GRAND TOTAL	419	4.163E 12					
GRAND MEAN	101165						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	13168.8	13.0
REPS.WHPL	18	17501.3	17.3
REPS.WHPL.SUBPL	260	36619.7	36.2

<sup>†</sup>Epsilon factor Error MS WAA = 0.6706

<sup>†</sup>Epsilon factor Error MS Segment = 0.1716

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 35.2 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of segments from plants  
labelled at 2 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	4.191E 9	2.096E 9			
REPS.WHPL STRATUM						
STRESS	1	4.839E 8	4.839E 8	0.654	0.432	
WAA	3	1.102E 11	3.674E 10	49.624	<.001	p<0.001
LIN	1	8.607E 10	8.607E 10	116.263	<.001	p<0.001
QUAD	1	2.307E 10	2.307E 10	31.162	<.001	p<0.001
CUB	1	1.070E 9	1.070E 9	1.446	0.249	
STRESS.WAA	3	1.348E 9	4.493E 8	0.607	0.621	
DEV.LIN	1	7.086E 8	7.086E 8	0.957	0.345	
DEV.QUAD	1	3.313E 8	3.313E 8	0.448	0.514	
DEV.CUB	1	3.080E 8	3.080E 8	0.416	0.529	
RESIDUAL	14	1.036E 10	7.403E 8			
TOTAL	21	1.224E 11	5.829E 9			
REPS.WHPL.SUBPL STRATUM						
SEGMENT	13	4.026E 11	3.097E 10	290.817	<.001	p<0.001
STRESS.SEGMENT	13	6.813E 9	5.241E 8	4.922	<.001	0.025>p>0.01
WAA.SEGMENT	39	9.066E 10	2.325E 9	21.832	<.001	p<0.001
LIN.DEV	13	6.938E 10	5.337E 9	50.121	<.001	p<0.001
QUAD.DEV	13	1.821E 10	1.401E 9	13.153	<.001	p<0.001
CUB.DEV	13	3.074E 9	2.364E 8	2.221	0.010	p>0.1
STRESS.WAA.SEGMENT	39	4.929E 9	1.264E 8	1.187	0.223	
DEV.LIN.DEV	13	2.392E 9	1.840E 8	1.728	0.057	
DEV.QUAD.DEV	13	1.732E 9	1.333E 8	1.252	0.245	
DEVIATIONS	13	8.043E 8	6.187E 7	0.581	0.868	
RESIDUAL	208	2.215E 10	1.065E 8			
TOTAL	312	5.271E 11	1.689E 9			
GRAND TOTAL	335	6.537E 11				
GRAND MEAN		31325				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	4325.5	13.8
REPS.WHPL	14	7271.8	23.2
REPS.WHPL.SUBPL	208	10318.9	32.9

<sup>†</sup>Epsilon factor Error MS WAA = 0.6214

<sup>†</sup>Epsilon factor Error MS Segment = 0.1860

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 35.3 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of segments from plants  
labelled at 4WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	1.605E 9	8.024E 8				
REPS.WHPL STRATUM							
STRESS	1	1.616E 9	1.616E 9	12.038	0.006		
WAA	2	1.055E 10	5.273E 9	39.282	<.001	p<0.001	
LIN	1	7.508E 9	7.508E 9	55.928	<.001	p<0.001	
QUAD	1	3.039E 9	3.039E 9	22.637	<.001	p<0.001	
STRESS.WAA	2	5.583E 7	2.792E 7	0.208	0.816		
DEV.LIN	1	2.215E 7	2.215E 7	0.165	0.693		
DEV.QUAD	1	3.368E 7	3.368E 7	0.251	0.627		
RESIDUAL	10	1.342E 9	1.342E 8				
TOTAL	15	1.356E 10	9.040E 8				
REPS.WHPL.SUBPL STRATUM							
SEGMENT	13	4.126E 10	3.174E 9	92.060	<.001	p<0.001	
STRESS.SEGMENT	13	6.941E 8	5.339E 7	1.549	0.106		
WAA.SEGMENT	26	9.805E 9	3.771E 8	10.938	<.001	p<0.001	
LIN.DEV	13	7.374E 9	5.673E 8	16.453	<.001	p<0.001	
QUAD.DEV	13	2.431E 9	1.870E 8	5.423	<.001	0.01>p>0.005	
STRESS.WAA.SEGMENT	26	7.126E 8	2.741E 7	0.795	0.749		
DEV.LIN.DEV	13	2.642E 8	2.032E 7	0.589	0.860		
DEV.QUAD.DEV	13	4.485E 8	3.450E 7	1.001	0.453		
RESIDUAL	156	5.378E 9	3.448E 7				
TOTAL	234	5.785E 10	2.472E 8				
GRAND TOTAL	251	7.302E 10					
GRAND MEAN		19280					

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	3090.6	16.0
REPS.WHPL	10	3096.5	16.1
REPS.WHPL.SUBPL	156	5871.7	30.5

<sup>†</sup>Epsilon factor Error MS WAA = 0.9304

<sup>†</sup>Epsilon factor Error MS Segment = 0.2037

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 35.4 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of segments from plants  
labelled at 6 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	1.094E 8	5.469E 7			
REPS.WHPL STRATUM						
STRESS	1	5.464E 7	5.464E 7	1.824	0.309	
RESIDUAL	2	5.990E 7	2.995E 7			
TOTAL	3	1.145E 8	3.818E 7			
REPS.WHPL.SUBPL STRATUM						
WAA	1	8.939E 8	8.939E 8	45.473	0.003	
STRESS.WAA	1	2.581E 7	2.581E 7	1.313	0.316	
RESIDUAL	4	7.863E 7	1.966E 7			
TOTAL	6	9.984E 8	1.664E 8			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEGMENT	13	3.377E 9	2.597E 8	109.891	<.001	p<0.001
STRESS.SEGMENT	13	4.039E 7	3.107E 6	1.315	0.216	
WAA.SEGMENT	13	6.447E 8	4.959E 7	20.981	<.001	p<0.001
STRESS.WAA.SEGMENT	13	1.495E 7	1.150E 6	0.486	0.928	
RESIDUAL	104	2.458E 8	2.364E 6			
TOTAL	156	4.322E 9	2.771E 7			
GRAND TOTAL	167	5.545E 9				
GRAND MEAN		7411				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	988.3	13.3
REPS.WHPL	2	1034.2	14.0
REPS.WHPL.SUBPL	4	1185.0	16.0
REPS.WHPL.SUBPL.SUBSUBPL	104	1537.4	20.7

<sup>†</sup>Epsilon factor Error MS WAA = 1.0000

<sup>†</sup>Epsilon factor Error MS Segment = 0.1184

Appendix 36 Analyses of variance : Total radioactivity of segments from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 36.1 VARIATE: Total radioactivity of segments (dpm segment<sup>-1</sup>) from plants labelled at A

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	8.391E 12	4.196E 12			
REPS.WHPL STRATUM						
STRESS	1	8.295E 11	8.295E 11	3.292	0.211	
RESIDUAL	2	5.039E 11	2.520E 11			
TOTAL	3	1.333E 12	4.445E 11			
REPS.WHPL.SUBPL STRATUM						
WAA	4	8.136E 12	2.034E 12	10.892	<.001	p<0.005
LIN	1	6.027E 12	6.027E 12	32.277	<.001	p<0.001
QUAD	1	1.743E 11	1.743E 11	0.933	0.348	
CUB	1	4.364E 11	4.364E 11	2.337	0.146	
DEVIATIONS	1	1.498E 12	1.498E 12	8.023	0.012	0.025>p>0.01
STRESS.WAA	4	9.464E 11	2.366E 11	1.267	0.324	
DEV.LIN	1	1.563E 10	1.563E 10	0.084	0.776	
DEV.QUAD	1	4.756E 11	4.756E 11	2.547	0.130	
DEV.CUB	1	3.072E 10	3.072E 10	0.165	0.690	
DEVIATIONS	1	4.244E 11	4.244E 11	2.273	0.151	
RESIDUAL	16	2.988E 12	1.867E 11			
TOTAL	24	1.207E 13	5.029E 11			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEGMENT	13	3.047E 14	2.344E 13	111.015	<.001	p<0.001
STRESS.SEGMENT	13	3.094E 12	2.380E 11	1.127	0.336	
WAA.SEGMENT	52	8.617E 13	1.657E 12	7.849	<.001	p<0.001
LIN.DEV	13	6.189E 13	4.761E 12	22.551	<.001	p<0.001
QUAD.DEV	13	7.556E 12	5.813E 11	2.753	0.001	0.1>p>0.05
CUB.DEV	13	1.110E 13	8.536E 11	4.043	<.001	0.025>p>0.01
DEVIATIONS	13	5.627E 12	4.329E 11	2.050	0.018	p>0.1
STRESS.WAA.SEGMENT	52	5.437E 12	1.046E 11	0.495	0.998	
DEV.LIN.DEV	13	1.492E 12	1.148E 11	0.544	0.896	
DEV.QUAD.DEV	13	2.312E 12	1.779E 11	0.843	0.615	
DEVIATIONS	26	1.632E 12	6.276E 10	0.297	1.000	
RESIDUAL	260	5.489E 13	2.111E 11			
TOTAL	390	4.543E 14	1.165E 12			
GRAND TOTAL	419	4.761E 14				
GRAND MEAN		1065140				
***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****						
STRATUM	DF	SE	CV%			
REPS	2	173116.3	16.3			
REPS.WHPL	2	59994.7	5.6			
REPS.WHPL.SUBPL	16	115493.5	10.8			
REPS.WHPL.SUBPL.SUBSUBPL	260	459477.3	43.1			

<sup>†</sup>Epsilon factor Error MS WAA = 0.7401  
<sup>†</sup>Epsilon factor Error MS Segment = 0.1764

Appendix 36.2 VARIATE: Total radioactivity of segments (dpm segment<sup>-1</sup>) from plants labelled at 2 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	1.307E 12	6.537E 11			
REPS.WHPL STRATUM						
STRESS	1	6.108E 11	6.108E 11	1.809	0.200	
WAA	3	1.150E 12	3.833E 11	1.135	0.369	
LIN	1	6.420E 11	6.420E 11	1.901	0.190	
QUAD	1	9.328E 10	9.328E 10	0.276	0.607	
CUB	1	4.145E 11	4.145E 11	1.227	0.287	
STRESS.WAA	3	8.958E 11	2.986E 11	0.884	0.473	
DEV.LIN	1	0.000E 0	0.000E 0	0.000		
DEV.QUAD	1	7.326E 11	7.326E 11	2.169	0.163	
DEV.CUB	1	1.498E 11	1.498E 11	0.444	0.516	
RESIDUAL	14	4.728E 12	3.377E 11			
TOTAL	21	7.385E 12	3.516E 11			
REPS.WHPL.SUBPL STRATUM						
SEGMENT	13	2.571E 15	1.977E 14	750.757	<.001	p<0.001
STRESS.SEGMENT	13	8.472E 12	6.517E 11	2.474	0.004	p>0.1
WAA.SEGMENT	39	8.333E 13	2.137E 12	8.113	<.001	p<0.005
LIN.DEV	13	3.455E 13	2.658E 12	10.090	<.001	p<0.005
QUAD.DEV	13	3.594E 13	2.765E 12	10.496	<.001	p<0.005
CUB.DEV	13	1.284E 13	9.880E 11	3.751	<.001	p>0.1
STRESS.WAA.SEGMENT	39	1.082E 13	2.773E 11	1.053	0.395	
DEV.LIN.DEV	13	2.760E 12	2.123E 11	0.806	0.653	
DEV.QUAD.DEV	13	5.795E 12	4.458E 11	1.693	0.064	
DEVIATIONS	13	2.261E 12	1.739E 11	0.660	0.800	
RESIDUAL	208	5.478E 13	2.634E 11			
TOTAL	312	2.728E 15	8.744E 12			
GRAND TOTAL	335	2.737E 15				
GRAND MEAN		1013388				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	76399.8	7.5
REPS.WHPL	14	155317.2	15.3
REPS.WHPL.SUBPL	208	513210.4	50.6

<sup>†</sup>Epsilon factor Error MS WAA = 0.6644

<sup>†</sup>Epsilon factor Error MS Segment = 0.0883

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 36.3 VARIATE: Total radioactivity of segments (dpm segment<sup>-1</sup>) from plants labelled at 4 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	2.010E 12	1.005E 12			
REPS.WHPL STRATUM						
STRESS	1	1.383E 12	1.383E 12	11.559	0.007	
WAA	2	3.330E 11	1.665E 11	1.392	0.293	
LIN	1	0.000E 0	0.000E 0	0.000		
QUAD	1	3.328E 11	3.328E 11	2.782	0.126	
STRESS.WAA	2	1.580E 11	7.901E 10	0.660	0.538	
DEV.LIN	1	1.246E 11	1.246E 11	1.041	0.332	
DEV.QUAD	1	3.345E 10	3.345E 10	0.280	0.608	
RESIDUAL	10	1.196E 12	1.196E 11			
TOTAL	15	3.070E 12	2.047E 11			
REPS.WHPL.SUBPL STRATUM						
SEGMENT	13	4.030E 14	3.100E 13	177.275	<.001	p<0.001
STRESS.SEGMENT	13	6.988E 12	5.376E 11	3.074	<.001	p>0.1
WAA.SEGMENT	26	1.304E 13	5.016E 11	2.869	<.001	0.1>p>0.05
LIN.DEV	13	1.230E 13	9.463E 11	5.412	<.001	0.05>p>0.025
QUAD.DEV	13	7.392E 11	5.686E 10	0.325	0.987	
STRESS.WAA.SEGMENT	26	3.339E 12	1.284E 11	0.734	0.820	
DEV.LIN.DEV	13	2.671E 12	2.055E 11	1.175	0.302	
DEV.QUAD.DEV	13	6.681E 11	5.139E 10	0.294	0.992	
RESIDUAL	156	2.728E 13	1.749E 11			
TOTAL	234	4.536E 14	1.938E 12			
GRAND TOTAL	251	4.587E 14				
GRAND MEAN		521036				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	109390.6	21.0
REPS.WHPL	10	92435.7	17.7
REPS.WHPL.SUBPL	156	418153.1	80.3

<sup>†</sup>Epsilon factor Error MS WAA = 0.6270

<sup>†</sup>Epsilon factor Error MS Segment = 0.0806

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 36.4 VARIATE: Total radioactivity of segments (dpm segment<sup>-1</sup>) from plants labelled at 6 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	4.308E 10	2.154E 10			
REPS.WHPL STRATUM						
STRESS	1	5.053E 10	5.053E 10	3.066	0.222	
RESIDUAL	2	3.297E 10	1.648E 10			
TOTAL	3	8.350E 10	2.783E 10			
REPS.WHPL.SUBPL STRATUM						
WAA	1	5.168E 10	5.168E 10	5.409	0.081	
STRESS.WAA	1	7.841E 9	7.841E 9	0.821	0.416	
RESIDUAL	4	3.822E 10	9.554E 9			
TOTAL	6	9.773E 10	1.629E 10			
REPS.WHPL.SUBPL.SUBSUBPL STRATUM						
SEGMENT	13	1.346E 13	1.035E 12	363.114	<.001	p<0.001
STRESS.SEGMENT	13	1.095E 11	8.419E 9	2.954	0.001	p>0.1
WAA.SEGMENT	13	3.460E 11	2.661E 10	9.336	<.001	0.025>p>0.01
STRESS.WAA.SEGMENT	13	1.808E 10	1.391E 9	0.488	0.927	
RESIDUAL	104	2.964E 11	2.850E 9			
TOTAL	156	1.423E 13	9.119E 10			
GRAND TOTAL	167	1.445E 13				
GRAND MEAN		154020				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	19613.3	12.7
REPS.WHPL	2	24262.4	15.8
REPS.WHPL.SUBPL	4	26123.9	17.0
REPS.WHPL.SUBPL.SUBSUBPL	104	53389.8	34.7

<sup>†</sup>Epsilon factor Error MS WAA = 1.0000

<sup>†</sup>Epsilon factor Error MS Segment = 0.0868

Appendix 37 Analyses of variance : VARIATE: Specific radioactivity of the whole stem from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 37.1 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole stem of plants labelled at A

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	7.424E 9	3.712E 9			
REPS.WHPL STRATUM						
STRESS	1	1.154E 8	1.154E 8	0.076	0.809	
RESIDUAL	2	3.041E 9	1.521E 9			
TOTAL	3	3.157E 9	1.052E 9			
REPS.WHPL.SUBPL STRATUM						
WAA	4	2.606E 10	6.515E 9	9.766	<.001	0.01>p>0.005
LIN	1	2.029E 10	2.029E 10	30.408	<.001	p<0.001
QUAD	1	3.913E 8	3.913E 8	0.587	0.455	
CUB	1	2.173E 9	2.173E 9	3.258	0.090	
DEVIATIONS	1	3.211E 9	3.211E 9	4.813	0.043	p>0.05
STRESS.WAA	4	4.908E 8	1.227E 8	0.184	0.943	
DEV.LIN	1	5.677E 6	5.677E 6	0.009	0.928	
DEV.QUAD	1	1.675E 8	1.675E 8	0.251	0.623	
DEV.CUB	1	3.153E 8	3.153E 8	0.473	0.502	
DEVIATIONS	1	2.306E 6	2.306E 6	0.003	0.954	
RESIDUAL	16	1.067E 10	6.671E 8			
TOTAL	24	3.723E 10	1.551E 9			
GRAND TOTAL	29	4.781E 10				
GRAND MEAN		84363				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	19267.0	22.8
REPS.WHPL	2	17439.6	20.7
REPS.WHPL.SUBPL	16	25828.6	30.6

<sup>†</sup>Epsilon factor Error MS WAA = 0.4384

Appendix 37.2 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole stem of plants  
labelled at 2 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	2.292E	8	1.146E	8			
REPS.PLOT STRATUM								
STRESS	1	8.987E	6	8.987E	6	0.105	0.751	
WAA	3	5.259E	9	1.753E	9	20.468	<.001	p<0.005
LIN	1	4.213E	9	4.213E	9	49.196	<.001	p<0.001
QUAD	1	9.680E	8	9.680E	8	11.303	0.005	0.025>p>0.01
CUB	1	7.752E	7	7.752E	7	0.905	0.358	
STRESS.WAA	3	1.508E	8	5.027E	7	0.587	0.633	
DEV.LIN	1	5.097E	7	5.097E	7	0.595	0.453	
DEV.QUAD	1	6.655E	7	6.655E	7	0.777	0.393	
DEV.CUB	1	3.329E	7	3.329E	7	0.389	0.543	
RESIDUAL	14	1.199E	9	8.564E	7			
TOTAL	21	6.618E	9	3.151E	8			
GRAND TOTAL	23	6.847E	9					
GRAND MEAN		19004						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	3785.1	19.9
REPS.PLOT	14	9254.4	48.7

<sup>†</sup>Epsilon factor Error MS WAA = 0.4072

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 37.3 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole stem of plants  
labelled at 4 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	1.431E	8 7.154E	7		
REPS.WHPL STRATUM						
STRESS	1	1.879E	8 1.879E	8	3.433	0.205
RESIDUAL	2	1.095E	8 5.473E	7		
TOTAL	3	2.974E	8 9.912E	7		
REPS.WHPL.SUBPL STRATUM						
WAA	2	1.302E	9 6.511E	8	152.046	<.001 p<0.001
LIN	1	1.080E	9 1.080E	9	252.315	<.001 p<0.001
QUAD	1	2.217E	8 2.217E	8	51.777	<.001 p<0.001
STRESS.WAA	2	1.034E	7 5.169E	6	1.207	0.348
DEV.LIN	1	9.366E	6 9.366E	6	2.187	0.177
DEV.QUAD	1	9.724E	5 9.724E	5	0.227	0.646
RESIDUAL	8	3.426E	7 4.282E	6		
TOTAL	12	1.347E	9 1.122E	8		
GRAND TOTAL	17	1.787E	9			
GRAND MEAN		21808				

\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	3453.0	15.8
REPS.WHPL	2	4271.3	19.6
REPS.WHPL.SUBPL	8	2069.4	9.5

<sup>†</sup>Epsilon factor Error MS WAA = 0.7582

Appendix 37.4 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole stem of plants  
labelled at 6 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	23041697	11520848			
REPS.WHPL STRATUM						
STRESS	1	12162211	12162211	1.695	0.323	
RESIDUAL	2	14347259	7173630			
TOTAL	3	26509470	8836490			
REPS.WHPL.SUBPL STRATUM						
WAA	1	150949820	150949820	41.097	0.003	
STRESS.WAA	1	1074307	1074307	0.292	0.617	
RESIDUAL	4	14691964	3672991			
TOTAL	6	166716090	27786015			
GRAND TOTAL	11	216267256				
GRAND MEAN		10604				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1697.1	16.0
REPS.WHPL	2	1893.9	17.9
REPS.WHPL.SUBPL	4	1916.5	18.1

<sup>†</sup>Epsilon factor Error MS WAA = 1.0000

Appendix 38 Analyses of variance : VARIATE: Total radioactivity of the whole stem from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 38.1 VARIATE: Total radioactivity of whole stem (dpm stem<sup>-1</sup>) of plants labelled at A

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	2.693E 13	1.346E 13			
REPS.WHPL STRATUM						
STRESS	1	1.152E 11	1.152E 11	0.031	0.877	
RESIDUAL	2	7.529E 12	3.765E 12			
TOTAL	3	7.645E 12	2.548E 12			
REPS.WHPL.SUBPL STRATUM						
WAA	4	9.137E 13	2.284E 13	11.353	<.001	0.01>p>0.005
LIN	1	5.609E 13	5.609E 13	27.877	<.001	p<0.001
QUAD	1	1.617E 12	1.617E 12	0.804	0.383	
CUB	1	9.361E 12	9.361E 12	4.653	0.047	
DEVIATIONS	1	2.430E 13	2.430E 13	12.078	0.003	0.025>p>0.01
STRESS.WAA	4	2.989E 12	7.472E 11	0.371	0.826	
DEV.LIN	1	5.090E 11	5.090E 11	0.253	0.622	
DEV.QUAD	1	7.162E 11	7.162E 11	0.356	0.559	
DEV.CUB	1	1.460E 12	1.460E 12	0.725	0.407	
DEVIATIONS	1	3.042E 11	3.042E 11	0.151	0.703	
RESIDUAL	16	3.219E 13	2.012E 12			
TOTAL	24	1.265E 14	5.273E 12			
GRAND TOTAL	29	1.611E 14				
GRAND MEAN		5027428				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1160334.3	23.1
REPS.WHPL	2	867724.4	17.3
REPS.WHPL.SUBPL	16	1418432.6	28.2

<sup>†</sup>Epsilon factor Error MS WAA = 0.4422

Appendix 38.2 VARIATE: Total radioactivity of whole stem (dpm stem<sup>-1</sup>) of plants  
labelled at 2 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	4.830E 11	2.415E 11				
REPS.PLOT STRATUM							
STRESS	1	1.247E 10	1.247E 10	0.063	0.806		
WAA	3	1.234E 13	4.114E 12	20.695	<.001	p<0.005	
LIN	1	9.717E 12	9.717E 12	48.884	<.001	p<0.001	
QUAD	1	2.199E 12	2.199E 12	11.064	0.005	0.025>p>0.01	
CUB	1	4.246E 11	4.246E 11	2.136	0.166		
STRESS.WAA	3	2.491E 11	8.303E 10	0.418	0.743		
DEV.LIN	1	6.586E 10	6.586E 10	0.331	0.574		
DEV.QUAD	1	1.247E 11	1.247E 11	0.627	0.442		
DEV.CUB	1	5.853E 10	5.853E 10	0.294	0.596		
RESIDUAL	14	2.783E 12	1.988E 11				
TOTAL	21	1.539E 13	7.327E 11				
GRAND TOTAL	23	1.587E 13					
GRAND MEAN		997983					

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	173749.0	17.4
REPS.PLOT	14	445850.7	44.7

<sup>†</sup>Epsilon factor Error MS WAA = 0.4019

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 38.3 VARIATE: Total radioactivity of whole stem (dpm stem<sup>-1</sup>) of plants  
labelled at 4 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	5.103E 11	2.552E 11			
REPS.WHPL STRATUM						
STRESS	1	6.184E 11	6.184E 11	5.147	0.151	
RESIDUAL	2	2.403E 11	1.202E 11			
TOTAL	3	8.588E 11	2.863E 11			
REPS.WHPL.SUBPL STRATUM						
TIME	2	2.299E 12	1.150E 12	104.086	<.001	p<0.001
LIN	1	2.104E 12	2.104E 12	190.472	<.001	p<0.001
QUAD	1	1.955E 11	1.955E 11	17.699	0.003	p<0.005
STRESS.TIME	2	4.909E 10	2.454E 10	2.222	0.171	
DEV.LIN	1	4.690E 9	4.690E 9	0.425	0.533	
DEV.QUAD	1	4.440E 10	4.440E 10	4.019	0.080	
RESIDUAL	8	8.837E 10	1.105E 10			
TOTAL	12	2.437E 12	2.031E 11			
GRAND TOTAL	17	3.806E 12				
GRAND MEAN		1210403				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	206223.4	17.0
REPS.WHPL	2	200136.6	16.5
REPS.WHPL.SUBPL	8	105100.6	8.7

<sup>†</sup>Epsilon factor Error MS WAA = 0.8456

Appendix 38.4 VARIATE: Total radioactivity of whole stem (dpm stem<sup>-1</sup>) of plants  
labelled at 6 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	1.002E 11	5.012E 10			
REPS.WHPL STRATUM						
STRESS	1	6.495E 10	6.495E 10	2.071	0.287	
RESIDUAL	2	6.271E 10	3.136E 10			
TOTAL	3	1.277E 11	4.255E 10			
REPS.WHPL.SUBPL STRATUM						
WAA	1	5.734E 11	5.734E 11	40.530	0.003	
STRESS.WAA	1	4.087E 9	4.087E 9	0.289	0.619	
RESIDUAL	4	5.660E 10	1.415E 10			
TOTAL	6	6.341E 11	1.057E 11			
GRAND TOTAL	11	8.620E 11				
GRAND MEAN		646509				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	111937.2	17.3
REPS.WHPL	2	125210.6	19.4
REPS.WHPL.SUBPL	4	118948.8	18.4

<sup>†</sup>Epsilon factor Error MS WAA = 1.0000

Appendix 39 Analyses of variance : VARIATE: Specific radioactivity of the whole shoot from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 39.1 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole shoot of plants labelled at A

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	3.328E 9	1.664E 9					
REPS.WHPL STRATUM								
STRESS	1	5.786E 6	5.786E 6	0.030	0.878			
RESIDUAL	2	3.847E 8	1.924E 8					
TOTAL	3	3.905E 8	1.302E 8					
REPS.WHPL.SUBPL STRATUM								
WAA	4	1.386E 10	3.464E 9	30.881	<.001		p<0.001	
LIN	1	1.214E 10	1.214E 10	108.262	<.001		p<0.001	
QUAD	1	8.242E 8	8.242E 8	7.348	0.015		0.05>p>0.025	
CUB	1	4.402E 8	4.402E 8	3.924	0.065			
DEVIATIONS	1	4.476E 8	4.476E 8	3.990	0.063			
STRESS.WAA	4	1.449E 8	3.621E 7	0.323	0.859			
DEV.LIN	1	2.826E 5	2.826E 5	0.003	0.961			
DEV.QUAD	1	9.807E 7	9.807E 7	0.874	0.364			
DEV.CUB	1	2.287E 6	2.287E 6	0.020	0.888			
DEVIATIONS	1	4.421E 7	4.421E 7	0.394	0.539			
RESIDUAL	16	1.795E 9	1.122E 8					
TOTAL	24	1.580E 10	6.581E 8					
GRAND TOTAL	29	1.951E 10						
GRAND MEAN		82680						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	12899.7	15.6
REPS.WHPL	2	6202.7	7.5
REPS.WHPL.SUBPL	16	10591.1	12.8

<sup>†</sup>Epsilon factor Error MS WAA = 0.3639

Appendix 39.2 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole shoot of plants  
labelled at 2 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	2.524E	8	1.262E	8			
REPS.PLOT STRATUM								
STRESS	1	5.777E	6	5.777E	6	0.149	0.705	
WAA	3	3.779E	9	1.260E	9	32.555	<.001	p<0.001
LIN	1	2.755E	9	2.755E	9	71.203	<.001	p<0.001
QUAD	1	9.812E	8	9.812E	8	25.361	<.001	p<0.005
CUB	1	4.263E	7	4.263E	7	1.102	0.312	
STRESS.WAA	3	9.052E	7	3.017E	7	0.780	0.525	
DEV.LIN	1	7.327E	7	7.327E	7	1.894	0.190	
DEV.QUAD	1	1.374E	7	1.374E	7	0.355	0.561	
DEV.CUB	1	3.505E	6	3.505E	6	0.091	0.768	
RESIDUAL	14	5.417E	8	3.869E	7			
TOTAL	21	4.417E	9	2.103E	8			
GRAND TOTAL	23	4.669E	9					
GRAND MEAN		22153						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	3971.6	17.9
REPS.PLOT	14	6220.2	28.1

<sup>†</sup>Epsilon factor Error MS WAA = 0.4085

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 39.3 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole shoot of plants  
labelled at 4 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	90796465	45398233			
REPS.PLOT STRATUM						
STRESS	1	99361198	99361198	12.209	0.006	
WAA	2	592504136	296252068	36.403	<.001	p<0.001
LIN	1	468293088	468293088	57.543	<.001	p<0.001
QUAD	1	124211056	124211056	15.263	0.003	0.01>p>0.005
STRESS.WAA	2	2039528	1019764	0.125	0.884	
DEV.LIN	1	2010527	2010527	0.247	0.630	
DEV.QUAD	1	29000	29000	0.004	0.954	
RESIDUAL	10	81380880	8138088			
TOTAL	15	775285728	51685715			
GRAND TOTAL	17	866082192				
GRAND MEAN		15798				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	2750.7	17.4
REPS.PLOT	10	2852.7	18.1

<sup>†</sup>Epsilon factor Error MS WAA = 0.6927

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 39.4 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole shoot of plants  
labelled at 6 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	9256003	4628001			
REPS.WHPL STRATUM						
STRESS	1	4883546	4883546	2.034	0.290	
RESIDUAL	2	4801607	2400804			
TOTAL	3	9685153	3228384			
REPS.WHPL.SUBPL STRATUM						
WAA	1	72114185	72114185	49.443	0.002	
STRESS.WAA	1	2214519	2214519	1.518	0.285	
RESIDUAL	4	5834155	1458539			
TOTAL	6	80162859	13360477			
GRAND TOTAL	11	99104014				
GRAND MEAN		6915				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1075.6	15.6
REPS.WHPL	2	1095.6	15.8
REPS.WHPL.SUBPL	4	1207.7	17.5

<sup>†</sup>Epsilon factor Error MS WAA = 1.0000

Appendix 40 Analyses of variance : VARIATE: Total radioactivity of the whole shoot from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 40.1 VARIATE: Total radioactivity of whole shoot (dpm shoot<sup>-1</sup>) of plants labelled at anthesis

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	9.733E 13	4.866E 13			
REPS.WHPL STRATUM						
STRESS	1	1.485E 13	1.485E 13	3.779	0.191	
RESIDUAL	2	7.859E 12	3.929E 12			
TOTAL	3	2.271E 13	7.570E 12			
REPS.WHPL.SUBPL STRATUM						
WAA	4	2.789E 14	6.972E 13	30.962	<.001	p<0.001
LIN	1	2.315E 14	2.315E 14	102.817	<.001	p<0.001
QUAD	1	5.775E 12	5.775E 12	2.565	0.129	
CUB	1	1.835E 13	1.835E 13	8.150	0.011	0.025>p>0.01
DEVIATIONS	1	2.323E 13	2.323E 13	10.316	0.005	0.025>p>0.01
STRESS.WAA	4	1.042E 13	2.604E 12	1.156	0.366	
DEV.LIN	1	3.632E 10	3.632E 10	0.016	0.901	
DEV.QUAD	1	4.832E 12	4.832E 12	2.146	0.162	
DEV.CUB	1	1.258E 12	1.258E 12	0.559	0.466	
DEVIATIONS	1	4.291E 12	4.291E 12	1.905	0.186	
RESIDUAL	16	3.603E 13	2.252E 12			
TOTAL	24	3.253E 14	1.356E 13			
GRAND TOTAL	29	4.454E 14				
GRAND MEAN	12334224					

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	2206012.3	17.9
REPS.WHPL	2	886485.6	7.2
REPS.WHPL.SUBPL	16	1500611.7	12.2

<sup>†</sup>Epsilon factor Error MS WAA = 0.4600

Appendix 40.2 VARIATE: Total radioactivity of whole shoot (dpm shoot<sup>-1</sup>) of plants labelled at 2 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	4.019E 12	2.010E 12			
REPS.PLOT STRATUM						
STRESS	1	2.707E 9	2.707E 9	0.004	0.949	
WAA	3	8.863E 13	2.954E 13	46.961	<.001	p<0.001
LIN	1	6.594E 13	6.594E 13	104.811	<.001	p<0.001
QUAD	1	2.125E 13	2.125E 13	33.777	<.001	p<0.001
CUB	1	1.444E 12	1.444E 12	2.295	0.152	
STRESS.WAA	3	1.774E 12	5.914E 11	0.940	0.448	
DEV.LIN	1	1.315E 12	1.315E 12	2.089	0.170	
DEV.QUAD	1	4.511E 11	4.511E 11	0.717	0.411	
DEV.CUB	1	8.678E 9	8.678E 9	0.014	0.908	
RESIDUAL	14	8.808E 12	6.291E 11			
TOTAL	21	9.922E 13	4.725E 12			
GRAND TOTAL	23	1.032E 14				
GRAND MEAN		3244340				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	501203.7	15.4
REPS.PLOT	14	793164.3	24.4

<sup>†</sup>Epsilon factor Error MS WAA = 0.4629

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 40.3 VARIATE: Total radioactivity of whole shoot (dpm shoot<sup>-1</sup>) of plants labelled at 4 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F	PR(adj) <sup>†</sup>
REPS STRATUM	2	2.130E 12	1.065E 12					
REPS.PLOT STRATUM								
STRESS	1	2.426E 12	2.426E 12	14.825	0.003			
WAA	2	1.237E 13	6.185E 12	37.787	<.001		p<0.001	
LIN	1	1.060E 13	1.060E 13	64.751	<.001		p<0.001	
QUAD	1	1.772E 12	1.772E 12	10.824	0.008		0.025>p>0.01	
STRESS.WAA	2	1.247E 11	6.234E 10	0.381	0.693			
DEV.LIN	1	1.135E 11	1.135E 11	0.693	0.424			
DEV.QUAD	1	1.120E 10	1.120E 10	0.068	0.799			
RESIDUAL	10	1.637E 12	1.637E 11					
TOTAL	15	1.656E 13	1.104E 12					
GRAND TOTAL	17	1.869E 13						
GRAND MEAN		2232167						

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	421356.5	18.9
REPS.PLOT	10	404566.0	18.1

<sup>†</sup>Epsilon factor Error MS WAA = 0.5979

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 40.4 VARIATE: Total radioactivity of whole shoot (dpm shoot<sup>-1</sup>) of plants labelled at 6 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	2.559E 11	1.280E 11			
REPS.WHPL STRATUM						
STRESS	1	2.459E 11	2.459E 11	3.470	0.204	
RESIDUAL	2	1.417E 11	7.087E 10			
TOTAL	3	3.877E 11	1.292E 11			
REPS.WHPL.SUBPL STRATUM						
WAA	1	1.662E 12	1.662E 12	37.644	0.004	
STRESS.WAA	1	9.259E 10	9.259E 10	2.097	0.221	
RESIDUAL	4	1.766E 11	4.415E 10			
TOTAL	6	1.931E 12	3.219E 11			
GRAND TOTAL	11	2.575E 12				
GRAND MEAN		999661				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	178851.2	17.9
REPS.WHPL	2	188247.6	18.8
REPS.WHPL.SUBPL	4	210129.2	21.0

<sup>†</sup>Epsilon factor Error MS WAA = 1.0000

Appendix 41 Analyses of variance : VARIATE: Specific radioactivity of the whole plant from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 41.1 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole plant of plants labelled at A

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	2.652E 9	1.326E 9				
REPS.PLOT STRATUM							
STRESS	1	4.276E 7	4.276E 7	0.334	0.570		
WAA	4	2.497E 10	6.243E 9	48.764	<.001	p<0.001	
LIN	1	2.291E 10	2.291E 10	178.948	<.001	p<0.001	
QUAD	1	1.049E 9	1.049E 9	8.191	0.010	0.05>p>0.025	
CUB	1	4.025E 8	4.025E 8	3.144	0.093		
DEVIATIONS	1	6.109E 8	6.109E 8	4.772	0.042	0.10>p>0.05	
STRESS.WAA	4	1.448E 8	3.620E 7	0.283	0.885		
DEV.LIN	1	2.612E 6	2.612E 6	0.020	0.888		
DEV.QUAD	1	7.769E 7	7.769E 7	0.607	0.446		
DEV.CUB	1	9.313E 6	9.313E 6	0.073	0.790		
DEVIATIONS	1	5.517E 7	5.517E 7	0.431	0.520		
RESIDUAL	18	2.304E 9	1.280E 8				
TOTAL	27	2.746E 10	1.017E 9				
GRAND TOTAL	29	3.012E 10					
GRAND MEAN		76829					

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	11516.1	15.0
REPS.PLOT	18	11314.9	14.7

<sup>†</sup>Epsilon factor Error MS WAA = 0.3421

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 41.2 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole plant of plants labelled at 2 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F	PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	3.500E	8 1.750E	8			
REPS.PLOT STRATUM							
STRESS	1	4.506E	8 4.506E	8	4.175	0.060	
WAA	3	3.190E	9 1.063E	9	9.852	<.001	p<0.005
LIN	1	2.938E	9 2.938E	9	27.220	<.001	p<0.001
QUAD	1	1.012E	8 1.012E	8	0.938	0.349	
CUB	1	1.510E	8 1.510E	8	1.399	0.257	
STRESS.WAA	3	6.349E	7 2.116E	7	0.196	0.897	
DEV.LIN	1	5.860E	6 5.860E	6	0.054	0.819	
DEV.QUAD	1	5.752E	7 5.752E	7	0.533	0.477	
DEV.CUB	1	1.094E	5 1.094E	5	0.001	0.975	
RESIDUAL	14	1.511E	9 1.079E	8			
TOTAL	21	5.215E	9 2.483E	8			
GRAND TOTAL	23	5.565E	9				
GRAND MEAN		61844					

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	4677.2	7.6
REPS.PLOT	14	10389.1	16.8

<sup>†</sup>Epsilon factor Error MS WAA = 0.7643

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 41.3 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole plant of plants labelled at 4 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	361497336	180748668			
REPS.PLOT STRATUM						
STRESS	1	144760702	144760702	6.573	0.028	
WAA	2	153757638	76878819	3.491	0.071	
LIN	1	18798140	18798140	0.854	0.377	
QUAD	1	134959500	134959500	6.128	0.033	0.05>p>0.025
STRESS.WAA	2	18766757	9383379	0.426	0.664	
DEV.LIN	1	11517302	11517302	0.523	0.486	
DEV.QUAD	1	7249455	7249455	0.329	0.579	
RESIDUAL	10	220232664	22023266			
TOTAL	15	537517760	35834517			
GRAND TOTAL	17	899015096				
GRAND MEAN		28094				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	5488.6	19.5
REPS.PLOT	10	4692.9	16.7

<sup>†</sup>Epsilon factor Error MS WAA = 0.7418

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 41.4 VARIATE: Specific radioactivity (dpm g<sup>-1</sup>) of whole plant of plants labelled at 6 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	7257110	3628555			
REPS.WHPL STRATUM						
STRESS	1	1388029	1388029	0.741	0.480	
RESIDUAL	2	3746810	1873405			
TOTAL	3	5134839	1711613			
REPS.WHPL.SUBPL STRATUM						
WAA	1	9035815	9035815	6.433	0.064	
STRESS.WAA	1	1511554	1511554	1.076	0.358	
RESIDUAL	4	5618553	1404638			
TOTAL	6	16165921	2694320			
GRAND TOTAL	11	28557870				
GRAND MEAN		8045				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	952.4	11.8
REPS.WHPL	2	967.8	12.0
REPS.WHPL.SUBPL	4	1185.2	14.7

<sup>†</sup>Epsilon factor Error MS WAA = 1.0000

Appendix 42 Analyses of variance : VARIATE: Total radioactivity of the whole plant from plants labelled on four occasions during grain fill : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 42.1 VARIATE: Total radioactivity of whole plant (dpm plant<sup>-1</sup>) of plants labelled at A

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	1.175E 14	5.874E 13			
REPS.WHPL STRATUM						
STRESS	1	1.161E 13	1.161E 13	3.292	0.211	
RESIDUAL	2	7.055E 12	3.527E 12			
TOTAL	3	1.867E 13	6.223E 12			
REPS.WHPL.SUBPL STRATUM						
WAA	4	1.139E 14	2.848E 13	10.892	<.001	0.025>p>0.001
LIN	1	8.438E 13	8.438E 13	32.277	<.001	p<0.001
QUAD	1	2.440E 12	2.440E 12	0.933	0.348	
CUB	1	6.109E 12	6.109E 12	2.337	0.146	
DEVIATIONS	1	2.097E 13	2.097E 13	8.023	0.012	0.05>p>0.025
STRESS.WAA	4	1.325E 13	3.313E 12	1.267	0.324	
DEV.LIN	1	2.189E 11	2.189E 11	0.084	0.776	
DEV.QUAD	1	6.659E 12	6.659E 12	2.547	0.130	
DEV.CUB	1	4.301E 11	4.301E 11	0.165	0.690	
DEVIATIONS	1	5.942E 12	5.942E 12	2.273	0.151	
RESIDUAL	16	4.183E 13	2.614E 12			
TOTAL	24	1.690E 14	7.041E 12			
GRAND TOTAL	29	3.051E 14				
GRAND MEAN		14911955				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	2423627.7	16.3
REPS.WHPL	2	839925.4	5.6
REPS.WHPL.SUBPL	16	1616909.0	10.8

<sup>†</sup>Epsilon factor Error MS WAA = 0.3924

Appendix 42.2 VARIATE: Total radioactivity of whole plant (dpm plant<sup>-1</sup>) of plants labelled at 2 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	1.830E 13	9.152E 12			
REPS.PLOT STRATUM						
STRESS	1	8.551E 12	8.551E 12	1.809	0.200	
WAA	3	1.610E 13	5.366E 12	1.135	0.369	
LIN	1	8.988E 12	8.988E 12	1.901	0.190	
QUAD	1	1.306E 12	1.306E 12	0.276	0.607	
CUB	1	5.804E 12	5.804E 12	1.227	0.287	
STRESS.WAA	3	1.254E 13	4.180E 12	0.884	0.473	
DEV.LIN	1	1.883E 11	1.883E 11	0.040	0.845	
DEV.QUAD	1	1.026E 13	1.026E 13	2.169	0.163	
DEV.CUB	1	2.097E 12	2.097E 12	0.444	0.516	
RESIDUAL	14	6.619E 13	4.728E 12			
TOTAL	21	1.034E 14	4.923E 12			
GRAND TOTAL	23	1.217E 14				
GRAND MEAN		14187432				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1069597.8	7.5
REPS.PLOT	14	2174440.3	15.3

<sup>†</sup>Epsilon factor Error MS WAA = 0.7775

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 42.3 VARIATE: Total radioactivity of whole plant (dpm plant<sup>-1</sup>) of plants labelled at 4 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	2.814E 13	1.407E 13			
REPS.PLOT STRATUM						
STRESS	1	1.936E 13	1.936E 13	11.559	0.007	
WAA	2	4.661E 12	2.331E 12	1.392	0.293	
LIN	1	2.288E 9	2.288E 9	0.001	0.971	
QUAD	1	4.659E 12	4.659E 12	2.782	0.126	
STRESS.WAA	2	2.212E 12	1.106E 12	0.660	0.538	
DEV.LIN	1	1.744E 12	1.744E 12	1.041	0.332	
DEV.QUAD	1	4.683E 11	4.683E 11	0.280	0.608	
RESIDUAL	10	1.675E 13	1.675E 12			
TOTAL	15	4.298E 13	2.865E 12			
GRAND TOTAL	17	7.112E 13				
GRAND MEAN		7294502				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	1531469.0	21.0
REPS.PLOT	10	1294099.6	17.7

<sup>†</sup>Epsilon factor Error MS WAA = 0.7142

NOTE: Since Error MS WAA > Error MS Stress, Error MS WAA was pooled with Error MS Stress

Appendix 42.4 VARIATE: Total radioactivity of whole plant (dpm plant<sup>-1</sup>) of plants labelled at 6 WAA

SOURCE OF VARIATION	DF	SS	MS	VR	F PR	F PR(adj) <sup>†</sup>
REPS STRATUM	2	6.032E 11	3.016E 11			
REPS.WHPL STRATUM						
STRESS	1	7.074E 11	7.074E 11	3.066	0.222	
RESIDUAL	2	4.615E 11	2.308E 11			
TOTAL	3	1.169E 12	3.896E 11			
REPS.WHPL.SUBPL STRATUM						
WAA	1	7.235E 11	7.235E 11	5.409	0.081	
STRESS.WAA	1	1.098E 11	1.098E 11	0.821	0.416	
RESIDUAL	4	5.350E 11	1.338E 11			
TOTAL	6	1.368E 12	2.280E 11			
GRAND TOTAL	11	3.140E 12				
GRAND MEAN		2156286				

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	274586.5	12.7
REPS.WHPL	2	339673.0	15.8
REPS.WHPL.SUBPL	4	365734.1	17.0

<sup>†</sup>Epsilon factor Error MS WAA = 1.0000

Appendix 43 Analysis of variance : Grain yield (g plant<sup>-1</sup>, primary plus secondary ears) at harvest maturity : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	59.79	29.90		
REPS.PLOTS STRATUM					
STRESS	1	719.42	719.42	25.762	0.037
RESIDUAL	2	55.85	27.93		
TOTAL	3	775.27	258.42		
GRAND TOTAL	5	835.06			
GRAND MEAN		150.3			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	3.87	2.6
REPS.PLOTS	2	5.28	3.5

Appendix 44 Analyses of variance : yield components and cob production (primary ear only) at harvest maturity : 1988/89 maize single cross hybrid <sup>14</sup>C labelling trial, Faculty of Agriculture

Appendix 44.1 VARIATE: Kernels ear<sup>-1</sup>

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	2638.6	1319.3		
REPS.PLOTS STRATUM					
STRESS	1	6332.3	6332.3	11.308	0.078
RESIDUAL	2	1120.0	560.0		
TOTAL	3	7452.3	2484.1		
GRAND TOTAL	5	10090.9			
GRAND MEAN		481.6			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	25.68	5.3
REPS.PLOTS	2	23.66	4.9

Appendix 44.2 VARIATE: Kernels row<sup>-1</sup>

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	1.309	0.654		
REPS.PLOTS STRATUM					
STRESS	1	74.198	74.198	24.266	0.039
RESIDUAL	2	6.115	3.058		
TOTAL	3	80.313	26.771		
GRAND TOTAL	5	81.622			
GRAND MEAN		34.16			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.572	1.7
REPS.PLOTS	2	1.749	5.1

Appendix 44.3 VARIATE: Rows ear<sup>-1</sup>

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	1.333	0.667		
REPS.PLOTS STRATUM					
STRESS	1	1.500	1.500	0.750	0.478
RESIDUAL	2	4.000	2.000		
TOTAL	3	5.500	1.833		
GRAND TOTAL	5	6.833			
GRAND MEAN		14.17			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.577	4.1
REPS.PLOTS	2	1.414	10.0

Appendix 44.4 VARIATE: Mass kernel<sup>-1</sup> (g)

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	0.00109200	0.00054600		
REPS.PLOTS STRATUM					
STRESS	1	0.00001667	0.00001667	1.316	0.370
RESIDUAL	2	0.00002533	0.00001267		
TOTAL	3	0.00004200	0.00001400		
GRAND TOTAL	5	0.00113400			
GRAND MEAN		0.3110			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.01652	5.3
REPS.PLOTS	2	0.00356	1.1

Appendix 44.5 VARIATE: Cob production (g plant<sup>-1</sup>)

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	1.423	0.712		
REPS.PLOTS STRATUM					
STRESS	1	14.727	14.727	2.085	0.286
RESIDUAL	2	14.123	7.062		
TOTAL	3	28.850	9.617		
GRAND TOTAL	5	30.273			
GRAND MEAN		17.6			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.60	3.4
REPS.PLOTS	2	2.66	15.1

Appendix 45 VARIATE: Secondary ear grain yield (g plant<sup>-1</sup>) at harvest maturity :  
1988/89 maize single cross hybrid <sup>14</sup>C labelling trial, Faculty of Agriculture

SOURCE OF VARIATION	DF	SS	MS	VR	F PR
REPS STRATUM	2	0.17693	0.08847		
REPS.PLOTS STRATUM					
STRESS	1	0.10667	0.10667	4.030	0.182
RESIDUAL	2	0.05293	0.02647		
TOTAL	3	0.15960	0.05320		
GRAND TOTAL	5	0.33653			
GRAND MEAN		0.747			

\*\*\*\*\* STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION \*\*\*\*\*

STRATUM	DF	SE	CV%
REPS	2	0.2103	28.2
REPS.PLOTS	2	0.1627	21.8

Appendix 46 Segment dry mass (g segment<sup>-1</sup>) on each sampling occasion of each labelling occasion : 1988/89  
maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 46.1 Dry mass of segments (g segment<sup>-1</sup>) from a maize hybrid subjected to water stress (S) and lack of water stress (NS) and labelled at anthesis and sampled at two weekly intervals from anthesis to eight weeks after anthesis (WAA)

Stress treatment	WAA	Segment													
		Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear
S	0	5,1	6,2	5,0	8,8	10,4	11,9	15,2	1,3	16,6	38,5	2,8	3,2	11,4	4,7
	2	5,5	5,3	5,0	9,1	10,9	12,1	14,9	1,8	15,4	33,3	15,0	11,4	16,4	1,9
	4	5,2	5,4	4,9	8,4	10,2	10,4	10,2	2,3	17,5	33,9	59,9	16,0	13,7	1,3
	6	3,5	5,0	4,9	9,6	11,7	11,8	12,5	2,5	17,2	28,0	96,8	18,0	12,2	1,0
	8	2,9	3,6	5,1	9,3	11,7	12,3	13,9	2,5	18,9	27,7	126,0	17,0	10,7	1,5
NS	0	5,9	6,2	4,8	9,2	11,2	11,6	12,7	1,3	21,5	39,3	2,4	3,6	10,9	5,6
	2	6,2	6,3	7,4	10,2	12,3	11,2	13,7	2,3	17,6	37,2	13,6	17,6	22,9	2,4
	4	4,9	5,4	4,8	8,7	10,2	10,6	11,0	2,8	18,6	40,7	67,7	18,3	18,7	1,7
	6	5,7	7,6	6,8	11,8	14,5	14,3	12,9	3,1	20,1	33,4	110,6	22,8	13,9	1,7
	8	3,2	6,0	6,1	10,5	12,7	13,7	17,9	3,0	19,7	31,3	139,6	21,6	13,8	1,9

Appendix 46.2 Dry mass of segments (g segment<sup>-1</sup>) from a maize hybrid subjected to water stress (S) and lack of water stress (NS) and labelled at two weeks after anthesis (WAA) and sampled at two weekly intervals from two weeks after anthesis to eight weeks after anthesis

Stress treatment	WAA	Segment													
		Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear
S	2	5,6	5,0	5,0	8,6	9,6	9,8	11,4	1,9	24,0	37,0	36,9	14,7	14,3	2,1
	4	5,0	4,1	4,4	8,1	9,5	10,4	10,7	2,4	18,3	37,8	82,0	15,5	10,7	1,1
	6	3,5	7,0	6,0	10,6	12,5	14,5	11,0	2,9	20,1	29,8	115,2	18,1	10,6	0,5
	8	5,0	5,0	5,0	9,1	10,7	11,4	11,3	2,3	17,6	25,6	113,8	15,4	9,8	1,1
NS	2	5,0	5,0	4,5	7,7	9,4	10,1	12,2	1,9	19,1	42,0	38,9	19,2	16,0	2,9
	4	5,6	4,9	4,5	7,8	9,2	10,1	10,1	2,6	17,4	41,4	83,2	19,4	14,7	1,6
	6	3,4	5,5	4,9	10,0	12,8	13,4	15,3	3,3	18,3	32,8	109,8	18,3	11,9	1,0
	8	4,4	5,5	5,2	9,6	11,3	12,4	13,2	2,8	17,7	28,8	143,4	21,4	14,9	1,2

Appendix 46.3 Dry mass of segments (g segment<sup>-1</sup>) from a maize hybrid subjected to water stress (S) and lack of water stress (NS) and labelled at four weeks after anthesis (WAA) and sampled at two weekly intervals from four weeks after anthesis to eight weeks after anthesis

Stress treatment	WAA	Segment													
		Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear
S	4	5,6	5,2	6,1	8,0	9,3	10,1	10,7	2,6	15,6	38,0	97,0	16,8	10,6	1,0
	6	4,5	5,6	5,3	9,5	12,2	12,0	12,8	2,7	19,0	27,6	114,3	17,7	10,1	1,0
	8	5,1	5,1	4,7	9,7	10,8	11,9	13,0	2,3	19,1	29,3	116,6	14,5	7,7	0,6
NS	4	5,7	5,4	4,6	8,1	9,4	9,8	9,7	3,0	17,2	36,6	106,8	19,8	12,7	1,7
	6	5,0	5,7	5,5	9,8	12,7	13,3	14,6	3,0	19,0	32,3	130,0	19,2	11,1	1,0
	8	4,2	5,4	5,3	9,5	10,6	14,3	11,9	2,0	17,9	32,1	145,3	12,7	7,5	0,5

Appendix 46.4 Dry mass of segments (g segment<sup>-1</sup>) from a maize hybrid subjected to water stress (S) and lack of water stress (NS) and labelled at six weeks after anthesis (WAA) and sampled at two weekly intervals from six weeks after anthesis to eight weeks after anthesis

Stress treatment	WAA	Segment													
		Tassel	Top	A1	B1	B2	B3	B4	Shank	Sheaths	Laminae	Grain	Cob	Husks	2° ear
S	6	3,4	5,1	5,1	10,1	11,9	12,1	12,7	3,0	19,1	26,4	112,9	17,5	9,2	0,8
	8	3,7	5,7	5,0	8,9	11,0	14,3	11,6	2,4	19,5	25,4	110,7	16,0	10,6	0,6
NS	6	5,1	5,6	5,0	9,9	12,1	12,6	13,6	3,4	19,1	32,4	131,9	20,8	12,7	1,1
	8	4,7	5,9	5,7	9,8	11,4	13,5	12,3	3,0	19,4	29,7	141,4	18,2	11,7	0,7

Appendix 47 Whole stem dry mass (g stem<sup>-1</sup>) on each sampling occasion of each labelling occasion : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 47.1 Whole stem dry mass (g stem<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis				
	0	2	4	6	8
S	58,7	59,0	51,7	57,9	58,3
NS	57,0	63,4	53,4	70,8	69,9

Appendix 47.2 Whole stem dry mass (g stem<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from two weeks after anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis			
	2	4	6	8
S	51,3	49,5	64,5	54,9
NS	50,7	49,1	65,2	60,0

Appendix 47.3 Whole stem dry mass (g stem<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from four weeks after anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis		
	4	6	8
S	52,1	60,1	57,5
NS	49,8	64,6	58,9

Appendix 47.4 Whole stem dry mass (g stem<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from six weeks after anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis	
	6	8
S	59,9	58,7
NS	62,1	61,6

Appendix 48 Whole shoot dry mass (g shoot<sup>-1</sup>) on each sampling occasion of each labelling occasion : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 48.1 Whole shoot dry mass (g shoot<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis				
	0	2	4	6	8
S	138,1	143,0	139,2	137,9	136,9
NS	143,8	167,2	156,2	168,4	161,3

Appendix 48.2 Whole shoot dry mass (g shoot<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from two weeks after anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis			
	2	4	6	8
S	148,8	137,9	147,1	129,2
NS	154,7	149,2	151,3	148,3

Appendix 48.3 Whole shoot dry mass (g shoot<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from four weeks after anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis		
	4	6	8
S	139,7	140,0	133,7
NS	143,6	152,2	133,8

Appendix 48.4 Whole shoot dry mass (g shoot<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from six weeks after anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis	
	6	8
S	136,3	134,5
NS	153,3	146,0

Appendix 49 Whole plant dry mass (g plant<sup>-1</sup>) on each sampling occasion of each labelling occasion : 1988/89 maize single cross hybrid <sup>14</sup>C-labelling trial, Faculty of Agriculture

Appendix 49.1 Whole plant dry mass (g plant<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis				
	0	2	4	6	8
S	140,8	158,0	199,1	234,7	262,9
NS	146,2	180,8	224,0	279,0	300,8

Appendix 49.2 Whole plant dry mass (g plant<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from two weeks after anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis			
	2	4	6	8
S	185,8	219,9	262,3	243,0
NS	193,6	232,5	261,1	291,7

Appendix 49.3 Whole plant dry mass (g plant<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from four weeks after anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis		
	4	6	8
S	236,7	254,3	250,3
NS	250,4	282,2	279,2

Appendix 49.4 Whole plant dry mass (g plant<sup>-1</sup>) of a maize hybrid subjected to water stress (S) and lack of water stress (NS) during grain fill and sampled at two weekly intervals from six weeks after anthesis to eight weeks after anthesis

Stress treatment	Weeks after anthesis	
	6	8
S	249,2	245,2
NS	285,2	287,4