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

by

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DECLARATION

I declare that the results contained in this thesis are from my own original work, except as acknowledged herein.

P.E. SHANAHAN

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LIST OF ABBREVIATIONS FREQUENTLY USED IN CHAPTERS 2 to 5

A - Anthesis

dpm - decays per minute

EMS - Error mean square

Leaf Ψw - Leaf water potential

MGF - Mid-grain fill

NS - Non-significant

NS - Non-stress

PM - Physiological maturity

RS - Reducing sugars

S - Stress

SR - Specific radioactivity

TNC - Total non-structural carbohydrate(s)

TR - Total radioactivity

TS - Total sugars

WAA - Weeks after anthesis, eg. one week after anthesis = 1 WAA

ABSTRACT

Stems of maize plants may serve as reservoirs for photosynthate produced in the leaves which may then be utilized for cell growth and maintenance requirements of the plants, and in particular for grain requirements during grain fill. Experiments were designed to ascertain the extent to which non-structural carbohydrates accumulate and are depleted in the stem and ears of locally cultivated maize hybrids during grain fill under conditions of water stress. Maize plants were grown: (i) under field conditions; (ii) under a rain-out shelter; and (iii) in pots placed inside a growth tunnel during grain fill. In the latter experiment whole maize plants were exposed to $^{14}CO_2$ at selected intervals during grain fill.

In the field trial large differences in the accumulation and depletion of total non-structural carbohydrates (TNC) were found between the six hybrids tested. The water stress conditions that prevailed from mid-grain fill (MGF) to physiological maturity (PM) resulted in TNC content levels being lower at PM than at anthesis in all hybrids except for SR 52. Total non-structural carbohydrate content in the whole stem of PNR 6427, CG 4602 and PNR 473 declined from anthesis to PM. In contrast TNC content in the whole stem of SA 60 and HL 1 declined from anthesis to MGF and then increased substantially in SA 60 and marginally in HL 1 from MGF to PM.

In the rain-out shelter trial, water stress resulted in a 38 % reduction in final grain yield in SA 6 compared to 25 % in

K78Y x I137TN. The greater tolerance to water stress of the more modern hybrid K78Y x I137TN compared to the obsolete hybrid SA 6 may be attributed to a number of factors, namely: (i) K78Y x I137TN recorded a higher leaf area index 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 water potential 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.

In the ^{14}C-labelling pot trial, the maize single cross hybrid B254W X M162W generally depleted TNC in vegetative organs in the latter half of grain fill under stress conditions, while under non-stress conditions TNC continued to accumulate in vegetative organs until PM. Both stressed and non-stressed plants assimilated less ^{14}C on consecutive labelling occasions during grain fill. The amount of ^{14}C assimilated at six weeks after anthesis was only 12,1 and 16,3 % of that assimilated at anthesis in stressed and non-stressed plants, respectively. Stressed and non-stressed plants labelled at anthesis translocated a smaller proportion of assimilated ^{14}C to the grain during grain fill than plants labelled later. Consequently, stressed and non-stressed plants labelled at anthesis recorded the highest proportion of whole plant ^{14}C recovered in the whole shoot at PM compared to

plants labelled on any of the other occasions. At anthesis the primary ear was not yet established as the major sink for photosynthate and much of the ^{14}C assimilated at anthesis was utilized for final structural growth of the whole shoot including the cob and husks of the primary ear. Stressed and non-stressed plants assimilated similar amounts of ^{14}C at anthesis and two weeks after anthesis, however, stressed plants assimilated less ^{14}C than non-stressed plants at four and six weeks after anthesis. Forty-eight hours after each labelling occasion, the stressed plants had partitioned a higher proportion of assimilated ^{14}C to the grain than the non-stressed plants. However, by PM the non-stressed plants had partitioned an equal or greater proportion of whole plant ^{14}C recovered at PM to the grain compared to the stressed plants. Radioactivity associated with component non-structural carbohydrates, was determined using ion-exchange column chromatography and thin-layer chromatography. These procedures provided detailed data of the partitioning of ^{14}C among glucose, fructose, sucrose and starch.

INTRODUCTION

The production of maize (Zea mays L.) in southern Africa provides a significant part of the nutritional requirements of the greater human population. The Department of Agriculture estimates that 35 % of the carbohydrate, 15 % of the fat and 31 % of the protein requirements in South Africa's daily diet are supplied directly by maize products such as maize meal, maize rice and samp (Anon, 1989a). Approximately R2 x 10^9 worth of these products is used annually by the South African consumer. Indirectly, maize also plays an important rôle in feeding South Africa through its use as an animal feed by South Africa's egg, broiler, dairy, pig and red meat industries. These industries buy in the region of R1,2 x 10^9 worth of maize annually, either directly or in the form of balanced feeds manufactured by the stock feed manufacturing industry. In terms of industrial consumption of maize products, the wet milling industry which produces starch, glucose and a wide range of modified starch products depends on the maize industry for its major input and purchases in the region of R95 x 10^6 worth of maize annually (Anon, 1989a). In South Africa the maize industry plays an extremely important rôle in the domestic economy. Almost a quarter of South Africa's estimated 60 000 white farmers produce maize for the commercial market each year, although it is estimated that 80 % of the annual maize production is produced by 15 to 20 % of these farmers (Anon, 1989a). Maize producers also provide direct employment for an estimated work force of 150 000 and provide food and shelter for a further 1,2 x 10^6 people (Anon, 1989a). The maize industry is an important consumer of raw materials from

standard of living allowing for the purchase of alternative food substitutes such as bread which sells at the same price as maize meal but has the added benefit of being an already prepared meal. It may be expected that as urbanisation continues to occur, the decline in the consumption of white maize may persist (Wolthers, 1988). However, there may be a countering force, namely the rapid increase in the human population of South Africa which is expected to reach 70×10^6 by the year 2020 (Human Sciences Research Council, 1991). Unless these large numbers of humans can be actively employed in the economy of South Africa, maize meal may once again become an attractive food for those surviving on the proverbial 'bread line'. The apparent decline in the usage of yellow maize, which is largely used for animal feed, is due to: (i) competition from alternative grains, such as grain sorghum (Sorghum bicolor L. Moench), wheat (Triticum aestivum) and barley (Hordeum spp.); (ii) a decline in recent years in feedlotting because of uneconomic red meat prices; and (iii) on farm conversion of maize into feeds thus bypassing the Maize Board (Wolthers, 1988).

To counter the decline in the usage of maize, new food products of maize must be developed that are attractive to the consumer and also require the minimum time for preparation. Additionally, new non-food products derived from maize will have to be developed for use, particularly in the building, paper and pharmaceutical industries (McGill, 1988). If the future of the maize industry in South Africa is to be a bright one then much research and development will have to be done in order to utilize tailor-made maize genotypes for the production of food and non-

food products that effectively compete with alternative products on the market.

Another ongoing challenge facing the maize industry in South Africa and, in fact, all human activity, is the availability of water. South Africa is situated within the high pressure belt of the middle latitudes of the southern hemisphere; warm dry descending air associated with high pressure systems occurring over the greater part of the country most of the time, which is unfavourable for the formation of precipitation. The average annual rainfall of about 497 mm for South Africa as a whole is well below the world average of 860 mm. A comparatively narrow region along the eastern and southern coastlines is moderately well-watered, but the greater part of the interior and the western portion of the country is arid or semi-arid. For instance, the mean annual rainfall on the east coast in the vicinity of Durban is 1 070 mm, while that for Port Nolloth at the same latitude on the west coast is a mere 58 mm. The highest rainfall occurs in the mountain ranges of the south-western Cape and in the Drakensberg, where the mean annual rainfall exceeds 3 000 mm in places. In general, 65 % of the country receives less than 500 mm of rain annually, which is regarded as the minimum for successful dryland farming. Twenty-one percent of the country receives less than 200 mm. South Africa is also periodically affected by severe and prolonged droughts. The greater part of the country was drought-stricken from 1960 to 1966, while the longest drought on record was from 1925 to 1933. The drought that commenced in 1978 and was largely broken in 1985 provided new cumulative lows in runoff records in many areas.

Droughts are often terminated by severe floods. As a consequence of the low frequency of cloud cover over much of South Africa, the high proportion of solar radiation that reaches the earth's surface provides an abundance of energy to evaporate water from land and water surfaces and cause its loss to the atmosphere. There are only a few isolated areas in South Africa where the average annual potential evaporation is less than the average annual rainfall. However, over most of the country the average annual potential evaporation ranges from about 1 100 mm to more than 3 000 mm and is well in excess of the annual rainfall. In the north-western Cape evaporation exceeds rainfall by a factor of 25:1. In areas with low rainfall and high potential evaporation the loss of water from storage dams due to evaporation is of great consequence, particularly for further water resource development. Additionally, high evaporation losses in low rainfall areas decreases the potential amount of rainfall runoff collected in storage dams (Anon, 1986).

The combined average annual runoff of South Africa's rivers is estimated to be 53,5 x 10^9 m^3. In some areas the highly variable river flow can have periods of up to 10 consecutive years of less than average flow. This must be allowed for in both the planning and the operation of water supply systems. Because of this variability and the high evaporation losses from storage, it is estimated that, with the present state of knowledge and technology, only about 62 % or 33,0 x 10^9 m^3 of the mean annual runoff can be exploited economically. In addition about 5,4 x 10^9 m^3 per annum may be obtainable from underground sources (Anon, 1986). According to Green (1984) South Africa is 90 % of

the way toward developing its water resources to accommodate this annual storage potential. The requirements of agriculture (irrigation) of $9,7 \times 10^9$ m^3 a^{-1} plus $5,2 \times 10^9$ m^3 a^{-1} of other direct users in 1990 represented 45 % of the annual storage potential (Table 1). By the year 2010 it is anticipated that $11,9 \times 10^9$ m^3 a^{-1} will be used by agriculture with $9,5 \times 10^9$ m^3 a^{-1} consumed by other direct users, in total representing 65 % of the total storage potential (Anon, 1986). On the surface the figures indicate that South Africa's potential water supply will easily meet the country's total water requirements. However, the

Table 1 Expected total use and percentage of total demand of the water resources of the Republic of South Africa (Anon, 1986)

Demand sector	1980		1990		2000		2010	
	(million m^3 a^{-1})	(%)	(million m^3 a^{-1})	(%)	(million m^3 a^{-1})	(%)	(million m^3 a^{-1})	(%)
Direct use								
Municipal and domestic	1 516	9,3	2 281	12,0	3 220	14,4	4 477	17,3
Industrial	1 031	6,3	1 448	7,6	2 043	9,1	2 961	11,4
Mining	466	2,9	511	2,7	582	2,6	649	2,5
Power generation	282	1,7	444	2,3	779	3,5	900	3,5
Irrigation	8 504	52,2	9 695	50,9	10 974	48,9	11 885	45,9
Stock-watering	262	1,6	288	1,5	316	1,4	358	1,4
Nature conservation	178	1,1	182	1,0	187	0,8	191	0,7
Indirect use								
Forestry run-off reduction	1 284	7,9	1 427	7,5	1 570	7,0	1 700	6,6
Ecological use, estuaries and lakes	2 768	17,0	2 767	14,5	2 767	12,3	2 767	10,7
Total	16 291	100,0	19 043	100,0	22 438	100,0	25 888	100,0

scenario during periods of drought reveals the situation to be somewhat precarious. In 1984, during the 1978 to 1985 drought, half of the 70 state irrigation schemes had to cut farmers' water quotas by between 50 and 100 %. Should a drought of similar proportions occur again in the future, with a greater proportion of the potential storage being utilized and little excess available as an emergency supply, the situation could well be catastrophic (Green, 1984).

Clearly, with the erratic rainfall that occurs in South Africa, the storage of water and the subsequent utilization thereof for irrigation is an important part of crop production in South Africa. In 1990 irrigation of crops accounted for 50,9 % of the water consumed directly and indirectly in South Africa (Table 1; Anon, 1986). Currently 1,2 x 10^6 ha of land are irrigated in South Africa (Green, 1991; personal communication) which includes almost all the fruit and vegetable production, a considerable proportion of the vineyards and a smaller proportion of sugarcane (Saccharum officinarum), wheat, cotton (Gossypium hirsutum), maize and fodder production (Green, 1984). It is estimated that the maximum area that could be economically irrigated with present technology and infrastructure is 1,4 x 10^6 ha. Thus approximately 86 % of the land suitable for irrigation is already being irrigated (Robbroeck, 1983). However, the 1,2 x 10^6 ha of land currently irrigated represents only 12 % of the total land under cultivation of just over 10 x 10^6 ha (Anon, 1989a). It is therefore apparent that the greater proportion of the cultivated crops are rain grown and with the limited availability of land suitable for irrigation, it appears likely that much of South

Africa's major food crops will largely be dependant on rainfall in the years to come. Additionally, the Department of Water Affairs has indicated that attempts to increase water savings in the agricultural sector will not only be achieved through improved irrigation techniques and management skills but also through the greater use of crop genotypes specifically bred for cultivation under rain grown conditions (Anon, 1986).

In terms of social and economic upliftment, irrigation is often seen as an important means of developing small farms or subsistence communities. However, Mr J-C Legoupil, head of the research and development division of the Institute of Tropical Agronomic Research in France, who visited South Africa in 1985, pointed out that the high cost of irrigation development and the scarcity of water in the whole region requires much thinking and research if irrigation is to be used as an efficient tool for development (Anon, 1985). He further pointed out that despite considerable initial investment and high running costs, irrigation projects encounter various problems - technical, management, training, agricultural policy, finance - which condemn them to failure. In Africa each year more irrigated land is abandoned than developed. Mr Legoupil made the general statement that in contrast to initial expectations, irrigation in many developing countries in Africa does not at present offer a solution to the vagaries of climate or contribute effectively to self-sufficiency of food production. Although it may be expected that advances in irrigation technology may make it possible for certain areas to become viable irrigation schemes, it is obvious that irrigation is not the panacea to all of

Africa's food shortages. This provides further incentive for the cultivation of selectively chosen food crops that have been specifically bred for cultivation under rain grown conditions.

In South Africa the greater proportion of maize cultivation occurs under rain grown conditions. The mean long term total rainfall during the normal growing season of maize in each of the main maize producing regions is, apart from Natal and Eastern Transvaal, marginal for maize production (Table 2). Importantly, however, is that the rainfall does not occur evenly and well distributed over the growing season, and drought conditions can occur at any stage during the growing season of maize. Thus the low and unreliable rainfall that occurs in the main maize

Table 2 Long term annual (LTA) monthly rainfall and average yield for the major maize producing regions[a]

Region	LTA-Monthly rainfall (mm)[b]							Yield (t ha^{-1})
	Oct	Nov	Dec	Jan	Feb	Mar	Total	Average 1979/80-1988/89
Natal	69,9	98,2	121,1	141,3	112,7	98,2	641,1	2,546
E-Tvl	71,3	124,3	125,6	124,9	105,1	84,1	635,3	2,904
PWV	64,6	106,2	112,8	125,6	95,8	77,4	582,4	2,799
N-Tvl	47,9	95,6	111,0	117,3	105,6	74,7	552,1	1,888
E-OFS	68,6	95,5	101,3	109,8	87,8	73,2	536,2	1,598
W-Tvl	42,7	71,3	85,0	105,5	88,3	84,2	477,0	1,676
N-OFS	52,6	74,7	77,3	92,9	75,8	73,8	447,1	1,919
N-Cape	29,8	47,7	62,8	85,5	74,0	75,2	375,0	1,356

a Data supplied by the Agrometeorological Department of the Grain Crops Research Institute, Potchefstroom

b The average of between 6 and 14 stations for each region. Planting dates may affect the total.

producing areas is largely responsible for rather dismal average yields recorded in each region, with the overall mean maize yield in South Africa for the 1979/80 to 1988/89 seasons of 1,922 t ha^{-1}. With the greater proportion of maize cultivated under natural rainfall conditions in South Africa and the associated low yields, the challenge to maize breeders is to produce hybrids with increased yield potential for rain grown conditions. This necessarily entails improving the drought tolerance characteristics of maize genotypes. However, the physiological, biochemical and morphological traits that provide maize genotypes (and, in fact, all crops in general) with a greater tolerance to periods of water deficits, is a matter of much debate and controversy amongst plant scientists. It is often reported in the literature that non-structural carbohydrates accumulate in the vegetative organs, particularly the stem, of maize (Westgate and Boyer, 1985a), wheat, barley (Bidinger, Musgrave and Fischer, 1977), rice (Oryza sativa) (Murata and Matsushima, 1975) and sorghum (Constable and Hearn, 1978) and may be subsequently remobilized to the developing grain when the production of current photosynthate is reduced or totally inhibited. Furthermore it is suggested that the remobilization of non-structural carbohydrate to the grain may enable crop species to continue linear grain fill until the production of current photosynthate is resumed. Failing the resumption of current photosynthate production, remobilization of stored non-structural carbohydrate may at least enable the crop species to realise a higher proportion of its potential yield. Based on these reports it was decided to ascertain the extent to which non-structural carbohydrates accumulate and are

depleted in the stem of locally cultivated maize hybrids during grain fill under conditions of water stress. An assessment could then be made of the importance of the remobilization of non-structural carbohydrates to the grain under environmental conditions that inhibit photosynthesis as a trait providing maize genotypes with a measure of drought tolerance. The study was conducted in three phases: (i) a pilot study was conducted on six maize hybrids grown under field conditions in order to determine whether differences exist amongst commonly grown hybrids in the extent to which non-structural carbohydrates accumulate and are depleted in the stem during grain fill (Chapter 2). A repeat study was conducted under field conditions in 1986/87 in order to determine the influence of environmental conditions on the accumulation and depletion of non-structural carbohydrates in the stem (data in press); (ii) in order to more effectively induce water stress two single cross maize hybrids were grown under a rain-out shelter in 1986/87 and the fluctuation in non-structural carbohydrates in the first pair of internodes above and below the primary ear was monitored during grain fill under stress and non-stress conditions (Chapter 3); and (iii) in order to determine the time course of the mobilization of 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 exposed to $^{14}CO_2$ at selected intervals during grain fill. The extent to which the assimilation of $^{14}CO_2$ and the distribution and remobilization of ^{14}C-labelled photosynthate among the various organs is affected by water stress was determined by recovering and analyzing the amount of ^{14}C in the various organs at selected intervals during grain fill (Chapter 4).

CHAPTER 1

LITERATURE REVIEW

1.1 Introduction

Carbohydrates in higher plants, as the initial products of photosynthesis, are the fundamental energy source and primary metabolic structures from which all other metabolites are synthesized such as amino acids, lipids, nucleic acids, hormones and phenolic compounds. Carbohydrates occur in plants as structural and non-structural components. Non-structural carbohydrates are those that can be accumulated and then readily mobilized and translocated for utilization in other plant organs. Thus non-structural carbohydrates are important in that they may function as a reserve of energy that may be used when carbohydrate utilization exceeds photosynthetic production. Non-structural carbohydrates are comprised of non-structural sugars and non-structural polysaccharides. The monosaccharides glucose and fructose, and the disaccharides sucrose and maltose are the predominant sugars found in grass and legume tissues. In maize, glucose and fructose comprise virtually all of the reducing sugars, with sucrose all of the non-reducing sugars. The polysaccharide starch, which occurs in high levels in the kernel and in low levels in the vegetative tissue, is the remaining major component of non-structural carbohydrates in maize. The non-structural carbohydrates that accumulate in the vegetative organs of maize can be utilized for continued plant growth and development if photosynthetic activity is reduced or inadequate often as a result of unfavourable environmental conditions.

Utilization of reserve non-structural carbohydrates for continued grain fill when photosynthesis is inhibited by unfavourable environmental conditions, may enable some maize genotypes to realize a greater proportion of their potential yield (depending on the timing, severity and duration of the environmental stress). Thus studying the partitioning patterns of non-structural carbohydrates in maize under favourable and unfavourable environmental conditions will provide a clearer understanding of the physiological basis for the differential tolerances shown by maize genotypes to limiting environmental conditions and particularly, in terms of this study, to water deficits.

1.2 Occurrence and biochemistry of the predominant non-structural carbohydrates in maize

1.2.1 Monosaccharides - glucose and fructose

Glucose and fructose occur in all vascular plants as products of hydrolysis either of their phosphate esters or especially their disaccharide, sucrose. They can also be derived from their polymers, starch and fructan. Concentrations of these sugars vary widely but may constitute over 50 % by mass of the edible portion in some fruits (e.g. date (Phoenix dactylifera). They are both substrates for the enzyme hexokinase, which initiates their entry into metabolism, as sources of energy (via glycolysis, the oxidative pentose phosphate pathway and the tricarboxylic acid cycle, reviewed by ap Rees, 1980), as C skeletons for synthesis from intermediates of these pathways and

as unchanged building blocks for the synthesis of oligo- and polysaccharides.

$$\text{Glucose} + \text{ATP} \xrightarrow[Mg^{2+}]{\text{Hexokinase}} \text{Glucose-6-phosphate} + \text{ADP}$$

$$\text{Fructose} \qquad\qquad \text{Fructose-6-phosphate} \qquad (1.1)$$

(Lewis, 1984).

Glucose and fructose are six C membered molecules and are therefore referred to as hexoses. The functional group of glucose is an aldehyde and that of fructose is a ketone, and they therefore respectively belong to the groups aldohexoses and ketohexoses. It is now known that monosaccharides with five or more C exist as cyclic (ring) structures with an oxygen bridge between the carbonyl group and another C of the same molecule. Chemically, ring closure involves hemiacetal formation, where the carbonyl group (aldehyde or ketone) reacts with an alcohol. A five membered ring containing four C and an oxygen is called a furanose ring and a six membered ring containing five C and an oxygen is called a pyranose ring. The pyranose form of glucose and the furanose form of fructose commonly occur in nature (Figure 1.1). In the α-form of the ring structure the hydroxyl group on C-1 is cis to the hydroxyl on C-2, whereas in the β-form it is trans. Although ring formation removes some of the characteristic reactions of the aldehyde or ketone group, monosaccharides may show some of the properties of a carbonyl function and are often referred to as reducing sugars. This is because the α- and β-forms may be interconverted via the free aldehyde or ketone and in solution a monosaccharide may exist in equilibrium, partly as the free aldehyde or ketone together with the α- and β-forms of the various possible rings (Duffus and Duffus, 1984; Lewis, 1984).

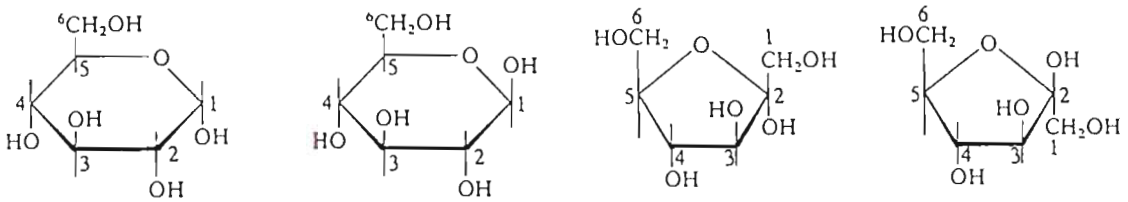


Figure 1.1 Pyranose forms of glucose and furanose forms of fructose (Duffus and Duffus, 1984)

Although glucose and fructose are freely involved in plant metabolism, it is their derivatives, the hexose phosphates and hexose nucleotides that, in the main, are formed or consumed as intermediary metabolites in carbohydrate synthesis and utilization.

1.2.1.1 Hexose phosphates

Hexose formation

Hexose phosphates are formed as intermediates in the synthesis of starch in the chloroplast, and sucrose in the cytosol. They are also formed during the uptake of sucrose from the extracellular space across the cell wall by action of invertases associated with the cell wall in certain plant tissues such as sugarcane storage cells (Glasziou, 1961). Hexose phosphates are also produced during the breakdown of reserve sucrose stored in

vacuoles and starch stored as granules in the chloroplast and amyloplast. Hexose phosphates are formed as intermediates in the mobilization of reserve lipids and the conversion thereof to sucrose (Glasziou and Gayler, 1972; Lewis, 1984).

Phosphated monosaccharides link the fixation of CO_2 during photosynthesis to the synthesis of more complex carbohydrates. Carbon dioxide fixed during the reductive pentose phosphate cycle in the chloroplast is made available for further metabolism as the phosphorylated three C monosaccharide glyceraldehyde-3-phosphate (GAP). The GAP may be used inside the chloroplast to form starch granules or GAP may be exported from the chloroplast to the cytosol via a specific phosphate translocator as dihydroxyacetone phosphate (DHAP). In well developed leaves exporting C to the rest of the plant, a major function of DHAP is in the synthesis of sucrose. Whether GAP is used inside the chloroplast in the synthesis of starch, or exported and synthesized to sucrose, it is initially converted to the hexose monophosphate glucose-1-phosphate (G1P) through the following reactions:

DHAP ⇌ GAP → Fructose-1,6-bisphosphate (FBP)

catalysed by triosephosphate isomerase and aldolase, respectively (1.2)

FBP → Fructose-6-phosphate (F6P) + Pi

catalysed by fructose-1,6-bisphosphatase (1.3)

F6P ⇌ Glucose-6-phosphate (G6P)

catalysed by phosphohexoisomerase (1.4)

G6P → G1P

catalysed by phosphoglucomutase (1.5)

(Duffus and Duffus, 1984; Lewis, 1984).
The utilization of G1P for sucrose and starch synthesis is discussed in Sections 1.2.2.1 and 1.2.3.2.

Sucrose translocated from the leaves to the other non-photosynthetic parts of the plant is a major source of hexose phosphates for plant metabolism. Movement of sucrose from the phloem to sink cells may occur via the intracellular connections or symplast as in the roots of pea (Pisum spp.) seedlings and maize; or substantial amounts of sucrose may move through the extracellular space or apoplast as in sugarcane storage tissue. In sugarcane storage tissue and the placenta - chalazal tissue of maize, evidence indicates that a cell wall invertase hydrolyses sucrose taken up from the apoplast. However, the appreciable number of plant tissues that have been shown to take up sucrose from the apoplast without prior hydrolysis (e.g. sugarbeet (Beta vulgaris) storage tissue) demonstrates that cell wall invertase is not a universal feature of plants, (ap Rees, 1988). Nonetheless, sucrose absorbed from the apoplast, or delivered via the symplast, will almost certainly arrive in the cytosol as sucrose. Production of hexose phosphates from this sucrose will involve acid invertase, alkaline invertase, or sucrose synthase, singly or in combination. Apart from its association with the cell wall, acid invertase appears to be confined to the vacuole and is therefore unlikely to be involved in sucrose metabolism in the cytosol. Alkaline invertase is probably present in most, if not all, living cells of higher plants. Sucrose synthase is almost certainly universally distributed and is one of the major proteins of plants. Fructose

produced by sucrose synthase will be metabolized to hexose phosphates via cytosolic fructokinase (ap Rees, 1988). The fate of the other product of sucrose synthase, UDP-glucose, is not clear but available evidence strongly indicates that it is the glucosyl donor for cellulose, and that pectic substances and hemicellulose are formed from diphospho-sugars that are made by direct interconversion from UDP-glucose. The other major polysaccharide formed from sucrose via a nucleoside diphospho-sugar donor is starch. The predominant precursor in the formation of starch catalysed by starch synthase is ADP-glucose and not UDP-glucose. There is evidence of a positive correlation between sucrose synthase and starch synthesis in maize endosperm. This implies that there is a route from UDP-glucose to ADP-glucose, involving hexose phosphates as intermediates. One of the most likely routes is the UDP-glucose pyrophosphorylase catalysed reaction:

UDP-glucose + PPi ⇌ G1P + UTP. (1.6)

If UDP-glucose pyrophosphorylase converts the product of sucrose synthase to G1P, then sucrose breakdown will be dependant upon a supply of PPi. The enzymes ATP or UTP pyrophosphohydrolase have been suggested as producing the necessary PPi in the following way:

ATP → PPi + AMP. (1.7)

So far these enzymes have not been isolated in the cytosol of plant tissues examined. An alternative source of PPi is PPi:fructose-6-phosphate-1-phosphotransferase [PFK(PPi)]. Collectively the reactions mentioned will function in the following way to convert the products of sucrose breakdown to F6P (for further metabolism) and ADP-glucose (for starch synthesis):

Sucrose + UDP ⇌ fructose + UDP-glucose (1.8)

catalysed by sucrose synthase

Fructose + UTP → F6P + UDP (1.9)

catalysed by fructokinase

UDP-glucose + PPi ⇌ G1P + UTP (1.10)

catalysed by UDP-glucose pyrophosphorylase

FBP + Pi ⇌ F6P + PPi (1.11)

catalysed by PFK(PPi)

G1P + ATP → ADP-glucose + PPi (1.12)

catalysed by ADP-glucose pyrophosphorylase.

As the reaction catalysed by PFK(PPi) is close to equilibrium in vivo, the enzyme may function in either direction depending upon whether there is a demand for PPi for sucrose breakdown or a need for the removal of PPi during sucrose synthesis (ap Rees, 1984; Hall and Rao, 1987; ap Rees, 1988).

Hexose phosphates are also formed as intermediates in the mobilization of reserve lipids and the conversion thereof to sucrose (pathway recently reviewed by ap Rees, 1988). From studies conducted on germinating castor bean (Ricinus communis), it appears that the initial step in the mobilization of reserve lipids is the hydrolysis of fat by a lipase to yield glycerol and fatty acids. The fatty acids are subjected to β-oxidation in the glyoxysome which generates considerable reducing power ($NADH_2$) and ATP, and large amounts of acetyl-CoA. The acetyl-CoA then enters the glyoxylate cycle, which is a modified form of the tricarboxylic acid (TCA) cycle in which the steps involving CO_2 release are bypassed. Citrate synthase catalyses the condensation of acetyl-CoA with the acceptor oxaloacetate. One

molecule of citrate is thus formed. Following conversion of citrate to isocitrate in a reaction catalysed by aconitase, succinate and glyoxylate are formed in a freely reversible reaction catalysed by isocitrate lyase. The glyoxylate formed condenses with a second molecule of acetyl-CoA to form malate. The malate thus formed enters the cytosol from the glyoxysome, is oxidized to oxaloacetate (by malate dehydrogenase) which is then converted to phosphenolpyruvate by phosphenolpyruvate carboxykinase. Subsequent reactions involve the conversion of phosphenolpyruvate to G1P by the reversal of glycolysis. Sucrose is then derived from G1P in a series of reactions described later. Considerable $NADH_2$ is formed by β-oxidation in the glyoxysome, but this organelle is unable to oxidize $NADH_2$ directly. The $NADH_2$ formed in the glyoxysome is reoxidized by glyoxysomal malate dehydrogenase which catalyses the reduction of oxaloacetate to malate by $NADH_2$. This malate (together with the succinate formed by isocitrate lyase) is then transferred to the mitochondria where malate dehydrogenase catalyses the reduction of NAD by the conversion of malate to oxaloacetate. The $NADH_2$ thus formed is used in the electron transport chain to form ATP. The oxaloacetate moves back to the glyoxysome via a shuttle involving glutamate, aspartate, and α-ketoglutarate (Duffus and Duffus, 1984; ap Rees, 1988).

Hexose phosphate utilization or consumption

As described earlier hexose phosphates are utilized during their conversion to sucrose, starch and structural polysaccharides. A major utilization of hexose phosphates is both their complete

oxidation to CO_2 forming the high energy compounds of $NADH_2$ and ATP, and their partial oxidation to provide intermediates for biosynthesis. Glycolysis and the oxidative pentose phosphate (OPP) pathway are the only two pathways of carbohydrate oxidation known in plants, and predominantly occur in the cytosol. Both pathways are well reviewed (ap Rees, 1985).

Through the action of sucrose synthase, UDP-glucose pyrophosphorylase and fructokinase, the products of sucrose degradation enter glycolysis as G1P and F6P. Through the conversion of G1P to G6P by phosphoglucomutase and F6P to G6P by phosphohexoisomerase, entry of sucrose degradation products into the OPP pathway is possible. During starch degradation the action of α-amylases, β-amylases, α-glucosidases, D-enzyme, phosphorylases, phosphoglucomutase and hexokinase (among others) enables the entry of G6P into glycolysis and the OPP pathway. (Duffus and Duffus, 1984; ap Rees, 1988).

1.2.1.2 Hexose nucleotides

Sugar nucleotides play an important rôle in the synthesis of sucrose and polysaccharides such as starch and cellulose. The following reaction is involved in the conversion of G1P to the sugar nucleotide UDP-glucose:

G1P + UTP ⇌ UDP-glucose + PPi

catalysed by UDP-glucose pyrophosphorylase. (1.13)

Other sugar nucleotide pyrophosphorylases exist that require the monosaccharide be phosphorylated on the C-1 position. Specific kinases that occur in plants that do phosphorylate the C-1

position of the monosaccharide include L-arabinokinase and D-galacturonokinase. However, D-glucose, D-fructose and D-mannose are phosphorylated by hexokinases that result in the formation of the 6-phospho derivatives. Isomerases may then convert F6P to G6P or mannose-6-phosphate and these, in turn, may be converted to G1P or mannose-1-phosphate. The nucleotide sugars may then be formed from the 1-phosphoglycosyl derivatives and the respective nucleoside triphosphate (NTP) in a reversible reaction catalysed by a pyrophosphorylase enzyme:

NTP + glycosyl-1-phosphate ⇌ NDP-glucose + PPi (1.14)

(Feingold and Avigad, 1980; Duffus and Duffus, 1984).

The UDP-glucose may be used as a direct precursor in the formation of sucrose and cellulose. Although UDP-glucose may serve as a precursor to the formation of starch, the starch synthase enzymes show a preference for ADP-glucose. Conversion of UDP-glucose to ADP-glucose occurs via G1P. The UDP-glucose and fructose are released in the degradation of sucrose by sucrose synthase. Fructose may be used in the synthesis of GDP-mannose and also, after conversion to G1P, in the synthesis of UDP-glucose. The UDP-glucose may be converted directly to its epimer UDP-D-galactose by the epimerase enzyme UDP-D-glucose-4-epimerase. Another epimerase UDP-L-arabinose-4-epimerase catalyses the interconversion of the epimers UDP-L-arabinose and UDP-D-xylose (Duffus and Duffus, 1984).

The UDP-glucose is also used as a direct precursor to the formation of UDP-glucuronic acid, which is a direct precursor of UDP-D-galacturonic acid and UDP-D-xylose, in a reaction catalysed by UDP-D-glucose dehydrogenase. The formation of UDP-D-

galacturonic acid from UDP-D-glucuronic acid is catalysed by UDP-D-glucuronate-4-epimerase. Xylose is derived from UDP-D-glucuronic acid following decarboxylation in a reaction catalysed by UDP-D-glucuronate decarboxylase (Duffus and Duffus, 1984).

1.2.2 Sucrose

Sucrose is the most common form in which sugar is transported in higher plants. The reasons for this are not clear but are suspected to involve its relatively unreactive chemical structure. In animal systems, the more reactive monosaccharide, glucose, can be used for transport because the transport system (the blood stream) is extracellular. Blood glucose is effectively sequestered outside the cytosol and does not encounter cellular enzymes until it is taken up across a plasma membrane. In green plant cells, sugars are synthesized internally within the cytosol, but the cell also has a full complement of glycolytic enzymes for energy maintenance during the dark period. Thus an inert molecule is an advantage, preventing a futile cycle of simultaneous carbohydrate synthesis and degradation (Lucas and Madore, 1988). The importance of sucrose in plants is related to the fact that it plays three vital and inter-related roles in plant metabolism. It is a major product of photosynthesis, the principal form of translocated C and the dominant storage sugar. Most of the world production of sucrose comes from two sources: sugarcane, which supplies 55 % of the world requirement for sucrose, and sugarbeet which supplies 45 % (Davies, 1974).

Sucrose is a disaccharide formed by the glycosidic linkage of the pyranose form of glucose to the furanose form of fructose. Since sucrose is also non-reducing, the linkage must be between C-1 of glucose and C-2 of fructose. The linkage is β with respect to the hydroxyl of fructose and α with respect to the hydroxyl of glucose. The full name for sucrose is β-D-fructofuranosyl-α-D-glucopyranoside. The solubility of sucrose in water is exceedingly high (179 g 100 $m\ell^{-1}$, 0°C; 487 g 100 $m\ell^{-1}$, 100°C) and most biological activities are not affected by sucrose even at high concentrations. Thus sucrose is further suited for being the mobilisation form of sugar from one tissue to another. The free energy of hydrolysis for sucrose is $\Delta G' = 29,3$ kJ which is larger than the -16,8 kJ for the α-(1→4) glycosidic linkage in the starch molecule (Akazawa and Okamoto, 1980) and almost as large as that for the sugar nucleotides (-30,6 kJ for ATP) (Lewis, 1984).

1.2.2.1 Synthesis of sucrose

Sucrose is synthesized in the cytosol from triose phosphates (DHAP and GAP) exported from the chloroplasts via a specific phosphate translocator in the chloroplast envelope, in exchange for Pi. In the cytoplasm the triose phosphates are converted to G1P through a series of reactions (reactions 1.2 to 1.5). Through reaction 1.13, G1P is converted to the sugar nucleotide UDP-glucose. There are two pathways for conversion of UDP-glucose to sucrose. In plants such as sugarcane:

UDP-glucose + F6P → sucrose-6-phosphate + UDP

catalysed by sucrose phosphate synthase; (1.15)

Sucrose-6-phosphate + H_2O → sucrose + Pi

catalysed by sucrose phosphatase. (1.16)

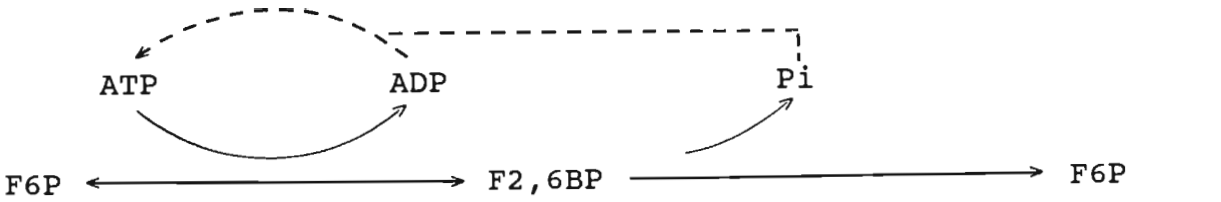
In some other plants the following pathway exists:

UDP-glucose + fructose → UDP + sucrose

catalysed by sucrose synthase. (1.17)

Sucrose may be hydrolysed to fructose and glucose in a reaction catalysed by invertase. Both acid and neutral invertases are present in plant tissues and in general appear to be involved in sugar uptake. For example, sucrose derived from leaf photosynthesis can be stored in sugarcane stems only after first being hydrolysed by an acid invertase localized in the cell walls. Invertase may be involved in the formation of reducing sugars in potato (Solanum tuberosum) tubers as a result of sucrose hydrolysis during cold storage (Duffus and Duffus, 1984; Hall and Rao, 1987).

Sucrose synthesis in the leaves needs to be regulated by balancing availability of photosynthate (triose phosphates) against demand by plant sinks for sucrose. The regulatory metabolite fructose-2,6-bisphosphate (F2,6BP) present in the cytosol of leaves at micromolar concentration is a potent inhibitor of the cytosolic fructose-1,6-bisphosphatase (FBPase) enzyme. The FBPase is a key enzyme in sucrose synthesis as it catalyses the first irreversible reaction in the conversion of triose phosphates to sucrose in the cytosol (F1,6BP → F6P + Pi; reactions 1.2 to 1.5). Fructose-2,6-bisphosphate is synthesized by two enzymes in the following manner:



Fructose-6-phosphate,2-kinase (F6P,2Kase)

F6P and Pi activate F6P,2Kase

DHAP and 3-phosphoglycerate (PGA) inhibit F6P,2Kase

Fructose-2,6-bisphosphatase (F2,6BPase)

F6P and Pi inhibit F2,6BPase

(In maize DHAP and PGA also inhibit F2,6BPase). (1.18)

The concentration of F2,6BP will depend on the activity of these two enzymes, which synthesize and degrade it. Fructose-6-phosphate,2-kinase can catalyse both the formation of F2,6BP and its degradation, whereas F2,6BPase only catalyses the degradation of F2,6BP. The activity of F6P,2Kase and F2,6BPase can be modified by metabolites. Fructose-6-phosphate,2-kinase is activated by F6P and Pi, whereas F2,6BPase is inhibited by its products F6P and Pi. Furthermore, F6P,2Kase is inhibited by 3-phosphoglycerate (PGA) and DHAP; DHAP is the major triose phosphate, accounting for 98 % of the total triose phosphates.

Fructose-2,6-bisphosphate functions to control sucrose metabolism in the leaves in the following way. In the light, chloroplasts export triose phosphates to the cytosol where they are converted to sucrose. The rate of triose phosphate conversion to sucrose must be regulated with respect to the rate of CO_2 assimilation (which determines triose phosphate availability); without such regulation, stromal metabolism could be depleted rapidly and photosynthesis strongly inhibited under suboptimal conditions. A feed-forward control of photosynthetic sucrose formation involving F2,6BP and FBPase exists which prevents this from happening. As photosynthesis is reduced under limiting

in less inhibition of the cytosolic FBPase. The resulting increase of G1P, and decline of Pi, will stimulate UDP-glucose pyrophosphorylase (reaction 1.13) and sucrose phosphate synthase (reaction 1.15) (Huber, 1986; Stitt, 1986).

It appears that in maize some of the enzymes involved in sucrose synthesis are enriched in the mesophyll cells, and it has been established that F6P,2Kase and F2,6BPase are almost certainly exclusively located in the mesophyll tissue. Starch synthesis has been shown to be primarily located in the bundle sheath cells of maize, so it appears that the enzymes and regulatory mechanisms of sucrose and starch metabolism are strictly compartmented between the mesophyll and bundle sheath cells (Huber, 1986).

1.2.2.2 Sucrose utilization

After synthesis sucrose may be utilised in the cell of synthesis for respiratory requirements through glycolysis and the TCA cycle or the OPP pathway. Intermediary metabolites of these pathways may be used for the synthesis of carbohydrates (mono, oligo and polysaccharides), proteins, lipids, nucleic acids etc. Sucrose may also be stored in the cell of synthesis. Most of the sucrose produced during photosynthesis will, however, be translocated to other sinks of the plant where it may also be respired, used in the production of other metabolites and/or stored. In cereals, much of the sucrose translocated to the developing grain is converted to starch. The protein synthesized in the developing grain contains the full range of amino acids, whereas the amino

acids entering the developing grain from the phloem are limited largely to aspartate/asparagine and glutamate/glutamine. It appears that the C skeletons required for the synthesis of the other amino acids are derived from intermediates of carbohydrate degradation mostly from the TCA cycle. The fatty acids for the synthesis of storage triglycerides are most likely derived from acetyl-CoA, a product of pyruvate oxidation (Duffus and Duffus, 1984).

Uptake and storage of sucrose has been extensively studied in the stem cells of sugarcane. After hydrolysis in the apoplast by invertase, tightly bound to the cell wall, glucose and fructose are transported into the cytosol of the storage cells where they may be rapidly reconverted to sucrose by a sequence of reactions involving hexokinase, phosphohexoisomerase, phosphoglucomutase, UDP-glucose pyrophosphorylase, sucrose phosphate synthase and sucrose phosphatase. The final reaction is accompanied by the transfer of sucrose into the vacuole. On the other hand, the mechanism of sucrose unloading and storage in sugarbeet roots appears to be rather different. In this case it appears that sucrose enters the vacuole without hydrolysis. The high vacuolar concentrations suggest that transport across the tonoplast involves active transport, possibly similar to that for phloem loading (ap Rees, 1988).

1.2.3 Starch

1.2.3.1 Structure, occurrence and location

The starch grain itself varies in both size (1 to 100 μm in diameter) and shape (spherical, polygonal, elliptical, grooved, etc.) between species and with environmental conditions. Czaja (1978) describes 14 morphological types and discusses their taxonomic distribution. The grains consist principally of two polymers, amylose and amylopectin, although material of an intermediate nature also occurs, especially in starches rich in amylose. Although little studied compared to the two main polymers, this material may be important in the synthesis of the granules themselves (Banks and Greenwood, 1975 cited by Lewis, 1984.)

Amylose is an essentially linear, helically structured α-D-(1→4) glucan with a degree of polymerisation of several thousand. A few α-D-(1→6) linked branches are present (Banks and Greenwood, 1975 cited by Lewis, 1984). This is the component of starch which binds iodine and stains blue. The iodine occupies the cavity of the helix in which there are six glucose residues per turn. Amylopectin, an even larger molecule ($DP>10^4$), is a large branched glucan consisting of α-D-(1→4) linked chains with an average length of 19 to 26 units joined together by α-D-(1→6) linkages (about 4 to 5 % of the total). This stains purple but does not bind iodine appreciably, probably because the large number of branch points disrupts formation of the iodine-binding helix. The chains of both polymers may be regarded as repeated

units of maltose with isomaltose as the disaccharide linking the chains in the amylopectin. This determines that amylose essentially has one reducing and one non-reducing end, whereas amylopectin has one reducing but many non-reducing terminal glucosyl units (Lewis, 1984).

The amount of starch produced by the edible portion of three grain crops (wheat, rice and maize) and three tuber crops (potato, yam (Dioscorea esculenta) and cassava (Manihot esculenta) in a year exceeds 7×10^8 t, of which about 6×10^8 t is contributed by the cereal grains (Jenner, 1982). Starch accumulates to the greatest amount in the grain of cereal crops. Starch normally accounts for 65 to 75 % of the dry mass of the caryopsis of grasses in their mature dry state. As most of this starch is deposited in the endosperm, the embryo and pericarp containing very little, values for the endosperm alone exceed 80 %. Isolated mutations of maize and barley have much less than the normal 75 % starch in the grain. For example, mutations of barley (notch-1 and notch-2) with starch contents depressed by about 50 % and a mutation of maize (shrunken-2) with only 25 to 30 % as much starch as normal (Jenner, 1982). The seeds of legumes have a lower percentage of starch than grass seeds but because they are heavier the seeds of pea and bean (Phaseolus spp.) contain as much starch as the heaviest of the grass seeds. Field pea (Pisum arvense) has 16 % starch and garden pea (Pisum sativum) has 32 % starch in the seed on a dry mass basis (Jenner, 1982). All fleshy fruits contain starch, but in many only traces can be detected, and the only starch granules to be found are restricted to the chlorophyllous layers on the outside of the

fruit. Among temperate fruits, the pome fruits are the only ones in which much starch is deposited in non-chlorophyllous regions e.g. apple (Malus pumila) variation of 6 to 34 % starch according to genotype. The tropical fruits such as the banana (Musax paradisiaca) can contain nearly 90 % of the dry mass of the pulp as starch. Vegetative underground storage organs can contain, depending on genotype, 60 to 80 % starch as dry mass in potato, 88,7 % starch as dry mass in yam root and 27 to 30 % starch as dry mass in cassava root (Jenner, 1982).

It is clear from the above discussion that the occurrence and distribution of starch varies between species and between genotypes within species. The occurrence and distribution of starch also varies between different parts of the plant and within leaves, during the diurnal cycle and ontogenetic development of the plant. In isolated chloroplasts, starch can be identified as an early product of photosynthesis. In intact plants, starch is synthesised during the day and mobilised by night and can account for up to 30 % of the total CO_2 assimilated (Herold, 1984). This diurnal variation as seen in foliage levels is the shortest detectable cycle in starch metabolism. More gradual losses and gains occur in other organs of the plant with ontogenetic development. Kalt-Torres, Kerr, Usada and Huber (1987) found that in 22 day old maize plants (leaf eight emerging from whorl) starch levels in the leaves varied between less than 10 mg dm^{-2} at sunrise and a peak of 40 mg dm^{-2} at sunset; the latter value representing 76 % of the non-structural carbohydrate pool. In the immature and mature maize stem, starch does not constitute a significant proportion of the dry mass. However,

the maize stem may be forced to accumulate large amounts of starch when grain development is prevented (Freeman, Bocan and Zobel, 1972). Freeman et al. (1972) found that starch granules from stems of mature maize plants and sorghum plants were about a third as large as average granules from endosperm tissue of the same species and contained only 1/3 to 1/2 as much amylose.

The primary site for starch deposition in cereal grains is the endosperm of the seed. Starch may be found in detectable quantities in the endosperm of barley as early as three days after fertilization (Baxter and Duffus, 1971). In maize during the transition from endosperm cell division (lag phase) to cell enlargement (linear grain fill phase) the rate of starch deposition rose from 0,005 mg kernel^{-1} day^{-1} (10 d after silking) to 7,44 mg kernel^{-1} day^{-1} (16 d after silking). Between 10 and 12 d after silking the proportion of the dry mass attributable to starch rose from 1,5 to 9,2 % (Tsai, Salamini and Nelson, 1970). Deposition rates of endosperm starch as high as 10 mg kernel^{-1} day^{-1} during the linear phase of grain fill have been recorded for maize. In contrast much lower rates of 1 to 2 mg kernel^{-1} day^{-1} have been recorded for the smaller grained cereals such as wheat, oat (Avena sativa), rice, barley and rye (Secale cereale) (Jenner, 1982). As the photosynthetically active parts of the plant become senescent and there is a progressive loss of photosynthetic capacity of the plant, termination of grain fill occurs in the maize kernel by the formation of a suberized layer of tissue between the pedicel and the endosperm, the so-called black layer formation (Daynard and Duncan, 1969).

1.2.3.2 Starch synthesis and pattern of granule formation

Under conditions where the CO_2 fixation rate in chloroplasts exceeds the rate at which triose phosphates can be converted to sucrose in the cytoplasm, synthesis of starch occurs in the chloroplast stroma (Hall and Rao, 1987). The pathway to starch begins with the conversion of triose phosphates (GAP and DHAP) to G1P through a series of reactions (reactions 1.2 to 1.5). The next step is the reaction of G1P with ATP or UTP as follows:

G1P + ATP(UTP) → ADP(UDP)-glucose + PPi

catalysed by ADP(UDP)-glucose pyrophosphorylase. (1.19)

ADP(UDP)-glucose may also be formed by reversal of the sucrose synthase reaction:

sucrose + ADP(UDP) ⇌ fructose + ADP(UDP)-glucose. (1.20)

The question of which reaction is the major route for the formation of starch is still contentious and is dependent on plant species and organ. Since sucrose synthesis does not occur in the stroma of the chloroplast and there is mostly an export of triose phosphates from the stroma it is uncertain which sugar nucleotide (ADP-glucose or UDP-glucose) is used by starch synthase in the formation of starch in leaves. In leaves, starch synthase is solely specific for ADP-glucose. Moreover, starch synthases in tissue of storage organs also appear to be specific for ADP-glucose. Only storage organ tissue starch synthase bound to starch granules can utilize UDP-glucose in addition to ADP-glucose. However, the rate of glucosyl transfer from UDP-glucose is usually 1/3 to 1/10 that observed for ADP-glucose (Preiss and Levi, 1979). In reserve tissue storing starch, sucrose is

considered to be the primary substrate for starch synthesis. The principal products of sucrose metabolism are UDP- and ADP-glucose, fructose and some glucose. Since the preferred nucleotide donor for starch synthesis is considered to be ADP-glucose, the principal fate of the three remaining products is probably conversion to ADP-glucose (Duffus and Duffus, 1984).

The shrunken-1 mutation that reduces sucrose synthase activity in maize endosperm reduces starch accumulation by 30 % while the shrunken-2 and brittle-2 mutations that decrease ADP-glucose pyrophosphorylase activity decrease starch accumulation by 70 to 75 %. The findings in these studies of the mutant endosperms suggest that practically all starch synthesis in maize endosperm is via the sugar nucleotide or ADP-glucose pathway and via the starch synthase reaction (Preiss, 1982). Once formed ADP(UDP)-glucose can transfer glucose to lengthen the amylose chain of a starch molecule in the following way:

$(C_6H_{10}O_5)n + ADP(UDP)\text{-glucose} \rightarrow (C_6H_{10}O_5)n+1 + ADP(UDP)$ (1.21)

catalysed by starch synthase (Bassham, 1979).

Alternatively, starch phosphorylase may catalyse the formation of starch in the following way:

$G1P + (C_6H_{10}O_5)n \rightleftharpoons Pi + (C_6H_{10}O_5)n+1.$ (1.22)

However, the high [Pi] to [G1P] in leaves and storage organ tissue would favour starch degradation by this enzyme. Nonetheless, the possibility that phosphorylases may under certain circumstances function synthetically cannot be discounted (Jenner, 1982; Duffus and Duffus, 1984).

Formation of the α-D-(1→6) branch point linkages in amylopectin is catalysed by a branching enzyme also called the Q-enzyme (Preiss, 1982).

The partitioning of triose phosphates between sucrose synthesis in the cytoplasm and starch formation in the chloroplast is regulated by a number of factors. The final step of the sucrose biosynthesis pathway in the cytoplasm liberates Pi and this Pi must be re-imported into the chloroplast in order to export triose phosphates into the cytoplasm via the phosphate translocator in the chloroplast envelope. Another potential control of sucrose synthesis is via the regulation of the activity of FBPase. This enzyme which hydrolyses FBP is inhibited by F2,6BP, a cytoplasmic metabolite, whose concentration in leaves varies with incident light intensity (Section 1.2.2.1). A third controlling factor is the availability of Pi in the stroma for photosynthesis. Photosynthesis is maximal when processes such as sucrose synthesis in the cytoplasm release Pi so that it may be returned to the stroma at a non-limiting rate. However, should sucrose synthesis decrease resulting in a decrease in the export of triose phosphates, photosynthesis can only proceed as fast as Pi is released from the synthesis of starch in the stroma by the action of the enzyme ADP-glucose pyrophosphorylase. It appears that when [PGA] is high and stromal [Pi] is low, the activity of ADP-glucose pyrophosphorylase is greatly increased. This allosteric activation of the enzyme by a high [PGA]/[Pi] ratio ensures that it is most active when conditions best favour starch synthesis (Edwards and Walker, 1983; Hall and Rao, 1987).

The synthesis and accumulation of starch occurs in the non-photosynthetic plastids or amyloplasts such as maize endosperm as well as in the photosynthetic plastids or chloroplasts. In chloroplasts starch turnover is rapid whereas in amyloplasts starch synthesis predominates during grain fill. The initiation of the first α-(1→4) bond within the plastid is still a matter for debate. There appear to be three possibilities: (i) primers (short lengths of α-D-(1→4)-glucose) are produced by specific enzymes; (ii) starch synthase can catalyse de novo the formation of α-(1→4) bonds; or (iii) the enzymes of synthesis have a small priming section as part of their molecular structure (Jenner, 1982). Actual growth of the starch granule has not been studied in vivo. Concepts on starch growth have been developed from studies of granules obtained destructively from a more or less heterogeneous collection of cells (Jenner, 1982). Evidence from in vivo ^{14}C incorporation into granules of storage organs (potato tuber, maize endosperm, bean and tobacco (Nicotiana tobacum) leaves) supports the postulate that the starch granule grows by apposition of material to its surface (Jenner, 1982). Recent models show the radial arrangement of amylopectin molecules from the centre of the granule with double helixes of the outer chain of amylopectin creating the 'concentric growth rings' observed in light studies as a result of periodic variations in refractive index (Kainuma, 1988). Amylose may exist in a random or helical arrangement without binding to an amylopectin molecule (Kainuma, 1988). All starches have a lower content of amylose than amylopectin and overall the amylose content is generally in the range 11 to 35 %. However, again enormous differences exist between species, and between genotypes within species. For

example, the amylose percentage of maize starch ranges from 20 to 36 %, potato starch from 18 to 23 % and rice from 8 to 37 % (Duffus and Duffus, 1984).

The starch granules grow steadily in size within the surrounding double membrane of the plastid reaching a maximum average diameter in wheat kernels of 20 to 30 μm, in maize kernels of 25 μm and in potato tubers of 100 μm (Duffus and Duffus, 1984). The starch grains of maize endosperm are round, but they may take on polygonal shapes as the endosperm cells become packed with expanding starch granules (Boyer and Shannon, 1987). Wheat endosperm starch grains have a characteristic lenticular shape with a peripheral groove. Starch granules in leaves are very small and disc shaped as a result of constant formation and degradation (Duffus and Duffus, 1984).

1.2.3.3 Starch degradation

Starch degradation occurs in three stages: (i) starch granules are broken down to maltodextrins; (ii) the maltodextrins are converted to glucose and G1P; and (iii) the glucose and G1P are metabolized or transported to cells that require them. Initial attack on the starch granule is by an endoamylase, α-amylase. This enzyme hydrolyses α-(1→4) linkages in both amylose and amylopectin. The products of hydrolysis by this enzyme retain the α-configuration and only slowly undergo mutorotation. Final products of amylose hydrolysis by α-amylase are dependent on the concentration of the enzyme. With low concentrations of enzyme, traces of glucose, maltose, maltotriose and maltodextrins of 6 to

8 glycosyl units are the final products. With high concentrations of the enzyme, the products are maltose (about 90 %), maltotriose and glucose. The α-amylase hydrolyses both the outer and inner chains of amylopectin but its action is hindered at the α-(1→6) branch points. The products of hydrolysis are glucose, maltose, maltotriose and α-dextrins (branched oligosaccharides usually containing 5 to 10 glucosyl units) (Duffus and Duffus, 1984; Stitt and Steup, 1985; Steup, 1988).

The β-amylase (or exoamylase) hydrolyses alternate α-(1→4) linkages in starch-type polysaccharides releasing maltose from the non-reducing ends of the molecule. Some amyloses are completely hydrolysed by β-amylase but others are not. The β-amylase only attacks external chains of amylopectin and cannot bypass the α-(1→6) branch points to attack the interior. Final products of hydrolysis are maltose whose reducing group has the β configuration, and high molecular mass limit dextrins with two or three glucose residues external to the branch points. Phosphorylases in the presence of inorganic phosphate attack polysaccharides containing α-(1→4) linked D-glucose residues releasing G1P. Phosphorylase will degrade amylose and the outer chains of amylopectin but it is probable that it can attack starch granules only after breakdown has been started by α-amylase. The α-glucosidases hydrolyse the α-(1→4) linkages of dextrins from the non-reducing end specifically releasing glucose. D-enzyme is a transglucosylase which catalyses the reversible condensation of α-(1→4) glucans giving a redistribution of the glucosyl residues and releasing free

glucose. This enzyme may function to produce primers for the synthesis of amylose or to help in starch degradation by producing from small limit dextrins larger molecules which can be readily attacked by phosphorylase. Debranching enzymes hydrolyse the α-D-(1→6) glycosidic linkages in amylopectin and α-dextrins (Duffus and Duffus, 1984; Stitt and Steup, 1985; Steup, 1988).

Starch degradation in germinating barley seeds begins with the conversion of 'latent' β-amylase to the 'active' form by thiol reducing agents. Activation of β-amylase follows the release of gibberellins from the embryo or their exogenous application. Unlike β-amylase, α-amylase is synthesised de novo during germination. This synthesis occurs in the aleurone layer of barley and is triggered by endogenous or exogenous gibberellin. Following synthesis, α-amylase is secreted into the endosperm. In seeds other than barley, α-amylase synthesis may occur in the scutellum as has been reported for maize (Duffus and Duffus, 1984).

In leaf cells α-amylase and phosphorylase largely occur within the chloroplast whereas β-amylase and the other enzymes mentioned occur in the cytoplasm. Major products of starch degradation in leaves are PGA, maltose, glucose and small amounts of G6P and ribose-5-phosphate. Some of the products of starch degradation will be used as substrate for chloroplast metabolism. Most of the products, however, will be exported from the chloroplast as triose phosphates, PGA and sugars. These in turn are available

for metabolism in the cytosol and could be respired or used for the synthesis of sucrose (Duffus and Duffus, 1984; Stitt, 1984).

Control of starch degradation is again largely determined by rates of photosynthesis. During the night the ratio of [PGA]/[Pi] is low. The activity of the allosteric enzyme ADP-glucose pyrophosphorylase is reduced. Export of triose phosphates out of the chloroplast increases in response to respiration and sucrose synthesis in the cytoplasm. Starch degradation occurs in order to supply triose phosphates and sugars for export to the cytosol (Duffus and Duffus, 1984; Stitt, 1984).

1.3 Carbohydrate partitioning as influenced by translocation and source-sink relations

Translocation in plants is the process whereby photosynthate is transported from sites of production or remobilization ('sources') to regions of utilization or storage ('sinks'). The translocation pathway occurs within the cytoplasm of cells (symplastic transfer) or in the extracellular space (apoplastic transfer). Symplastic translocation includes short distance transfer from cell to cell via intercellular connections called plasmodesmata and long distance transfer within the cells of the phloem. The phloem tissue within the vascular bundles consists of elongated sieve elements arranged end to end in longitudinal rows to make the conducting sieve tubes. Associated with and connected to the sieve tubes by plasmodesmata are companion cells. Companion cells are formed by divisions of sieve element

precursors so that sieve elements and their companion cells are ontogenetically related. In general, companion cells resemble secretory cells in their ultrastructure, and their ability to deliver sugar into the sieve tube against a positive gradient suggest a secretory function. The protoplasts of companion cells are those characteristic of metabolically active cells. Their nuclei and nucleoli are relatively large. The cells contain plastids, often differentiated as chloroplasts, numerous large mitochondria, and some endoplasmic reticulum. In certain taxa of dicotyledons, companion cells develop cell wall ingrowths emphasizing their secretory nature (Esau, 1977).

1.3.1 Translocation

The process of translocation may be divided into three broad processes: (i) phloem loading; (ii) phloem transport; and (iii) phloem unloading.

1.3.1.1 Phloem loading

Phloem loading is the selective and active accumulation of sucrose in the sieve tube elements from surrounding source cells. To simplify the discussion the movement of sucrose from the sites of synthesis in the cytosols of leaf mesophyll cells to the phloem will be considered. The process of phloem loading involves two main steps: (i) the transfer of sucrose from mesophyll cells to the region of the sieve tube elements; and (ii) the uptake or loading of sucrose into the sieve tube elements (Giaquinta, 1983).

Transfer to sieve tube region

Transfer of sucrose from the mesophyll cells to the sieve tubes may be symplastic, apoplastic, or a combination of both (Giaquinta, 1983; Daie, 1985). If symplastic transport occurs it would be expected that mesophyll cells would retain ^{14}C photosynthate being transferred to the sieve tubes. Very little leakage of ^{14}C photosynthate occurred from isolated and intact mesophyll cells from Papaver spp. and Spinacia spp. (Kaiser, Paul and Bassham, 1979).

A symplastic transfer of sucrose between the mesophyll and bundle sheath cells of C_4 plants is also indicated. In maize for example extensive plasmodesmatal connections exist among the mesophyll cells and between individual mesophyll and bundle sheath cells (Evert, Eschrich and Heyser, 1978). In maize leaves, the outer tangential and radial walls of the bundle sheath cells contain a continuous suberin lamella whereas the inner tangential walls contain suberin mainly at the sites of plasmodesmata aggregation (Evert, Eschrich and Heyser, 1977). This further indicates that the movement of photosynthate through the bundle sheath is restricted largely to a symplastic pathway.

Although structural studies of the distribution and frequency of plasmodesmatal connections of the various leaf cells for different plant species are sparse, it appears from available evidence that the movement of photosynthate from the mesophyll cells to the region of the sieve tube occurs via a symplastic route.

Transfer into or loading of the sieve tube elements

There is currently intense debate over whether the transfer of photosynthate into the sieve tube-companion cell complex of the phloem from the surrounding mesophyll cells occurs through the symplast or apoplast (Lucas and Madore, 1988). Studies conducted in the 1970s and early 1980s had erroneously concluded that the kinetic analyses of the uptake of exogenously supplied sucrose to excised and intact leaf tissue reflected solely the transport mechanism operating at the sieve element-companion cell complex (Giaquinta, 1983; Lucas and Madore, 1988). Kinetic analysis studies conducted in the 1970s and early 1980s on the uptake of exogenously supplied sucrose to excised and intact leaf tissue indicated that uptake of sucrose across the plasmalemma of leaf tissue occurs via the combination of a saturable, energy dependent process and a first order linear kinetic mechanism. The saturable component has been assumed to indicate the presence of a sucrose-H^+ cotransport mechanism whereas it is not certain whether the linear component represents simple diffusion or facilitated diffusion through the lipid bilayer (Lucas and Madore, 1988). It was then theorized that phloem loading involved the exudation of photosynthate from the mesophyll cells into the apoplast and the active loading of this photosynthate from the apoplast into the sieve elements by the sucrose-H^+ cotransport system. The sucrose-H^+ cotransport system is thought to operate through the cotransport of sucrose with protons moving down their electrochemical gradient maintained by a proton-pumping ATPase at the plasmalemma. The influx of protons accompanied by sucrose is coupled to a charge compensating efflux

of K^+ ions. It has also been suggested that the exudation of photosynthate from the mesophyll cells in the region of the sieve elements involves an active proton cotransport mechanism. Anatomical studies have, however, revealed no specific morphological features indicating the specialization of mesophyll cells in the region of the sieve elements for active exudation of photosynthate (Giaquinta, 1983). However, kinetic analyses indicated the presence of a saturable and linear component of sucrose uptake in parenchyma tissue of sugarbeet petiole slices (Maynard and Lucas, 1982) and inner parenchyma, chlorenchyma and vascular bundles of mature onion (Allium cepa) leaves (Wilson, Oross and Lucas, 1985).

It appears then that the presence of a saturable and a linear component of uptake must be an ubiquitous feature of the plasma membranes of a wide variety of cell types within the mature leaf. Kinetic analyses obtained on leaf tissue therefore represents the retrieval of sugars by the various tissues and cannot be equated with the specific process of phloem loading per se (Lucas and Madore, 1988). From an anatomical viewpoint it has long been known that there are plasmodesmatal connections between the mesophyll and sieve element-companion cell complex. However, it has often been argued in favour of apoplastic transfer that low frequency of plasmodesmatal connections, as in sugarbeet, would prevent the expeditious transport of photosynthate from mesophyll cells to sieve tube elements if it occurred via the symplasm (Evert and Mierzwa, 1986). However, frequency analysis does not take into consideration the variation in plasmodesmatal structural diversity and efficiency (Lucas and Madore, 1988).

By injecting fluorescent dyes into the cytosol of single mesophyll cells and monitoring its movement the transport rôle of the symplastic network may be determined. Madore and Lucas (1986) micro-injected Lucifer Yellow CH, an intensely fluorescent 4-aminonapthalimide dye into mesophyll cells of sugarbeet and morning glory (Ipomoea tricolor). In order to overcome the problem of dye that is injected into the vacuole (rather than the cytoplasm) not passing through the tonoplast, the dye was encapsulated in small (0,2 μm diameter) phospholipid vesicles (liposomes). Any dye injected into the vacuole then fused with the tonoplast and the dye was released into the cytoplasm. Subsequent cell to cell movement of the dye indicated the existence of symplastic continuity from the mesophyll to the minor veins of the source leaf of the plants studied. Thus the free permeability of the relatively small Lucifer Yellow molecule (457 daltons) suggests that there is no barrier to the diffusion of small molecules through the leaf symplast. Extension of the dye tracing techniques to other plant species may shed light on the transport potential of symplastic networks. Evidence has accrued that the plasmodesmata may, in fact, regulate the flow of solutes through the symplasm (Erwee and Goodwin, 1985). Lucas and Madore (1988) from the available evidence speculate the existence of H^+-ATPase protein(s) in the neck regions of the plasmodesmata controlling the flow of solutes through the symplasm.

The selectivity of the phloem in transporting specific ('phloem-mobile') photosynthate, has also been used as an argument in support of an apoplastic loading step, as selective release of

solutes to the apoplast by the mesophyll, or selective retrieval of solutes by the phloem could determine which compounds are transported (Giaquinta, 1983). Although the specific mechanism of selectivity is not known, the ability of Cucurbita pepo mesophyll cells (and other non-phloem tissue) to take up exogenous [^{14}C]stachyose (used by members of the Cucurbitaceae in conjunction with sucrose as a transport sugar) and [^{14}C]galactose, and then metabolize these sugars resulting in labelled sucrose being found as the transport sugar in the phloem (Madore and Web, 1981), may indicate the rôle of non-phloem tissue in symplastically supplying phloem mobile photosynthate to the sieve tubes. In addition, the possibility that sugars may leak out of mesophyll and phloem tissue, may provide the need for uptake systems that retrieve these leaked solutes (Lucas and Madore, 1988). It has been suggested that the tremendously high sugar levels in the phloem may result in a passive leakage of solutes through phloem membrane 'pores' with a steady recapture along the path ('pump and leak' system) maintaining the pressure flow over a long distance (Gifford and Evans, 1981).

In summary: the existence of an operative symplastic network between mesophyll cells and sieve tubes; the apparent ubiquitous distribution of linear and saturable components of sucrose uptake among phloem and non-phloem tissue; metabolism of non-transportable forms of sugars to transportable forms by non-phloem tissue and the possible existence of retrieval systems in phloem and non-phloem tissue argues in favour of symplastic transfer of photosynthate from mesophyll cells to the sieve tube.

However, the possibility of apoplastic phloem loading occurring in specific tissues of specific plants cannot be ruled out.

1.3.1.2 Phloem transport or inter-organ transport

Whether photosynthate is taken up from the apoplast into phloem parenchyma or companion cells via a proton cotransport mechanism or arrives in the phloem parenchyma or companion cells symplastically from the mesophyll cells, evidence suggests that the transfer from the companion cells to the sieve elements occurs symplastically. In the sieve tubes, sugar (in most species almost solely sucrose) reaches very high levels, normally in the range of 200 to 800 mM. This uptake of sucrose in the companion cell–sieve tube complex leads to osmotic uptake of water and hence to a considerable hydrostatic pressure in these cells. Sucrose then moves down the osmotic pressure gradient (Gifford and Evans, 1981). Fisher (1978) found in soybean (Glycine max) that there was a sufficient gradient in sieve tube sucrose between source leaf and sink to create a hydrostatic pressure gradient to drive Münch-type mass flow at the observed rate.

Minor vein sieve tubes extend into stems as bundles and as isolated vascular strands. Numerous bridging strands occur between and within bundles in lamina, petiole and stem; and in grasses many anastomoses also occur at the nodes. This enables photosynthate transported in the phloem to reach all parts of the plant. The complications of this network of sieve tubes is that sinks must establish sufficient gradients to drive the movement

of photosynthate through the various links to them (Giaquinta, 1983).

1.3.1.3 Phloem unloading

To exit from the lumen of the phloem, solutes can either cross the sieve tube plasma membrane into the cell wall (apoplast) and diffuse to sink cells, or pass into the symplasm of adjacent cells via plasmodesmata. Unloading via the symplasm will rely on bulk flow of solution through the plasmodesmata or solute diffusion in the absence of solvent flow. In sink tissues considerable variation exists in the frequency of plasmodesmatal connections from sieve tubes to companion cells, phloem parenchyma or other intermediary cells (Thorne, 1986). Companion cells, vascular parenchyma and other cells in some species are again implicated in functioning as transfer cells, actively unloading photosynthate from the sieve tubes to the sink cells.

The anatomical features and physiological characteristics of the various sink tissues found within a plant and among plant species suggest that several mechanisms and structural specializations regulate phloem unloading. For instance apoplastic unloading is required in some reproductive tissue, e.g. maize kernels, bean and soybean seeds, because there are no plasmodesmatal connections between the maternal phloem strands and the developing endosperm (Thorne, 1982; Thorne and Giaquinta, 1984).

Figure 1.2 (Thorne, 1986) illustrates three generalized types of unloading, and serves as an overview of the processes. In Figure

1.2 a highly stylized sieve tube is shown connected to an adjacent receiver cell by a plasmodesma. Small circles on the perimeter of these components of the transport system represent membrane-bound carriers or sites of selective or facilitated transport.

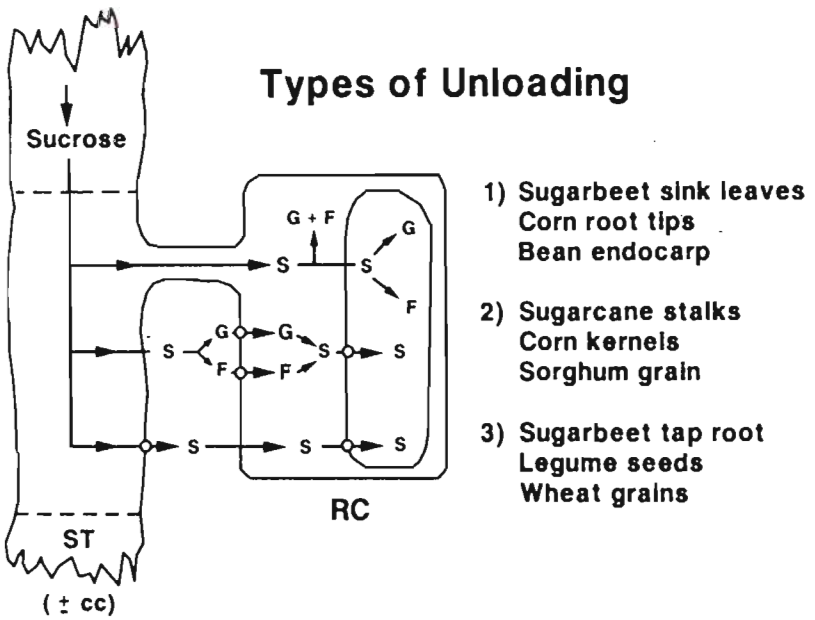


Figure 1.2 Stylized summary of representative unloading mechanisms. ST, sieve tube; RC, receiver cell or sink cell; CC, companion cell; S, sucrose; G, glucose; F, fructose. The receiver cell's vacuole is represented by an oval, and plasmodesma is shown connecting the sieve tube and receiver cell in type 1. Small circles represent solute carriers (Thorne, 1986, P.213)

In type 1 loading the symplastic pathway as shown may be favoured energetically over an apoplastic route since membrane transport is avoided. The possible hydrolysis of sucrose within the cytoplasm or vacuole is shown after entry into the receiver cell.

Type 2 unloading has been extensively studied in sugarcane stems (Glasziou and Gayler, 1972). Sucrose unloading in sugarcane involves a rather complex series of steps: (i) unloading of sucrose from the sieve tubes into the apoplast; (ii) hydrolysis of sucrose by a cell wall invertase; (iii) hexose accumulation into the cytoplasm of storage parenchyma; and (iv) sucrose synthesis in the vacuole. Several lines of evidence indicate that sucrose hydrolysis is the rate limiting step of unloading in sugarcane.

Type 3 unloading also involves the exit of photosynthate from the sieve tubes into the apoplast prior to their accumulation by the receiver cells. In these species, however, sucrose is accumulated by receiver cells without being hydrolysed. Lack of randomization following uptake of asymmetrically labelled sucrose has been used as an indicator that sucrose is not hydrolysed and resynthesized during uptake.

1.3.2 Regulation of the partitioning of translocated photosynthate

Efforts to understand the factors determining the allocation or partitioning of photosynthate among plant organs are motivated by efforts to increase the harvestable yield or economic product of the plant.

From the perspective of agricultural scientists, partitioning of photosynthate occurs between harvestable and non-harvestable organs of the crop. Increases in the yield of the harvestable

component of the crop have been achieved by increasing the so-called harvest index (HI) of the plant defined by Donald (1962) as the ratio of the economic or harvestable yield to total biomass production (HI = economic yield/biological yield). Increases in the HI of crops have largely been achieved through improved cultural practices (fertilization, crop density, weed control, etc.) combined with the selection for genotypes with raised yield quantity and quality. However, as apparent yield plateaus in crops are reached greater effort is being made to improve the efficiency of both the production and partitioning of photosynthate so that greater amounts of photosynthate are transferred to the harvestable organs of the crop for every unit of resource (water, applied nutrients, etc.) used (Snyder and Carlson, 1984).

The production, translocation, partitioning and accumulation of photosynthate within the plant are controlled genetically and moderated by the environment. Raising both the quantity and quality of crop yield may be achieved by selecting for genotypes with increased partitioning into the economic yield or by manipulating the processes involved in the production and partitioning of photosynthate (by, for example, application of exogenous hormones or removal of competitive sinks). Clearly, upper limits exist to the degree to which photosynthate may be partitioned to the harvestable organs without jeopardizing the capacity of the plant to support the yield component both structurally and nutritionally.

Any efforts to increase crop productivity by improving the efficiency of the production and partitioning of photosynthate must be based on strategies that have a clear understanding of the genetically governed, but environmentally influenced, regulation of photosynthate production and partitioning. Regulation of the amount of photosynthate available for the growth and maintenance of the various plant organs may occur during: (i) production or remobilization in the source; (ii) loading of photosynthate from the source into the translocation pathway; (iii) the process of translocation; (iv) unloading of the photosynthate from the translocation pathway; and (v) during uptake and compartmentation or utilization in the sink.

Simply put, the debate is whether the patterns of photosynthate partitioning and final harvestable yield are determined or limited by processes at the source (including phloem loading) often termed source activity or source strength, or by the process of translocation or finally by processes at the sink including phloem unloading often termed sink activity or sink strength.

1.3.2.1 Source strength and export of photosynthate

Photosynthate production

At the whole plant level production of photosynthate is determined by whole plant photosynthesis. Potential gross photosynthesis of a plant is a product of the photosynthetic

activity or rate per unit area of photosynthetic tissue (usually expressed as the CO_2 exchange rate per unit leaf area (CER)) and the total photosynthetic tissue area (usually expressed as leaf area). Although researchers have found considerable variation among species in CER (Yoshida, 1972) there is no evidence to suggest that selection for increased yields in crops has selected for genetic increases in the CER of, among others, wheat (Dunstone, Gifford and Evans, 1973), maize (Duncan and Hesketh, 1968) and sugarcane (Bull, 1971). In fact, highest CER of wheat, sorghum, pearl millet (Pennisetum typhoides) and cotton have been found in the wild relatives, not in modern genotypes. The CER of crops appears to be correlated with variation in ribulose bisphosphate carboxylase content, specific leaf mass (leaf dry mass per unit area) and stomatal and mesophyll cell conductance. However, selection for increased ribulose bisphosphate carboxylase content may be at the expense of other important enzymes. Selection for specific leaf mass may be negatively correlated with leaf area. Attempts to select for improved stomatal conductance through increased stomatal frequency, length and aperture size are often negated by being negatively correlated, and by final stomatal conductance being determined by the optimal ratio of water loss to C gain (Gifford and Evans, 1981; Edwards and Walker, 1983). Direct selection for increased CER is not always successful either, since it has been possible to select for tall fescues with high growth rate but low CER and vice versa (Wilhelm and Nelson, 1978). A high CER capacity or potential of a crop may, on the other hand, be cancelled by limiting environmental factors such as low ambient CO_2 levels,

incident radiation levels, mineral and water availability, etc. (discussed in Section 1.3.2.5).

Total gross photosynthesis of a plant is also determined by the area of photosynthetic tissue that intercepts incident solar radiation. Since selection for increased yields via increased CER has proved ambiguous, leaf area index (LAI = leaf area per unit ground area) has been widely used as a determinant of dry mass production (Yoshida, 1972). Although increasing LAI raises dry mass production, this relationship is not linear nor does it hold indefinitely because the increased mutual shading of the leaves is accompanied by a decrease in the mean photosynthetic rate per unit leaf area. Additionally LAI does not solely determine the amount of incident solar radiation intercepted; light interception by a canopy of leaves is strongly influenced by the shape, angle, and azimuthal orientation, vertical separation and horizontal arrangement, persistence of photosynthetic tissue and absorption by non-leaf structures (Yoshida, 1972). Of these factors leaf angle in relation to LAI has been singled out as an important factor in the dry mass production of a crop. Mathematical models demonstrate that erect leaves are the most efficient arrangement for maximum photosynthesis when LAI is large. Thus to summarise on a whole plant or crop level the photosynthetic production of photosynthate, assuming optimal growing conditions, is determined largely by the interaction of LAI, leaf photosynthetic rate and leaf angle (Yoshida, 1972).

At the cellular level the availability of photosynthate for export from photosynthetic tissue, which for most plants is sucrose, is determined by the host of processes involved in the metabolism of sucrose. The simplistic view of sucrose export from a source leaf being regulated by the rate of photosynthesis and sink demand is no longer acceptable in the light of recent research advances.

The control of the partitioning of reduced CO_2 in the form of triose phosphates between the metabolism of starch in the chloroplast and sucrose metabolism in the cytosol has been discussed in Sections 1.2.2.1 and 1.2.3.2. Since export of triose phosphates from the chloroplast occurs by a counter exchange of inorganic phosphate, the synthesis and export and/or compartmentation of sucrose, which results in the release of inorganic phosphate, directly determines the amount of triose phosphates exported to the cytosol. The Pi released from sucrose synthesis is re-imported into the chloroplast and utilized for the regeneration of ribulose bisphosphate in order to maintain CO_2 fixation. Low sink requirement for sucrose results in the conversion of triose phosphate to starch releasing Pi for the regeneration of ribulose bisphosphate. A constant production and export of sucrose in response to demand by sinks could result in inhibition of source leaf photosynthesis through depletion of the reductive pentose phosphate pathway metabolite pools. Sucrose synthesis itself must therefore be kept under strict metabolic control. The metabolic control mechanisms employed appear to be directly or indirectly regulated by the metabolite F2,6BP (Section 1.2.2.1).

Of the C fixed by the plant in the form of triose phosphates half is allocated for immediate export and subsequent partitioning among sinks (Fondy and Geiger, 1982). A part of the newly fixed C is retained in vacuoles and cytoplasm, serving as reserve C, and in some cases as osmoticum. A portion of newly fixed C is usually stored as reserve carbohydrates, sucrose, starch and fructans. Leaf reserves provide for export later in the day, during subsequent periods of development as well as under stress. Stored material buffers against changes in metabolite levels when C fixation declines (Fondy and Geiger, 1982). Part of both newly fixed and reserve C is allocated for respiration and for leaf biomass, including synthesis of photosynthetic apparatus and structures for its effective display. Besides maintaining current structure, leaf biomass also contributes to expansion of leaf area and thickness, important for light interception, photochemistry and C metabolism (Fondy and Geiger, 1982)

Regulation during phloem loading

Mechanisms exist in the mesophyll cells for controlling the amount of sucrose synthesised for export in response to variations in sink demand (Section 1.2.2.1 and 1.2.3.2). Whether further control mechanisms exist or are even required to regulate the process of phloem loading in response to changes in sink demand remains equivocal.

If apoplastic transfer of photosynthate from mesophyll cells to the companion cell/sieve tube complex occurs involving the putative carrier mediated sucrose : H^+ cotransport plus ATPase

proton pump, then regulation of phloem loading may be exerted in the following ways. High sucrose concentration in the phloem may through mass action prevent the dissociation of the hypothetical carrier-substrate complex on the inside surface of the plasmalemma. The activity of the ATPase proton pump in sugarbeet roots may be activated by sucrose in the presence of the substrate MgATP and Na^+. In contrast to phloem loading responding to internal phloem sucrose concentrations, it has been suggested that phloem loading may respond to changes in sieve tube turgor (Giaquinta, 1983). The possibility that the ATPase complex is the transducer of turgor pressure changes through structural changes, induced by membrane compression at high turgor, affecting ATPase activity is discussed by Reinhold and Kaplan (1984).

1.3.2.2 Regulation during translocation

The available evidence indicates that the phloem network does not regulate the movement of photosynthate through it. Experiments involving incisions in the culm of wheat (Wardlaw and Moncur, 1976) and sorghum (Muchow and Wilson, 1976) have shown that dry mass accumulation in the grain was not reduced by restricting phloem cross section. Lush and Evans (1974) have suggested that when photosynthesis in C_4 grasses is driven high enough sucrose concentrations in the bundle sheaths may exceed those of the sieve tubes such that loading occurs down a gradient. But even then the proportion of photosynthate retained by the leaf did not increase, indicating that an upper limit to translocation capacity out of the leaf had not been reached. The existence of

alternative routes for the flow of photosynthate from source to sink and the development of the phloem system to meet the potential needs of a sink as in the wheat peduncle means that there is enough flexibility for translocation not to limit flow from sources to sinks in most situations (Gifford and Evans, 1981).

1.3.2.3 Sink strength and import of photosynthate

Regulation during phloem unloading

The process of phloem unloading and the ability of the sink to absorb unloaded photosynthate appear to play a very significant rôle in the distribution pattern or partitioning of photosynthate within the plant. Photosynthate may be transferred out of the sieve tube apoplastically, i.e. across the plasmalemma or it may be transferred symplastically to sink tissue via plasmodesmata connections. Control of unloading thus depends on the mechanism of unloading, apoplastic or symplastic, employed. The control of apoplastic unloading has been studied in the bean stem. In the bean stem, the transfer of photosynthate from the conducting tissue to the adjacent storage cells occurs via the apoplast. However, this apoplastic unloading appears, in addition to simple diffusion, to involve facilitated movement, for it is affected by plant growth regulators. The plasmodesmatal frequency between phloem tissue and the adjacent tissue is sufficient for some involvement of symplastic unloading in the bean stem. It has been suggested that symplastic movement may be controlled by pressure sensitive valves in the plasmodesmatal connections.

Once apoplastic transport is saturated as a result of high sugar concentration in the free space, symplastic unloading would begin and become the principle route of unloading (Ho, 1988).

On the other hand, the unloading of photosynthate into the pedicel of the maize kernel was not inhibited by metabolic inhibitors, indicating that unloading may not be an energy dependent carrier mediated transport process but rather a passive diffusional one. A reduction in turgor of the unloading cells in the pedicel of the maize kernel has been identified as the cause of reduced unloading. In unloading tissue such as the seed coat of legumes with a putative sucrose : H^+ cotransport mechanism involved in unloading, the activity of the ATPase enzyme may be affected by high free space turgor pressure (Reinhold and Kaplan, 1984; Thorne, 1986).

The rôle of sink activity in regulating photosynthate partitioning

(i) Sink strength

Most research suggest that the source controls the supply and timing of sucrose for export (Fondy and Geiger, 1982). However, once sucrose is loaded there is no evidence to suggest that the source controls its eventual destination to the available competing sinks (Gifford and Evans, 1981). If the Münch hypothesis of mass flow of photosynthate in the phloem is correct, then flux rates to sinks are related to the sucrose gradient between source and sink. This hypothesis may explain

the rôle of the sink in controlling sucrose export from source leaves. The sucrose gradient in the phloem between source and sink can be maximized by increasing sucrose concentrations in the sieve elements at the source or reducing them at the sink. Increasing the sucrose concentration at the site of the phloem loading would increase transport but it would also either inhibit further sucrose export from the mesophyll cells or result in a depletion of intermediate metabolites of the reductive pentose phosphate cycle. The more 'physiologically sound' strategy would be for the sinks to direct the flow of photosynthate from source tissue through removal and utilization of photosynthate at the site of unloading (Wyse, 1986).

Sink tissue may 'receive' or 'import' photosynthate apoplastically involving sucrose : H^+ cotransport or symplastically via direct plasmodesmatal connections between phloem tissue and sink tissue. The ability of a sink to attract photosynthate in competition with other sinks is termed the sink strength, as described by the following equation:

Sink strength (g day^{-1}) = sink size (g) x sink activity (g g^{-1} day^{-1}); (1.23)

here sink activity is expressed as relative growth rate (Daie, 1985). The proportion of imported photosynthate used for respiration by sink organs can be substantial. Thus, sink strength of a sink organ, measured as an absolute growth rate or net accumulation rate of dry mass, fails to assess the true ability of a sink organ to receive photosynthate and is more a measure of apparent sink strength. The import rate of photosynthate, measured as the sum of the net C gain and

respiratory C loss by a sink organ, should give a more appropriate estimate of the actual sink strength (Ho, 1988).

Actual sink strength would be affected by the availability of photosynthate supply and the proximity of the sink to receive or attract photosynthate. This intrinsic ability of a sink is the potential sink strength. It is genetically determined and can be fully expressed when the supply of photosynthate is sufficient to meet the demand and the environmental conditions for the metabolic activity of the sink organ are optimal (Ho, 1988).

Ho (1988) on the other hand, feels sink size should be defined as the physical constraint upon a sink organ's photosynthate import. The number of metabolically active cells in the sink organ may be a suitable measure of sink size. For instance, among wheat genotypes, the final grain dry mass is potentially determined by the number of cells in the endosperm and the number of plastids in each endosperm cell. By measuring the number of storage cells or the storage organelles within, sink size can be quantified.

Sink activity may be determined by the processes occurring in sink tissue which promote the net uptake of photosynthate such as: (i) chemical alteration of the unloaded photosynthate (i.e. hydrolysis of sucrose to hexoses, formation of starch, etc); (ii) compartmentation within apoplastic or symplastic pools; and (iii) utilization of photosynthate for growth (Thorne, 1986). All of these processes are likely to be energy dependent and so import of photosynthate by sink tissue may be controlled by these

metabolic activities. It has been suggested that when any of these processes is affected, the sucrose concentration in the free space at the point of unloading will be raised. As a result, the sucrose concentration gradient between the source and sink required to sustain the rate of import would decrease (Ho, 1988). This phenomenon has been demonstrated in tomato (Lycopersicon lycopersicum) where the import rate of the fruit can be reduced by lowering fruit temperature to decrease both respiration and sucrose hydrolysis (Walker, Ho and Baker, 1978).

(ii) Characteristics of sink organs

In general, once sucrose or hexoses enter the cytosol of a sink cell, they will be either stored as sugars in the cytosol or in the vacuole, or used as substrates for respiration or biosynthesis. The storage of sugars is either by chemical compartmentation (conversion to another sugar or to starch) or by physical compartmentation (in the vacuole, separated from the cytosol by the tonoplast). The utilization of sugars provides either energy or structural materials for cell growth. By compartmentation or utilization of imported sugars, the sugar level in the cytosol of a sink cell is kept low. Based on the proportion of imported sugars being utilized or stored inside the sink cell, all sink cells can be classified as utilization sink cells or storage sink cells, respectively. Before cell differentiation all sink cells are utilization sink cells. After differentiation, some sink cells may remain as utilization sink cells (e.g. in fibrous roots), while some may change to storage sink cells (e.g. endosperm of grains). In general most cells in

the meristem tissue are utilization sink cells, and most cells in the storage organs are storage sink cells. However, in source organs such as mature leaves some of the cells (e.g. phloem parenchyma cells) can be classified as storage sink cells. The function of a sink organ changes with development; thus the same sink organ may have either or both sink cells at different times. For instance, sugarbeet roots may have mainly utilization sink cells in the fibrous roots during early growth, but may have mainly storage sink cells in the tap roots during later growth. In this sense the function of a sink organ is determined by the predominant type of sink cell it contains (Ho, 1986).

(iii) Competition between sinks

Competition for available photosynthate among sink organs means that the competitive ability or strength of a sink may determine the availability of photosynthate for import. Although competition may be amplified when photosynthate supply is limited, the comparative (relative) competitive abilities of the various sink organs change with plant development thus altering the priority of partitioning between sinks. For instance, in tomato, a developing inflorescence is a weaker sink for photosynthate than expanding leaves, but a truss with growing fruit is a stronger sink than young leaves and roots. Thus when dry mass production was reduced, the limited amount of mobile photosynthate was mainly imported by the developing young leaves to sustain growth, and the initiating inflorescence was aborted. The potential sink strength of the inflorescence increased from flowering to fruiting stage and the priority between sinks for

photosynthate in the order of roots > young leaves > inflorescence in a flowering plant changed to the order of fruit > young leaves > flowers > roots in a fruiting tomato plant (Ho, 1988).

By altering the potential sink strength of an individual sink the priority of photosynthate partitioning can be changed. Winter wheat grain yield was successfully improved by introducing the Norin 10 dwarfing gene Gai/Rht, which shortened the stem. The higher yield of the semi-dwarf winter wheat was due to a greater number of grains, which may in turn be due to reduced maximal stem growth when 90 % of the ear dry mass was normally accumulated (Brooking and Kirby, 1981).

1.3.2.4 Hormonal regulation of source sink interactions

The host of processes that occur during the production and translocation of photosynthate from source to sink provide sites for the regulation of photosynthate partitioning. Induction of these regulatory mechanisms may be achieved by changes in the turgor pressure gradient between source and sink. Continued import of photosynthate by sink tissue reduces turgor pressure at the site of unloading which then reduces turgor pressure at the site of loading thereby increasing loading which facilitates photosynthate movement towards the sites of unloading. The rôle of the ATPase enzyme in sensing and translating turgor pressure changes into changes in the proton-motive force which provided the energy for sucrose uptake has been mentioned (Section

1.3.2.1). However, from studies conducted on plant hormones it is clear that they are involved in many aspects of growth and differentiation and therefore it is most likely that they may play a key rôle in source-sink interactions.

During plant growth various organs and tissues undergo rather orderly transitions from sink to source metabolism. The import-export transition that occurs during leaf development is perhaps the most well studied of these transition events, but is not the only case. A sink to source transition does not necessarily involve the development of photosynthetic capacity, more often it is simply the result of remobilization of previously stored reserves in what were previously storage sinks. This type of transition is exemplified by storage organs such as taproots, or storage tissues such as the sugarcane stem parenchyma or the paraveinal mesophyll layer of the soybean leaf, in which mobilization of stored reserves is induced by the production of new, often reproductive, sink tissues. Mobilization of structural components by senescing leaves prior to abscission is another case in point. It is well recognized that these transition phases during plant growth are regulated by the interaction of specific phytohormones on specific target cells or tissues (Daie, 1985; Ho, 1988).

The effect of hormones on partitioning patterns has been studied in plants exposed to exogenously applied hormones. Interpretation of the effects of exogenously applied hormones being direct or indirect remains equivocal.

Effects at the source

Gibberellic acid (GA_3) and kinetin have been shown to enhance photosynthetic activity whereas abscisic acid (ABA) generally is believed to lead to a reduction of photosynthesis through its effects on stomatal closure, although ABA may inhibit photosynthesis directly. Phytohormones may modify C end-product formation. For example GA_3 and indole acetic acid (IAA) enhanced and ABA inhibited sucrose phosphate synthase activity in sugarbeet and bean leaves (Daie, 1985).

Abscisic acid, IAA, and GA_3 have all been shown to influence phloem loading. Abscisic acid significantly reduced phloem loading in bean and castor bean whereas IAA enhanced phloem loading in both species. The mechanism by which plant growth regulators control phloem transport is unclear. The contested suggestion was made that IAA and ABA regulate ATPase-mediated proton pumping responsible for the establishment of a proton gradient across the plasmalemma (Daie, 1985).

Effects at the sink

Phytohormones may regulate both sink size and activity. It has been shown that ABA stimulates and IAA inhibits membrane transport of sugar thereby influencing sink activity in sugarbeet tap root. Correlations between ABA levels and sugar import in fruits have further implicated this hormone in the control of photosynthate partitioning (Daie, 1985; Lucas and Madore, 1988).

The study of the effects of hormones on source-sink interactions, however, remain complicated by the difficulty in separating effects of stimulation of growth on photosynthate transport processes from the effects of stimulation of transport on growth phenomena. Additionally the degree to which phytohormones regulate both source and sink activity is not clear. Patrick (1982) has proposed two possible models for the control of photosynthate partitioning at the whole plant level. In the 'sink' model, control is mediated solely by photosynthate transport within the sink, and changes in photosynthate pool size provide the signal to co-ordinate supply to the sink. The photosynthate pool at the sink region may be considered a 'barometer' reflecting the balance between photosynthate supply and utilization as well as possibly determining rates of these processes. In the 'supply-sink' model, sink produced hormones integrate the photosynthate supply with utilization by controlling both processes. 'Sink' control could be an adequate strategy when photosynthate concentrations are not limiting. Under conditions of limited photosynthate concentration, the 'supply-sink' strategy could ensure greater flow of photosynthate to the sink region than that generated by 'sink' control. In this case, sink produced hormones would also mediate regulation of supply processes.

Control of sink activity by gene action

An area that has received little attention to date is the rôle of gene action in controlling sink activity. Certainly, gene action will determine both the sequence and rate of development

of sink organs within a plant. For example, in developing maize kernels a 40-fold increase in DNA content per cell was observed 10 to 12 d after pollination. It is during this period that cell differentiation is occurring and enzymes are being synthesized for the metabolism of photosynthate into starch. This may indicate a mechanism for gene amplification at a time when rapid increases in metabolism are occurring (Wyse, 1986).

Hormones may regulate the activity of already formed enzymes and they may also be involved in regulating gene expression thus controlling the production of enzymes involved in plant metabolism. Regulation of gene expression may thus determine the competitive ability of a sink by controlling the timing and intensity of metabolic activity in the sink organ (Wyse, 1986).

1.3.2.5 Environmental effects on photosynthate partitioning

The final pattern of partitioning of photosynthate to harvestable and non-harvestable organs in the plant is determined by the interaction of the genetic potential with environmental influences.

Temperature

Temperature affects the rate and duration of dry mass accumulation in crops thus influencing dry mass partitioning (Tollenaar, 1989). Leaf photosynthetic rates of maize increased substantially between 15 and 31°C (Duncan and Hesketh, 1968), but

changes in dry mass of young maize canopies at the 12 leaf stage showed a curvilinear response to temperature in the range 11 to 31°C with an optimum at approximately 19°C (Tollenaar, 1989). It has often been reported that the root : shoot ratio tends to decline, whereas the partitioning of photosynthate into new leaf area increases with an increase in temperature (Potter and Jones, 1977). Super-optimal or sub-optimal temperatures may adversely affect the growth and development of the various organs of a plant thus affecting partitioning patterns. Super-optimal temperatures during pollination and kernel endosperm cell division in maize affect kernel number (Herrero and Johnson, 1981) and mass kernel^{-1} (Jones, Roessler and Ouattar, 1985), respectively.

Temperature changes will affect the growth rate of the plant organs and it is therefore expected that temperature would indirectly affect translocation rates. However, since translocation is associated with metabolically active cells, it is possible that temperature may directly affect translocation rates. Local reduction in the temperature of stem and petiole tissue inhibits the movement of applied ^{32}P and ^{14}C photosynthate (Wardlaw, 1968).

Although it is one matter to measure the effects of temperature on photosynthate partitioning it is another to pinpoint which of the processes in the source-translocation path-sink system cause the responses to temperature. Obviously for field-grown crops it is not possible to control temperature although for greenhouse grown crops control of shoot and root temperatures is possible

but not always feasible. The most acceptable approaches in taking advantage of temperature effects on partitioning are by genotype selection and by planting date (Snyder and Carlson, 1984).

Light

Light affects plant growth and development both quantitatively and inductively. Increased duration and intensity of light intercepted by a crop increases biomass production. Inductive stimulii, sensed as photoperiod or as alterations in the spectral quality of light in the crop canopy can cause significant changes in photosynthate partitioning, which can lead to increases in crop productivity. It is debatable whether light acts directly on photosynthate transport and metabolism or whether altered patterns of photosynthate partitioning result from light induced changes in morphological development (Snyder and Carlson, 1984).

The effect of photoperiod and light intensity on photosynthesis and on the allocation of triose phosphates to sucrose and starch synthesis as regulated by F2,6BP has been discussed in Section 1.2.2.1. The interaction of sink demand with this control mechanism again makes interpretation of cause and effect of light on partitioning patterns difficult.

Experiments involving the artificial shading of plants to determine effects on partitioning patterns may not simulate naturally occurring low light effects of differing densities of canopies. The physiological responses of plants under shading

conditions may differ for the following reasons: (i) the upper portion of the canopy receives nearly full radiation; this is not true under shade; (ii) the photosynthetic photon flux density and the spectral gradients in the canopy would be different in the shaded canopy; and (iii) temperature gradients would differ (Snyder and Carlson, 1984; Patrick, 1988).

Water and minerals

Although the effects of temperature and water stress are usually confounded they are discussed separately here for convenience.

Deficiencies in water and mineral nutrients result in a smaller source and sink, lower photosynthetic rates, and altered partitioning patterns. Water and nitrogen deficiencies usually increase the proportion of root to total biomass, as well as root to shoot. On the other hand, harvest index in maize declines from an optimum as levels of NPK fertilization increase (Snyder and Carlson, 1984). Again, since macro- and micronutrients are required for normal cell maintenance and growth, and since translocation involves metabolically active cells, it is difficult to isolate the effects of altered nutrition on the source-translocation path-sink system.

Water stress tends to alter partitioning, with an overall decrease in biomass and an increase in the concentration of sucrose in both sugarbeet and sugarcane, but total economic yield may decrease if water stress becomes too severe (Snyder and Carlson, 1984). Osmoregulation may play an important rôle in the

tolerance of crop species to drought (Morgan, 1984). Maintenance of turgor in sink cells enables growth to continue thus maintaining a demand for translocated photosynthate. Without turgor maintenance growth slows and photosynthate is diverted to sinks with less negative water potentials. Under conditions of severe water deficits photosynthate may be remobilized from storage sites in vegetative organs such as the stem (Snyder and Carlson, 1984).

Carbon dioxide

Exposure of crop plants to increased levels of CO_2 in order to increase photosynthate production has had mixed results. Plants with the C_4 pathway appear to be less responsive than C_3 plants. Rice exposed to high CO_2 levels partitioned relatively more dry mass to the roots than to the leaves compared to partitioning at lower CO_2 levels. In contrast growth of maize was promoted less by high CO_2 levels and suppressed less by low CO_2 levels (Snyder and Carlson, 1984).

Stand density

Biological yield becomes asymptotic with increasing plant density. For root crops such as sugarbeet the highest economic yield per unit of land is produced at stand densities less than that needed to produce maximum aboveground yield. The proportion of taproot to leaves decreases as stand density increases for sugarbeet. Increasing stand density in maize decreases HI. Increasing stand density in cereals is complicated by a reduction

in tillering thus economic yield may not be dramatically affected (Snyder and Carlson, 1984).

Existing stand densities recommended may often represent the upper limit of population density stresses that the crop can tolerate under most conditions. However, when water or nutrient stress occurs, economic yield may be greater at lower stand densities than those recommended (Stoskopf, 1981).

1.4 Non-structural carbohydrate partitioning in maize grown under favourable environmental conditions

Economic yield production in plants is dependent on the synthesis, accumulation, storage, remobilization and translocation of numerous biochemical substances. Quantitative analysis of the specific biochemical fractions in plant components at different stages in the growth and development of crop species should help advance our understanding of physiological processes that determine crop productivity under yield limiting and non-limiting environmental conditions (Fairey and Daynard, 1978).

1.4.1 Growth and development of maize

A description of the growth and development of maize highlights the changes in source-sink relations as the different organs are formed and mature. In a period of 4½ months (18 weeks) maize develops from a small seed to a plant 2,0 to 3,5 m tall. During this period the maize plant passes through two main growth

phases: the germination plus vegetative phase, and the reproductive phase.

Under conditions of adequate soil moisture and temperature, germination begins with the emergence of the radicle from the seed coat. The coleoptile emerges shortly after and then the seminal roots are produced. After the seedling is established the maize plant begins to form the roots and leaves to support ear formation. All new leaves are produced within the first 3 to 4 weeks of the plant's development by the apical meristem which is still at or below ground level. As the leaves grow they emerge through the whorl of the other developing leaves. The rôle of nutrient and water uptake is taken over from the seminal roots by adventitious roots emanating from the basal nodal region. Brace roots develop from nodes above the crown at tassel emergence and play a physically supportive and limited nutrient absorbing rôle. By the time five or six leaves have emerged, the apical meristem has been raised above ground by limited stem elongation. Although 20 or so leaves may be produced only 14 or 15 are generally present on the plant at the completion of the vegetative stage.

When the plant is approximately 0,6 m high and the full number of leaves has been formed (not all are yet visible), the apical meristem undergoes a transition which heralds the reproductive phase as tassel initiation begins. This is followed shortly by ear initiation involving the elongation of axillary meristems basipetally on the stem. At this stage rapid stem elongation

occurs and the plant increases in stem height and girth and leaf size.

Five to six weeks elapse from tassel initiation to tassel emergence. After the tassel emerges the rate of vegetative development slows down. During this period pollen formation takes priority over ear formation in terms of available photosynthate. Two to three days after pollen shed begins, each potential ovule produces a tube-like structure called a silk that grows until it emerges from the husks surrounding the ear. The silks from the middle to base of the ear emerge first, and those from the tip appear last. Pollen grains germinate on the silks, and each pollen grain produces a pollen tube which grows down the center of an individual silk, but only one pollen grain succeeds in fertilizing each ovule. Fertilization of each ovule is completed in about a day.

After fertilization has occurred the ear becomes established as the major sink for available photosynthate. However, the cob is the major area of growth for the first 10 to 14 d. This is followed by a period of linear deposition of dry mass in the kernels. Physiological maturity is reached when kernels on the ear have achieved maximum dry mass accumulation. Maturity is indicated by development of the so-called 'black layer', a region of suberized material which develops between the basal endosperm and the vascular area in the pedicel (kernel base) (Aldrich, Scott and Leng, 1975; Tollenaar, 1977).

1.4.2 Carbohydrate partitioning during the vegetative phase

During the vegetative stage, from germination to anthesis, photosynthate is initially used to establish the root system, the leaf canopy and for limited internode growth. Once tassel initiation is complete rapid stem elongation commences and photosynthate is largely used for the synthesis of structural tissue in the stem (Tollenaar, 1977).

Young maize leaves are initially largely heterotrophic, that is they depend in part on photosynthate imported from other regions of the plant while retaining and using all the photosynthate they produce (Wardlaw, 1968; Turgeon, 1989). Once the leaves are 30 to 60 % of their full size they begin to export their own products of photosynthesis. When leaves are full sized they become autotrophic, that is they produce an excess of photosynthate and act as the plant's major sources of transport sugar (Wardlaw, 1968; Turgeon, 1989). It appears that leaves are most photosynthetically active in exporting photosynthate soon after reaching their maximum size (Wardlaw, 1968). This sink to source transition of leaves is accompanied by a number of morphological and biochemical changes. Sieve tube maturation occurs as the complete vein network is established (Turgeon, 1989). When the leaves function as sinks sucrose translocated to them is hydrolysed and used for respiration and the synthesis of other metabolites. Sucrose phosphate synthase is not detectable in sink leaves but is in source leaves. Thus one of the biochemical changes associated with the sink to source

transition is related to increased levels of sucrose synthesis catalysed by sucrose phosphate synthase (Duffus and Duffus, 1984).

The position of the leaves in relation to the various sink tissues determines the photosynthate distribution pattern. Photosynthate is generally translocated from the leaves to the nearest sink, although the relative strengths of competing sinks may override the influence of distance. Thus lower leaves usually supply the roots, upper leaves supply the shoot apices and intermediate leaves supply both. However, with ontogeny of the plant the pattern of photosynthate distribution will change, most markedly when the reproductive organ(s) is produced (Wardlaw, 1968).

There does not seem to be a surplus production of photosynthate during vegetative growth as judged by the low levels of accumulated non-structural carbohydrates recorded in the stem of maize (Simmons and Jones, 1985). This is understandable considering the large increases in root and shoot dry mass recorded during the vegetative phase. Under favourable environmental conditions and depending on genotype, non-structural carbohydrates in excess to grain requirements may begin to accumulate in the stem after fertilization (Campbell, 1964) once final increases in stem and leaf size have ceased.

By labelling one maize cultivar with $^{14}CO_2$ during the pre- and post-silking periods, Simmons and Jones (1985) were able to measure the relative distribution of radioactivity between grain

and stover at maturity. These data, in conjunction with measurements of changes in aboveground plant dry mass, facilitated the mathematical estimation of the contribution of pre-silking photosynthate to grain yield. Results obtained showed that less than 10 % of final grain yield could be attributed to pre-silking assimilates. Simmons and Jones (1985) postulated that most of the ^{14}C detected in the grain from pre-silking labelling was translocated with N remobilized from vegetative organs. It was further suggested by Simmons and Jones (1985) that although small quantitatively, pre-silking assimilates could be extremely important for optimum development of the grain.

1.4.3 Carbohydrate partitioning during the reproductive phase

The reproductive phase of growth commences with the fertilization by pollen grains of the ovules. After fertilization the conditions are set for the developing kernels to become the predominant sinks. Initially, however, assimilates are still partitioned to the stem, leaves and cob, with rapid accumulation of dry mass in the kernels occurring 15 to 18 d after mid-silking (Daynard and Duncan, 1969; Tollenaar, 1977).

Since photosynthate does not significantly begin to accumulate in the stem until after silking, it is generally accepted that photosynthate produced after anthesis contributes the most to grain yield. Estimates vary from 90 to 95 % of grain dry mass contributed to by photosynthate produced after flowering (Hanway,

1962; Allison, 1969; Milthorpe and Moorby, 1969). The supply of photosynthate to the grain may come from two sources, viz photosynthate produced from current photosynthesis and photosynthate stored in the various plant organs. All of the aboveground component organs of the maize plant (apart from the tassel proper) are capable of supplying either or both currently produced or stored photosynthate to the grain. However, there is not much data on the relative contributions of current and stored photosynthate by the component organs to the non-structural carbohydrates accumulated in the grain. What is certain, however, from the studies conducted to date is that the distribution and utilization patterns of non-structural carbohydrates vary with the nature of the component organ, position of the organ in the crop canopy and continued reproductive development of the maize plant.

1.4.3.1 Leaves and sheaths

It has been estimated that the upper leaves, stem and ear are responsible for supporting 80 to 90 % of the grain growth for wheat and rye whereas the lower leaves of rice and maize support grain growth to a greater extent. This is possibly due to a lower rate of leaf senescence in tropical species allowing for extended photosynthesis in the lower leaves compared to temperate species (Allison and Watson, 1966; Wardlaw, 1968). Apart from the diurnal synthesis, storage and remobilization of starch in the leaves, it can be safely assumed that while the leaves are photosynthetically active the photosynthate translocated out of the leaves during favourable environmental conditions are

products of current photosynthesis. However, during senescence of the leaves, loss of dry mass indicates the remobilization and translocation out of the leaves of metabolites such as amino acids, proteins and lipids. Data on the exact contribution made to photosynthate accumulation in the grain by photosynthesis in the leaves relative to other photosynthetic organs such as the stem and ear husks is scarce. Milthorpe and Moorby (1969) estimate that in maize approximately half the kernel carbohydrates come from the top six leaves, one-third from the middle four to five leaves and one-sixth from the bottom four to five leaves, the approximate proportions varying with the environment and source and sink strengths.

Palmer, Heichel and Musgrave (1973) labelled maize plants with ^{14}C at four different leaf positions in order to reveal patterns of translocation. The first and third leaves above the ear as well as the first leaf below the ear exported ^{14}C mainly to kernels of the developing ear. Export was more rapid from the upper leaves than from ones at lower positions. Movement of ^{14}C from the fifth leaf below the ear was much slower than the upper three leaves, but kernels of the developing ear ultimately became the principal sink for ^{14}C exported by this leaf. However, appreciable label from the fifth leaf below the ear accumulated in the lower stem and roots.

Fairey and Daynard (1978) found that in the single cross maize hybrids tested, the concentration of sugars in the dry mass of leaves increased acropetally. Sugar concentrations in the leaves were found to be at their lowest when last sampled 31 d after

mid-silking. Fairey and Daynard (1978) theorised that these trends may have resulted from the lower illuminance of basal leaves as well as from the gradual acropetal progression of leaf senescence in the crop canopy throughout the grain filling period.

Westgate and Boyer (1985a) found in their control plants that there was a rapid increase in total ethanol soluble sugar content in composite samples of all leaves from early grain fill to mid-grain fill. Thereafter levels declined to pre-anthesis levels. A similar pattern was followed by total reducing sugars content.

The work of Below, Christensen, Reed and Hageman (1981) illustrates how the partitioning of non-structural carbohydrates from the leaves to the grain is influenced by water deficits. In the first leaf below the ear leaf an initial decrease in carbohydrate content between 5 and 9 days after anthesis (DAA) was noted and was concurrent with the initiation of rapid grain fill and a severe droughty period. Subsequent to this, carbohydrate content in the selected leaf increased during the same periods (between 18 and 21 DAA, and between 31 and 34 DAA) as apparent changes in the linear rate of ear dry mass accumulation occurred. Between 21 and 31 DAA a decrease in leaf carbohydrate was again consistent with a droughty period. From 31 DAA until grain maturity leaf carbohydrates increased in sympathy with the gradual cessation of ear dry mass accumulation and the occurrence of favourable temperature and moisture regimes. When all the maize leaves of the plant were composited,

an overall decline in both dry mass and non-structural carbohydrate content occurred during grain fill.

Allison and Watson (1966) found that the leaf sheaths provide almost one-fifth of the total plant leaf area. With the assumption that the photosynthetic rates of the sheaths and laminae are similar, they estimated that the sheaths contributed about one-fifth, and the laminae about four-fifths, of the plant dry mass produced by the leaves after silking.

1.4.3.2 Stem

Although the stem tissue cells contain chloroplasts and are therefore capable of photosynthesis the contribution of stem photosynthesis to grain dry mass accumulation has not been reported. Besides containing the vascular connections between the leaves and the tassel, ear and roots it appears that the stem may serve as a temporary storage site for non-structural carbohydrates. It is not clear whether non-structural carbohydrates accumulate in the stem as a result of photosynthate production exceeding the requirements of the grain or as a result of specific competition for, and storage of, non-structural carbohydrates by the stem. It has also proved difficult to distinguish between non-structural carbohydrates that occur in the translocation pathway, and pools that are stored in the pith parenchyma cells. A clear definition of what is meant by 'stored' non-structural carbohydrates is also required in terms of period of storage, since there may be a rapid exchange between non-structural carbohydrates in the parenchyma cells with those

in the translocation pathway. What is certain, however, is that levels of non-structural carbohydrates in the stem vary with genotype, ontogeny and environmental influences, and these factors determine the extent to which non-structural carbohydrates are mobilized out of the stem and into the developing grain.

Under favourable environmental conditions the depletion or accumulation of non-structural carbohydrates in the stem may be interpreted as indicating, respectively, a source or sink limitation to final grain yield. Since sink capacity often determines source capacity and vice versa it may be difficult to determine the limiting factor (Tollenaar, 1977). It appears that maize grown in the far temperate regions of Canada often shows a source limitation inferred by the relocation of stem and husk carbohydrates to the grain in the latter part of the grain filling period (Tollenaar, 1977). Declining temperatures and solar irradiance, early frosts and aging of the leaves during the latter part of the growing season cause a considerable decline in leaf photosynthetic rate and LAI (Tollenaar, 1977). The following research reports demonstrate the existence of a source limitation in maize grown in far temperate regions as inferred by a decline in stem non-structural carbohydrate levels.

In a study conducted over a two year period on six hybrids, Daynard, Tanner and Hume (1969) found that stem dry mass and stem soluble solids (mostly carbohydrates) composition (%) and content (mass (plant part)$^{-1}$) declined initially until 2 to 3 weeks after mid-silking and then declined as rapid ear development occurred.

They found no corresponding decrease in stem residue dry mass which indicated that losses in stem dry mass were as a result of movement of soluble carbohydrates from the stem to the ear. These workers suggested that the accumulation of carbohydrate in the stem immediately after silking was most likely due to a limited ear sink capacity in relation to source capacity. The depletion in stem carbohydrates was as a result of either or both an enlarged ear sink capacity or reduced photosynthetic capacity.

The period of maximum accumulation of non-structural carbohydrates in the maize stem occurs after anthesis. Hume and Campbell (1972) estimated the soluble solids in maize stems by taking refractometer readings of expressed sap, and total sugars were measured by the Shaffer-Somogyi method. Total soluble solids were found to increase until 2 to 3 weeks after silk emergence, then decline as grain dry mass increased. Soluble solid concentrations in the stem declined at ear formation and silking suggesting utilization of soluble solids for organ development. Concentration decreases in internodes near the top of the plant also suggested that soluble solids were being utilized by the tassel during anthesis. Largest amounts of soluble solids and total sugars were found to accumulate in the second to fifth elongated internodes above ground level, ear development usually occurring immediately above the fifth internode. Soluble solids represented close to 50 % of the stem dry mass during the period from one week before silking until four weeks after silking. Although soluble solids and total sugars gradually disappeared from all internodes as grain fill proceeded, the difference between soluble solids and stem dry

mass, which represents structural material, remained almost constant. Within the three year period that Hume and Campbell (1972) conducted their studies, losses of soluble solids from the stem during grain fill averaged about 900 kg ha^{-1}. From studies with ^{14}C it was calculated that 25 % of the label incorporated in the early grain filling period was lost in respiration. Using this figure, the calculated amount of soluble solids from stem storage incorporated into grain then averaged 675 kg ha^{-1}, and ranged from 1 050 kg ha^{-1} to 185 kg ha^{-1} over seasons.

Fairey and Daynard (1978) growing maize plants under nutrient culture in the field found that during the early stages of grain development the percentage of sugars (assessed using the calorimetric method of Dubois, Gilles, Hamilton, Rebers and Smith (1956)) in whole plant dry mass remained relatively constant (21,6 to 23,6 %). Once the developing grain became established as the principal sink, sugar composition (and content) declined markedly to 8,3 %. However, starch concentration in whole plant dry mass (extracted using the procedure of Hilliard and Daynard (1974), and quantisized using the method of Dubois et al. (1956)) increased from 2 % at early grain fill to 16 % with advancing grain maturity. In the stem, soluble carbohydrates accumulated during the early stages of kernel growth, concentration of sugars increased acropetally, and then declined towards grain maturity. The greatest relative decline in stem sugars occurred in the internodes above the ear. In support of Hume and Campbell's (1972) work, Fairey and Daynard (1978) found the proportion of dry mass in the tissue residue following non-structural carbohydrate extraction remained constant throughout the period

of their study. Thus the most evident change in chemical composition of the whole plant dry mass from 10 to 31 d after silking was the utilization of soluble sugars in the synthesis of starch and components of residual matter in the grain.

Additionally, Fairey and Daynard (1978) noted that sugars constituted the principal storage carbohydrates in the stem whereas starch formed less than 2 % of stem dry mass and the dry mass of vegetative organs as a whole. In maize, as with most other cereal crops such as sorghum, the principal storage site for starch is the endosperm of the grain. Some workers (Welton, Morris and Hartzler, 1930; Mühling, 1963 cited by Fairey and Daynard, 1978) were unable to detect any starch in the maize stem. However, Kemp and Henson (1934) reported up to 4,7 % starch in the dry mass of mature stems of dent maize and Nishikawa and Kudo (1973) cited by Fairey and Daynard (1978) found 11 to 17 % starch in stem dry mass during grain filling at plant populations that were high enough to induce barrenness. Fairey and Daynard (1978) concluded that the rôle of starch as a storage carbohydrate in the maize stem is not clear.

The characteristics of maize stem starch was investigated in a comparative study of the endosperm and stem starch of one maize and one sorghum cultivar conducted by Freeman et al. (1972). The maize cultivar was a cytoplasmic sterile version of a commercially available cultivar. Without the development of an ear the maize cultivar accumulated large quantities of starch in the stem. The sorghum cultivar had been specifically bred to accumulate large quantities of sucrose in the stem at the expense

of starch synthesis in the grain. The sorghum endosperm and the maize and sorghum stem starch granules were found to have an average molecular size between 75 and 80 % that of normal maize endosperm. Stem starches were estimated by iodine affinity to contain only 1/3 to 1/2 as much amylose as endosperm starches.

Maize grown in temperate, subtropical and tropical environments may, on the other hand, show either a source or a sink limitation to final yield depending on the interaction of genotype with environmental factors.

An apparent sink limitation was indicated in maize grown in the subtropical conditions of Rhodesia (now Zimbabwe) by Allison and Watson (1966). Stem dry mass remained constant in plants after flowering and it was necessary to defoliate plants by 50 % to induce a reduction in stem dry mass. That the utilization of stem carbohydrates is dependent on population density was later demonstrated by Allison, Wilson and Williams (1975). At 2,47 plants m^{-2}, stem mass increased after flowering and then remained fairly constant until final harvest; but with 4,94 plants m^{-2} stem mass decreased from flowering to final harvest. Lucas (1981) tested two old cultivars and two new high yielding cultivars in the tropical conditions of Nigeria. He found a considerable loss in stem dry mass towards the end of grain mass accumulation and concluded that photosynthate in the stem of tropical maize cultivars may also contribute to the grain as reported for far temperate maize cultivars.

In the temperate conditions of Ohio (USA), Welton et al. (1930) investigated the distribution of reducing sugars and sucrose in the internodes of two maize cultivars (Clarage, 1927; Burr Leaming, 1928). Levels of starch were not determined as there was not enough to be tested. Plants were sampled on a weekly basis from tasselling until maturity. All data were expressed on a fresh mass basis. Sucrose composition was found to increase acropetally in both cultivars, declining in the very top internodes in the cultivar Clarage. In the Burr Leaming cultivar reducing sugar composition declined acropetally while in Clarage, levels first increased acropetally and then decreased at the top internodes. By averaging the values of all internodal segments for each sampling date, changes in the average composition of the stem over the reproductive phase were determined. In Clarage sucrose composition first increased until the ear was fully developed and thereafter declined. Reducing sugar composition declined over the grain fill period. In Burr Leaming sucrose composition increased gradually throughout grain fill while reducing sugar composition fluctuated considerably but showed an overall decline.

Remobilization of stem sucrose was observed in five maize inbreds grown in temperate conditions at Brookhaven (USA). In their study Van Reen and Singleton (1952) found the sucrose composition in stems of the five maize inbreds rose rapidly from late whorl stage, through pollination and into early ear formation. During later stages of ear development the sucrose composition in the stems decreased which these workers took to indicate translocation of stored carbohydrates to the ear. This was more

pronounced in one of the inbred lines which was a good grain producer, leading to the conclusion that the high yielding characteristics of the line was due to its ability to translocate most or all of the high early stem sucrose content to the ear.

Further indication that the remobilization of vegetative photosynthate reserves for grain requirements occurs in temperate maize cultivars was demonstrated by the study of Hanway and Russell (1969). They found that in 11 maize hybrids grown under field conditions in Iowa (USA), dry mass accumulated in non-grain parts of the plants such as the stem, leaves, sheaths, cobs, shank, silks and husks after silking. Towards the end of the season dry mass declined in these non-grain plant parts and it was suggested that photosynthate was translocated to the grain.

On the other hand, in the temperate conditions of Illinois (USA), Below et al. (1981) found that three out of five single cross hybrids studied had more aboveground vegetative (stover) dry mass at grain maturity than at anthesis, while the loss of stover dry mass by the other two hybrids was negligible. The increase in stover dry mass was accounted for by an increase in non-structural carbohydrate content in the stem. By 42 d after anthesis when the bulk of the ear mass had been acquired, the average gain in stover dry mass was 12 %, while the loss of stover reduced N was 28 %. The research results presented so far in this section emphasise the importance of the stem and other vegetative organs in supplementing the supply of carbohydrate from the leaves to the developing grain. Below et al. (1981), on the other hand, theorised that since carbohydrates are thought

to be stored in the stem of maize plants and remobilized for grain fill during periods of low photosynthesis, their results indicate that photosynthetic capacity was adequate while nitrate reduction capacity was inadequate for ear demands. Current indications are that availability of N is important in establishing and maintaining a photosynthetically active leaf canopy and in the initiation and development of sink capacity in rice (Murata and Matsushima, 1975). A seed storage protein, zein, has been implicated in playing an undetermined rôle in the development of the maize ear (Tsai, Huber and Warren, 1978).

The interaction between C and N metabolism in determining final grain yield was further demonstrated in a follow-up study conducted by Swank, Below, Lambert and Hageman (1982). They compared the 'stay green' (late leaf senescence) single cross hybrid FS854 with four other single cross hybrids. The hybrid FS854 had set the world yield record in 1975 of 21,3 t ha^{-1} under non-irrigated conditions. Swank et al. (1982) from the results of their study attributed the high yield of this hybrid to the following physiological traits: (i) the continued accumulation of reduced N by aboveground parts throughout grain fill; (ii) the continued accumulation of dry mass by aboveground parts throughout grain fill indicating the maintenance of photosynthetic capacity; (iii) the maintenance of high rates of dry mass and reduced N accumulation by the kernels in the final stages of grain fill; and (iv) the stem had the lowest concentration of carbohydrate during the first 44 d of grain fill and the highest concentrations of amino N and reduced N throughout grain fill compared to that of the other hybrids.

Swank et al. (1982) suggested that the ability of the hybrid to continually take up N extended leaf duration and photosynthetic capacity for a greater period thus ensuring longer duration of grain fill.

1.4.3.3 Carbohydrate partitioning in other organs

Palmer et al. (1973) found that about 70 to 85 % of the ^{14}C assimilated by leaves above the ear and deposited in cobs and husks was subsequently remobilized and accumulated in the kernels within the two weeks following initial labelling 15 to 18 d after fertilization. A figure of 5 to 10 % of the label initially assimilated was estimated for photosynthate first accumulating in the stem and then being transferred to the kernels. Palmer et al. (1973) feel that their data suggest that the cobs and husks may be the principal reservoirs of C that allow linear dry mass accumulation in kernels during periods of fluctuating rates of photosynthesis.

Allison and Watson (1966) found that shading the ear husks had no effect on final grain yield. As the ear husks and leaves have been found to have similar photosynthetic rates and since the photosynthetic area of the ear husks was only 2 % of the photosynthetic area, Allison and Watson (1966) concluded that the photosynthetic contribution of husks to final grain yield is about 2 %. Hesketh and Musgrave (1962) showed that the ear husks did contribute to grain yield through their own photosynthesis. Fairey and Daynard (1978) demonstrated the importance of the husks as temporary storage sites of non-structural carbohydrates

before remobilization for grain fill occurs. A decline from 40 to 14 % of husk dry mass between 17 and 31 d after silking was measured. Salvador and Pearce (1988) found that complete removal of husks resulted in grain yield loss of nearly 18 % and concluded that this reflects the importance of husks in maintaining the ears internal environment and as storage organs for sugars.

In the study conducted by Fairey and Daynard (1978) high concentrations (40 to 55 % dry mass) of sugars as well as a relatively constant concentration of 3 % dry mass of free amino acids plus amides were observed in the shank throughout this study, a reflection of the translocation function of that organ.

The rôle of the roots as a reservoir from which photosynthate can be drawn is not often studied, probably due to the difficulties involved with root sampling. Levels of non-structural carbohydrates in the roots appear to be low. Concentrations of less than 5 % sugar declining with grain fill have been measured (Conrad, 1937; Fairey and Daynard, 1978). However, starch levels are either undetectable (Conrad, 1937) or present at concentrations of less than 1 % (Fairey and Daynard, 1978). The roots of the maize plant may play an important rôle in supplying the organic N needs of the plant during kernel growth. Fairey and Daynard (1978) have shown the concentrations of free amino acid plus amide in the roots declined during grain fill while concentrations increased in the stem internodes. They proposed that the increased concentration in the internodes may have been caused, in part, by the translocation of N compounds from

senescent leaves and the mobilization of reduced N compounds from the root system.

It appears that the patterns of photosynthate production, accumulation and utilization depend on the specific interaction of genotype with environmental factors. The environmental factors that may exert an influence are temperature, light, water and nutrient availability and population density (Section 1.3.2.5). Thus in order to ascertain whether a specific genotype genetically controls the patterns of carbohydrate partitioning it will be necessary to test the genotype under controlled and optimal environmental conditions. It is also clear that N in addition to C availability in the plant plays a critical rôle in determining final yield. Since C and N metabolism are linked through photosynthesis (Wallsgrove, Keys, Lea and Miflin, 1983) it may be necessary to study both reduced N and non-structural carbohydrate partitioning patterns in order to understand the physiological determinants of yield.

1.5 Manipulated source-sink relations

Altering source-sink relations by manipulating the growth and development or by complete removal of source and/or sink tissue affects the partitioning of photosynthate among the harvestable and non-harvestable organs of the plant. Alterations in source-sink relations occur naturally through organ damage by hail, insects and disease and through poor growth due to unfavourable environmental conditions. These conditions can be simulated artificially by the physical manipulation of source-sink

relations. Source manipulations involve leaf removal and shading, sink manipulations involve complete or partial prevention of pollination and ear tissue removal. Both source and sink activity may be affected by water and nutrient deficiencies.

1.5.1 Leaf tissue removal

When alternate laminae were removed at silking (thus half defoliating plants) leaf area duration was decreased by 40 %, and the subsequent production of dry mass decreased nearly proportionately, so that net assimilation rate was not affected but grain mass was decreased by only 32 %. Stem mass decreased from two weeks after flowering in half-defoliated plants, but remained nearly constant in intact (control) plants (Allison and Watson, 1966). The decrease in stem mass caused by defoliation suggested that previously stored dry mass was moved to the grain. It is also possible that depletion of photosynthetic products in the remaining leaves increased their photosynthetic rate, or that in the maize hybrid tested there was a production of photosynthate in excess of grain storage capacity, thus defoliation resulted in a less than expected reduction in grain mass (see also Kiesselbach, 1948).

Jones and Simmons (1983) have shown that the effects of reduced photosynthate supply through leaf defoliation on final yield are dependent upon the stage of grain development. In their study a reduction of photosynthate supply by total defoliation before kernel number per ear has been completely established (12 d after

mid-silking) substantially reduced the number of kernels ear^{-1} and the mass $kernel^{-1}$. Total defoliation after the onset of linear kernel growth (24 d after mid-silking) did not significantly reduce the number of kernels ear^{-1} but did significantly decrease mass $kernel^{-1}$. Both these treatments resulted in a decline in the soluble carbohydrate content in the internode above the ear which was more rapid for the later defoliated plants. These data agree with the results of Tollenaar and Daynard (1978a&b) and Frey (1981), suggesting that maize does alter the number of kernels ear^{-1} in order to compensate for reductions in photosynthate supply that occur during the first three weeks after mid-silking. After this time, compensation for reduced photosynthate availability occurs by a reduction in kernel growth rate and duration of grain fill, with enhanced remobilization of soluble carbohydrates from vegetative organs such as the stem.

Similarly Egharevba, Horrocks and Zuber (1976) found that number of kernels was greatly reduced by 62,3 % when plants were completely defoliated 10 d after mid-silking. Partial or complete defoliation 20 d or more after mid-silking resulted in yield decreases largely related to a decline in mass $kernel^{-1}$. These workers also studied the effects of complete defoliation above and complete defoliation below the ear but found no significant differences in yield components.

Allison (1969) grew the maize hybrid SR 52 at five population densities, namely 2,30, 3,52, 4,79, 6,05 and 7,38 plants m^{-2}. Before flowering, between 6 and 10 weeks after sowing, the percentage of the total dry mass in the leaves increased with

population density; for example, at 10 weeks 26 and 34 % of the total dry mass was in the leaf laminae, with population densities of 2,30 and 7,38 plants m^{-2}, respectively. After flowering the proportion of the total dry mass increment allocated to the grain was higher than other plant parts, and this proportion increased with population density. It appeared that the greater proportion of dry mass that moved to the grain when population density increased was at the expense of the stem, husks and cob. Stem mass increased until 3 to 4 weeks after flowering then remained constant in the population of 2,30 plants m^{-2}, decreased moderately in populations of 3,52 and 4,79 plants m^{-2}, and decreased to such an extent in populations of 6,05 and 7,38 plants m^{-2} that at final harvest it massed the same as it had 10 weeks after sowing. Thus it appears that the sink is limiting in widely spaced crops and some of the photosynthate which could be translocated to the grain remains in the stem. Should photosynthesis cease prematurely this surplus photosynthate may be remobilized and used for continued grain fill and final yield may be less affected. In a follow up study Allison et al. (1975) tested the interaction of population density and defoliation on the availability of surplus photosynthate stored in the stem for continued grain fill. Plants were grown at two population densities of 2,47 and 4,94 plants m^{-2} and defoliation (all leaf laminae removed) was carried out at 122 and 143 d after planting. Silking occured at 81 and 83 d after planting in the low and high population density, respectively. Defoliation caused a greater decrease in stem mass at final harvests in plants grown at the lower population density than the higher. Defoliation also caused a

relatively greater decrease in final grain mass in the higher than the lower population density, the decreases were 57 and 16 % in the high, and 47 and 11 % in the low density with the earlier and the later defoliation, respectively. These results confirmed those of Allison (1969) that lower population density may result in more photosynthate being stored in the stem which is remobilized and translocated to the grain should photosynthesis prematurely cease due to, for example, water stress.

1.5.2 The effects of shade

Reed, Singletary, Schussler, Williamson and Christy (1988) shaded (50 % interception of incident light) maize plants during either vegetative growth (10 d after seedling emergence to initial pollen shed), flowering (initial pollen shed to the onset of linear grain dry mass accumulation), or grain fill (onset of linear grain dry mass accumulation to physiological maturity). Photosynthesis was measured on plots from 9 d before flowering to grain maturity, and the plants were sampled at intervals during this period for measurement of dry mass and reduced N content of plant parts of the aboveground vegetation (stover) and ear. Shading during the vegetative phase resulted in only a small decrease in kernel number and no significant effect on kernel mass. Shading during the vegetative stage resulted in whole plant dry mass accumulation and whole plant reduced N content not recovering to control levels during flowering and grain fill. However, photosynthesis recovered to levels comparable to control levels during flowering and grain fill.

Thus there was adequate photosynthate during the development periods when kernel number and kernel mass were established.

On the other hand, when plants were shaded during flowering, photosynthesis, plant dry mass and whole plant reduced N content decreased by 50 % and kernel abortion increased relative to controls during period. Although whole plant reduced N content decreased during the treatment by approximately 50 % relative to the controls, the N concentration in aborting kernels was higher than in non-aborting kernels through late flowering and early grain fill. It appears that the physiological requirements for photosynthate were greater than those for reduced N during establishment of kernel number. After shading was removed at the end of flowering, photosynthesis and plant dry mass accumulation returned to control levels throughout grain fill resulting in a significant decline in kernel number but a non-significant decrease in kernel mass compared to the controls.

Similarly, shading plants during grain fill decreased photosynthesis, aboveground plant dry mass, and whole plant reduced N content during the treatment by approximately 50 %. Mass kernel^{-1} was significantly reduced by 12 % and yield was significantly reduced by 19 % whereas kernels ear^{-1} was not significantly reduced compared to the controls. Ear dry mass and reduced N content decreased by approximately 25 % relative to the controls. Remobilization of dry mass from the stover increased from 7,0 g in the control to 24,2 g in response to shade stress during grain fill. Both the control plants and the plants exposed to shade during grain fill showed an equivalently large

decrease in the reduced N content of the stover during grain fill. This suggests that availability of newly reduced N was more limiting than availability of photosynthate for grain dry mass accumulation of controls. Both dry mass and reduced N were remobilized from the stover of the plants exposed to shade during grain fill, indicating that the reduction in photosynthesis had forced the mobilization of stored photosynthate to the ear and restricted the amount of photosynthate available for the reduction of newly taken up NO_3^-. It appears from these results that even under normal light conditions the amount of photosynthate partitioned to the reduction of newly taken up NO_3^- is limiting and this is exacerbated when shading reduces photosynthesis.

The limited effects of shading during the vegetative phase on final yield of maize as found by Reed et al. (1988) contrasts with the study of Early, McIlrath, Seif and Hageman (1967). They found that extreme shading (80 to 90 % interception of incident light) during vegetative development greatly reduced both vegetative growth and kernel number relative to the controls.

Setter and Flannigan (1986) conducted a study to determine to what extent sugar and starch depletion from maize stem responds to shade and ear temperature treatments. When ear temperature was controlled at 6, 16, 25 and 32°C from 18 to 27 days after pollination (DAP), plants had similar glucose, sucrose and starch concentrations in laminae and sheaths at all temperatures. However, sucrose concentrations in a composite sample of cobs, shanks and husks, and in stems were higher in plants with the 6°C

ear temperature than in plants with the 25°C ear temperature treatment. When plants were shaded to exclude 85 % of light and ear temperatures were controlled during the period from 34 to 44 DAP, sugar and starch concentrations in leaf sheaths and laminae were not affected. Glucose, sucrose and starch concentrations in certain stem fractions were higher in plants with 6°C treatments than in corresponding stem fractions of plants with higher ear temperature. The differences between total sugar content in stems of the 6°C treatment and the content in stems of the 16, 25 and 32°C treatments were 3,6, 4,1 and 4,1 g plant^{-1}, respectively. These differences were not attributed to respiratory losses because, at the end of the treatment period, stem and ear respiration rates among plants with various ear temperatures were not discernibly different. Setter and Flannigan (1986) concluded that it is more likely that temperature induced increases in kernel sink strength at the middle and late kernel fill stages increase the extent of carbohydrate redistribution from vegetative plant parts to kernels.

1.5.3 Partial or complete prevention of fertilization

Reduced sink capacity of maize through prevention of pollination or ear tissue removal results in often significant changes in the production and partitioning of photosynthate in the rest of the plant.

Moss (1962) found that preventing the growth of maize kernels caused photosynthate to accumulate in the leaves slowing

photosynthetic rate. Allison and Watson (1966), on the other hand, found that when pollination was prevented and no kernels formed, net assimilation rate during the first month after flowering was unaffected as dry mass in the stem and husks increased. Thus photosynthesis may not initially have been affected because these organs could accommodate the surplus photosynthate during the first few weeks after silking. In their ^{14}C labelling studies Palmer et al. (1973) found plants bearing partly fertilized ears accumulated large amounts of ^{14}C in the stem, roots and, to a lesser extent, husks, compared with completely fertilized controls. In unpollinated maize hybrids, Campbell (1964) recorded a rapid accumulation of stem soluble solids with final concentrations of between 15 and 17 % being attained. These results appear to indicate that in plants without developing ears, the surplus photosynthate accumulates as soluble solids in vegetative tissue such as the stem and are not utilized for the synthesis of structural material. Hume and Campbell (1972) found that when pollination and subsequent grain formation was prevented, stem soluble solids accumulated to even higher levels at the end of the growing season than were present in the weeks immediately following anthesis. However, stem soluble solids did temporarily decline in the stem of the barren maize plants three weeks after silking coinciding with the development of husk and cob. Root lodging may also restrict ear development and cause soluble solids to accumulate in maize stems (Hume and Campbell, 1972).

1.5.4 Ear tissue removal

Kiesselbach (1948) found that ear removal caused the yield of maize stems and leaves to increase by 59 %, but the overall fodder yield was decreased by 27 % when compared to plants with ears. This indicates that although the stems and leaves have some carbohydrate storage capacity, it is apparently much less than that of a normal ear.

It is often observed that removal of flowers causes delayed senescence in many plants (Leopold, 1961). The observation of Moss (1962) that the leaves of maize plants on which pollination had been prevented were still green towards the end of the season and had a higher rate of assimilation than leaves of pollinated plants which were by then senescent, appears to be another case in point. However, in direct contrast are the results of Allison and Weinmann (1970) who found that removal of ears after flowering caused premature senescence of the leaves above the ear, preceded by the appearance of a purplish red colour. The upper leaves of the earless plants contained more than twice as much total sugar and more than three times as much starch as those of intact plants. Their suggestion that abnormal concentrations of non-structural carbohydrates might interfere with the functions of the leaf and hence lead to premature senescence adds to the general consensus of other workers who have found similar results.

Christensen, Below and Hageman, (1981) found that ear removal initiates not only an earlier onset but an enhanced rate of leaf

senescence in maize. Other characteristics these workers noted associated with ear removal were: (i) marked decrease in dry mass and reduced N accumulation by the whole plant; (ii) progressive, parallel decreases in leaf reduced N, nitrate reductase activity, and chlorophyll; and (iii) increases in carbohydrate content of both the leaf and stem and of reduced N in the stem. It appears that the reduction in the sink capacity of the plant by ear removal resulted in a decrease in photosynthesis. The stem served as an alternative sink to the ear resulting in the mobilization of reduced N from the leaves. The enhanced mobilization of reduced N out of the leaves was suggested by these workers as being a major cause of the earlier onset and enhanced rate of senescence.

Jones and Simmons (1983) observed the effect of enhanced photosynthate supply by reducing the number of kernels at the ear tip by 20 to 40 % per ear at 12 and 24 d after silking. Enhanced photosynthate supply per kernel by kernel removal at either date did not significantly affect the pattern of kernel development, kernel growth rate and duration or final kernel mass. Carbohydrate concentration of the kernels at maturity was also not affected but N concentration of the grain was. Soluble carbohydrate and N concentration in the internode above the ear of plants in which ear size was reduced was higher than in control plants. The lack of a significant response by the grain to photosynthate enhancement may indicate that kernel growth rates and final seed size have approached their upper genetic limits. Factors other than photosynthate supply appear to limit final kernel growth rates and mass in the hybrid studied.

The effect of removal of the husks on final yield of the maize plant remains contentious. The husks have been shown to contribute photosynthate to the grain from both their own photosynthesis (Hesketh and Musgrave, 1962) and from remobilized photosynthate (Fairey and Daynard, 1978). Tollenaar and Daynard (1978b) reported that dehusking ears 9 d after the appearance of the first silks had no effect on grain yield determined at 20 d post-silking. Salvador and Pearce (1988) carried out four different dehusking treatments, viz: (i) husks peeled down from the ear and left down; (ii) husks ripped off entirely, exposing the shank; (iii) husks cut off with scissors; and (iv) husks peeled down and immediately replaced and fastened about the ear with a rubber band. All ears were covered in brown paper bags for protection and unbagged and bagged intact ears were included as controls. Treatments were compared at 15 d after 80 % silking. Treatments in which husks remained on the ear after peeling decreased yield less (8,6 %) than did those in which husks were removed entirely (17,7 %); the average yield decrease for all treatments involving husk manipulation was 14,3 %. Since dehusking was carried out during the grain filling period the greater reduction in kernel mass than kernel number which was recorded was expected. Unfortunately since these workers did not analyse non-structural carbohydrates in the ear husks it is not possible to state whether yield losses were due to either altered ear environment as a result of husk removal or the prevention of the remobilization of photosynthate from the husks to the developing grain. Since the husks do play a rôle in supplying current and remobilized stored photosynthate to the developing grain it appears that the reduction in grain yield was partly due

to a reduction in photosynthate supply from husks during grain fill which the leaves of the plant did not compensate for.

The reason for dehusking having no effect in the experiment of Tollenaar and Daynard (1978b) may be due to the loss of photosynthate supply from the husks during kernel set being easily compensated for by the leaves of the plant.

1.6 Non-structural carbohydrate partitioning in maize grown under conditions of water deficits

It is not the objective of this section to review all the physiological responses and adaptions of plants to water deficits and the reader is rather referred to the following excellent reviews on the subject: Hsiao (1973); Sullivan and Eastin (1974); Boyer and McPherson (1975); Turner and Begg (1981); Shulze (1986) and Turner (1986a&b).

1.6.1 Vegetative growth phase

Cell enlargement is more sensitive to water deficits than photosynthesis (Boyer, 1973; Hsiao, 1973). For example, rates of leaf enlargement are most rapid when leaf water potential (Ψw) is -0,15 to -0,25 MPa, and they decline rapidly when leaf Ψw falls below these values. In maize, sunflower (Helianthus annuus) and soybean leaf enlargement was reduced by 25 % of the well watered controls or less when leaf Ψw decreased to -0,4 MPa. Water deficits during vegetative development will then firstly inhibit leaf and stem enlargement. Root growth, on the other

hand, appears to be either unaffected or often stimulated by water deficits that inhibit leaf and stem growth (McPherson and Boyer, 1977; Jurgens, Johnson and Boyer, 1978; Sharp and Davies, 1979; Meyer and Boyer, 1981; Westgate and Boyer, 1985b). It appears that as water deficits increase, more of the available photosynthate is partitioned to the developing root system (Hsiao and Acevedo, 1974; Sharp and Davies, 1979). This may provide an explanation for the reduction in the shoot to root ratio recorded for plants exposed to water deficits compared to controls. It is not only the growth of new leaf area that may be affected by water deficits but the senescence rate of existing leaf tissue may also be accelerated during water deficits (Boyer and McPherson, 1975) and in conjunction with a decrease in leaf enlargement overall LAI will be reduced. Since a decrease in LAI due to senescence is irreversible the photosynthetic capacity of the plant will be reduced and the supply of photosynthate during the reproductive phase may be limiting (Boyer and McPherson, 1975). Greater water deficits are necessary before photosynthetic rate per unit leaf area is reduced (Turner and Begg, 1978). Plant maturity may, however, affect the response of photosynthetic activity to water deficits. Boyer (1970a&b) found that in vegetative maize (approximately 30 d after planting), photosynthesis declined to 70 % of that in well watered plants when leaf Ψw decreased to -1,2 MPa. In their study of maize exposed to water deficits for most of the grain filling period, McPherson and Boyer (1977) found that at a leaf Ψw of -1,8 to -2,0 MPa, the rate of photosynthesis per unit leaf area was 15 % of the controls. Westgate and Boyer (1985a) found that photosynthesis was completely inhibited when the leaf Ψw in

maize plants subjected to water deficits during grain fill reached -1,6 to -1,8 MPa. Initially photosynthesis declines as a result of stomatal closure (Boyer, 1970b), but as water deficits become more severe the biochemical and biophysical reactions of photosynthesis are affected (Boyer, 1970b).

1.6.2 Reproductive growth phase

Reproductive development in maize commences with the transition of the apical meristem to tassel initiation. Spikelets are then produced on the tassel and at the same time ear differentiation occurs on the topmost axillary meristem. Spikelet primordia are produced acropetally along the ear. The development of ears from lower axillary meristems occurs basipetally (Tollenaar, 1977). The rate and duration of the ear spikelet initiation period determines the number of spikelets available for fertilization. Water deficits that inhibit the photosynthetic activity of the leaves may limit the number of spikelets initiated (Claasen and Shaw, 1970). The development of both male and female floret primordia within the spikelets may also be retarded (Husain and Aspinall, 1970). Unfortunately research reports are not always clear on whether water deficits affect spikelet initiation or the development of spikelets into mature kernels.

1.6.2.1 The flowering period

The flowering period of the reproductive phase from tassel emergence, including pollen shed and silk emergence, to fertilization determines the number of spikelets fertilized i.e.

the potential number of kernels set per plant. There is abundant evidence that water deficits during flowering cause a reduction in the number of kernels set by the plant, thus reducing the sink potential of the plant (Tollenaar, 1977)

Research evidence points to a number of effects of water deficits during flowering that may cause a reduction in final kernel number. Drought stress during embryo sac formation may cause the egg cell to abort (Moss and Downey, 1971). Silk emergence may be retarded, thus by the time silks emerge no viable pollen remains (Herrero and Johnson, 1981). Pollen viability and pollen tube development may also be disrupted, although Herrero and Johnson (1981) have shown that high temperatures affect pollen development more than drought stress.

Although the effects of water deficits on flowering as described are well documented, the physiological factors that cause the sensitivity of each phase of flowering to water deficits are less well understood. Westgate and Boyer (1986a) have shown that when water was withheld from maize plants, leaf Ψw decreased to -1,7 MPa and silk Ψw decreased to -1,2 MPa, whereas pollen Ψw remained unaffected. It was suggested that silks are in moderate hydraulic contact with the vegetative plant whereas pollen grains are not, thus low plant water status affects silks more than pollen. However, Herrero and Johnson (1981) found that at similar ear leaf Ψw, silk elongation was slower on drought stressed than well watered plants. They concluded that factors additional to plant water status control silk growth.

The effect of desiccation on the hormonal balance of the maize plant thus disrupting flowering has been suggested by Moss and Downey (1971). In their study a decrease in femaleness of drought stressed plants was manifested in the abortion of embryo sacs, delayed silk development, and the presence of male florets in ear spikelets. Applied auxins are known to increase the femaleness of maize plants indicated by male sterility and female florets being formed on the tassel (Heslop-Harrison, 1961). Drought stress causes an increase in the activity of IAA-oxidase (Darbyshire, 1971), and thus a reduction in endogenous auxin levels.

On the other hand, the physiological basis for the sensitivity of flowering to drought stress may be viewed in terms of the availability of photosynthate for cell division and growth. Prior to silking, in the transition stage between vegetative and reproductive growth, a rapid increase in leaf and stem dry mass occurs; as leaf size and stem girth and size increase photosynthate is converted to structural material (Westgate and Boyer, 1985a). There is thus little excess non-structural carbohydrate to accumulate in the leaves and stem (Westgate and Boyer, 1985a). This infers that the processes of flowering are largely dependent on current photosynthate for energy and growth requirements. Water deficits during flowering that inhibit photosynthesis reduce the supply of current photosynthate and since reserve levels are low the processes that determine kernel sink potential are retarded. Westgate and Boyer (1985a) have shown that an inability of silks to maintain turgor potential at low leaf Ψw (-1,6 to -1,8 MPa) may be due to a lack of reserves

during silking preventing the silks from accumulating sufficient solutes and maintaining a favourable osmotic potential. Unavailability of photosynthate reserves may be one of the factors additional to plant water status that Herrero and Johnson (1981) concluded control silk growth. Simmons and Jones (1985) have shown that under favourable environmental conditions the quantitatively small amount of stored photosynthate formed prior to silking may contribute less than 10 % to final grain yield. These workers pointed out, however, that pre-silking photosynthate may be important in determining optimum grain development. In general the host of substrates and metabolites required for normal plant metabolism whether they be carbohydrates, lipids, proteins, nucleic acids, hormones or phenolic compounds depend for their formation on the initial products of photosynthesis.

The process of fertilization, during which the pollen grain lands on the stigmatic surface, germinates, the pollen tube grows down within the silk, fertilization takes place and the early embryo is formed, is sensitive to severe water deficits. Westgate and Boyer (1986b) conducted a study in which embryos failed to develop and endosperm cell division did not commence in maize plants exposed to water deficits that almost completely inhibited photosynthesis (leaf Ψw -1,7 MPa). At this low leaf Ψw the silk Ψw was -1,2 MPa. In control plants pollen with a high Ψw (-1,5 to -3,0 MPa) placed on silks with a high Ψw (-0,3 to -0,5 MPa) produced about 550 kernels ear^{-1}. Pollen of low Ψw (up to -12,5 MPa) placed on the control plant silks also produced grain of a similar high rate. However, when pollen with either

high or low Ψw was placed on the silks of stressed plants with a low silk Ψw (-1,2 MPa), the grain did not develop. The failure of the grain to grow could not be attributed to insufficient water on the the silk surfaces as pollen germinated and the pollen tube grew within the silks. The egg sac was invariably fertilized but the embryo did not develop beyond 2 to 3 d. Since leaf Ψw was low enough to completely inhibit photosynthesis and levels of carbohydrate reserves recorded during fertilization were low, these workers suggested that a lack of photosynthate had severely inhibited further grain development.

1.6.2.2 The period of grain fill

The period of grain fill, following fertilization and terminated by physiological maturity (or black layer formation), is characterized by three different phases of grain development. The first, called the lag phase, is a period during which cell division is predominant and kernel dry mass increase is minimal. The lag phase actually commences at silk emergence and extends for 10 to 20 d. The second, or linear phase, is a period of rapid dry mass increase due to the conversion of sugars to starch in the endosperm. In this period more than 90 % of the grain dry mass is accumulated. During the third phase, the rate of dry mass accumulation declines and then terminates with physiological maturity (Johnson and Tanner, 1972). The severity and phase at which water deficits occur during grain fill determines the reduction in final grain yield.

In the two to three weeks after fertilization with the structural development of the stem complete, non-structural carbohydrate levels increase resulting in further increases in the stem dry mass. Leaf dry mass continues to increase peaking at approximately mid-grain fill as a result of both structural development and increases in non-structural carbohydrate levels. After mid-grain fill leaf dry mass decreases due to the mobilization of non-structural carbohydrates, proteins and lipids out of the leaves (Westgate and Boyer, 1985a).

Ouattar, Jones and Crookston (1987a) have shown that long term water deficits imposed from early lag phase until maturity did not affect kernel growth rate for approximately 24 d. Grain filling then terminated abruptly resulting in a 50 % decrease in final kernel mass. Since the water deficits resulted in leaf Ψw of -1,8 to -1,9 MPa (point at which photosynthesis is inhibited (McPherson and Boyer, 1977)) no further whole shoot mass gain was recorded. Stem soluble sugar levels were still low when water deficits were imposed, placing a restriction on the rate and duration of endosperm cell division and grain fill.

Ouattar, Jones, Crookston and Kajeiou, (1987b) have shown that water deficits imposed from the linear-filling phase until maturity (depending on timing, severity and duration) did not significantly reduce the rate of kernel mass gain nor the final kernel mass. Although leaf Ψw declined to below -1,8 MPa, endosperm water, osmotic and turgor potentials were not affected by soil water deficits. (Similar results were obtained by Westgate and Boyer (1986c)). Ouattar *et al.* (1987b) postulated

that the grain is hydraulically uncoupled from the leaf. Endosperm Ψw were low (-1,0 to -1,2 MPa) during endosperm cell division but increased (-0,2 to -0,6 MPa) during the linear-fill period. Ouattar et al. (1987b) suggested that this may be due to the lower endosperm osmotic potential in association with the higher endosperm sugar concentration recorded during endosperm cell division as compared to a higher endosperm osmotic potential during the linear-fill period when soluble sugar concentration decreased due to rapid conversion into starch. Thus the continued kernel growth and maintenance of favourable turgor in the grain were not as a result of osmoregulatory adaption. Ouattar et al. (1987b) compare their results to those of Munns, Brady and Barlow (1979) who reported that the apical meristem of wheat and barley had the ability to osmoregulate under severe water deficits. Ouattar et al. (1987b) postulated that the difference between the stem apex and grain responses may be due to the fact that the osmotically active compounds such as sugars and amino acids do not accumulate in the grain but are rapidly and regularly used for starch and protein synthesis. This is not the case in the apex where organic substances are either oxidized in the respiration process or accumulated as sugars and amino acids. As Westgate and Boyer (1985a) had reported, Ouattar et al. (1987b) found that stem soluble sugar concentration had increased to high levels (approximately 270 g kg^{-1} dry mass) at the onset of the linear-filling phase of grain fill. Thus they attributed the continuation of kernel mass increase when photosynthesis had ceased to the remobilization of stem carbohydrate reserves to the grain as evidenced by the rapid decline in both relative stem mass and total stem sugar

concentrations. Stem moisture content had remained high (700 to 900 g kg^{-1} fresh mass) and relatively unaffected by long term water deficits indicating that the kernel water status was coupled more to stem water content. Thus the favourable moisture status of the grain together with a high stem water content were thought to be the factors that allowed for remobilization of stem carbohydrate reserves and their utilization for kernel growth. Evidence points to photosynthesis being more sensitive to water deficits than translocation (McPherson and Boyer, 1977; Jurgens et al., 1978). Thus water deficits that occur during the linear phase of grain fill may severely affect the source capacity of the maize plant rather than kernel sink capacity.

Other workers have also shown that continued grain mass accumulation under conditions of water deficits is achieved by the remobilization and transport of stored carbohydrates from vegetative organs, primarily the stem, to the grain. Jurgens et al. (1978) found that grain dry mass continued to increase as whole shoot dry mass (including the grain) began to decline in maize plants subjected to a continuous water deficit (leaf Ψw -1,5 to -1,9 MPa) from 10 d after mid-silking. This indicated that continued grain growth was maintained while current photosynthate production had ceased by the redistribution of reserve carbohydrate mostly from the stem to the grain. Labelling plants with ^{14}C before mid-silking in the same study resulted in 10,5 % of the ^{14}C accumulating in the grain of the controls and 13,1 % accumulating in the grain of stressed plants. These results indicated that more reserves were used for grain filling in the stressed plants than in the controls. Similarly

McPherson and Boyer (1977) found that continued grain mass gain was achieved at the expense of dry mass in other shoot parts, mostly the stem, in maize plants subjected to water deficits (leaf Ψw -1,8 to 2,0 MPa) during grain fill. Westgate and Boyer (1985a) found that the greatest losses of dry mass were incurred by the leaves and stem of maize, subjected to water deficits that completely inhibited photosynthesis from mid-grain fill to maturity, as reserve carbohydrates were mobilized to the grain. On the other hand, imposition of water deficits at silk emergence that completely inhibited photosynthesis (leaf Ψw -1,6 to -1,8 MPa) resulted in only a slight decline in leaf and stem dry mass as mobilizable reserve carbohydrates had not yet accumulated.

1.6.3 Selection of genotypes tolerant to water deficits

It is apparent that considerable variations in the relative strengths of the source and the sink occur in maize inbreds and hybrids grown under similar environmental conditions. Determination of the balancing of source capacity to sink capacity and thus photosynthate partitioning patterns has been attributed to a range of physiological factors such as continued nitrate uptake during grain fill (Swank et al., 1982) and endogenous growth substances (Lenton, 1984). Overall a certain degree of flexibility exists for the improvement of maize genotypes through the manipulation of the factors regulating source and sink activity in maize grown under favourable and unfavourable environmental conditions.

Breeding programmes directed towards selecting for drought tolerance are faced with having to reconcile two conflicting requirements: that of reducing transpirational loss of the plant while at the same time allowing maximum CO_2 uptake and dry mass production (Stanhill, 1986). Turner (1986b) has outlined four basic approaches to breeding maize genotypes with drought tolerance. The first is to breed for high yields under optimal conditions and assume that the rank order of genotypes will persist in suboptimal conditions. The strategy employed here may simply be singling out those genotypes which record high yields i.e. selection once the finished product is produced. Alternatively it may be attempted to directly incorporate physiological traits that are thought to improve the efficiency of photosynthate partitioning to the economic yield i.e. attempting to improve on the processes that produce the finished product. The second approach is to breed for maximum yield in the suboptimal target environment. The third approach, often used in conjunction with the second, is the identification and incorporation of a range of traits that confer a measure of drought tolerance. These traits may not be the same as the ones that improve yield under favourable environmental conditions and may, in fact, be antagonistic to high yields under optimal conditions. The fourth approach which is a simplified version of the third is to select for a single drought tolerance trait in an established programme. Some examples of the traits are stomatal activity (McCree, 1974), osmoregulation (Morgan, 1984), high levels of endogenous abscisic acid and proline levels (Quarrie, 1980), high hydraulic resistance of roots (Passioura,

1986) and decreased cuticular transpiration rates (Greenfield, Noble and Jarvie, 1987).

It is clear from the research reports detailed that the availability of stem non-structural carbohydrates for remobilization to the grain during reduced photosynthetic capacity enables some maize genotypes to realize a greater percentage of their potential yield. Thus it may be argued that the utilization of stem non-structural carbohydrates for grain fill under environmental conditions that inhibit photosynthesis provides another useful selection criterion for drought tolerance. However, the extent to which the remobilization of stem reserves to the grain occurs depends on the kernel sink strength. Thus decreased sensitivity of the reproductive growth phases that determine kernel number and size must also be selected for. This may be achieved by selecting for those genotypes that have completed leaf and stem structural growth before fertilization occurs. This would ensure that photosynthate would be available to meet the requirements for kernel set instead of being utilized for synthesis of stem and leaf structural tissue. Photosynthate in excess to those requirements would then accumulate in the stem and be available for remobilization should photosynthesis be inhibited during kernel set. Similarly excess photosynthate produced during grain fill would accumulate in the stem and could be utilized during periods of reduced photosynthesis. It may, however, be difficult to determine whether photosynthate is actively accumulated in the stem in competition with the developing grain.

The capacity to accumulate and then utilize stem reserves would only be an advantageous characteristic for maize cultivars and hybrids grown in regions that have a high likelihood of drought occurring during grain fill. Should drought not occur, high amounts of carbohydrates left in the stem at the end of grain fill may be regarded as wasted yield. This will have to be weighed against the risk of large yield losses being incurred should cultivars and hybrids be grown without 'built in insurance'. In addition, high levels of stem carbohydrates are an advantageous characteristic in maize used for silage, fodder and as stover fed to animals in the field after harvest since the nutritional quality of the whole plant is increased.

CHAPTER 2

1985/86 MAIZE HYBRID RAIN GROWN FIELD TRIAL

2.1 Introduction

Twelve maize hybrids (Table 2.1) were grown under field conditions with the probable assumption that drought periods would occur during grain fill resulting in the depletion of available non-structural carbohydrates in the stem to supplement the supply of carbohydrate to the grain. Of the twelve hybrids, six were chosen for non-structural carbohydrate analysis, namely PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1. PNR 473 is recognized to be a hybrid with good drought tolerance and high yield potential. However, the Pioneer^{R} Seed Company (Pioneer

Table 2.1 Twelve maize hybrids grown in the 1985/86 rain grown trial, Faculty of Agriculture

Pedigree	Source
PNR 542	ex Pioneer 1984
SA 4MS	ex Potchefstroom 1984
SNK 2244	ex Sensako 1984
PNR 6427	ex Pioneer 1984
SA 60	ex Pietermaritzburg 1960
CG 4602	ex Ciba-Geigy 1984
SR 52	ex Saffola 1983
PNR 473	ex Pioneer 1984
HL 1	ex Saffola 1985
SX 16	ex Saffola 1983
CG 4502	ex Ciba-Geigy 1985
PNR 95	ex Pioneer 1983

Seed Company Catalogue, 1985) rates its standability as 4, out of a scale of 1 to 5, where 1 is excellent and 5 is poor. Its poor standability is thought to be due to its tendency to deplete non-structural carbohydrates in the stem at the expense of stem structural strength and resistance to microbial infection of the stem tissue. On the other hand, PNR 6427 represents an improvement on PNR 473 with a standability rating of 2, yet retaining good drought tolerance characteristics. SA 60 is an obsolete hybrid released in 1960. Until recently SA 60 was included in national co-operative maize trials in order to estimate the relative yield improvements of new hybrid releases. SA 60 has poor drought tolerance characteristics but nonetheless serves as a useful benchmark genotype. CG 4602 is purported to have a high yield capacity but moderate drought tolerance characteristics. SR 52 is a high yielding hybrid released in Southern Rhodesia (now Zimbabwe) in 1960 and is more adapted to the short day-length conditions of the sub-tropics. Under favourable environmental conditions and at a plant population density of 2,47 plants m^2, Allison et al. (1975) found that the stem dry mass of SR 52 increased until just after flowering and then remained fairly constant until physiological maturity. They concluded that under normal circumstances depletion of stem reserves did not occur in SR 52. HL 1 is a hybrid developed in South Africa by Dr H.O. Gevers (Department of Agricultural Development, summer grains sub-centre, Cedara) specifically for its high kernel lysine content. Farmers who have planted HL 1 report that it is apparently sensitive to drought at flowering as reduced yields are incurred at maturity.

Although the design of this experiment made no comparison between water stress and non-stress conditions it was nonetheless hoped that differences would be detected between the hybrids in the extent to which non-structural carbohydrates are accumulated and depleted in the stem under the environmental conditions which prevailed during this trial.

2.2 Materials and methods

A site description for this trial conducted on land at the Faculty of Agriculture, University of Natal is provided in Appendix 1.

2.2.1 Field trial cultural and sampling procedures

Cultural procedures

Twelve maize hybrids (Table 2.1) were planted in a randomized complete blocks design with three replications at the University of Natal on the 5 December 1985 (Appendix 14). Hand-jabbers were used to plant seed spaced 0,25 m apart in 0,8 m rows in plots at a uniform depth of 10 cm. Thus there were 4 rows per gross plot of 13,6 m^2. Three seeds were planted per hill, and later thinned to a single plant. In accordance with soil analysis conducted by Cedara Fertilizer Advisory Service (Appendix 11) the trial was fertilized with 50 kg N ha^{-1} applied as LAN (28) at planting and a further 50 kg N ha^{-1} when the crop was approximately 0,5 m high. No phosphate nor potash was applied. Plants were protected from cutworm (*Agrostis* spp.) and stalkborer (*Busseola fusca*) by

pesticides, and weed control was maintained by hand weeding. The trial was irrigated until anthesis whereupon stress was allowed to develop by withdrawing supplementary irrigation.

Sampling procedures

It was decided to select six of the 12 hybrids for further analyses. The six chosen were PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1 and data for these six hybrids only are presented. Whole plants of each hybrid were sampled just after fertilization was completed at anthesis (A), mid-grain fill (MGF) and at physiological maturity (PM) as assessed by grain black layer formation (Daynard and Duncan, 1969; Rench and Shaw, 1971). Two plants per plot were sampled between 10h00 and 12h00. Sampled plant stems were cut at the soil surface and leaves and tassels were discarded. The entire stem was divided into paired internode sections above and below the primary ear, with the primary ear being separated into the shank, grain and cob (Figure 2.1). For purposes of this thesis 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 corresponding segments of the two plants sampled per plot were grouped together to form composite samples.

Each composite sample was placed in a brown paper bag and dried at 70°C in a forced draught oven for 48 h. Samples were then weighed and milled to pass through a 1 mm mesh. The milled material was placed in 30 mℓ plastic bottles, dried again at

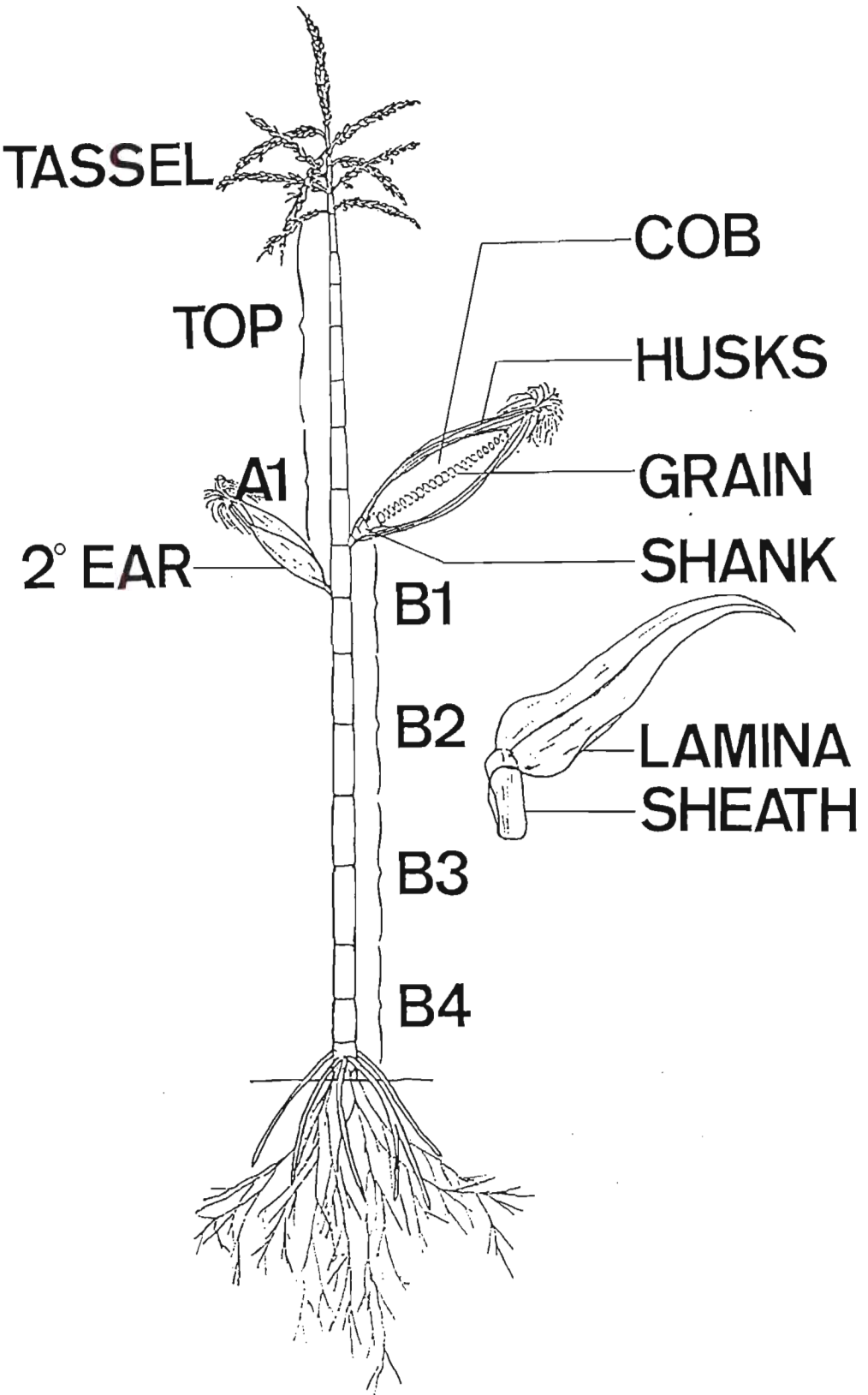


Figure 2.1 Labels used in this thesis for segments sub-sampled from maize plants. The stem segments were labelled according to their position relative to the primary ear (A - above and B - below, the primary ear)

70°C, stoppered and stored until carbohydrate analysis could be conducted.

Leaf area

Leaf area was determined *in situ* for plants from one of the inner two rows. A portable hand-held leaf area meter (LI-COR LI-3000) was used to determine leaf area at maximum canopy (approximately two weeks after anthesis). Since the leaf area was determined on leaves attached to the plant the area of the sheaths was excluded. Additionally some non-photosynthetic (necrotic) leaf tissue was also metered.

Yield analysis

Plants were left to dry out in the field for three weeks after attaining physiological maturity. Nett plots were then hand harvested. Ears were dehusked and shelled using a hand driven maize sheller. Grain mass per nett plot was then determined. These values were then corrected to 12,5 % moisture content and expressed as grain mass (g) per square metre (m^2) ground area.

Additionally, from five randomly selected primary ears per plot the following yield components were determined: rows ear^{-1}; kernels row^{-1} and mass $kernel^{-1}$ (mean of 50 kernels from each of the five ears sampled).

2.2.2 Non-structural carbohydrate analysis

Total non-structural carbohydrates were determined using the modified Weinmann technique (Weinmann, 1947) described by Smith (1981). Sugars were extracted from samples in 80 % (v/v) ethanol. Aliquots of this extract were then analyzed for reducing power using the Shaeffer-Somogyi copper-iodometric titration method (Heinze and Murneek, 1940) to provide a measure of free reducing sugars (RS). In order to determine levels of total sugars (TS) separate aliquots were hydrolysed with 1 M H_2SO_4 before testing for reducing power. Non-reducing sugars were obtained from the difference between TS and RS. Tissue starch in the residue following ethanol extraction was enzymatically hydrolysed to glucose monomer units using Clarase 4000 (R) (Serevac (PTY) Ltd). Aliquots of this extraction were then analyzed for reducing power. Values for total non-structural carbohydrates (TNC) were obtained from the sum of TS and starch. All data at this stage were expressed as component non-structural carbohydrate percentage (composition). By multiplying the percentage values by the dry mass of the original tissue the data was then expressed as component non-structural carbohydrate content in grams. The component non-structural carbohydrate composition and content values for the stem can be compared on a per internode basis or, by summing content values for internodes for each respective hybrid, on a whole plant stem basis. In addition the cob and grain were analyzed for non-structural carbohydrate composition and content.

2.2.3 Statistical analysis and presentation of data

All biometrical analysis was conducted using the GENSTAT Version 4.04 statistical computer package. In order to compare data for each internodal position from each sampling date the trial was analyzed as a split split plot, with hybrid as whole-plot factor, growth stage as sub-plot factor and stem segment as subsub-plot factor. The data for the individual stem segments, including the shank, were summed together providing data for the whole plant stem. The data were analyzed as a split plot with hybrid as the whole-plot factor, and growth stage at which sampling occurred as the sub-plot factor. The data for the grain and cob were each individually analyzed as split plots as for the whole plant stem data.

In order to analyze the data as a split plot in time the following conditions have to be met: (i) homogeneity of error variance for sampling dates; and (ii) identical correlations between measurements for any two sampling dates. This is technically referred to as compound symmetry (Box, 1950; Cole and Grizzle, 1966). Growth of plants is, however, usually characterised by increasing variability over time and by decreasing correlation between two periods as the time difference between sampling dates increases (Causton and Venus, 1981). Consequently if there are more than just a few sampling dates, the split plot in time will usually estimate growth curves imprecisely, and the F-test for the treatment x sampling date interaction will likely produce too many significant results (Greenhouse and Geisser, 1959; Gill, 1978).

In order to test the validity of the split plot in time analysis the data were subjected to the GENSTAT REPMEAS MACRO (Payne and Dixon, 1984). This macro provides the following tests on the data: (i) Box's test of equality covariance matrices; (ii) Box's chi-squared test of covariance matrices; and (iii) Box's F-test of symmetry of covariance matrices. In addition the REPMEAS MACRO provides the Greenhouse-Geisser epsilon factor (Greenhouse and Geisser, 1959). This factor is used to multiply the degrees of freedom (DF1 and DF2) for those F-tests involving the Error Mean Square (EMS) for growth stage (sampling date) and if the factor is less than one the value of F attached to the newly calculated degrees of freedom is higher thus making the F-test for statistical significance more stringent. Additionally since the EMS for stem segments (subsub-plot factor) is calculated over growth stages the stem segments were treated as seven 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. Thus there are two epsilon factors for the split split plot analysis, one for the growth stage EMS, and one for the plant segment EMS. These two epsilon factors are presented at the bottom of the analyses of variance tables in the Appendices, as well as the new F-test levels of significance after epsilon factor adjustment. Occasionally the EMS for growth stage was larger than the EMS for hybrid. 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 six hybrids x three growth stages the whole-plot factor, 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 growth stage before pooling was done. The epsilon factor does not affect the degrees of freedom used to calculate least significant differences (LSD's) and the original degrees of freedom attached to the relevant EMS are used to determine the required t-values (Stielau, 1990; personal communication).

In the split plot analysis of the whole stem, cob and grain data 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 growth stage. Occasionally the EMS for growth stage was larger than the EMS for hybrid. In these situations a weighted pooling of the two EMS's was conducted, .e. the trial was analyzed as a factorial of six hybrids x three growth stages. 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 growth stage before pooling was done.

In the analysis of variance the sum of squares for growth stage was partitioned into linear and quadratic regression effects providing a description of the fluctuation in levels of non-structural carbohydrate components as a function of weeks after anthesis. 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 <u>per se</u> unless the treatment factor was not involved in a significant interaction. Since the coefficient of variation (C.V.) for each

component non-structural carbohydrate was usually above 20 %, the degree of interaction between the treatment factors hybrid, growth stage and stem segment (the latter treatment factor is not relevant to the whole stem, cob and grain data) would have to be substantial in order to provide a significant F-test for that interaction. Consequently the overall F-test for the highest order interaction for each component non-structural carbohydrate was usually non-significant. Occasionally, however, a component regression effect of the highest order interaction was significant when the overall F-test was non-significant. Since the C.V.'s for the component non-structural carbohydrate data were high, it likely that the significant regression effect of the highest order interaction would not be repeatable over seasons and therefore for purposes of this experiment the highest order interaction was regarded as non-significant (Clarke, 1988; personal communication). Nonetheless, the data of the highest order interactions are graphically presented and discussed as they show important physiological trends in the changes in non-structural carbohydrates in the plant segments of each hybrid during grain fill. Least significant differences are only presented on the graphs of the significant highest order interactions. The first highest order interaction which was significant was that for starch composition of the stem segments (Section 2.3.1.5, Figure 2.7). The single asterisk (*) presented with the first cross-bar on the LSD's indicates the $p = 0,05$ significance level, while the two asterisks (**) presented with the second cross-bar on the LSD's indicates the $p = 0,01$ significance level. This format is followed throughout the

thesis although the asterisks are only presented with the LSD's on Figure 2.7.

The continual interconversions of glucose, fructose, sucrose and starch through various catabolic and anabolic pathways makes the interpretation of data very difficult. For example, a decline in stem sucrose content from one sampling date to another may be interpreted as remobilization and utilization of stem reserves. Besides the fact that in the intervening period between sampling dates sucrose content levels may have fluctuated to higher and lower levels, the overall decline in sucrose content may be associated with an increase in glucose and fructose levels. Clearly, analyzing the data using analysis of variance techniques does not provide information on the dynamic state of flux in which non-structural carbohydrate components exist. In order to facilitate the interpretation of data the content values for reducing sugars, sucrose and starch were expressed as the following ratios to one another at each sampling date:

$$\text{sucrose ratio} : \frac{\text{sucrose content}}{\text{reducing sugars content}}$$

$$\text{starch ratio} : \frac{\text{starch content}}{\text{sucrose content}}$$

These ratios enable the relative proportions of the non-structural carbohydrate components to be more readily assessed. The reducing sugars, sucrose and starch contents were further expressed as a percent of the TNC content in order to assess the relative contributions of the component carbohydrates to the TNC content of stem tissue. Throughout this thesis these data are presented in tabulated or graphical form for descriptive purposes

only, and therefore no analysis of variance tests are discussed nor presented for these data.

Cell contents can be broadly divided into five constituents: non-structural carbohydrate, amino acids and protein, lipid, fat, and organic acids; the structural carbohydrates, cellulose and hemicellulose, constitute the cell wall (Deinum and Struik, 1986). Since the protein and lipid fractions were not separately determined in this study, the protein, lipid, structural carbohydrate and mineral components have been collectively termed the residual fraction of the cell. The residual content of a plant segment was determined as the difference between the dry mass and the TNC content of that segment. The ratio of TNC content to residual content was derived in order to more readily assess their relative contributions to the dry mass of a plant segment.

2.2.4 Climatic conditions during grain fill

In order to assess the effects of water availability on the growth of the six maize hybrids, meteorological data (for the period 5 December 1985 (planting date) to the 15 April 1986 (physiological maturity), soil water data and genetic inputs on PNR 6427 were run through the CERES-Maize computer programme (Appendix 4). This programme is a simulation model of maize growth and development, and based on the inputs attempts to predict, amongst other parameters, final grain yield. This simulation model also outputs two stress-day indices, namely CSD1 and CSD2. CSD1 is the less sensitive index and provides an

indication of the extent to which photosynthesis is inhibited by water stress, while CSD2 is the more sensitive index and provides an indication of the extent to which 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 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. The values for CSD1 and CSD2 generated by the programme (Table 1, Appendix 4) indicate that from fertilization (21 February 1986) to just before MGF (20 March 1986), CSD1 and CSD2 were generally equal to zero indicating an adequate supply of water for the processes of photosynthesis and cell expansion. However, at MGF (21 March 1986) CSD1 and CSD2 were 0,32 and 0,54, respectively, increasing to 0,72 and 0,81, respectively, on the 22 March 1986 indicating conditions of water stress. This may explain the lower TNC content levels generally measured in the whole stem tissue of the six hybrids at MGF compared to A (Section 2.3.2.8). From 23 to 26 March 1986, CSD1 and CSD2 then declined to zero but a further severe water stress period developed from 27 March to 11 April 1986 as CSD1 and CSD1 increased from 0,52 and 0,68, respectively, to 1,00 for both indices during this period. However, an adequate water supply was apparently available from 12 April until PM on 15 April 1986 as CSD1 and CSD2 were both zero during this period. This may explain the reaccumulation of TNC in the whole stem of SA 60, SR 52 and HL 1 from MGF to PM, although TNC

levels at PM were less than at A (Section 2.3.2.8). This method of using the CSD1 and CSD2 stress-day factors generated by the CERES-Maize simulation model in order to obtain an index of the water stress conditions that the maize plants were exposed to has its obvious shortcomings, in particular the fact that genetic inputs are only available for PNR 6427. Nonetheless, the values obtained for CSD1 and CSD2 do roughly correspond with the changes in the levels in non-structural carbohydrates in the stems of the six maize hybrids. An interesting research programme would be to correlate the values of CSD1 and CSD2 with leaf area expansion data, photosynthetic activity and levels of stem non-structural carbohydrates.

In terms of rainfall during the grain filling period, the monthly rainfall totals for March and April 1986 were respectively 55,8 and 73,8 % of the long term monthly means (Appendix 6). These data reinforce the scenario indicated by the CSD1 and CSD2 stress indices that rainfall was limited during the grain filling period of the six hybrids, particularly during March which encompassed the mid-grain filling period.

2.3 Results and discussion

Analysis of selected samples by high pressure liquid chromatography showed that sucrose was the only non-reducing sugar present in detectable quantities (Appendix 17). Non-reducing sugars are therefore referred to as sucrose for the remainder of the thesis.

2.3.1 Non-structural carbohydrate analysis of stem segments

2.3.1.1 Reducing sugars composition

Main effects and first order interactions

The main effect for hybrid was significant (Table 2.2 and Appendix 18.1). SR 52 had the highest RS composition of 12,2 %, which was significantly ($p = 0,01$) higher than that of PNR 6427, SA 60, PNR 473 and HL 1, and significantly ($p = 0,05$) higher than that of CG 4602.

The main effects for growth stage and stem segment were significant. However, since these factors were involved in a significant higher order interaction their main effects are of limited interest.

The interactions of hybrid with stem segment and hybrid with growth stage were non-significant. There were no significant components of the latter interaction either.

The interaction of growth stage with stem segment was significant (Table 2.3). The growth stage(quadratic) x stem segment component of the interaction was also significant. This indicates that the stem segments had significantly different patterns of RS composition levels over the growth stages. The top, A1, B1 and B2 segments showed a similar stepwise decline in RS composition from A to PM. In the B3 segment RS composition declined markedly from A to MGF, and then remained constant from

Table 2.2 Mean stem segment reducing sugars composition (%) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
7,0	5,9	8,0	12,2	3,7	5,9
LSD (0,05)	3,4				
LSD (0,01)	4,6				

Table 2.3 Influence of three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), on stem segment reducing sugars composition (%) meaned for six maize hybrids

Growth stage	Stem segment							Growth stage means
	Top	A1	B1	B2	B3	B4	Shank	
A	7,6	8,2	7,7	10,1	10,2	12,0	8,1	9,1
MGF	5,8	7,5	7,2	7,5	6,1	5,3	10,0	7,1
PM	4,0	4,0	4,8	4,9	6,1	7,1	5,0	5,1
Stem segments means	5,8	6,6	6,6	7,5	7,5	8,1	7,7	

Body of table	LSD 0,05	LSD 0,01
Comparison of means at the same level of growth stage	1,8	2,4
Comparison of means at the same level of stem segment or with neither factor in common	2,9	3,9
Marginal means		
Comparison of growth stage means	2,4	3,2
Comparison of stem segment means	1,0	1,4

MGF to PM. In the B4 segment RS composition initially decreased from A to MGF and then increased from MGF to PM. The shank, too, had a different pattern of RS composition change over the growth stages, with levels initially increasing from A to MGF, and then declining from MGF to PM. The RS composition in the shank was significantly ($p = 0,01$) higher at MGF than in any of the other segments at MGF. All segments had significantly ($p \leq 0,05$) less RS composition at PM than at A.

Second order interaction of hybrid, growth stage and stem segment

The interaction of hybrid, growth stage and stem segment was non-significant (Figure 2.2). There were no significant components of the interaction either. However, there were apparent differences between hybrids in RS composition levels in the stem segments during grain fill.

Stem segment RS composition levels ranged from a low of 0,7 % (PNR 473, top segment at PM) to a high of 16,8 % (CG 4602, B2 segment at A).

Averaged over stem segments the patterns of RS composition changes over the growth stages were apparently different for each hybrid. The RS composition declined from A to PM in CG 4602 and PNR 473. On the other hand, RS composition in PNR 6427 initially remained constant from A to MGF before declining from MGF to PM. In SA 60 and HL 1 RS composition declined markedly from A to MGF before increasing slightly from MGF to PM. It is noteworthy that in addition to these general trends RS composition in the B3 and

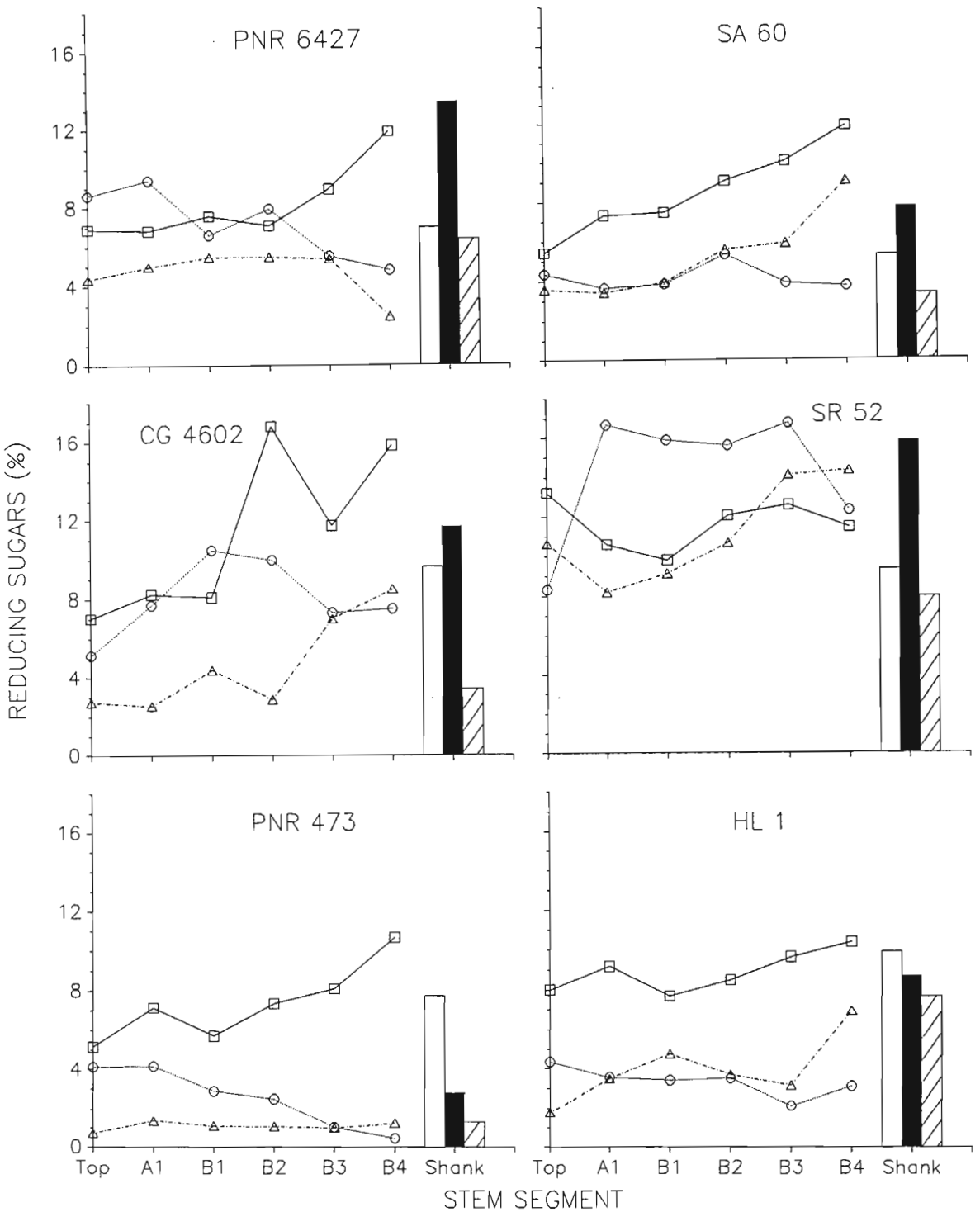


Figure 2.2 Fluctuation in reducing sugars composition in stem segments of six maize hybrids at anthesis (□—□□), mid-grain fill (○—○■) and physiological maturity (△·····△▨)

B4 segments at PM was as high or higher than those at MGF in SA 60, CG 4602, PNR 473 and HL 1.

Changes in RS composition levels in the shank did not always match the general patterns of the main stem segments and were apparently not consistently the same over growth stages for all hybrids. In PNR 6427, SA 60, CG 4602 and SR 52 RS composition increased in the shank from A to MGF and then declined to levels at PM less than at A. In SR 52 this pattern generally matched the changes observed in the main stem segments. The increase in RS composition of the shank from A to MGF was also particularly marked in SR 52 indicating that RS made up a major component of the shank dry mass at MGF. On the other hand, in PNR 473 and HL 1 RS composition levels in the shank peaked at A and then declined in a stepwise fashion to PM. The decline in RS composition from A to PM was more marked in PNR 473. Based on their relative abundance or predominance it appears that RS may play an important metabolic rôle in the shank at A in PNR 473 and HL 1, whereas in the other four hybrids RS appear to be important at MGF. It is not clear, however, whether the relative abundance of RS at these different growth stages indicates RS in storage or RS actively involved in anabolic and catabolic reactions.

2.3.1.2 Reducing sugars content

Main effects and first order interactions

The main effects of hybrid and stem segment were significant, while the main effect of growth stage was non-significant

(Appendix 18.2). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interaction of hybrid with growth stage was non-significant. There were no significant components of the interaction either.

Unlike RS composition, however, the interaction of hybrid with stem segment was significant indicating that the variation in RS content among the stem segments was not consistent over all hybrids (Table 2.4). Perusal of the interaction table reveals that almost every 2 x 2 table within it indicates a non-additive relationship between the factors hybrid and stem segment. This points to the fact that the pattern of RS content changes over the stem segments was unique to each hybrid. CG 4602, SR 52, PNR 473 and HL 1 all showed an increase in RS content from the top segment down to the B3 segment. The RS content was, however, lower in the B4 segment than in the B3 segment in these four hybrids. Reducing sugars content in PNR 6427 increased from the top to a maximum in the B2 segment and then declined from the B2 to the B4 segment. The RS content in SA 60 declined from the top to the A1 segment and then increased from the A1 segment through to the B4 segment. In CG 4602 RS content increased significantly ($p = 0,05$) from the A1 to B1 segments and also from the B1 to B2 segments. In particular, SR 52 showed substantial significant ($p \leq 0,05$) increases in RS content from the A1 to B3 segments while RS content in the B4 segment was markedly significantly ($p = 0,01$) less than the B3 segment. The RS content in the B4 segment of CG 4602 was also significantly ($p = 0,05$) lower than

Table 2.4 Influence of maize hybrid on stem segment reducing sugars (RS) content (g segment^{-1}) meaned over three growth stages during grain fill

Hybrid	Stem segment							Hybrid means
	Top	A1	B1	B2	B3	B4	Shank	
PNR 6427	0,38	0,31	0,51	0,80	0,69	0,49	0,16	0,48
SA 60	0,41	0,36	0,62	1,01	1,05	1,05	0,15	0,66
CG 4602	0,25	0,37	0,83	1,31	1,40	0,94	0,17	0,75
SR 52	0,68	0,86	1,58	2,09	3,49	1,72	0,24	1,53
PNR 473	0,18	0,24	0,31	0,47	0,52	0,19	0,07	0,28
HL 1	0,30	0,33	0,60	0,64	0,73	0,56	0,25	0,49
Stem segments means	0,37	0,41	0,74	1,05	1,31	0,82	0,17	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,46	0,60
Comparison of means at the same level of stem segment or with neither factor in common	0,63	0,84
Marginal means		
Comparison of hybrid means	0,46	0,62
Comparison of stem segment means	0,19	0,25

the B3 segment. It is noteworthy that on an absolute basis RS content in the B4 segment of PNR 473 was markedly but non-significantly lower than the B3 segment, but on a relative basis RS content in the B3 segment was 2,7 times that in the B4 segment. The shank recorded the lowest RS content for all the hybrids with RS content in the shank of HL 1 the highest at

0,25 g segment^{-1} and the shank of PNR 473 the lowest at 0,07 g segment^{-1}. However, there were no significant differences in RS content of the shanks of the hybrids. The pattern of RS content distribution between the A1, B1 and shank segments (the shank arises from the axillary bud of the node shared between these segments) was generally similar in all the hybrids except SR 52. In comparison to the other hybrids the shank of SR 52 had much lower levels of RS content compared to that in the A1 and B1 segments. As the final grain yield of SR 52 was low in this trial (Section 2.3.3), this would appear to reflect decreased translocation of carbohydrate through the shank in response to low grain carbohydrate requirements resulting in the accumulation of non-structural carbohydrate in the main stem segments.

The interaction of growth stage with stem segment was significant (Table 2.5). The growth stage(linear and quadratic) x stem segment components of the interaction were also significant. This indicates that changes in RS content over the growth stages were not the same for all stem segments. Except for the A1 segment at PM being non-significantly less than the top segment in RS content, RS content increased from the top to the B3 segment at all three growth stages. The B4 segment had less RS content than the B3 segment at all growth stages. The shank recorded the lowest RS content levels at all growth stages. The top, A1 and B2 segments declined in RS content from A to PM. The B1 and shank segments initially increased in RS content from A to MGF and then declined from MGF to PM. Both the B3 and B4 segments initially declined in RS content from A to MGF and then increased from MGF to PM. At A the B3 segment had the highest

Table 2.5 Influence of three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM) on stem segment reducing sugars content (g segment^{-1}) meaned for six maize hybrids

Growth stage	Stem segment							Growth stage means
	Top	A1	B1	B2	B3	B4	Shank	
A	0,48	0,53	0,81	1,36	1,62	0,82	0,10	0,82
MGF	0,34	0,44	0,83	1,03	1,05	0,54	0,29	0,65
PM	0,29	0,28	0,59	0,77	1,27	1,12	0,13	0,63
Stem segments means	0,37	0,41	0,74	1,05	1,31	0,82	0,17	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of growth stage	0,32	0,43
Comparison of means at the same level of stem segment or with neither factor in common	0,44	0,59
Marginal means		
Comparison of growth stage means	NS	NS
Comparison of stem segment means	0,19	0,25

RS content which was significantly ($p = 0,01$) higher than the RS content in all the other segments except the B2 segment. At MGF the RS content in the B3 segment was also significantly ($p = 0,01$) higher than all the other segments except the B2 segment. The B3 segment at PM was significantly ($p = 0,01$) higher in RS content than all the other segments except B4 at PM.

Second order interaction of hybrid, growth stage and stem segment

The interaction of hybrid, growth stage and stem segment was non-significant (Figure 2.3). However, the hybrid x growth stage(linear) x stem segment component of the interaction was significant. This indicates that the changes in RS content of the stem segments over the growth stages were not consistently the same for all of the hybrids.

Reducing sugars content levels ranged from a low of 0,02 g segment^{-1} (PNR 473, B4 segment at MGF) to a high of 4,40 g segment^{-1} (SR 52, B3 segment at PM).

With the exception of SR 52, the distribution patterns of RS content were generally similar to that of RS composition. The RS content was generally highest at A in the main stem segments, with content increasing basipetally. Noteworthy however is that, unlike RS composition, the B4 segment in all six hybrids did not have the highest RS content at A. It would appear that the relative abundance of RS in the B4 segment was higher compared to the other main stem segments, while on an absolute basis RS levels were low in the B4 segment compared to the other main stem segments. Reducing sugars content, as with RS composition, declined from A to PM in PNR 6427, CG 4602 and PNR 473. With the water stress conditions that existed from MGF to PM (Section 2.2.4, Appendices 4 and 6) a possible reduction in the production of current photosynthate may have enhanced the utilization of existing RS pools during grain fill. On the other hand, RS content declined from A to MGF in SA 60 and HL 1, but increased

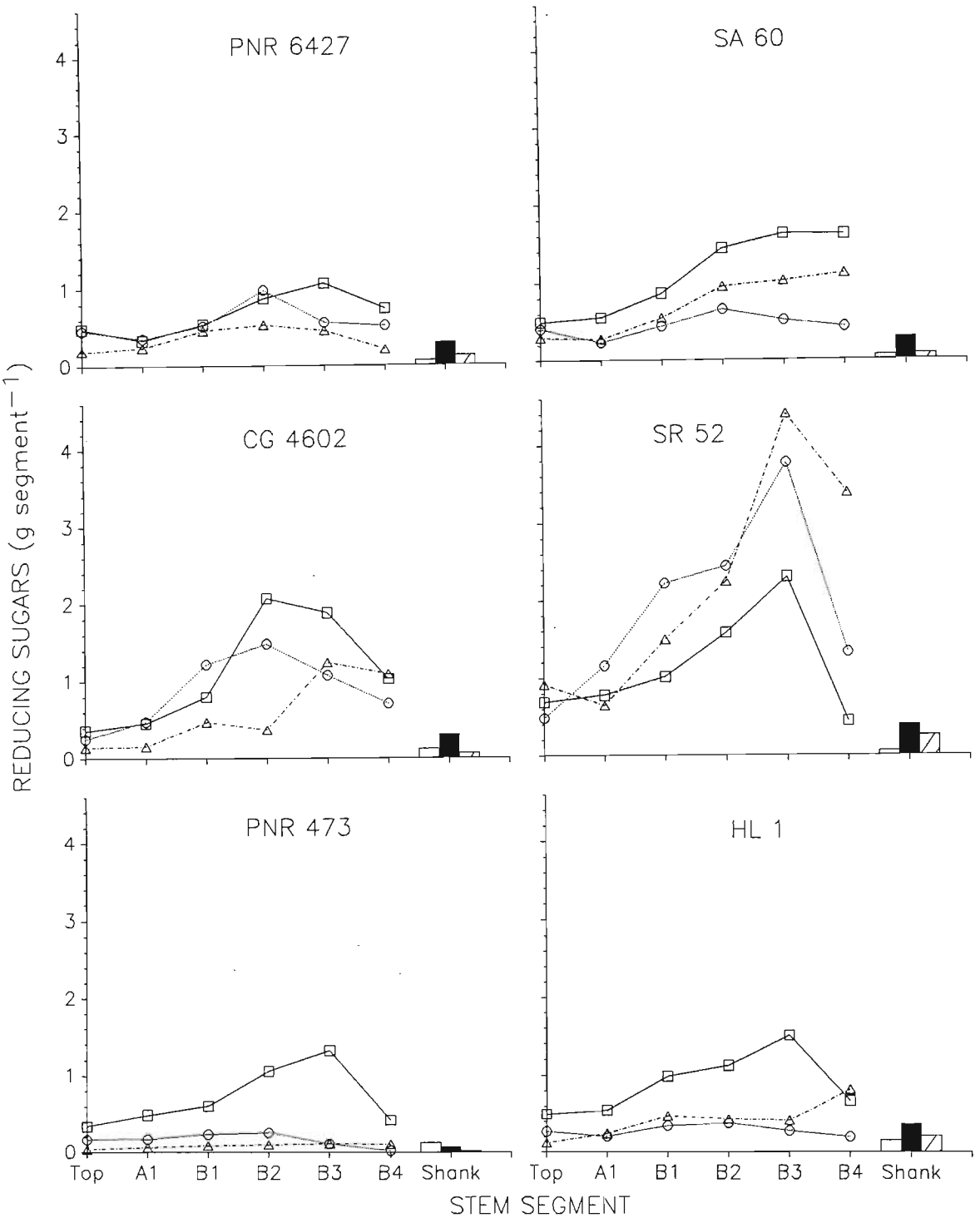


Figure 2.3 Fluctuation in reducing sugars content in stem segments of six maize hybrids at anthesis (□—□▭), mid-grain fill (○—○■) and physiological maturity (△····△▨)

from MGF to PM although levels remained lower than at A. This may indicate the restocking of RS pools with photosynthate produced from recently fixed CO_2 or the conversion of existing labile organic compounds in the stem segments to RS.

The RS content in SR 52 was generally higher in the main stem segments at both MGF and PM than at A. However, RS content was higher in the B3 and B4 segments at PM than at MGF, whereas the upper main stem segments (except for the top) were higher at MGF than at PM. Thus it appears that from MGF to PM some utilization of RS occurred in the A1, B1 and B2 segments and may have been enhanced by a reduction in the production of current photosynthate due to the water stress conditions that prevailed during this period.

Peak RS content in the shank of the hybrids coincided with peak grain fill at MGF. An exception was PNR 473 which had peak RS content in the shank at A. This may indicate that the major part of grain fill begins earlier in PNR 473 than the other hybrids tested, or that during mid-grain fill there was an undersupply of carbohydrate to the developing grain. It is possible that the water stress conditions that prevailed from MGF to PM enhanced the utilization of existing pools of RS to supplement the reduced supply of current photosynthate. This is supported by the marked reduction in RS content in the main stem segments of PNR 473 from A to MGF; with the small amounts of RS at MGF being further depleted to even lower levels at PM.

A good example of how composition data may be misleading in terms of the utilization or accumulation of a component carbohydrate is shown by the RS levels in the shank of HL 1. Whereas RS composition in the shank declined in a stepwise fashion from the highest level at A to the lowest level at PM, RS content was highest in the shank at MGF, and although lower at PM than at MGF, levels were higher at PM than at A. This indicates that the relative abundance of other organic components contributing to shank mass increased from A to MGF and the levels of these other components remained high relative to RS at PM.

Thus the considerable variations that existed in the RS content of the stem segments among hybrids and over growth stages, particularly in SR 52, provided for the significant hybrid with stem segment, and growth stage with stem segment interactions noted earlier.

It is apparent then that since RS occurred in relatively high abundance and since RS content levels do not remain static but generally decline in the main stem segments during grain fill while peaking in the shank during mid-grain fill, they play an important rôle in the metabolism of the plant during grain fill. However, whether or not a decline in RS levels indicates that this rôle is in being utilized for the requirements of the developing grain is not clear. Apart from direct translocation of RS (once converted to sucrose) from the stem segments to the developing grain, a decline in RS levels may be due to: (i) utilization for respiratory requirements; (ii) conversion to other non-structural carbohydrate components namely sucrose and

starch, or conversion to components of the residual fraction within a segment; and (iii) translocation from one stem segment to another followed by respiration or conversion to non-structural carbohydrate or residual components (ap Rees, 1980; Duffus and Duffus, 1984; ap Rees, 1988).

2.3.1.3 Sucrose composition

Main effects and first order interactions

The main effects of hybrid, growth stage and stem segment were significant (Appendix 18.3). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interaction of hybrid with growth stage was significant (Table 2.6). The hybrid x growth stage(linear) component of the interaction was also significant. This indicates that the fluctuations in sucrose composition over the growth stages differed significantly among the hybrids. All hybrids decreased in sucrose composition from A to MGF, and then, except for CG 4602, increased in sucrose composition from MGF to PM. Although sucrose composition in CG 4602 also declined from A to MGF, the difference of 6,8 % ($p = 0,01$) was less than that of the other five hybrids. Sucrose composition then declined marginally from MGF to PM in CG 4602. There were major differences between the other five hybrids in the changes in absolute amounts of sucrose composition over the growth stages. Sucrose composition declined by the largest amount of 11,3 % ($p = 0,01$) in SA 60 from

Table 2.6 Influence of maize hybrid on mean stem segment sucrose composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	Growth stage			Hybrid means
	A	MGF	PM	
PNR 6427	10,2	1,8	5,3	5,7
SA 60	12,2	0,9	6,3	6,5
CG 4602	10,5	3,7	3,4	5,9
SR 52	9,6	1,9	7,2	6,3
PNR 473	11,1	0,6	1,0	4,2
HL 1	9,3	0,8	2,3	4,1
Growth stage means	10,5	1,6	4,3	

Body of table	LSD	
	0,05	0,01
Comparisons of means	3,0	4,1
Marginal means		
Comparison of hybrid means	1,8	2,4
Comparison of growth stage means	1,2	1,7

A to MGF with the second largest decline of 10,5 % ($p = 0,01$) occurring in PNR 473. PNR 473 had the lowest sucrose composition of 0,6 % at MGF, but this level was not significantly less than the levels in any of the other hybrids at MGF. From MGF to PM sucrose composition increased by only 0,4 % (NS) in PNR 473 and by 1,5 % (NS) in HL 1. More marked increases from MGF to PM occurred in PNR 6427 of 3,5 % ($p = 0,05$), SR 52 of 5,3 % ($p = 0,01$) and in SA 60 of 5,4 % ($p = 0,01$).

The interaction of hybrid with stem segment was non-significant.

The interaction of growth stage with stem segment was significant (Table 2.7). The growth stage(linear and quadratic) x stem segment components of the interaction were also significant. This indicates that the fluctuations in sucrose composition over the growth stages was different for each of the seven segments. The outstanding feature of the means of the body of this interaction table is that all segments declined in sucrose composition from A to MGF, and then increased in sucrose composition from MGF to PM. Sucrose composition was significantly ($p = 0,01$) higher at A than at MGF and at PM for all segments. At PM, sucrose composition was significantly ($p \leq 0,05$) higher than at MGF for each segment except the B4 segment which was non-significantly higher. Again the significant interaction was due to differences between the segments in the changes in absolute amounts of sucrose composition over the growth stages. Sucrose composition of the top, A1 and B1 segments declined significantly ($p = 0,01$) by 9,5, 9,7 and 9,1 % respectively, from A to MGF. The B2, B3 and B4 segments declined significantly ($p = 0,01$) by 7,9, 7,0 and 5,5 % respectively, from A to MGF. Thus the change in sucrose composition from A to MGF was more marked for the upper top to B1 segments, while the change in sucrose composition was less marked for the lower segments, particularly the B4. In relation to the A1 and B1 segments, and in fact all the other main stem segments, the decline of 13,4 % ($p = 0,01$) from A to MGF in the shank was most marked. The decline in sucrose composition from A to MGF in all segments may indicate depletion of the sucrose

Table 2.7 Influence of three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), on stem segment sucrose composition (%) meaned for six maize hybrids

Growth stage	Stem segment							Growth stage means
	Top	A1	B1	B2	B3	B4	Shank	
A	11,0	11,7	10,9	9,8	8,4	6,8	14,7	10,5
MGF	1,5	2,0	1,8	1,9	1,4	1,3	1,3	1,6
PM	3,9	4,9	4,5	4,2	3,9	2,8	5,5	4,3
Stem segments means	5,5	6,2	5,8	5,3	4,6	3,6	7,2	

Body of table	LSD 0,05	LSD 0,01
Comparison of means at the same level of growth stage	1,5	2,0
Comparison of means at the same level of stem segment or with neither factor in common	1,9	2,5
Marginal means		
Comparison of growth stage means	1,2	1,7
Comparison of stem segment means	0,9	1,1

pool. It appears that depletion was more marked in the upper segments which are in closest proximity to the ear, particularly in the shank. The amounts by which sucrose composition increased from MGF to PM in each segment were 2,4 ($p = 0,05$), 2,9 ($p = 0,01$), 2,7 ($p = 0,01$), 2,3 ($p = 0,05$), 2,5 ($p = 0,01$) and 1,5 % (NS) for the top, A1, B1, B2, B3 and B4 segments, respectively. Thus while sucrose increased by similar amounts in the top, A1, B1, B2 and B3 segments, the B4 segment in comparison increased by much less. The shank sucrose composition

increased most markedly by 4,2 % ($p = 0,01$) from MGF to PM. This may indicate that as the rate of grain dry mass accumulation slowed after MGF and then ceased at PM, the relative proportion of sucrose increased in the shank.

Second order interaction of hybrid, growth stage and stem segment

The interaction of hybrid, growth stage and stem segment was non-significant (Figure 2.4). There were no significant components of the interaction either. However, there were apparent differences between hybrids in sucrose composition levels in the stem segments during grain fill.

Sucrose composition levels varied from a low of 0,1 % (PNR 473, B4 segment at PM) to a high of 17,2 % (SA 60, top segment at A).

Sucrose composition levels were generally highest in all stem segments of the six hybrids at A. The A1, B3 and B4 segments of SR 52 had slightly less sucrose composition at A than at PM. In contrast to RS composition sucrose composition was generally lower in the basal stem segments viz the B3 and B4 segments at A.

With the exception of the main stem segments of CG 4602, sucrose composition in all segments declined from A to MGF and then increased from MGF to PM. Although sucrose composition in all the segments rose substantially from MGF to PM in PNR 6427, SA 60 and SR 52, levels at PM did not generally exceed those at A. HL 1, and particularly PNR 473, showed a limited increase in

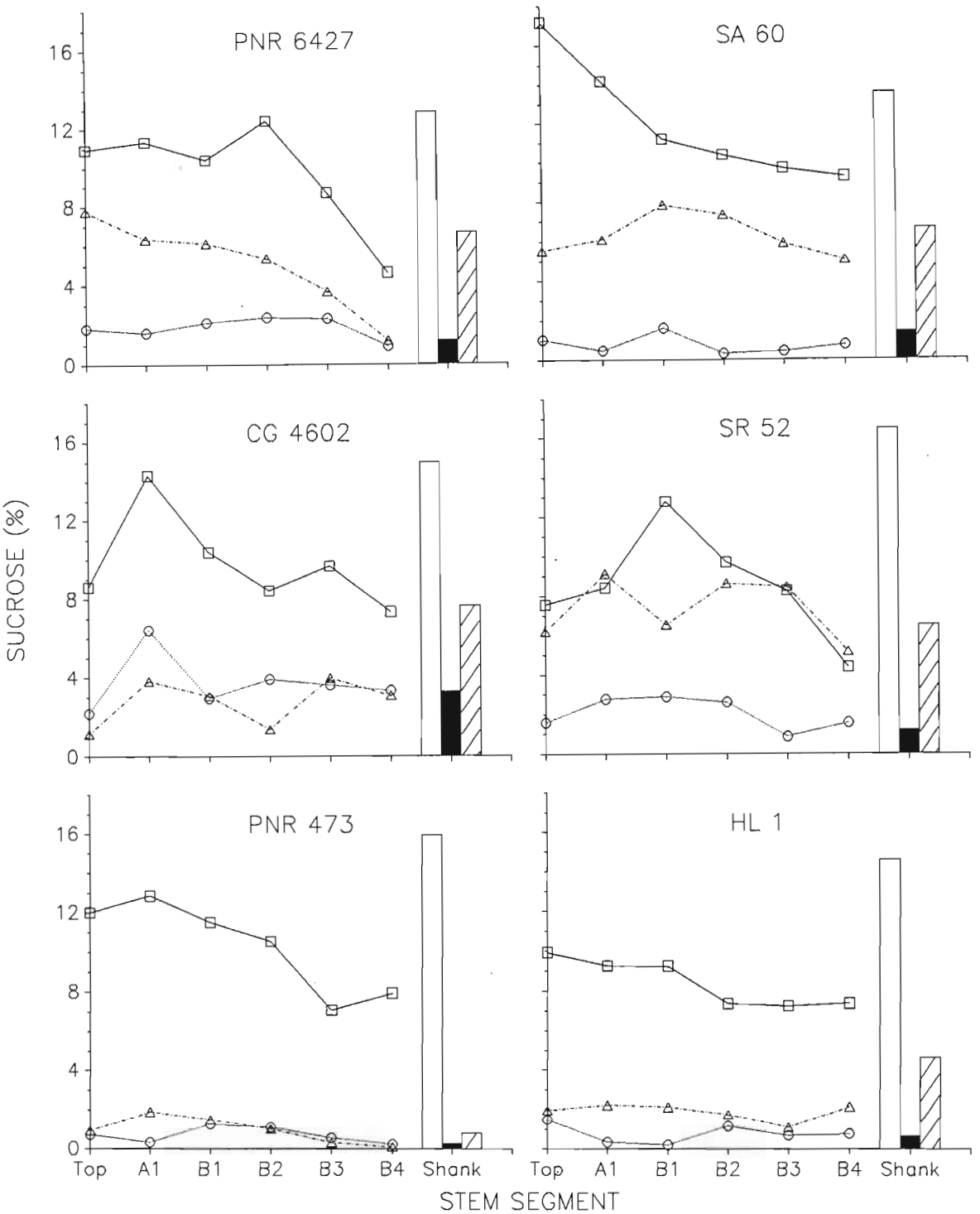


Figure 2.4 Fluctuation in sucrose composition in stem segments of six maize hybrids at anthesis (□—□ □), mid-grain fill (○—○ ■) and physiological maturity (△·····△ ▨)

sucrose composition levels from MGF to PM. In the main stem segments of CG 4602 sucrose composition generally declined from A to the lowest levels at PM. The shank of CG 4602 did, however, follow the general trend of all the segments of the other hybrids in decreasing in sucrose composition from A to MGF and then increasing from MGF to PM. The shank of CG 4602 had the highest sucrose composition at MGF and at PM. It is also noteworthy that in contrast to the general trend shown by the stem segment with growth stage interaction, the increase in sucrose composition from MGF to PM in the shank of PNR 473 was marginal compared to the other hybrids.

2.3.1.4 Sucrose content

Main effects and first order interactions

The main effect for hybrid was non-significant while the main effects for growth stage and stem segment were significant (Appendix 18.4). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interaction of hybrid with growth stage was significant (Table 2.8). The hybrid x growth stage(linear) component of the interaction was also significant. This indicates that although the hybrid means were not significantly different, the fluctuations in sucrose content over growth stages differed significantly among hybrids. All hybrids showed a decrease in sucrose content from A to MGF. This was followed by an increase

Table 2.8 Influence of maize hybrid on mean stem segment sucrose content (g segment^{-1}) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	Growth stage			Hybrid means
	A	MGF	PM	
PNR 6427	0,73	0,11	0,31	0,38
SA 60	1,19	0,08	0,71	0,66
CG 4602	0,82	0,33	0,30	0,48
SR 52	0,77	0,21	1,18	0,72
PNR 473	0,86	0,05	0,06	0,33
HL 1	0,76	0,06	0,18	0,33
Growth stage means	0,85	0,14	0,46	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,45	0,61
Comparison of means at the same level of growth stage or with neither factor in common	0,49	0,68
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of growth stage means	0,18	0,25

in sucrose content from MGF to PM, except in CG 4602 in which sucrose content declined from MGF to PM. Whereas sucrose content in all the other hybrids was lower at PM than at A, sucrose content in SR 52 was higher at PM than at A. Perusal of the means of the body of the interaction table reveals that the absolute amounts by which sucrose content increased or decreased were quite different for each hybrid. SA 60 had the highest

sucrose content at A of 1,19 g segment^{-1}, however, this was not significantly higher than the sucrose content in the other hybrids. Sucrose content declined from A to MGF by 0,62 ($p = 0,01$), 1,11 ($p = 0,01$), 0,49 ($p = 0,05$), 0,56 ($p = 0,05$), 0,81 ($p = 0,01$) and 0,70 g segment^{-1} ($p = 0,01$) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. While SA 60 decreased markedly in sucrose from A to MGF, CG 4602 declined comparatively the least and it had non-significantly the highest sucrose content at MGF. Sucrose content then increased from MGF to PM by 0,20 (NS), 0,63 ($p = 0,01$), 0,97 ($p = 0,01$), 0,01 (NS) and 0,12 g segment^{-1} (NS) in PNR 6427, SA 60, SR 52, PNR 473 and HL 1, respectively. Sucrose content declined slightly by 0,03 g segment^{-1} (NS) in CG 4602 from MGF to PM. Thus sucrose content increased markedly in SR 52 from MGF to PM compared to the other hybrids. Sucrose content also increased substantially in SA 60. Sucrose content in SR 52 at PM was significantly ($p = 0,01$) higher than that in the other hybrids at PM except SA 60. PNR 6427 increased in sucrose content slightly more (0,08 g segment^{-1}) than HL 1. On the opposite end of the scale was PNR 473 which hardly increased in sucrose content from MGF to PM.

The interaction of hybrid with stem segment was significant which indicates that the variation between stem segments in sucrose content differed significantly among hybrids (Table 2.9). Perusal of the interaction table reveals that almost every 2 x 2 table within it indicates a non-additive relationship between the factors hybrid and stem segment. This points to the fact that the pattern of sucrose content changes among the stem segments

Table 2.9 Influence of maize hybrid on stem segment sucrose content (g segment^{-1}) meaned over three growth stages during grain fill

Hybrid	Stem segment							Hybrid means
	Top	A1	B1	B2	B3	B4	Shank	
PNR 6427	0,41	0,33	0,49	0,71	0,47	0,17	0,09	0,38
SA 60	0,72	0,53	0,87	0,95	0,85	0,60	0,12	0,66
CG 4602	0,22	0,50	0,58	0,60	0,92	0,40	0,15	0,48
SR 52	0,34	0,51	0,93	1,18	1,44	0,52	0,11	0,72
PNR 473	0,29	0,34	0,48	0,58	0,41	0,09	0,08	0,33
HL 1	0,29	0,25	0,48	0,44	0,47	0,26	0,14	0,33
Stem segments means	0,38	0,41	0,64	0,74	0,76	0,34	0,12	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,27	0,36
Comparison of means at the same level of stem segment or with neither factor in common	0,41	0,57
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of stem segment means	0,11	0,15

was unique to each hybrid. Sucrose content was higher in the top segment than the A1 segment of PNR 6427, SA 60 and HL 1. Of the three, SA 60 had the greatest difference in sucrose content between the top and A1 segments of 0,19 g segment^{-1} (NS). Sucrose content increased from the top to B3 segments in CG 4602 and SR 52. In SR 52, however, sucrose content increased by the

comparatively large amounts, from the A1 to B1 segments and from the B1 to B2 segments, of 0,42 ($p = 0,01$) and 0,25 g segment^{-1} (NS), respectively. In PNR 6427 sucrose content also increased by a comparatively large amount of 0,22 g segment^{-1} (NS) from the B1 to B2 segments. Sucrose content also increased substantially from the B2 to B3 segments in SR 52 by 0,26 g segment^{-1} (NS). All the hybrids had less sucrose content in the B4 segment than the B3 segment. However, the difference in the amount of sucrose in these two segments was not the same for all the hybrids. Sucrose content was less in the B4 segment than the B3 segment by 0,30 ($p = 0,05$), 0,25 (NS), 0,52 ($p = 0,01$), 0,92 ($p = 0,01$), 0,32 ($p = 0,05$) and 0,21 g segment^{-1} (NS) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. Thus on an absolute basis SR 52 had substantially less sucrose in the B4 segment than the B3 segment. It is noteworthy that on an absolute basis the difference between sucrose content in the B3 and B4 segments was not as great in PNR 473, but on a relative basis sucrose content in the B3 segment was 4,55 times that in the B4 segment. The differences in sucrose content between the shank and the A1 and B1 segments may, as with RS content, provide some indication of the carbohydrate requirements of the grain. In comparison to the other hybrids sucrose content in the A1 and B1 segments of SA 60 and SR 52 was much higher than that in the shank. In the case of SR 52 this may again be a reflection of decreased translocation of carbohydrate through the shank in response to low grain carbohydrate requirement resulting in the accumulation of carbohydrate in the main stem. Although SA 60 did not yield as poorly as SR 52, it would appear that there was an excess production of photosynthate by the source in relation

to the requirements of the sinks including the stem and grain. Interestingly the differences in sucrose content between the shank and the A1 and B1 segments were the lowest in HL 1. This may indicate that the production of sucrose was in balance with utilization of sucrose by the sinks including the stem and grain, or that there was an over-utilization of the sucrose pool by the sinks in HL 1.

The interaction of growth stage with stem segment was significant (Table 2.10). The growth stage(linear and quadratic) x stem segment components of the interaction were also significant. This indicates that the fluctuations in sucrose content differed significantly among the segments over the growth stages. The outstanding feature of the means of the body of this interaction table is that all segments declined in sucrose content from A to MGF, and then increased in sucrose content from MGF to PM. Again the significant interaction is due to differences between the segments in the changes in absolute amounts of sucrose content over the growth stages. The top and A1 segments declined significantly ($p = 0,01$) by 0,68 and 0,65 g segment^{-1} respectively, from A to MGF. The B1, B2 and B3 segments declined significantly ($p = 0,01$) by 1,00, 1,07 and 1,09 g segment^{-1} respectively, from A to MGF. The B4 segment declined significantly ($p = 0,01$) by 0,34 g segment^{-1} from A to MGF. Thus the change in sucrose content from A to MGF was more marked for the B1, B2 and in particular, the B3 segments than the top and A1 segments. The B4 segment declined the least in comparison to the other main stem segments from A to MGF. The shank declined by 0,15 g segment^{-1} (NS) from A to MGF which was the lowest amount

Table 2.10 Influence of three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), on stem segment sucrose content (g segment^{-1}) meaned for six maize hybrids

Growth stage	Stem segment							Growth stage means
	Top	A1	B1	B2	B3	B4	Shank	
A	0,77	0,77	1,18	1,32	1,29	0,47	0,18	0,85
MGF	0,09	0,12	0,18	0,25	0,20	0,13	0,03	0,14
PM	0,28	0,33	0,55	0,67	0,79	0,43	0,14	0,46
Stem segments means	0,38	0,41	0,64	0,74	0,76	0,34	0,12	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of growth stage	0,19	0,25
Comparison of means at the same level of stem segment or with neither factor in common	0,26	0,34
Marginal means		
Comparison of growth stage means	0,18	0,25
Comparison of stem segment means	0,11	0,15

of all the segments. It is, however, important to note that sucrose content at MGF was one-sixth that at A in the shank. The more marked decline in sucrose content in the B1, B2 and B3 segments from A to MGF is not unexpected as they are large stem segments and are therefore capable of accumulating and supplying greater amounts of carbohydrates on an absolute basis. From MGF to PM sucrose content increased by 0,19 (NS), 0,21 (NS), 0,37 ($p = 0,01$), 0,42 ($p = 0,01$), 0,59 ($p = 0,01$) and

0,30 g segment^{-1} ($p = 0,05$) in the top, A1, B1, B2, B3 and B4 segments, respectively. Again sucrose increased to a greater extent in the larger segments, the largest being the B3 segment. The B4 segment was not as large as the B3 segment and therefore sucrose content did not increase by as large an amount in the B4 segment as in the B3 segment. The shank being the smallest segment increased by the smallest amount in sucrose content, namely 0,11 g segment^{-1}. However, sucrose content at PM was 4,66 times that at MGF in the shank indicating that on a relative basis the sucrose content in the shank did increase substantially.

Second order interaction of hybrid, growth stage and stem segment

The interaction of hybrid, growth stage and stem segment was just non-significant (Figure 2.5). The hybrid x growth stage(linear) x stem segment component of the interaction was also just non-significant. Thus there is some possibility that the variation in sucrose content in the stem segments over the growth stages was not consistently the same for all hybrids.

Sucrose plays three vital and inter-related rôles in plant metabolism. It is a major product of photosynthesis, the principle form of translocated C and the main storage sugar in the maize stem (Barr, 1939; ap Rees, 1984). A major problem in interpreting data on sucrose levels in stem tissue is the inability to distinguish between translocatory and storage forms of sucrose.

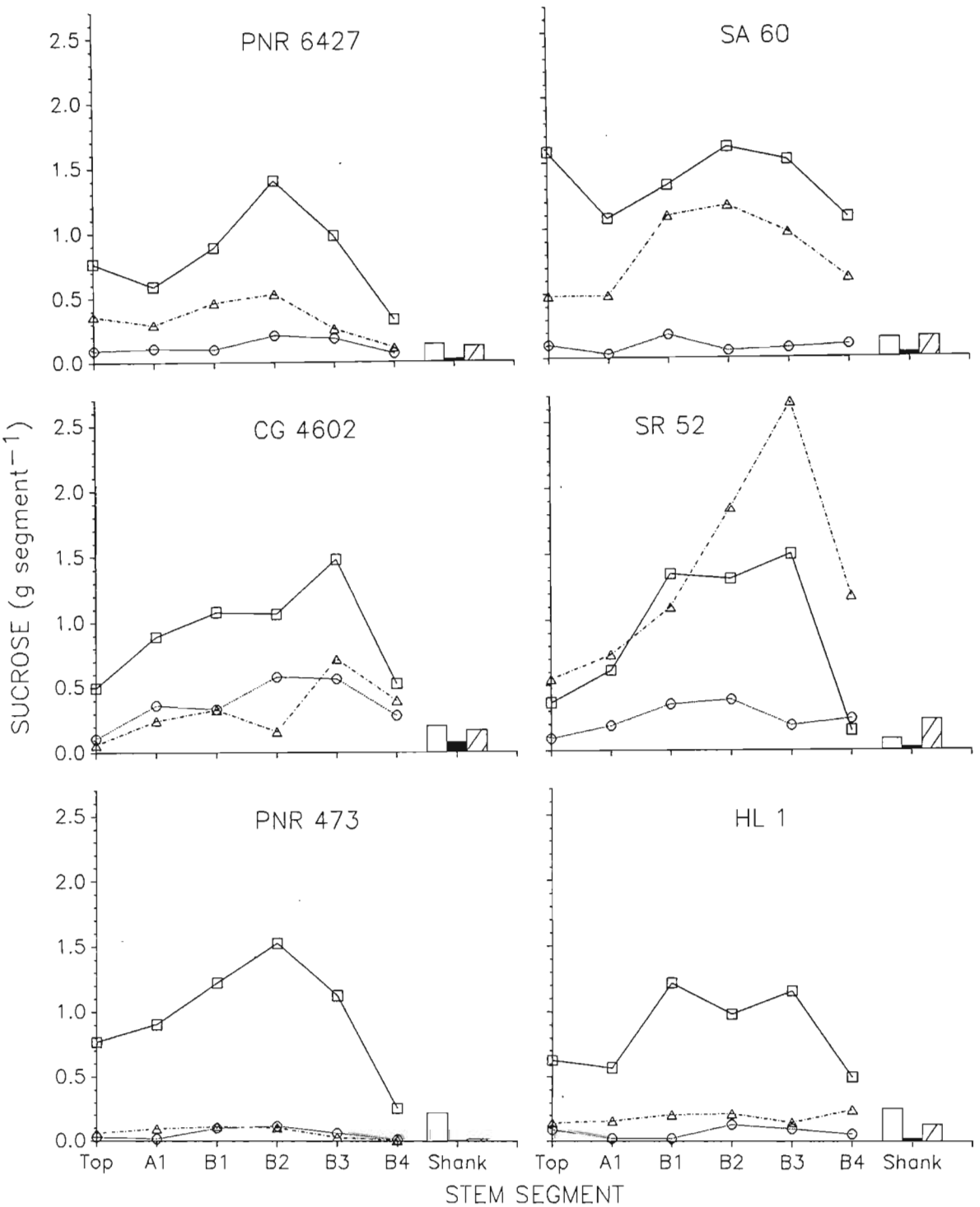


Figure 2.5 Fluctuation in sucrose content in stem segments of six maize hybrids at anthesis (□—□▭), mid-grain fill (○—○■) and physiological maturity (△·····△▨)

Sucrose content ranged from a low of 0,01 g segment^{-1} (PNR 473, B4 segment at PM) to a high of 2,65 g segment^{-1} (SR 52, B3 segment at PM).

Apart from SR 52, sucrose content in the main stem segments was at its highest at A. The B4 segment generally had the lowest amounts of sucrose at A. Since the leaves that originate from the nodes of the B4 segment had senesced at A, any carbohydrate in these segments would be translocate from upper segments with photosynthesising leaves. It appears that the supply of both reducing sugars and sucrose at A to the basal segments, which also support the carbohydrate requirements of the seminal and adventitious root systems, was limited. The priority requirements of carbohydrate in the plant at anthesis are likely to be for the processes of tasselling, ear development, silking, pollination and final increases in leaf and stem size (Tollenaar, 1977).

The ratio of sucrose content to RS content makes it possible to more readily assess the relative proportions of these non-structural carbohydrates (Table 2.11). Also, by graphically expressing the component non-structural carbohydrate contents as a percentage of the total non-structural carbohydrate content a summary of the changes in the relative proportions of the component carbohydrates is provided (Figure 2.6).

It is noteworthy that in all except the B3 and B4 segments, sucrose content at A exceeded RS content by as much as 3,29 times (SA 60, top segment) (Table 2.11, Figure 2.6). As with sucrose

Table 2.11 Ratio of sucrose content to reducing sugars (RS) content and ratio of starch content to sucrose content for stem segments of six maize hybrids sampled at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	Stem segment	A		MGF		PM	
		Sucrose : RS	Starch: sucrose	Sucrose : RS	Starch: sucrose	Sucrose : RS	Starch: sucrose
PNR 6427	Top	1,80	0,3	0,54	2,5	2,49	0,4
	A1	2,44	0,5	0,33	2,7	1,28	0,4
	B1	1,72	0,1	0,21	8,5	1,06	0,3
	B2	1,83	0,2	0,28	8,0	1,09	0,4
	B3	1,09	0,2	0,35	1,7	0,54	2,3
	B4	0,41	0,4	0,36	3,8	0,70	1,1
	Shank	2,48	0,6	0,08	5,3	1,09	0,7
SA 60	Top	3,29	0,1	0,43	2,2	1,37	0,4
	A1	2,30	0,3	0,12	18,0	1,40	0,4
	B1	1,49	0,1	0,43	4,3	2,10	0,2
	B2	1,13	0,4	0,37	7,4	1,21	0,3
	B3	1,00	0,4	0,31	14,3	3,54	0,3
	B4	0,92	0,4	0,33	4,5	0,57	0,5
	Shank	2,72	0,4	0,17	6,0	2,08	0,5
CG 4602	Top	1,43	1,4	0,76	6,5	0,24	127,2
	A1	2,09	0,3	0,82	1,9	1,62	0,6
	B1	1,43	0,3	0,29	1,2	2,41	0,5
	B2	0,66	0,5	0,39	0,3	0,38	31,8
	B3	0,81	0,6	1,43	0,2	0,46	1,2
	B4	0,51	0,8	0,81	1,7	0,26	40,3
	Shank	1,54	0,5	0,28	2,4	2,31	0,6
SR 52	Top	1,09	28,3	0,36	2,3	0,53	0,9
	A1	0,79	0,8	0,31	3,3	1,11	0,4
	B1	1,31	0,4	0,56	3,8	0,63	1,1
	B2	0,84	0,7	0,68	1,0	0,74	0,7
	B3	0,66	0,5	0,29	6,2	0,52	0,7
	B4	1,21	1,1	0,76	7,3	0,36	0,8
	Shank	1,93	0,4	0,15	5,7	0,78	0,5
PNR 473	Top	2,56	0,3	0,20	4,3	1,67	1,6
	A1	1,82	0,4	0,42	5,6	14,52	1,5
	B1	2,02	0,6	0,48	4,2	4,72	40,4
	B2	1,45	0,2	1,64	1,7	7,66	54,8
	B3	0,93	0,3	0,86	17,1	0,95	19,2
	B4	0,70	1,7	0,66	30,4	0,86	70,7
	Shank	2,22	0,4	0,10	75,0	4,98	2,5
HL 1	Top	1,30	0,4	0,42	3,4	1,54	4,4
	A1	1,02	0,3	0,12	7,4	0,58	1,9
	B1	1,22	0,5	0,10	47,9	4,35	0,7
	B2	0,87	0,9	0,55	3,2	3,47	1,4
	B3	0,74	0,4	1,27	3,5	0,36	18,0
	B4	0,63	0,8	0,32	2,0	0,92	0,2
	Shank	1,49	0,4	0,09	5,7	0,63	0,8
Sucrose : RS ratio			SE ($\bar{x}$)	1,33			
Starch : sucrose ratio			SE ($\bar{x}$)	14,7			

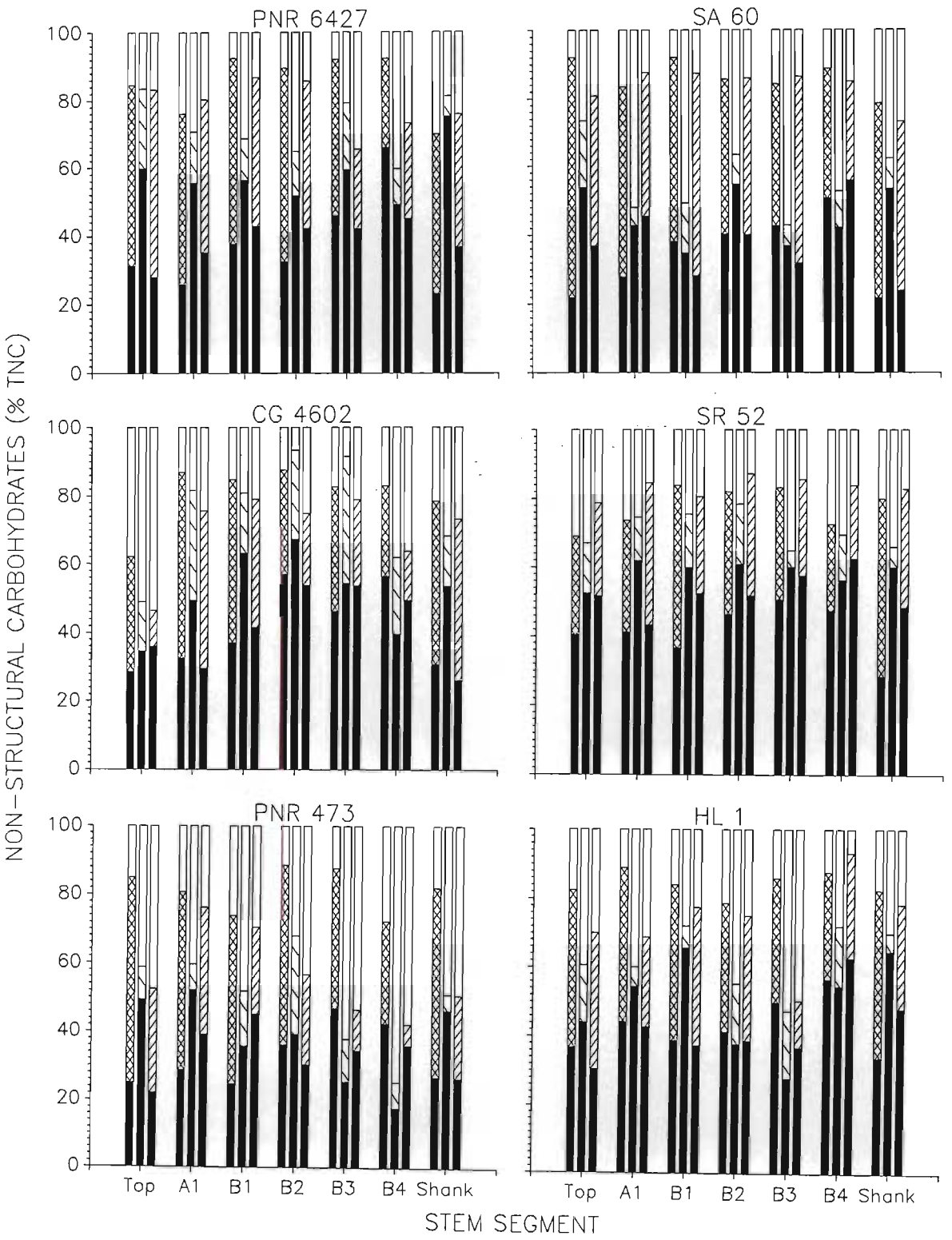
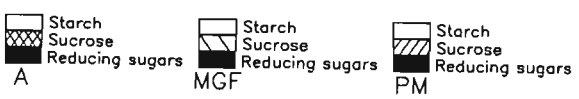


Figure 2.6 Fluctuation in component non-structural carbohydrate content expressed as a percentage of total non-structural carbohydrate (TNC) content in stem segments of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Key



composition, with the exception of the main stem segments of CG 4602, sucrose content in the main stem segments and the shank declined from A to MGF and then increased from MGF to PM. SA 60, PNR 473 and in particular HL 1 showed a marked decline in sucrose levels from A to MGF. SA 60 and in particular SR 52 showed a substantial increase in sucrose content levels from MGF to PM, with the average segment sucrose content at PM in SR 52 higher than at A. It will be recalled that apart from SR 52 the RS content also declined from A to MGF in the main segments and then from MGF to PM further declined in PNR 6427, CG 4602 and PNR 473 but increased in SA 60, SR 52 and HL 1. In the shank on the other hand, RS content had apart from PNR 473, increased from A to MGF and then declined from MGF to PM. Sucrose declined more relative to RS in the main stem segments from A to MGF as the ratio of sucrose to RS, with few exceptions, was less than one at MGF (Table 2.11, Figure 2.6). Sucrose levels then, with the odd exception, rose more relative to RS from MGF to PM as indicated by the increase in the ratio of sucrose content to RS content (Table 2.11, Figure 2.6).

The low levels of sucrose relative to RS at MGF may indicate the importance of RS in biochemical reactions during metabolically active periods such as peak grain fill. The high levels of RS content in the shank at MGF (apart from PNR 473) may be indicative of high rates of metabolic activity as all carbohydrate translocated to the developing grain passes through the shank. On the other hand, at A before rapid grain dry mass accumulation had begun sucrose and RS levels were, with the exception of SR 52, at their highest levels. At this stage the

sink potential of the ear had not fully developed and photosynthate surplus to grain requirements accumulated in the main stem segments. At A it is likely that sucrose occurred in the translocation pathway and in storage pools (Giaquinta, 1983). Should environmental conditions become limiting to the production of current photosynthate, sucrose in storage pools in the stem may provide an immediate supplementary supply of photosynthate for grain fill to continue (Franceschi, 1986). Sucrose content in the stem segments was generally lowest in all hybrids at MGF, coinciding with peak grain fill. With the high carbohydrate requirements of the grain at this stage it is likely that there will be little excess current photosynthate available to accumulate in the stem in the form of sucrose. In addition, respiratory losses would be high at MGF in order to supply the energy required to drive the remobilization and translocatory processes (Stoy, 1965). The water stress conditions that prevailed from MGF to PM would also reduce the production of current photosynthate thus enhancing the depletion of sucrose available in storage pools to meet the carbohydrate requirements of the grain. It is possible that the low levels of sucrose recorded at MGF were indicative of sucrose in the translocation pathway, with a considerably lower proportion of sucrose occurring in storage pools compared to that at A. That sucrose levels rose from MGF to PM with levels again higher than RS levels at PM, may be indicative of reduced utilization of the sucrose pool for grain fill requirements as the grain attained physiological maturity and for general cell maintenance requirements.

That all three first order interactions were significant and the just non-significance of the second order interaction is not unexpected in the light of the marked differences in the changes of sucrose content levels over the growth stages for each of the hybrids. As with RS the changes in sucrose levels in SR 52 during the reproductive phase were markedly different to the other five hybrids. Thus the data for SR 52 are an important component in causing significant interactions.

From the discussion above it becomes apparent that a reduction in sucrose content may not be coincident with an overall decline in TS (RS plus sucrose) levels within any one segment since sucrose may be converted to RS and vice versa. Total sugars content levels did, however, generally decline from their highest levels at A to their lowest levels at MGF and then increased from MGF to PM (Table 2.12). For example, TS content averaged over segments in PNR 473 at MGF was only 13,2 % of that at A. SR 52 was again the exception to the rule as TS content at MGF was 108,8 % of that at A. Importantly, however, is that the TS content values account for the interconversion of sucrose and RS, and the values indicate a general depletion from A to MGF of TS followed by a reaccumulation from MGF to PM. These data do not indicate what the TS were utilized for from A to MGF. This may become clearer once the data for the whole stem non-structural carbohydrate and residual content is examined (Section 2.3.2). It is also possible that the TS were utilized for starch synthesis within any one segment.

Table 2.12 Fluctuation in total sugars content (g segment^{-1}) in stem segments of six maize hybrids sampled at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	Stem segment	A	MGF	PM
PNR 6427	Top	1,26	0,55	0,55
	A1	0,93	0,47	0,53
	B1	1,43	0,62	0,92
	B2	2,27	1,19	1,06
	B3	2,04	0,74	0,71
	B4	1,07	0,59	0,32
	Shank	0,20	0,32	0,25
SA 60	Top	2,08	0,52	0,78
	A1	1,63	0,27	0,77
	B1	2,19	0,63	1,66
	B2	3,05	0,72	2,12
	B3	3,13	0,59	1,99
	B4	2,69	0,53	1,73
	Shank	0,21	0,33	0,24
CG 4602	Top	0,86	0,36	0,20
	A1	1,35	0,84	0,41
	B1	1,88	1,55	0,80
	B2	3,14	2,06	0,53
	B3	3,36	1,64	1,96
	B4	1,55	0,99	1,49
	Shank	0,33	0,39	0,24
SR 52	Top	1,06	0,58	1,46
	A1	1,39	1,35	1,38
	B1	2,36	2,57	2,59
	B2	2,89	2,83	4,09
	B3	3,80	3,96	7,04
	B4	0,59	1,57	4,56
	Shank	0,14	0,43	0,49
PNR 473	Top	1,11	0,19	0,10
	A1	1,40	0,19	0,16
	B1	1,84	0,34	0,20
	B2	2,59	0,37	0,20
	B3	2,45	0,18	0,15
	B4	0,69	0,04	0,12
	Shank	0,35	0,08	0,04
HL 1	Top	1,13	0,36	0,27
	A1	1,12	0,23	0,40
	B1	2,20	0,36	0,67
	B2	2,10	0,51	0,64
	B3	2,66	0,37	0,56
	B4	1,16	0,25	1,05
	Shank	0,42	0,39	0,35

$SE(\bar{x})$ = 0,38

The incidence of Diplodia zeae was high in the 1986 season and this, coupled with water stress (Mortimore and Ward, 1964), resulted in reduced yields for all hybrids. High sugar levels in the stem pith tissue apparently provides the maize plant with greater resistance to D. zeae stem rot (Craig and Hooker, 1961). Although SR 52 maintained comparatively high levels of sucrose in the stem throughout the grain filling period, it was severely affected by D. zeae which contributed to it recording the lowest grain yield of the hybrids tested.

2.3.1.5 Starch composition

Main effects and first order interactions

The main effects for hybrid, growth stage and stem segment were significant. The first order interactions of hybrid with growth stage, and growth stage with stem segment were both non-significant, while the first order interaction of hybrid with stem segment was significant. However, since the second order interaction was significant the main effects and first order interactions are of limited interest (Appendix 18.5).

Second order interaction of hybrid, growth stage and stem segment

The interaction of hybrid, growth stage and stem segment was significant (Figure 2.7). The hybrid x growth stage(linear and quadratic) x stem segment components of the interaction were also significant.

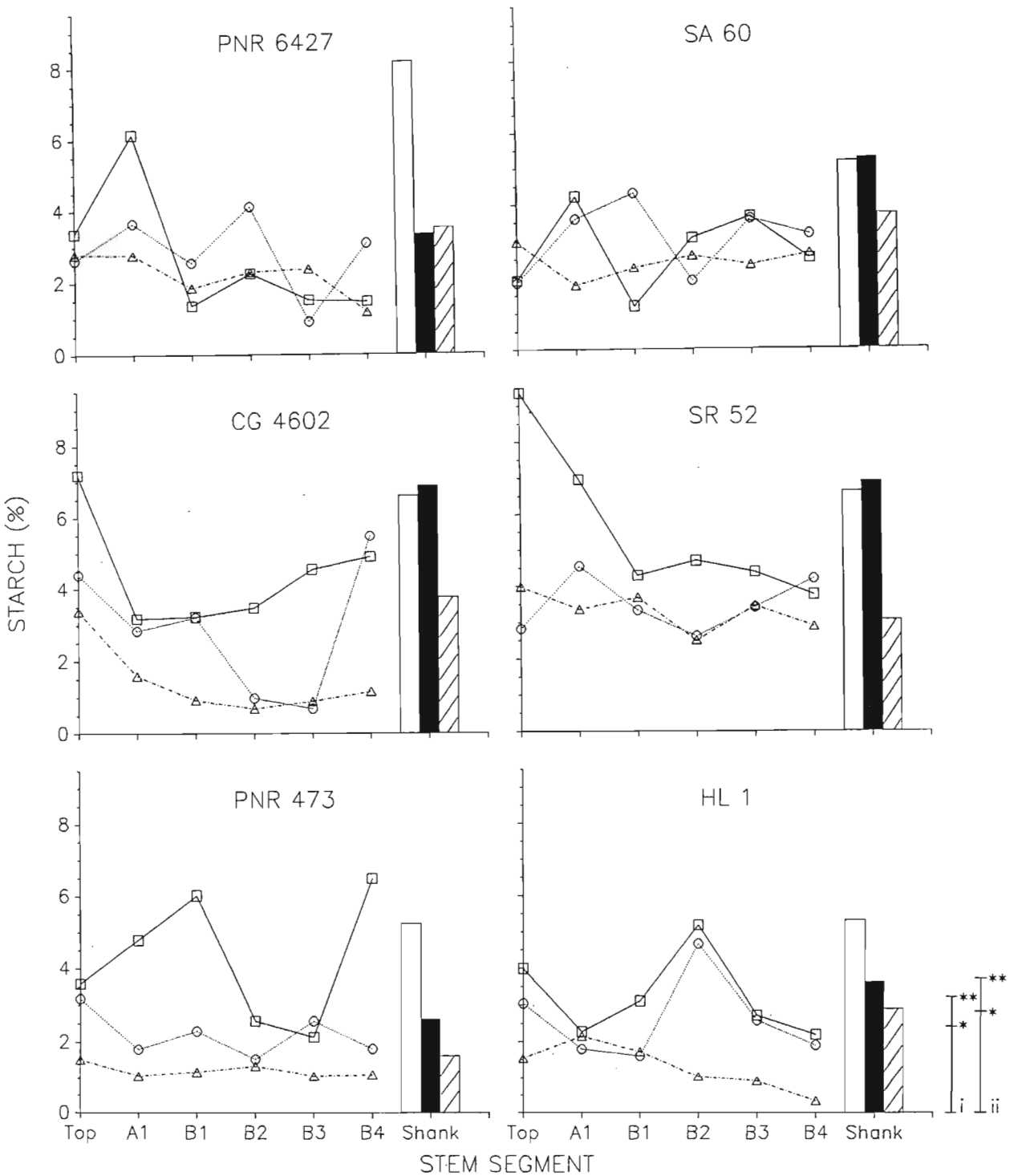


Figure 2.7 Fluctuation in starch composition in stem segments of six maize hybrids at anthesis (□—□□), mid-grain fill (○—○■) and physiological maturity (△·····△▨). Comparisons using LSD's of means at the same levels of (i) hybrid and growth stage; and (ii) stem segments or with no factor in common

Variation in starch composition is very different to that of sucrose. Although starch may occur in short and long term storage forms (Stitt and Steup, 1985), it does not occur as a translocate. It is clear after studying Figure 2.7 that the fluctuations in starch composition in the stem segments over the growth stages were extremely variable for each hybrid.

Starch composition ranged from a low of 0,3 % (HL 1, B4 segment at PM) to a high of 9,3 % (SR 52, top segment at A).

Starch composition was generally highest at A in the main stem segments of CG 4602, SR 52, PNR 473 and HL 1 (Figure 2.7). While starch composition was highest in the shank at A in PNR 473 and HL 1, in SA 60, CG 4602 and SR 52 starch composition was similar at A and MGF at which stages it was higher than at PM. In CG 4602 and SR 52 the top segment at A recorded the highest starch composition out of all their segments at all growth stages of 7,2 and 9,3 %, respectively. PNR 473 recorded its highest starch composition levels at A in the B4 segment of 6,5 % followed by the B1 segment of 6,0 %. In HL 1 the highest starch composition of 5,3 % was recorded at A in the shank. In PNR 6427 and SA 60 starch composition at A in the main stem segments was not consistently higher or lower than levels at MGF or PM. The shank of PNR 6427 at A had the highest starch composition of 8,1 % out of all its segments. This was also the highest starch composition recorded for shanks of all the hybrids at all growth stages. SA 60 recorded its highest starch composition of 5,2 % in the shank at MGF.

Starch composition generally declined from A to PM in the main stem segments of CG 4602, PNR 473 and HL 1, while levels at MGF and PM were fairly similar in SR 52. Starch composition initially increased in the shanks of CG 4602 and SR 52 from A to MGF before declining from MGF to PM. Starch composition in the shanks of PNR 473 and HL 1 declined in a stepwise fashion from A to PM. In PNR 6427 starch composition at MGF was lower in the top, A1 and B3 segments than at A, while in the B1, B2 and B4 segments starch composition was higher at MGF than at A. Starch composition in PNR 6427 at PM was generally lower than that at MGF in the main stem segments, but was still higher than that at A in the B1, B2 and B3 segments. Starch composition in the shank of PNR 6427 declined substantially from A to MGF, and increased slightly from MGF to PM. In SA 60 starch composition at MGF was generally as high as that at A in the main stem segments, while starch composition at PM was generally lower than that at A or MGF. The pattern of starch composition changes in the shank of SA 60 was similar to that in the shanks of CG 4602 and SR 52 with an initial slight increase from A to MGF and then a decline from MGF to PM. It is noteworthy that at PM starch composition levels were less variable among the main stem segments for all hybrids.

2.3.1.6 Starch content

Main effects and first order interactions

The main effects for hybrid and stem segment were significant (Appendix 18.6). However, since these factors were involved in

a significant higher order interaction their main effects are of limited interest.

The main effect for growth stage was significant (Table 2.13). However, since this factor was not involved in significant higher order interactions the changes in starch content over the growth stages may be assessed solely in terms of the main effect for growth stage. There was a significant negative linear effect which indicates that starch content declined from A to PM. Starch content was significantly ($p = 0,01$) higher at A than at PM while starch content at A was not significantly higher than at MGF, nor was starch content significantly higher at MGF than at PM.

The interaction of hybrid with growth stage was non-significant. There were no significant components of the interaction either.

The interaction of hybrid with stem segment was significant indicating that the variation in starch content between stem segments differed among the hybrids (Table 2.14). Perusal of the interaction table reveals that almost every 2 x 2 table within it indicates a non-additive relationship between the factors hybrid and stem segment. This points to the fact that the pattern of sucrose content over the stem segments was unique to each hybrid. Starch content increased from the top to the B3 segment in SA 60 and SR 52. While starch content increased by 0,15 g segment^{-1} (NS) from the B2 to B3 segments in SA 60, in SR 52 it increased by 0,35 g segment^{-1} ($p = 0,01$) in the same segments. In PNR 6427 starch content increased from the top to

Table 2.13 Mean starch content (g segment^{-1}) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM) of stem segments from six maize hybrids

Growth stage		
A	MGF	PM
0,32	0,26	0,20

LSD (0,05) 0,08

LSD (0,01) 0,10

Table 2.14 Influence of maize hybrid on stem segment starch content (g segment^{-1}) meaned over three growth stages during grain fill

Hybrid	Stem segment							Hybrid means
	Top	A1	B1	B2	B3	B4	Shank	
PNR 6427	0,16	0,21	0,17	0,32	0,18	0,14	0,08	0,18
SA 60	0,19	0,25	0,34	0,38	0,53	0,36	0,12	0,31
CG 4602	0,30	0,15	0,27	0,22	0,34	0,29	0,11	0,24
SR 52	0,32	0,36	0,47	0,48	0,83	0,45	0,10	0,43
PNR 473	0,17	0,16	0,32	0,23	0,24	0,18	0,06	0,20
HL 1	0,18	0,12	0,24	0,44	0,29	0,08	0,11	0,21
Stem segments means	0,22	0,21	0,30	0,35	0,40	0,25	0,10	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,17	0,22
Comparison of means at the same level of stem segment or with neither factor in common	0,19	0,25
Marginal means		
Comparison of hybrid means	0,11	0,15
Comparison of stem segment means	0,07	0,09

the A1 segments, but decreased in the B1 segment, increased from the B1 to the B2 segment by a relatively substantial amount of 0,15 g segment^{-1} (NS), then decreased in the B3 segment. Starch content was non-significantly higher in the top segment than the A1 segment in CG 4602 but increased from the A1 to the B1 segment, decreased in the B2 segment and then increased in the B3 segment. In PNR 473 starch content was relatively low in the top and A1 segments then increased quite markedly by 0,16 g segment^{-1} (NS) from the A1 to the B1 segment. Starch content then decreased from the B1 to the B2 segment and increased slightly from the B2 to the B3 segment. In HL 1 starch content declined slightly from the top to the A1 segment, increased in the B1 segment, and then increased by the most substantial amount of 0,20 g segment^{-1} ($p = 0,05$) from the B1 to the B2 segment. Starch content then declined by 0,15 g segment^{-1} (NS) from the B2 to B3 segments. All the hybrids had less starch content in the B4 segment than the B3 segment. However, the difference between these two segments in starch content was not the same for all the hybrids. Starch content was less in the B4 segment than in the B3 segment by 0,04 (NS), 0,17 (NS), 0,05 (NS), 0,38 ($p = 0,01$), 0,06 (NS) and 0,21 g segment^{-1} ($p = 0,05$) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. Thus SR 52 had substantially less starch content in the B4 segment than the B3 segment, while the B3 and B4 segments were not as markedly different in starch content in CG 4602, PNR 473 and particularly PNR 6427. In SR 52 the A1 segment had significantly ($p = 0,01$) higher starch content than the shank, the difference being 0,26 g segment^{-1}. The B1 segment of SR 52 also had significantly ($p = 0,01$) higher starch content

than the shank, the difference was 0,37 g segment^{-1}. SA 60 and PNR 473 had, respectively, 0,13 and 0,10 g segment^{-1} more starch content in the A1 segment than the shank, these differences were, however, non-significant. The B1 segment of these two hybrids had significantly ($p = 0,01$) more starch content than the shank, the differences were 0,22 and 0,26 g segment^{-1}, respectively. CG 4602 and HL 1 had the least marked and non-significant differences in starch content between the shank and the A1 and B1 segments. This may indicate that there was little photosynthate in excess to the requirements of the various sinks particularly the grain, to accumulate in the stem as starch.

The interaction of growth stage with stem segment was non-significant. There were no significant components of the interaction either.

Second order interaction of hybrid, growth stage and stem segment

The interaction of hybrid, growth stage and stem segment was non-significant (Figure 2.8). There were no significant components of the interaction either. However, there were apparent differences between hybrids in starch content levels in the stem segments during grain fill.

Starch content ranged from a low of 0,04 g segment^{-1} (HL 1, B4 segment at PM) to a high of 1,05 g segment^{-1} (SR 52, B3 segment at PM).

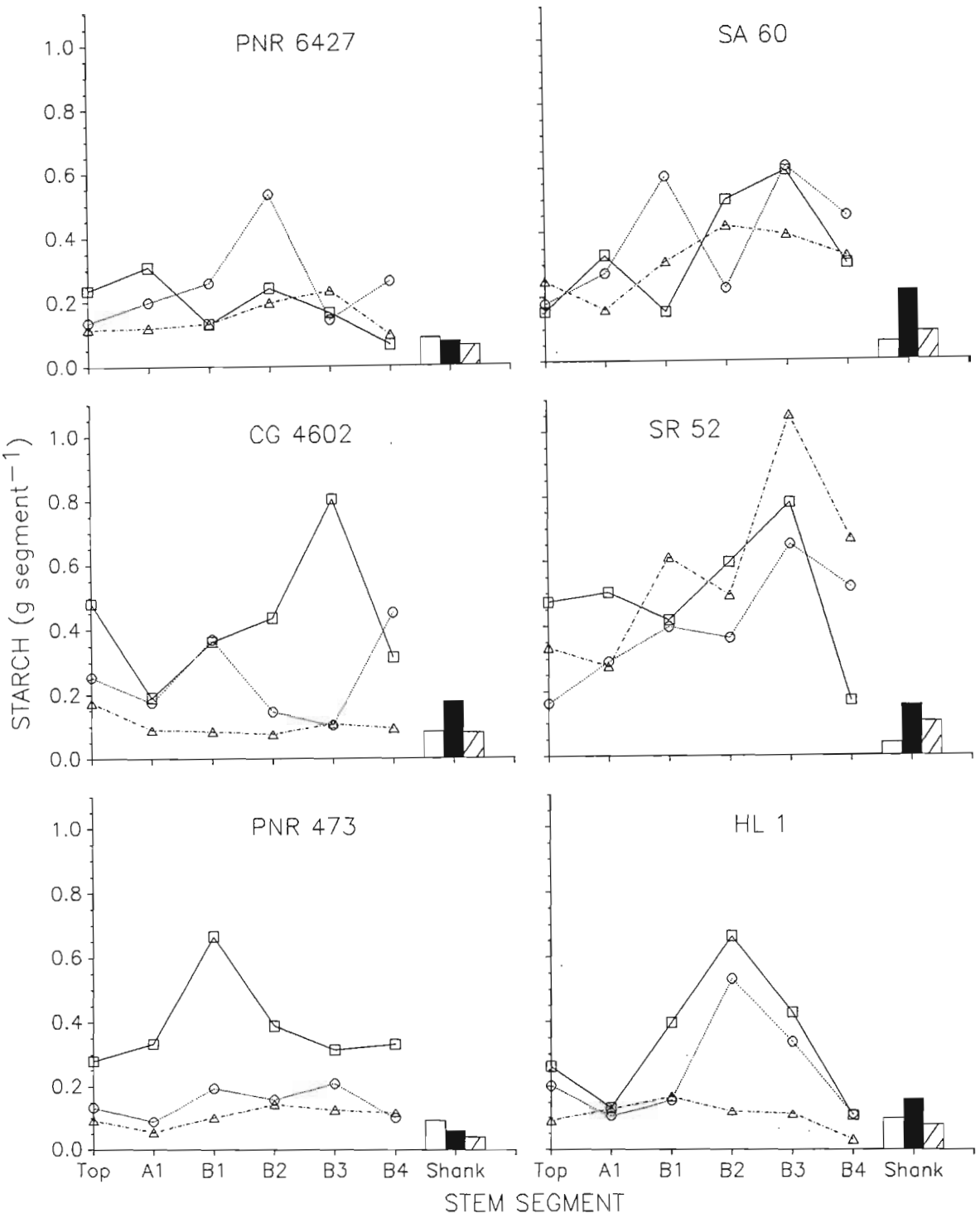


Figure 2.8 Fluctuation in starch content in stem segments of six maize hybrids at anthesis (□—□□), mid-grain fill (○—○■) and physiological maturity (△·····△▨)

As with starch composition, starch content levels were very variable among the stem segments of each hybrid over growth stages. Averaged over stem segments, starch content increased from A to MGF and then declined from MGF to PM in PNR 6427 and SA 60. In CG 4602, PNR 473 and HL 1 starch content averaged over stem segments declined from A to PM. In SR 52 starch content averaged over stem segments initially declined from A to MGF and then increased from MGF to PM. Depletion of starch reserves thus occurred in the latter phase of grain fill in PNR 6427 and SA 60, while depletion occurred over the entire grain filling period in CG 4602, PNR 473 and HL 1. It is possible that starch in the stem may serve as a long term storage form of carbohydrate which is mobilized to the grain after sucrose storage pools are depleted when the photosynthetic capacity of the maize plant is limited due to, for example, unfavourable environmental conditions (Franceschi, 1986).

It is interesting to note that starch content as with RS content was highest at MGF in the shanks of the hybrids except PNR 6427 and PNR 473. It will be remembered that sucrose content in the shank was at its lowest level for all hybrids at MGF. If sucrose levels were low in the shank at MGF, indicative of peak grain fill, the question may be posed as to why the hybrids were able to afford the conversion of sugars to starch. It is possible that shank starch may function as an emergency buffer supply of carbohydrate should current photosynthate production be reduced. Alternatively, it is possible that since the requirements for carbohydrate are at a maximum during MGF, the low levels of sucrose in the shank at MGF may be indicative of sucrose that is

in the translocation pathway with very little stored in vacuoles. Since it is likely that the rate at which carbohydrate in the form of sucrose is transferred to the ear is rapid during MGF, some excess carbohydrate is stored in the shank as starch and RS.

The ratio of starch to sucrose (Table 2.11, Figure 2.6) indicates that starch generally occurred in smaller amounts than sucrose at A and vice versa at MGF. At PM the ratio of starch to sucrose provides values with starch both higher and lower than sucrose levels. Some extreme values were recorded such as the amount of starch in the top segment of CG 4602 at PM being 127,2 times that of sucrose.

2.3.1.7 Total non-structural carbohydrate composition

Main effects and first order interactions for TNC composition

The main effects for hybrid and stem segment were significant (Appendix 18.7). However, since these factors were involved in a significant higher order interaction their main effects are of limited interest.

The main effect for growth stage was significant (Table 2.15). Since this factor was not involved in significant higher order interactions the changes in TNC composition over the growth stages may be assessed solely in terms of the main effect for growth stage. There was a significant negative linear effect superimposed with a significant positive quadratic effect which reflected the marked decline in TNC composition of 12,0 %

Table 2.15 Mean total non-structural carbohydrate composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM) of stem segments from six maize hybrids

Growth stage		
A	MGF	PM
23,8	11,8	11,5

LSD (0,05) 3,3
LSD (0,01) 4,4

(p = 0,01) from A to MGF followed by a marginal decline of 0,3 % (NS) from MGF to PM. The marked decline in TNC composition from A to MGF may indicate the utilization of the TNC pool in the stem segments by the various sinks in the plant and/or it may indicate that components of the residual fraction that contribute to dry mass increased in the stem segments relative to the TNC fraction.

The interaction of hybrid with growth stage was non-significant. There were no significant components of the interaction either.

The interaction of hybrid with stem segment was significant indicating that the variation in TNC composition among the stem segments was not consistent over all the hybrids (Table 2.16). The TNC composition was higher in the A1 segment than the top segment for all hybrids except HL 1. The difference between these segments of 3,0 % (NS) in CG 4602 was the most marked for all hybrids. The TNC composition was slightly higher in the A1 segment than the B1 segment for all hybrids. However, the

Table 2.16 Influence of maize hybrid on stem segment total non-structural carbohydrate composition (%) meaned over three growth stages during grain fill

Hybrid	Stem segment							Hybrid means
	Top	A1	B1	B2	B3	B4	Shank	
PNR 6427	16,4	17,7	14,7	16,4	13,1	10,5	20,7	15,6
SA 60	14,6	14,9	14,5	15,1	15,1	15,9	17,3	15,4
CG 4602	13,9	16,9	15,6	16,2	16,5	19,0	22,6	17,2
SR 52	21,2	23,5	22,7	23,0	24,1	19,9	24,6	22,7
PNR 473	10,6	11,8	11,2	9,7	7,9	10,0	12,8	10,6
HL 1	12,0	11,4	11,3	12,3	10,1	11,7	19,3	12,6
Stem segments means	14,8	16,0	15,0	15,4	14,4	14,5	19,5	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	3,5	4,5
Comparison of means at the same level of stem segment or with neither factor in common	5,6	7,5
Marginal means		
Comparison of hybrid means	4,7	6,3
Comparison of stem segment means	1,4	1,9

difference of 3,0 % (NS) between these segments in PNR 6427 was more marked than the other hybrids. Whereas TNC composition increased marginally from the B1 to B2 segments in all the other hybrids, in PNR 473 it decreased non-significantly by 1,5 %. While in the other hybrids TNC composition either declined or increased slightly from the B2 to the B3 segments, in PNR 6427 it declined markedly by 3,3 % (NS). The decline in TNC

composition from the B3 to B4 segments of 4,2 % in SR 52 was substantial and significant (p = 0,05). In PNR 6427 the decline of 2,6 % (NS) in TNC composition from the B3 to the B4 segment was not as great as that in SR 52. In the other hybrids TNC composition increased non-significantly from the B3 to B4 segments by 0,8, 2,5, 2,1 and 1,6 % in SA 60, CG 4602, PNR 473 and HL 1, respectively. The differences in TNC composition between the shank and the A1 and B1 segments may provide a more complete picture, than study of the component carbohydrates did, of the carbohydrate requirements of the grain. In all hybrids TNC composition in the shank was higher than that in either the A1 or the B1 segment. The difference in TNC composition between the shank and the A1 segment was only 1,1 (NS) and 1,0 % (NS), and between the shank and the B1 segment was only 1,9 (NS) and 1,6 % (NS) in SR 52 and PNR 473, respectively. On the other hand, the difference in TNC composition between the shank and the A1 segment was 5,7 (p = 0,01) and 7,9 % (p = 0,01), and between the shank and the B1 segment was 7,0 (p = 0,01) and 8,0 % (p = 0,01) in CG 4602 and HL 1, respectively. The difference in TNC composition between the shank and the A1 segment was 3,0 (NS) and 2,4 % (NS), and between the shank and the B1 segment was 6,0 (p = 0,01) and 2,8 % (NS) in PNR 6427 and SA 60, respectively. Therefore, on a relative or composition basis SR 52 and particularly PNR 473 partitioned low amounts of TNC to the shank and thus maintained, on average over the growth stages, low concentrations of TNC in the shank relative to the A1 and B1 main stem segments. On the other hand, CG 4602 and particularly HL 1 maintained high concentrations of TNC in the shank relative to the A1 and B1 segments. Compared to these four

hybrids PNR 6427 and SA 60 maintained intermediate concentrations of TNC in the shank on average over the growth stages. It is important, however, to point out that maintenance of high concentrations of TNC in the shank may not translate, in absolute terms, into high final grain yields. This is so because final yield is the integration over the entire grain filling period of the absolute amounts of photosynthate that have been translocated from the vegetative organs of the plant through the shank and into the grain. It is noteworthy that all hybrids recorded their highest TNC composition in the shank with SR 52 recording the highest value of 24,6 % which was significantly ($p = 0,01$) greater than the lowest value of 12,8 % recorded in PNR 473.

The interaction of growth stage with stem segment was non-significant. There were no significant components of the interaction either.

Second order interaction of hybrid, growth stage and stem segment for TNC composition

The interaction of hybrid, growth stage and stem segment was non-significant (Figure 2.9). There were no significant components of the interaction either.

The TNC composition ranged from a low of 2,4 % (PNR 473, B3 segment at PM) to a high of 32,3 % (SR 52, shank at A).

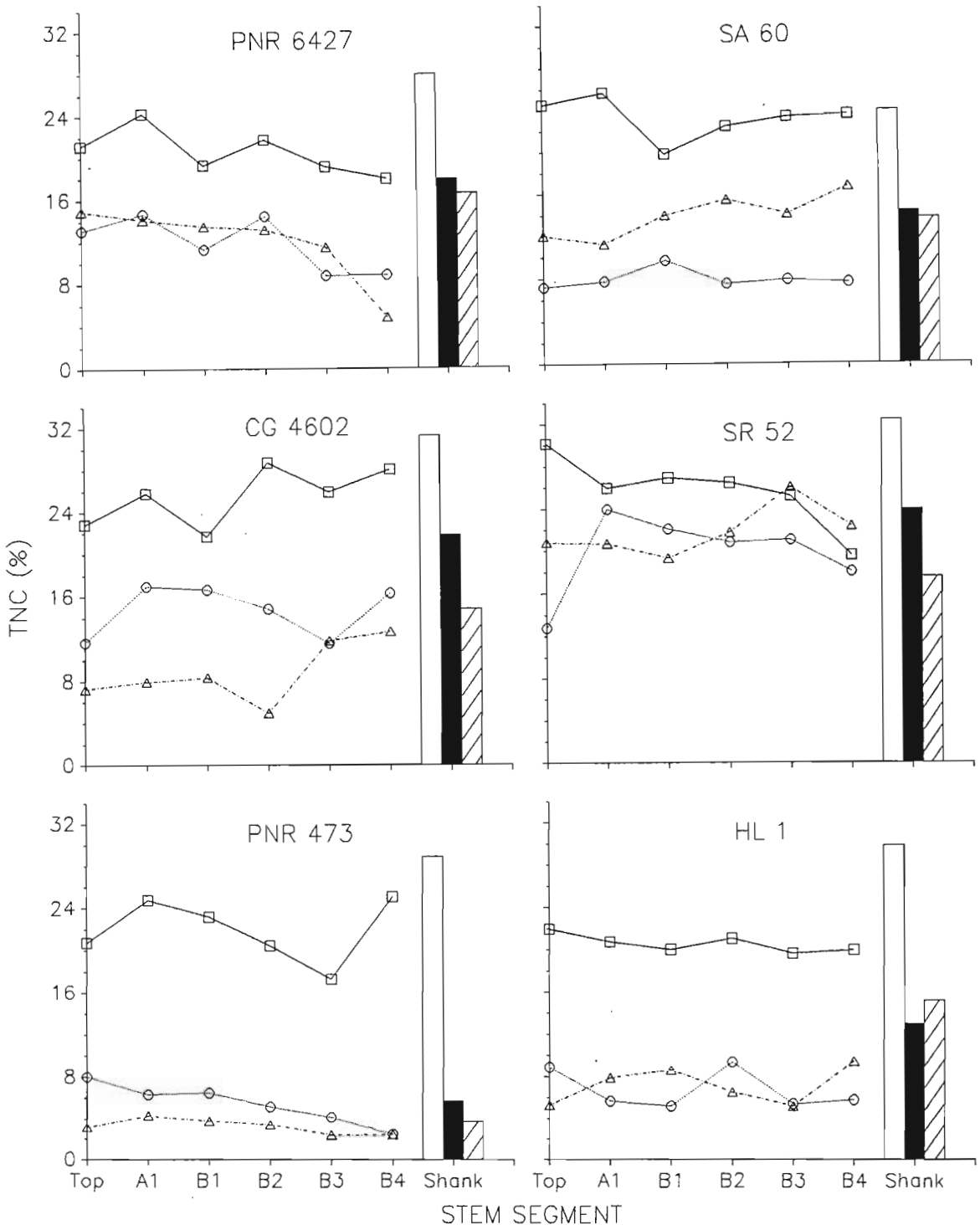


Figure 2.9 Fluctuation in total non-structural carbohydrate (TNC) composition in stem segments of six maize hybrids at anthesis (□—□□), mid-grain fill (○—○■) and physiological maturity (△·····△▨)

As indicated by the significant main effect for growth stage, TNC composition was highest in all segments of the hybrids at A (Figure 2.9). SR 52 was a minor exception here as the TNC composition in the B3 and B4 segments at A was less than at PM. The TNC composition in the shanks of all the hybrids except HL 1 did decline substantially from A to MGF and then less markedly from MGF to PM. In HL 1 TNC composition in the shank declined substantially from A to MGF and then increased slightly from MGF to PM. There was no apparent consistent trend for all the hybrids in TNC composition changes over the growth stages in the main stem segments. In PNR 6427 TNC composition generally declined from A to MGF and then remained constant from MGF to PM. In SA 60 TNC composition generally declined from A to MGF, and then increased from MGF to PM. In CG 4602 there was a stepwise decline in TNC composition from A to PM, although at PM the B3 and B4 segments maintained higher TNC composition levels than the other segments. In SR 52 TNC composition declined from A to MGF and then remained constant from MGF to PM, although TNC composition in the B3 and B4 segments was higher at PM than at A. The TNC composition in PNR 473 declined most markedly compared to the other hybrids from A to MGF and then declined only slightly from MGF to PM. The decline in TNC composition in HL 1 from A to MGF was also marked but TNC composition remained generally constant from MGF to PM.

2.3.1.8 Total non-structural carbohydrate content, residual content and segment dry mass

Main effects and first order interactions for TNC content

The main effects for hybrid, growth stage and stem segment were significant (Appendix 18.8). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interaction of hybrid with growth stage was non-significant. However, the hybrid x growth stage(linear) component of the interaction was significant (Table 2.17). PNR 6427, CG 4602 and PNR 473 all declined in TNC content from A to PM. The initial decline in TNC content from A to MGF was the most marked for these hybrids, particularly in PNR 473 which declined by 1,49 g segment^{-1} ($p = 0,05$). On the other hand, SA 60 and HL 1 initially declined markedly and significantly ($p = 0,05$) in TNC content from A to MGF but then from MGF to PM increased non-significantly in TNC content. SA 60 increased more markedly than HL 1 in TNC content from MGF to PM. In SR 52 TNC content increased significantly ($p = 0,05$) from A to PM particularly from A to MGF. At PM the TNC content of SR 52 was significantly ($p = 0,01$) higher than that of any of the other hybrids at PM.

Table 2.17 Influence of maize hybrid on mean stem segment total non-structural carbohydrate content (g segment^{-1}) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	Growth stage			Hybrid means
	A	MGF	PM	
PNR 6427	1,49	0,87	0,76	1,04
SA 60	2,44	0,87	1,60	1,64
CG 4602	2,16	1,36	0,90	1,48
SR 52	2,17	2,26	3,59	2,67
PNR 473	1,83	0,34	0,24	0,80
HL 1	1,84	0,58	0,67	1,03
Growth stage means	1,99	1,05	1,29	

Body of table	LSD	
	0,05	0,01
Comparisons of means	1,22	1,64
Marginal means		
Comparison of hybrid means	0,71	0,95
Comparison of growth stage means	0,50	0,67

The interaction of hybrid with stem segment was significant indicating that the variation in TNC content among the stem segments was not consistent over all the hybrids (Table 2.18). The TNC content was marginally and non-significantly higher in the top segment than the A1 segment by 0,10, 0,18 and 0,07 g segment^{-1} in PNR 6427, SA 60 and HL 1, respectively. On the other hand, in CG 4602, SR 52 and PNR 473 TNC content was non-significantly higher in the A1 than the top segment by 0,24,

Table 2.18 Influence of maize hybrid on stem segment total non-structural carbohydrate content (g segment^{-1}) meaned over three growth stages during grain fill

Hybrid	Stem segment							Hybrid means
	Top	A1	B1	B2	B3	B4	Shank	
PNR 6427	0,95	0,85	1,17	1,83	1,35	0,80	0,33	1,04
SA 60	1,32	1,14	1,84	2,34	2,43	2,01	0,38	1,64
CG 4602	0,78	1,02	1,68	2,13	2,66	1,63	0,43	1,48
SR 52	1,36	1,73	2,98	3,75	5,76	2,69	0,45	2,67
PNR 473	0,64	0,74	1,11	1,29	1,17	0,46	0,22	0,80
HL 1	0,77	0,70	1,32	1,52	1,48	0,91	0,49	1,03
Stem segments means	0,97	1,03	1,68	2,14	2,47	1,42	0,39	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,67	0,88
Comparison of means at the same level of stem segment or with neither factor in common	0,94	1,25
Marginal means		
Comparison of hybrid means	0,71	0,95
Comparison of stem segment means	1,41	1,85

0,37 and 0,10 g segment^{-1}, respectively. The TNC content was higher in the B1 segment than the A1 segment in all hybrids. Although the difference in TNC content between these two segments of 0,70 ($p = 0,05$), 0,66 (NS) and 0,62 g segment^{-1} (NS) in SA 60, CG 4602 and HL 1, respectively, were fairly similar, the difference of 1,25 g segment^{-1} ($p = 0,01$) in SR 52 was most marked. In PNR 6427 and PNR 473 the differences of 0,32 (NS) and

0,37 g segment^{-1} (NS) were less marked than the other hybrids. The TNC content further increased in all hybrids from the B1 to B2 segments. The difference between these two segments was most marked in PNR 6427 and SR 52, the differences being 0,66 (NS) and 0,77 g segment^{-1} ($p = 0,05$), respectively. From the B2 to the B3 segment TNC content increased in SA 60, CG 4602 and SR 52 but declined in PNR 6427, PNR 473 and HL 1. The increase of 2,01 g segment^{-1} ($p = 0,01$) in TNC content from the B2 to the B3 segment recorded in SR 52 was the most marked change compared to the other hybrids. Total non-structural carbohydrate content declined in all hybrids from the B3 to the B4 segment. The TNC content declined markedly from the B3 to the B4 segment by 1,03 ($p = 0,01$) and 0,71 g segment^{-1} ($p = 0,05$) in CG 4602 and PNR 473 respectively, and most markedly by 3,07 g segment^{-1} ($p = 0,01$) in SR 52. The differences between the shank and the A1 and the B1 segments in TNC content may, as with TNC composition, provide further insight into the carbohydrate requirements of the grain in each hybrid. In all hybrids TNC content in the shank was lower than that in either the A1 and B1 segments. Again this is in accordance with dry mass differences. The difference in TNC content between the shank and the A1 segment was only 0,52 g segment^{-1} (NS) in both PNR 6427 and PNR 473, and between the shank and the B1 segment was 0,84 ($p = 0,05$) and 0,89 g segment^{-1} ($p = 0,01$) in PNR 6427 and PNR 473, respectively. In HL 1 the differences between the shank and the A1 segment, and the shank and the B1 segment were the lowest of all the hybrids, these being 0,21 (NS) and 0,83 g segment^{-1} ($p = 0,05$), respectively. The differences were more marked in SA 60 and CG 4602. The differences between the

shank and the A1 segment were 0,76 ($p = 0,05$) and 0,59 g segment^{-1} (NS), and between the shank and the B1 segment were 1,46 ($p = 0,01$) and 1,25 g segment^{-1} ($p = 0,01$) in SA 60 and CG 4602, respectively. The most marked differences between the shank and the A1 segment, and the shank and the B1 segment of 1,28 ($p = 0,01$) and 2,53 g segment^{-1} ($p = 0,01$) respectively, were recorded in SR 52. Thus on an absolute basis there appears to be excess photosynthate in the A1 and B1 segments relative to the shank in SR 52. Both SA 60 and CG 4602 also had excess photosynthate in the A1 and B1 segments relative to the shank but not to the same extent as SR 52. PNR 6427 and PNR 473 apparently had more of a balance between non-structural carbohydrate in the stem and that in the shank en route to the grain. HL 1 had the least extreme differences in TNC content between the shank and the A1 and B1 segments and it may be inferred that there was a good balance between production of photosynthate and utilization by the developing grain. On the other hand, if the small differences in TNC content between the shank and the subtending A1 and B1 segments are coupled to overall low levels of TNC content in these segments and in the other stem segments, this may indicate an inadequate production of photosynthate (source limitation). Even if sink demand exceeds source supply, inferred by overall low levels of TNC content in the stem and shank, this may not necessarily result in low final grain yield. What may happen in this situation is that most of the current photosynthate is immediately, upon synthesis in the leaves, translocated to the grain and respired or converted to other organic compounds in the various plant organs. Thus little excess TNC accumulates in the stem and consequently little TNC

is detected in the stem. Averaged over growth stages, the B3 segment recorded the highest TNC content for SA 60, CG 4602, SR 52 and PNR 473 while the highest TNC content was recorded in the B2 segment for PNR 6427 and HL 1.

The interaction of growth stage with stem segment was significant (Table 2.19). The growth stage(linear and quadratic) x stem segment components of the interaction were also significant.

Table 2.19 Influence of three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), on stem segment total non-structural carbohydrate content (g segment^{-1}) meaned for six maize hybrids

Growth stage	Stem segment							Growth stage means
	Top	A1	B1	B2	B3	B4	Shank	
A	1,56	1,60	2,34	3,14	3,42	1,51	0,35	1,99
MGF	0,60	0,75	1,34	1,61	1,60	0,98	0,46	1,05
PM	0,74	0,74	1,37	1,68	2,40	1,77	0,34	1,29
Stem segments means	0,97	1,03	1,68	2,14	2,47	1,42	0,39	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of growth stage	0,47	0,62
Comparison of means at the same level of stem segment or with neither factor in common	0,67	0,89
Marginal means		
Comparison of growth stage means	0,50	0,67
Comparison of stem segment means	1,41	1,85

This indicates that the fluctuations in TNC content differed significantly among the segments over the growth stages. Apart from the shank, TNC content initially declined from A to MGF by 0,96 ($p = 0,01$), 0,85 ($p = 0,05$), 1,00 ($p = 0,01$), 1,53 ($p = 0,01$), 1,82 ($p = 0,01$) and 0,53 g segment^{-1} (NS) in the top, A1, B1, B2, B3 and B4 segments, respectively. Again the changes in TNC content were most marked in the largest segments particularly the B3 segment. The shank increased marginally by 0,11 g segment^{-1} (NS) from A to MGF. In all segments except the A1 and the shank, TNC content then increased from MGF to PM by 0,14 (NS), 0,03 (NS), 0,07 (NS), 0,80 ($p = 0,05$) and 0,79 g segment^{-1} ($p = 0,05$) in the top, B1, B2, B3 and B4 segments, respectively. Although the B4 segment was smaller than the B3 segment, the marked increase in TNC content was almost equal to that of the B3 segment. In the A1 segment TNC content declined by 0,01 g segment^{-1} (NS) and in the shank by 0,12 g segment^{-1} (NS).

Main effects and first order interactions for residual content

The main effect for hybrid was non-significant while the main effects for growth stage and stem segment were significant (Appendix 18.9). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interaction of hybrid with growth stage was significant (Table 2.20). The hybrid x growth stage(linear and quadratic) components of the interaction were also significant indicating

Table 2.20 Influence of maize hybrid on mean stem segment residual content (g segment^{-1}) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	Growth stage			Hybrid means
	A	MGF	PM	
PNR 6427	5,95	8,26	7,56	7,25
SA 60	7,97	10,93	9,72	9,54
CG 4602	6,32	7,90	7,44	7,22
SR 52	6,24	8,20	12,10	8,84
PNR 473	6,80	6,44	7,52	6,92
HL 1	6,95	8,19	7,94	7,69
Growth stage means	6,70	8,32	8,71	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	1,79	2,43
Comparison of means at the same level of growth stage or with neither factor in common	3,00	4,21
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of growth stage means	0,73	0,99

differences in patterns of residual content changes over the growth stages for the six hybrids. In PNR 6427, SA 60, CG 4602 and HL 1 residual content initially increased from A to MGF, and then declined from MGF to PM. In SR 52 residual content increased from A to PM. Residual content in PNR 473 initially declined from A to MGF, and then increased from MGF to PM. All hybrids did, however, have a higher residual content at PM than

at A, the difference was only significant ($p = 0,01$) in SR 52. The increase in residual content of 2,96 g segment^{-1} ($p = 0,01$) recorded by SA 60 from A to MGF was most marked compared to the other hybrids. While PNR 6427, SA 60, CG 4602, PNR 473 and HL 1 increased or decreased by approximately 1,00 g segment^{-1} or less in residual content from MGF to PM, SR 52 showed a most marked increase of 3,90 g segment^{-1} ($p = 0,01$).

The interaction of hybrid with stem segment was significant indicating that the variation in residual content among the stem segments was not consistent over all the hybrids (Table 2.21). Residual content was marginally and non-significantly higher in the top than the A1 segment by 0,71, 1,22, 0,33 and 0,22 g segment^{-1} in PNR 6427, SA 60, PNR 473 and HL 1 respectively, the difference being most marked in SA 60. On the other hand, residual content was higher in the A1 than the top segment by 0,06 (NS) and 0,73 g segment^{-1} (NS) in CG 4602 and SR 52, respectively. Residual content increased by large amounts from the A1 to the B1 segment, the differences of 4,49 ($p = 0,01$) and 4,55 g segment^{-1} ($p = 0,01$) in SA 60 and SR 52 respectively, were the most marked. Residual content increased by about 2,00 g segment^{-1} from the B1 to B2 segments in SA 60, CG 4602, SR 52 and PNR 473. The increase of 3,23 g segment^{-1} ($p = 0,01$) was more marked in PNR 6427 while the increase of 1,59 g segment^{-1} (NS) in HL 1 was the smallest of the hybrids. While residual content increased by 1,00 g segment^{-1} or less from the B2 to B3 segments in the other hybrids, in SR 52 it increased markedly by 4,32 g segment^{-1} ($p = 0,01$). Residual content declined substantially in all hybrids from the B3 to B4 segments; the

Table 2.21 Influence of maize hybrid on stem segment residual content (g segment^{-1}) meaned over three growth stages during grain fill

Hybrid	Stem segment							Hybrid means
	Top	A1	B1	B2	B3	B4	Shank	
PNR 6427	5,17	4,46	7,77	11,00	11,75	9,16	1,47	7,25
SA 60	7,93	6,71	11,20	13,95	14,00	10,82	2,17	9,54
CG 4602	4,93	4,99	8,86	11,04	12,67	6,50	1,55	7,22
SR 52	4,84	5,57	10,12	12,49	16,81	10,52	1,55	8,84
PNR 473	5,13	4,80	8,01	10,64	11,96	6,04	1,85	6,92
HL 1	5,61	5,39	9,56	11,15	12,54	7,26	2,35	7,69
Stem segments means	5,60	5,32	9,25	11,71	13,29	8,38	1,82	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	1,72	2,26
Comparison of means at the same level of stem segment or with neither factor in common	3,06	4,25
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of stem segment means	0,70	0,92

differences between these two segments of 2,59, 3,18, 6,17, 6,29, 5,92 and 5,28 g segment^{-1} in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1 respectively, were significant ($p = 0,01$). Thus the changes were most marked in CG 4602 and SR 52. In all hybrids residual content in the shank was lower than that in either the A1 and B1 segments. This is again in accordance with dry mass differences. The largest differences in residual

content between the shank and the A1 segment, and the shank and the B1 segment of 4,54 ($p = 0,01$) and 9,03 g segment^{-1} ($p = 0,01$) respectively, were recorded in SA 60.

The interaction of growth stage with stem segment was significant (Table 2.22). The growth stage(linear) x stem segment component of the interaction was also significant. This indicates that the fluctuations in residual content differed significantly among the

Table 2.22 Influence of three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), on stem segment residual content (g segment^{-1}) meaned for six maize hybrids

Growth stage	Stem segment							Growth stage means
	Top	A1	B1	B2	B3	B4	Shank	
A	5,11	4,92	8,39	10,33	12,20	5,14	0,82	6,70
MGF	5,82	5,37	9,73	12,18	13,58	8,96	2,59	8,32
PM	5,87	5,68	9,64	12,62	14,08	11,04	2,06	8,71
Stem segments means	5,60	5,32	9,25	11,71	13,29	8,38	1,82	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of growth stage	1,21	1,60
Comparison of means at the same level of stem segment or with neither factor in common	1,34	1,78
Marginal means		
Comparison of growth stage means	0,73	0,99
Comparison of stem segment means	0,70	0,92

segments over the growth stages. All segments increased in residual content from A to MGF but while the top, A1, B2, B3 and B4 segments further increased in residual content from MGF to PM, in the B1 and shank segments residual content declined. The increase in residual content from A to MGF was most marked in the B4 segment and the shank, the increases being 3,82 ($p = 0,01$) and 1,77 g segment^{-1} ($p = 0,05$), respectively. The increase of 2,08 g segment^{-1} ($p = 0,01$) in the B4 segment from MGF to PM was the most marked change in residual content for all the segments over these growth stages. It appears then, that on average over the hybrids the B4 segment accumulated considerable amounts of the residual fraction over the growth stages. This may further explain the tendency for this segment to accumulate smaller amounts of TNC content in comparison to the B3 segment in addition to the fact that the B4 segment was generally smaller than the B3 segment.

Main effects and first order interactions for stem segment dry mass

The main effect for hybrid was non-significant while the main effects for growth stage and stem segment were significant (Appendix 18.10). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The interaction of hybrid with growth stage was significant (Table 2.23). The hybrid x growth stage(linear) component of the interaction was also significant indicating differences in

Table 2.23 Influence of maize hybrid on mean stem segment dry mass (g segment^{-1}) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	Growth stage			Hybrid means
	A	MGF	PM	
PNR 6427	7,4	9,1	8,3	8,3
SA 60	10,4	11,8	11,3	11,2
CG 4602	8,5	9,3	8,3	8,7
SR 52	8,4	10,5	15,7	11,5
PNR 473	8,6	6,8	7,8	7,7
HL 1	8,8	8,8	8,6	8,7
Growth stage means	8,7	9,4	10,0	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	2,2	2,9
Comparison of means at the same level of growth stage or with neither factor in common	3,5	4,9
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of growth stage means	0,8	1,1

patterns of dry mass changes over the growth stages for the six hybrids. In all the hybrids except PNR 473 and HL 1, dry mass increased from A to MGF. Whereas SR 52 increased markedly in dry mass by 2,1 g segment^{-1} (NS) from A to MGF, PNR 473 declined by an almost equal amount, 1,8 g segment^{-1} (NS), from A to MGF. While average stem segment dry mass declined from MGF to PM in PNR 6427, SA 60, CG 4602 and HL 1, SR 52 further increased in dry

mass from MGF to PM. After the initial decrease from A to MGF, dry mass in PNR 473 increased from MGF to PM. The increase in dry mass in SR 52 of 5,2 g segment^{-1} from MGF to PM was the most marked change in dry mass over all the growth stages.

The interaction of hybrid with stem segment was significant indicating that the variations in dry mass among the stem segments were not consistent over all the hybrids (Table 2.24). Dry mass

Table 2.24 Influence of maize hybrid on stem segment dry mass (g segment^{-1}) meaned over three growth stages during grain fill

Hybrid	Stem segment							Hybrid means
	Top	A1	B1	B2	B3	B4	Shank	
PNR 6427	6,1	5,3	8,9	12,8	13,1	10,0	1,8	8,3
SA 60	9,3	7,9	13,0	16,3	16,4	12,8	2,5	11,2
CG 4602	5,7	6,0	10,5	13,2	15,3	8,1	2,0	8,7
SR 52	6,2	7,3	13,1	16,2	22,6	13,2	2,0	11,5
PNR 473	5,8	5,5	9,1	11,9	13,1	6,5	2,1	7,7
HL 1	6,4	6,1	10,9	12,7	14,0	8,2	2,8	8,7
Stem segments means	6,6	6,4	10,9	13,9	15,8	9,8	2,2	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	2,0	2,6
Comparison of means at the same level of stem segment or with neither factor in common	3,5	4,9
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of stem segment means	0,8	1,1

of the top segment was higher than the A1 segment in PNR 6427, SA 60, PNR 473 and HL 1, while the opposite was true for CG 4602 and SR 52. The difference in dry mass between these two segments of 1,4 g segment^{-1} (NS) in SA 60 was the most marked of the hybrids. Dry mass of the B1 segment was substantially higher than that of the A1 segment in all hybrids. Differences between these segments in dry mass of 3,6, 5,1, 4,5, 5,8, 3,6 and 4,8 g segment^{-1} in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1 respectively, were all significant ($p = 0,01$). Thus differences were again marked in SA 60 and SR 52. Dry mass further increased from the B1 to the B2 segment. The difference in dry mass between these segments of 1,8 g segment^{-1} (NS) in HL 1 was the smallest recorded, while SA 60 recorded the most marked difference of 3,3 g segment^{-1} ($p = 0,01$) compared to the other hybrids. While dry mass increased by 1,4 g segment^{-1} (NS) or less from the B2 to the B3 segment in all the other hybrids, in SR 52 the increase of 6,4 g segment^{-1} ($p = 0,01$) was marked in comparison. Dry mass in the B4 segment was significantly ($p = 0,01$) less than that in the B3 segment by 3,1, 3,6, 7,2, 9,4, 6,6 and 5,8 g segment^{-1} for PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. It is obvious that the A1 and B1 segments will be substantially greater in dry mass than the shank. However, large differences in dry mass between the shank and the A1 and B1 segments may indicate an accumulation of excess TNC in the main stem and/or conversion of excess TNC to the residual fraction in the main stem as a result of sink requirements, particularly the grain, being exceeded by source supply. The most marked differences between the shank and the A1 segment of 5,4 ($p = 0,01$) and 5,3 g segment^{-1} ($p = 0,01$) were

recorded in SA 60 and SR 52, respectively. The most marked differences between the shank and the B1 segment of 10,5 ($p = 0,01$) and 11,1 g segment^{-1} ($p = 0,01$) were also recorded in SA 60 and SR 52, respectively. The smallest differences between the shank and the A1 segment, and the shank and the B1 segment of 3,4 ($p = 0,01$) and 7,0 g segment^{-1} ($p = 0,01$) respectively, were recorded in PNR 473. Again it appears that excess carbohydrate accumulated as dry mass in the main stem segments in SA 60 and SR 52 while in complete contrast PNR 473 did not accumulate much carbohydrate as dry mass in the stem segments. It is noteworthy that SR 52 recorded significantly ($p = 0,01$) the highest dry mass of 22,6 g segment^{-1} in the B3 segment compared to all the segments of the other hybrids.

The interaction of growth stage with stem segment was significant (Table 2.25). The growth stage(linear) x stem segment component of the interaction was also significant. This indicates that the changes in dry mass differed significantly among the segments over the growth stages. Whereas the top, A1 and B3 segments declined slightly in dry mass from A to MGF, the other segments increased in dry mass. The increases of 3,3 ($p = 0,01$) and 1,9 g segment^{-1} ($p = 0,05$) in the B4 and shank segments, respectively, were the most marked changes in dry mass from A to MGF. From MGF to PM dry mass declined by 0,1 (NS) and 0,7 g segment^{-1} (NS) in the B1 and shank segments, respectively. In the other segments namely top, A1, B2, B3 and B4 the dry mass increased by 0,2 (NS), 0,3 (NS), 0,5 (NS), 1,3 (NS) and 2,9 g segment^{-1} ($p = 0,01$), respectively. Thus the increase in dry mass from MGF to PM was particularly marked in the B4 segment.

Table 2.25 Influence of three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), on stem segment dry mass (g segment^{-1}) meaned for six maize hybrids

Growth stage	Stem segment							Growth stage means
	Top	A1	B1	B2	B3	B4	Shank	
A	6,7	6,5	10,7	13,5	15,6	6,6	1,2	8,7
MGF	6,4	6,1	11,1	13,8	15,2	9,9	3,1	9,4
PM	6,6	6,4	11,0	14,3	16,5	12,8	2,4	10,0
Stem segments means	6,6	6,4	10,9	13,9	15,8	9,8	2,2	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of growth stage	1,4	1,8
Comparison of means at the same level of stem segment or with neither factor in common	1,6	2,1
Marginal means		
Comparison of growth stage means	0,9	1,2
Comparison of stem segment means	0,8	1,1

Second order interactions of hybrid, growth stage and stem segment for TNC content, residual content and stem segment dry mass

The interaction of hybrid, growth stage and stem segment for TNC content was non-significant (Figures 2.10 and 2.11). However, the hybrid x growth stage(linear) x stem segment component of the interaction was significant. This indicates that the variation

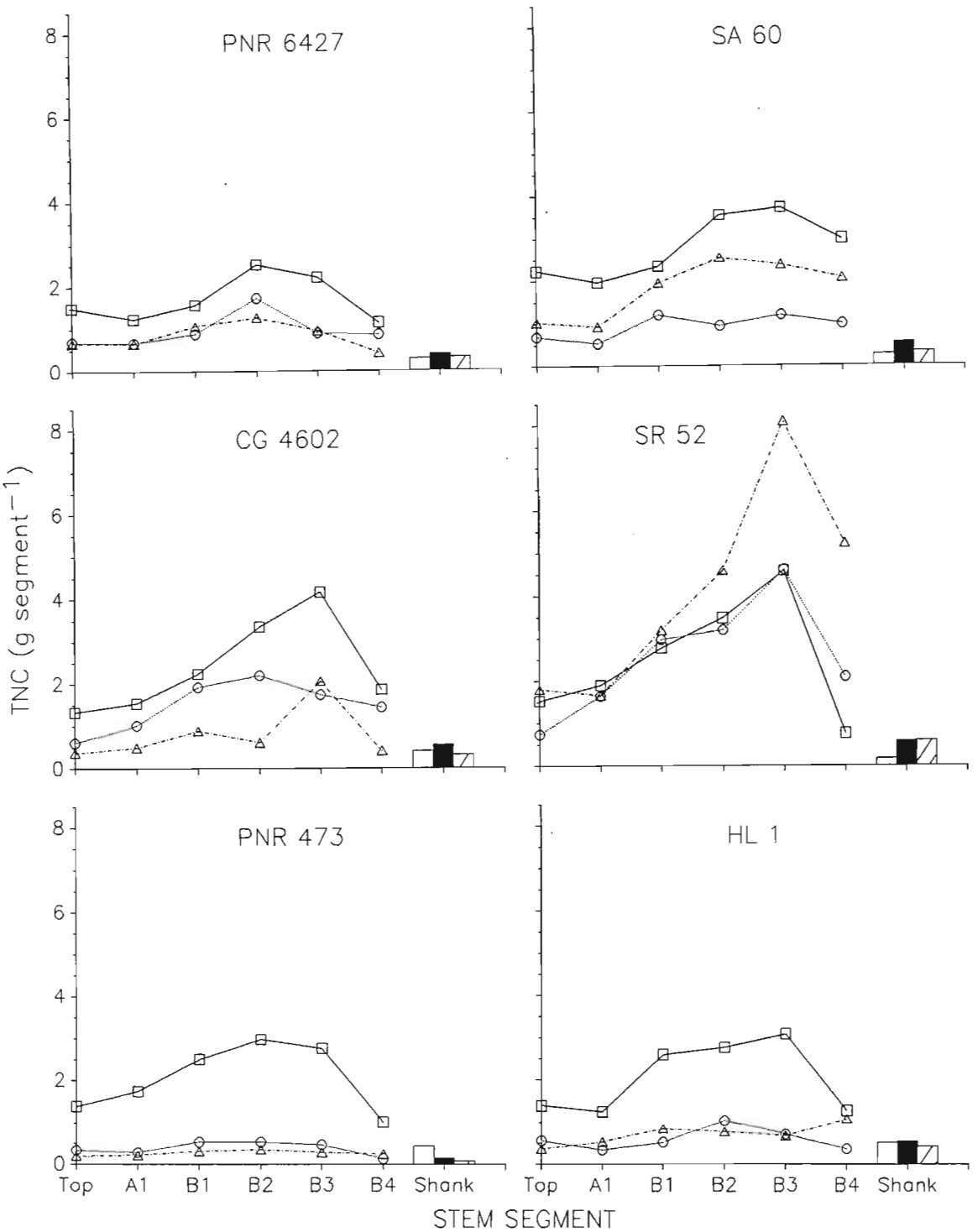


Figure 2.10 Fluctuation in total non-structural carbohydrate (TNC) content in stem segments of six maize hybrids at anthesis (□—□□), mid-grain fill (○—○■) and physiological maturity (△·····△▨)

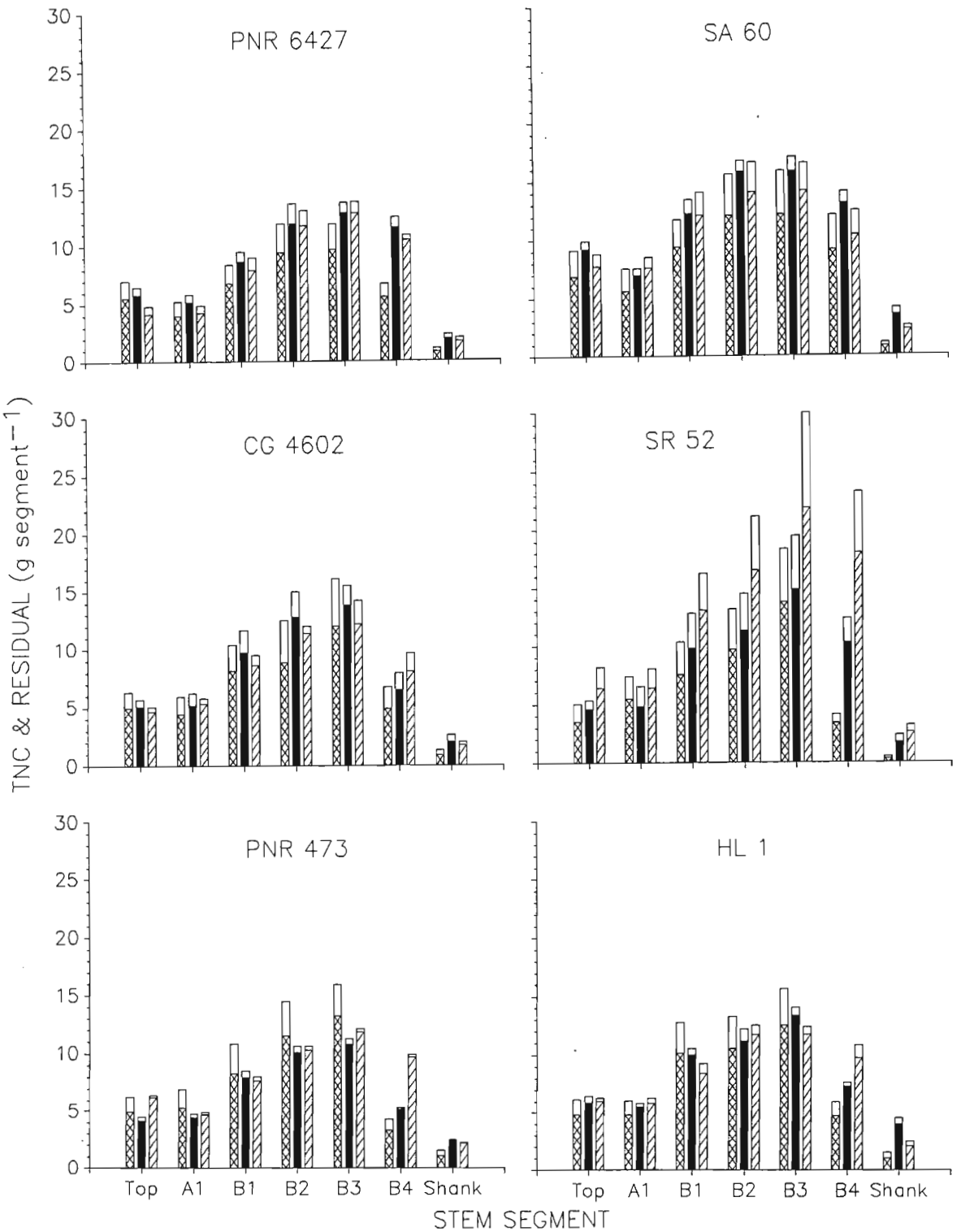


Figure 2.11 Fluctuation in total non-structural carbohydrate (TNC) content, residual content and dry mass of stem segments in six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

in TNC content in the stem segments over the growth stages was not consistently the same for all the hybrids.

The interaction of hybrid, growth stage and stem segment for residual content was non-significant (Figure 2.11). There were no significant components of the interaction either.

The interaction of hybrid, growth stage and stem segment for dry mass was just non-significant (Figure 2.11). However, the hybrid x growth stage(linear) x stem segment component of the interaction was significant. This indicates that the variation in dry mass in the stem segments over the growth stages was not consistently the same for all the hybrids.

The second order interactions for these variates are presented together in Figure 2.11 and the apparent variations in TNC content, residual content and stem segment dry mass are discussed with respect to one another. In order to get a better description of the relative amounts of TNC content to residual content, the ratio of TNC content to residual content is presented in Table 2.26.

In PNR 6427 the dry mass of all the segments except for the top generally increased from A to MGF (Figure 2.11). It is also apparent that there was a concomitant increase in the residual content and decrease in TNC content of most of the stem segments from A to MGF. The ratio of TNC content to residual content indicates that at MGF the amount of TNC relative to the amount of residual material was much less than at A (Table 2.26). The

Table 2.26 Ratio of total non-structural carbohydrate (TNC) content to residual content for stem segments of six maize hybrids sampled at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	Stem segment	A	MGF	PM
		TNC:Residual	TNC:Residual	TNC:Residual
PNR 6427	Top	0,27	0,16	0,18
	A1	0,33	0,18	0,17
	B1	0,24	0,13	0,16
	B2	0,28	0,18	0,17
	B3	0,24	0,10	0,14
	B4	0,22	0,10	0,05
	Shank	0,40	0,22	0,20
SA 60	Top	0,33	0,08	0,15
	A1	0,35	0,09	0,13
	B1	0,25	0,11	0,17
	B2	0,29	0,09	0,20
	B3	0,31	0,09	0,18
	B4	0,31	0,08	0,20
	Shank	0,32	0,17	0,16
CG 4602	Top	0,31	0,14	0,08
	A1	0,35	0,21	0,09
	B1	0,28	0,20	0,10
	B2	0,41	0,18	0,06
	B3	0,35	0,13	0,15
	B4	0,39	0,20	0,18
	Shank	0,46	0,28	0,18
SR 52	Top	0,44	0,16	0,28
	A1	0,35	0,34	0,27
	B1	0,37	0,30	0,25
	B2	0,36	0,28	0,29
	B3	0,34	0,29	0,38
	B4	0,26	0,23	0,31
	Shank	0,48	0,33	0,22
PNR 473	Top	0,27	0,09	0,03
	A1	0,33	0,68	0,05
	B1	0,30	0,07	0,04
	B2	0,26	0,06	0,04
	B3	0,21	0,04	0,02
	B4	0,34	0,03	0,03
	Shank	0,41	0,06	0,04
HL 1	Top	0,28	0,10	0,06
	A1	0,26	0,06	0,09
	B1	0,25	0,06	0,10
	B2	0,27	0,11	0,73
	B3	0,25	0,06	0,06
	B4	0,26	0,06	0,11
	Shank	0,43	0,15	0,19
TNC : Residual ratio SE ($\bar{x}$)			0,03	

lower levels of TNC content at MGF indicate that there was little excess current photosynthate available to accumulate in the stem and maintain TNC levels constant from A to MGF (Figures 2.10 and 2.11). Thus the general decline in TNC content from A to MGF noted in PNR 6427 may be due to depletion of the TNC pool for grain requirements and conversion of TNC to residual components in the stem segments. From MGF to PM the dry mass of the stem segments in this hybrid generally declined. In the top, A1, B1, B4 and shank segments this decline was, in the greater part, due to a decline in the residual content. The ratio of TNC content to residual content indicates that the amount of TNC relative to the residual components remained constant or increased slightly from MGF to PM.

In SA 60 the pattern was fairly similar to that in PNR 6427 from A to MGF with TNC content levels declining and residual content levels increasing in the stem segments (Figures 2.10 and 2.11). The water stress conditions that prevailed from MGF to PM would possibly have reduced the supply of current photosynthate, resulting in little excess current photosynthate being available to accumulate in the stem and maintain TNC levels constant from A to MGF. With the demand for carbohydrate by the grain peaking at MGF, it is likely that existing TNC pools in the stem were depleted to supplement the reduced supply of current photosynthate. On the other hand, since residual content in all stem segments of SA 60 increased from A to MGF it is also likely that part of the existing TNC pools was converted to residual components within the stem. However, from MGF to PM the amount of TNC relative to the residual components increased as a result

of decreases in the residual content and increases in the TNC content (Table 2.26). In fact, dry mass increased in the A1 and B1 segments from MGF to PM largely due to increases in the TNC content. It appears then that in SA 60 as grain fill ceased TNC accumulated in the stem segments and was not converted to residual components.

The changes in TNC content, residual content and stem segment dry mass were somewhat variable in the stem segments of CG 4602 (Figures 2.10 and 2.11). The ratio of TNC content to residual content declined in all segments from A to MGF as a result of both increases in residual content and decreases in TNC content (Table 2.26). In all except the B4 segment dry mass declined from MGF to PM. This decline was due to decreases in both TNC content and residual content. The ratio of TNC content to residual content further declined in all segments except the B3 segment from MGF to PM. This indicates that TNC content declined by a greater proportion than the residual content in CG 4602. The water stress conditions that prevailed from MGF to PM may have enhanced the depletion of existing TNC pools in the stem to supplement the supply of current photosynthate to the grain from mid (peak)-grain fill to PM. At PM most of the leaves of CG 4602 had senesced thus TNC did not reaccumulate in the stem at grain maturation as was the case with SA 60.

Dry mass increased in all segments except the A1 segment in SR 52 from A to PM (Figure 2.11). As TNC content did not change much from A to MGF the increase in dry mass was due to an increase in the residual content of the stem segments. Thus the decline in

the ratio of TNC content to residual content from A to MGF was due to increases in the residual content while TNC content remained constant or declined (Table 2.26). The increases in dry mass were substantial from MGF to PM particularly in the B3 segment. The ratio of TNC content to residual content increased from MGF to PM in the top, B2, B3 and B4 segments indicating that in these segments the proportional increase in TNC was greater than the residual components (Table 2.26). The TNC content was at a maximum in all segments at PM in SR 52 and it is clear that grain carbohydrate requirements were low and the stem segments served as alternative sinks for photosynthate.

In PNR 473 the dry mass of the stem segments declined from A to MGF except in the B4 and shank segments in which dry mass increased (Figure 2.11). The decline in dry mass was due, in the greater part, to a decline in the TNC content of the stem segments. This is supported by the markedly low TNC content to residual content ratio for all segments at MGF in PNR 473 (Table 2.26). The TNC content remained low in all the stem segments from MGF to PM although the dry mass did increase in the top, A1, B3 and most markedly in the B4 segments, largely as a result of increased residual content. It is likely that the water stress conditions that prevailed from MGF to PM reduced the production of current photosynthate. Thus it appears that there was little photosynthate available to accumulate as TNC in the stem segments of PNR 473 from MGF to PM, although photosynthate was still converted to residual components as late as PM.

In HL 1 dry mass of the stem segments did not fluctuate widely at all (Figure 2.11). The TNC content was generally highest in the segments at A except in the shank where TNC content was highest at MGF. Apart from the shank then, TNC content declined from A to MGF but the residual content increased in the top, A1, B2, B3, B4 and shank segments (Figure 2.10). In the B1 segment the residual content declined marginally from A to MGF. These changes in TNC content and residual content thus explain the recorded decline in the ratio of TNC content to residual content (Table 2.26). From MGF to PM dry mass decreased in the top, B1, B3 and shank segments, but increased in the A1, B2 and B4 segments. The TNC content from MGF to PM increased in the A1, B1 and B4 segments, and declined in the top, B2, B3 and shank segments. Residual content was lower at PM than at MGF in the B1, B3 and shank segments, but higher in the top, B2 and B4 segments. At PM only TNC content in the B4 segment of HL 1 approached levels near that at A, the difference was 0,19 g segment^{-1}. The lower TNC content levels at MGF and PM in the main stem segments compared to those at A may indicate the depletion of TNC pools to supplement the supply of current photosynthate to the grain. The water stress conditions that prevailed from MGF to PM may have enhanced the depletion of existing TNC pools in HL 1.

SR 52 recorded the highest mean stem segment dry mass of 11,5 g segment^{-1} followed in rank order by 11,2, 8,7, 8,7, 8,3 and 7,7 g segment^{-1} in SA 60, HL 1, CG 4602, PNR 6427 and PNR 473, respectively (Tables 2.23 and 2.24). These values were, however, not significantly different from one another. These values point

once again to the greater partitioning of photosynthate to stem dry mass in SR 52 and SA 60 while PNR 473 had, in comparison to the other hybrids, the lowest amount of photosynthate partitioned to stem dry mass.

2.3.2 Non-structural carbohydrate analysis of whole stem

2.3.2.1 Reducing sugars composition

The main effect for hybrid was significant (Table 2.27 and Appendix 19.1). SR 52 had significantly ($p \leq 0,05$) higher RS composition than any of the other hybrids. Apart from CG 4602 being significantly ($p = 0,05$) higher in RS composition than PNR 473, the other hybrids were non-significantly different from one another.

Table 2.27 Mean whole stem reducing sugars composition (%) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
6,6	6,2	8,4	12,9	3,6	5,6
LSD (0,05)	3,9				
LSD (0,01)	5,2				

The main effect for growth stage was significant (Table 2.28). There was a significant negative linear effect which indicates that the RS composition declined from A to PM, with the RS composition levels at A significantly ($p = 0,01$) higher than at PM. Levels at MGF were neither significantly lower than at A nor higher than at PM.

Table 2.28 Mean whole stem reducing sugars composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
9,4	6,9	5,4

LSD (0,05) 2,7
LSD (0,01) 3,7

The interaction of hybrid with growth stage was non-significant (Figure 2.12). There were no significant components of the interaction either. However, there were apparent differences between hybrids in RS composition levels in the whole stem during grain fill. Whole stem RS composition ranged from a low of 1,1 % in PNR 473 at PM to a high of 15,3 % in SR 52 at MGF. Whole stem RS composition declined in all hybrids, except SR 52, from A to MGF (Figure 2.12). The decline was more marked in SA 60, PNR 473 and particularly HL 1. In complete contrast, RS composition in the whole stem of SR 52 increased from A to MGF. From MGF to PM RS composition declined in all hybrids except SA 60 and HL 1 in which RS composition increased marginally.

2.3.2.2 Reducing sugars content

The main effect for hybrid was significant (Table 2.29 and Appendix 19.2). SR 52 had significantly ($p = 0,01$) higher RS content than any of the other hybrids. Apart from CG 4602 which had significantly ($p = 0,05$) higher RS content than PNR 473;

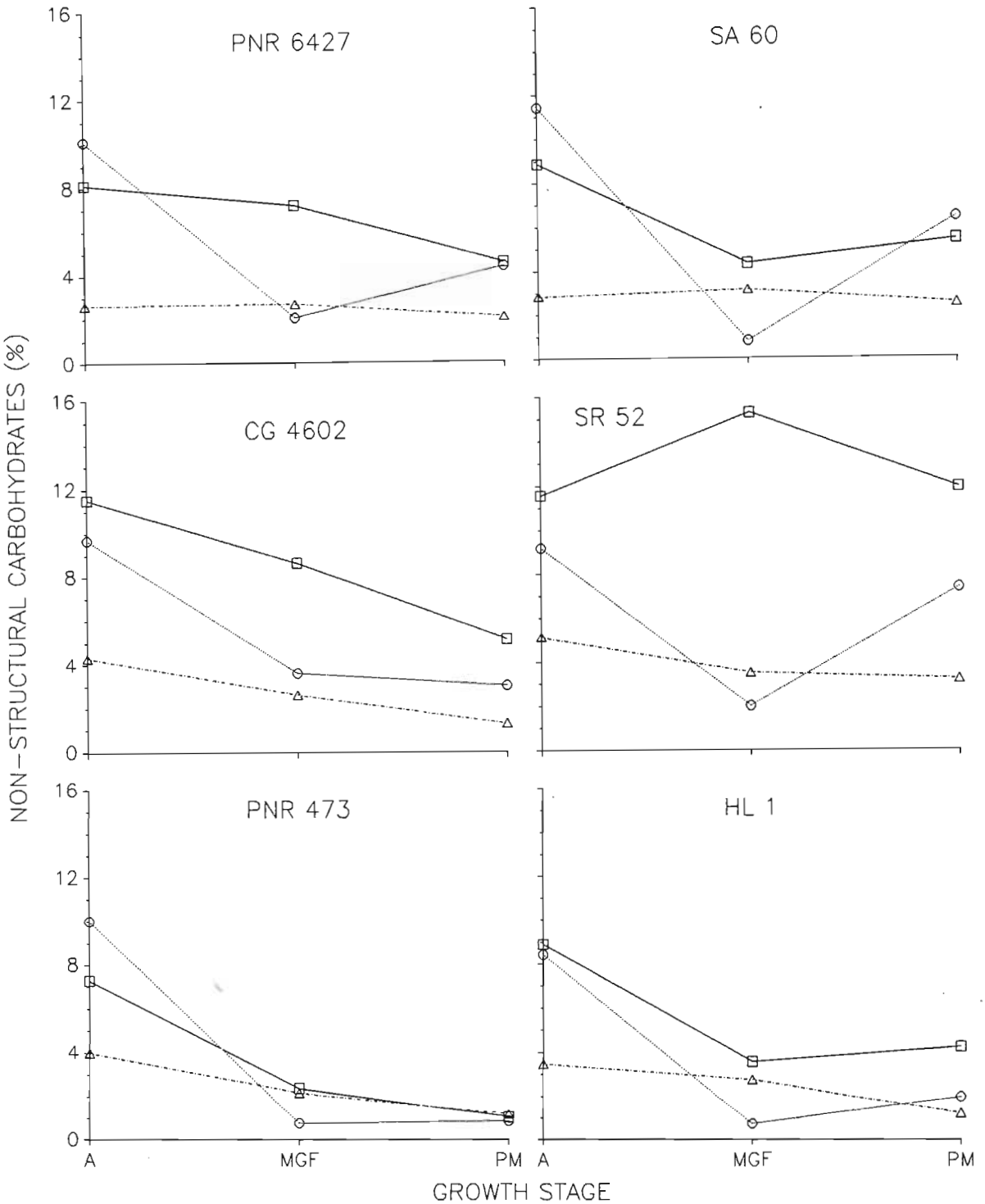


Figure 2.12 Fluctuation in reducing sugars (□——□), sucrose (○——○) and starch (△·····△) composition in whole stems of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

PNR 6427, SA 60, CG 4602, PNR 473 and HL 1 were not significantly different from one another.

Table 2.29 Mean whole stem reducing sugars content (g $stem^{-1}$) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
3,34	4,65	5,27	10,67	1,98	3,40
LSD (0,05)	3,24				
LSD (0,01)	4,35				

The main effect for growth stage was non-significant (Table 2.30). There were no significant components of the main effect either. However, the data do indicate a trend of RS content declining from A to PM.

Table 2.30 Mean whole stem reducing sugars content (g $stem^{-1}$) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
5,71	4,52	4,44
LSD (0,05) NS		
LSD (0,01) NS		

The interaction of hybrid with growth stage was non-significant (Figure 2.13). There were no significant components of the interaction either. However, there were apparent differences

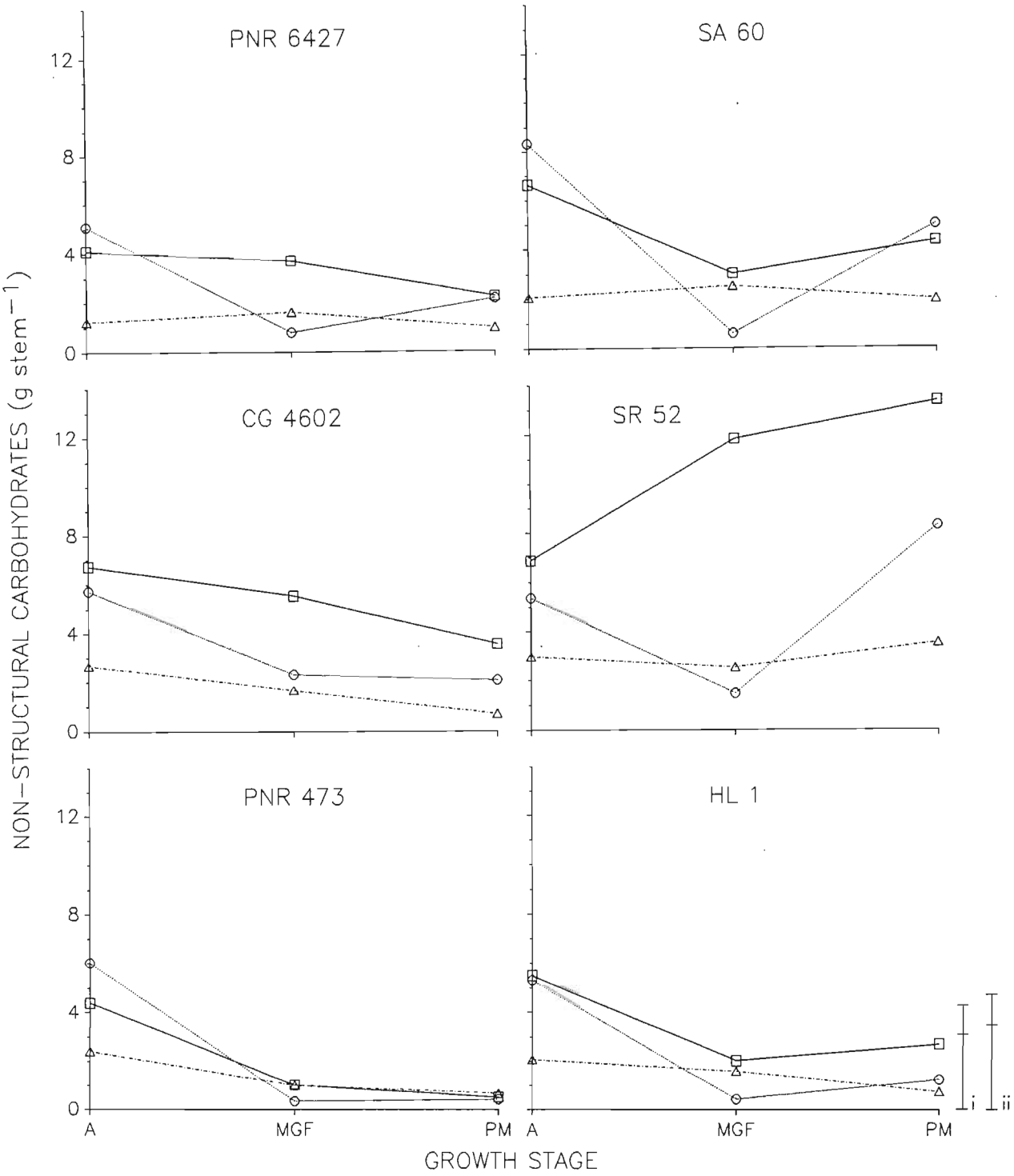


Figure 2.13 Fluctuation in reducing sugars (□——□), sucrose (○——○) and starch (△·····△) content in whole stems of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM).

Comparisons using LSD's of sucrose content means at the same level of (i) hybrid; and (ii) growth stage or with neither factor in common

between hybrids in the RS content levels in the whole stem during grain fill. Whole stem RS content ranged from a low of 0,53 g $stem^{-1}$ in PNR 473 at PM to a high of 13,34 g $stem^{-1}$ in SR 52 at PM. Whole stem RS content declined in all hybrids, except SR 52, from A to MGF (Figure 2.13). The decline was more marked in SA 60, PNR 473 and particularly HL 1. In complete contrast RS content in the whole stem of SR 52 increased from A to MGF. From MGF to PM RS content declined in PNR 6427, CG 4602 and PNR 473, but increased marginally in HL 1 and more substantially in SA 60 and SR 52.

2.3.2.3 Sucrose composition

The main effect for hybrid was non-significant (Table 2.31 and Appendix 19.3). However, SA 60 and SR 52 recorded the highest sucrose composition with HL 1 the lowest.

Table 2.31 Mean whole stem sucrose composition (%) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
5,5	6,2	5,4	6,2	3,9	3,7
LSD (0,05)	NS				
LSD (0,01)	NS				

The main effect for growth stage was significant (Table 2.32). There was a significant negative linear effect superimposed with a significant positive quadratic effect which indicated that sucrose composition initially declined from A to MGF and then

increased from MGF to PM. Sucrose composition was significantly ($p = 0,01$) higher at A than at MGF and PM. Sucrose composition declined markedly from A to MGF. Sucrose composition then increased from MGF to PM with levels at PM significantly ($p = 0,01$) greater than at MGF.

Table 2.32 Mean whole stem sucrose composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
9,8	1,7	4,0

LSD (0,05) 1,3
LSD (0,01) 1,8

The interaction of hybrid with growth stage was non-significant (Figure 2.12). There were no significant components of the interaction either. However, there were apparent differences between hybrids in sucrose composition levels in the whole stem during grain fill. Whole stem sucrose composition ranged from a low of 0,7 % in PNR 473 at MGF to a high of 11,4 % in SA 60 at A. Whole stem sucrose composition declined in all hybrids from A to MGF with the decline being most marked in SA 60 and least marked in CG 4602 (Figure 2.12). Sucrose composition then increased in all hybrids, except CG 4602, from MGF to PM, most markedly in SA 60 and SR 52 and least markedly in PNR 473. In CG 4602 sucrose composition declined marginally from MGF to PM.

2.3.2.4 Sucrose content

The main effect for hybrid was non-significant while the main effect for growth stage was significant (Appendix 19.4). However, since the first order interaction of hybrid with growth stage was significant these main effects are of limited interest.

The interaction of hybrid with growth stage was significant (Figure 2.13). The hybrid x growth stage(linear) component of the interaction was also significant. Whole stem sucrose content ranged from a low of 0,36 g $stem^{-1}$ in PNR 473 at MGF to a high of 8,33 g $stem^{-1}$ in SA 60 at A. Whole stem sucrose content declined from A to MGF in all hybrids by 4,31 ($p = 0,01$), 7,74 ($p = 0,01$), 3,43 ($p = 0,05$), 3,89 ($p = 0,05$), 5,67 ($p = 0,01$) and 4,86 g $stem^{-1}$ ($p = 0,01$) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively (Figure 2.13). Thus the decline was most marked in PNR 473 and particularly SA 60, and least marked in CG 4602. Sucrose content then increased from MGF to PM by 1,36 (NS), 4,38 ($p = 0,01$), 6,80 ($p = 0,01$), 0,07 (NS) and 0,80 g $stem^{-1}$ (NS) in PNR 6427, SA 60, SR 52, PNR 473 and HL 1 respectively, while it decreased by 0,23 g $stem^{-1}$ (NS) in CG 4602. Thus the increase was most marked in SA 60 and particularly SR 52, and least marked in PNR 473.

The ratio of sucrose content to RS content in the whole stem provides for an easier assessment of the relative proportions of the non-structural carbohydrates (Table 2.33). Also, by graphically expressing the component non-structural carbohydrate contents as a percentage of the total non-structural carbohydrate

content, a summary of the changes in the relative proportions of the component carbohydrates is provided (Figure 2.14).

Table 2.33 Ratio of sucrose content to reducing sugars (RS) content and ratio of starch content to sucrose content for the whole stem of six maize hybrids sampled at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	A		MGF		PM	
	Sucrose : RS	Starch: sucrose	Sucrose : RS	Starch: sucrose	Sucrose : RS	Starch: sucrose
PNR 6427	1,30	0,25	0,28	2,78	0,97	0,45
SA 60	1,33	0,26	0,24	4,71	1,13	0,37
CG 4602	0,85	0,46	0,44	0,76	0,63	1,17
SR 52	0,81	0,60	0,50	1,80	0,55	0,63
PNR 473	1,38	0,39	0,45	3,32	3,40	3,27
HL 1	0,94	0,48	0,29	3,71	1,09	0,80
Sucrose : RS ratio			SE ($\bar{x}$)	0,76		
Starch : sucrose ratio			SE ($\bar{x}$)	0,68		

At A sucrose content exceeded RS content by 1,30, 1,33 and 1,38 times in PNR 6427, SA 60 and PNR 473, respectively. In CG 4602, SR 52 and HL 1 whole stem RS content exceeded sucrose content (Table 2.33, Figure 2.14). While sucrose content declined in all hybrids from A to MGF, RS content also declined in all hybrids except SR 52 from A to MGF. Reducing sugars content exceeded sucrose content at MGF as the ratio was less than one in all hybrids. Sucrose declined more relative to RS in all hybrids from A to MGF as the ratio of sucrose to RS was lower at MGF than

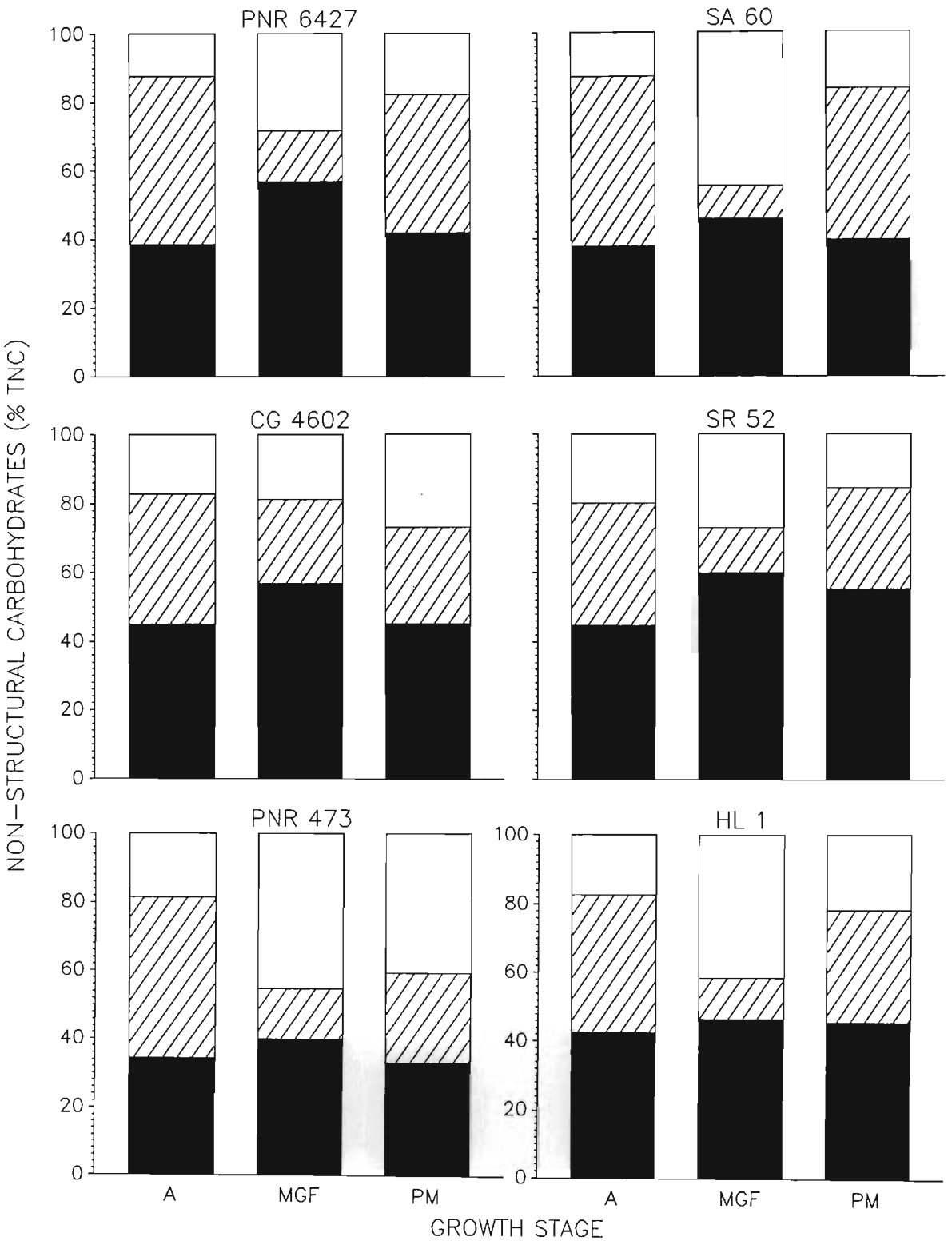


Figure 2.14 Fluctuation in component non-structural carbohydrate content expressed as a percentage of total non-structural carbohydrate (TNC) content in whole stems of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Key Starch, Sucrose, Reducing sugars

at A. The ratio of sucrose to RS increased in all hybrids from MGF to PM. Sucrose content exceeded RS content at PM in SA 60, HL 1 and most markedly in PNR 473. The ratio was almost one in PNR 6427 but sucrose content was still less than RS content in CG 4602 and SR 52. Thus there was a depletion of the sucrose pool and to a lesser extent, with the exception of SR 52, the RS pool from A to MGF in all hybrids. In all hybrids except CG 4602, levels of sucrose had increased from MGF to PM and in the case of SR 52 exceeded those at A. It is not certain at this stage which sinks in the hybrids utilized the sucrose pool in the whole stem from A to MGF. The increase in sucrose content from MGF to PM in all hybrids, except CG 4602, seems to indicate that once grain fill was completed there was enough photosynthetic activity in the leaves for current photosynthate to accumulate in the stem. In CG 4602 most leaves had senesced before grain black layer was reached and so there was no production of photosynthate surplus to grain requirements.

2.3.2.5 Starch composition

The main effect for hybrid was non-significant (Table 2.34 and

Table 2.34 Mean whole stem starch composition (%) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
2,5	2,8	2,7	4,0	2,5	2,5
LSD (0,05)	NS				
LSD (0,01)	NS				

Appendix 19.5). However, SR 52 recorded the highest starch composition while PNR 6427 and PNR 473 recorded the lowest.

The main effect for growth stage was significant (Table 2.35). There was a significant negative linear decline in starch composition from A to PM. Starch composition at A was significantly ($p = 0,05$) higher than at MGF and significantly ($p = 0,01$) higher than at PM. Starch composition at MGF was significantly ($p = 0,05$) higher than at PM.

Table 2.35 Mean whole stem starch composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
3,7	2,8	1,9

LSD (0,05) 0,8
LSD (0,01) 1,1

The interaction of hybrid with growth stage was non-significant (Figure 2.12). There were no significant components of the interaction either. However, there were apparent differences between hybrids in starch composition levels in the whole stem during grain fill. Whole stem starch composition ranged from a low of 1,2 % in PNR 473 at PM to a high of 5,2 % in SR 52 at A. From A to MGF starch composition increased marginally in PNR 6427 and SA 60, while levels declined in all the other hybrids with PNR 473 declining the most (Figure 2.12). Starch composition

then declined in all hybrids from MGF to PM with the smallest decline occurring in PNR 6427 and the largest in HL 1.

2.3.2.6 Starch content

The main effect for hybrid was significant (Table 2.36 and Appendix 19.6). SR 52 had significantly ($p = 0,05$) higher sucrose content than SA 60, and significantly ($p = 0,01$) higher starch content than all the other hybrids. SA 60 had significantly ($p = 0,05$) higher starch content than PNR 6427 and PNR 473. PNR 6427, CG 4602, PNR 473 and HL 1 were not significantly different in starch content from one another.

Table 2.36 Mean whole stem starch content (g $stem^{-1}$) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
1,27	2,17	1,68	3,01	1,37	1,47
LSD (0,05)	0,77				
LSD (0,01)	1,04				

The main effect for growth stage was significant (Table 2.37). There was a significant linear negative decline in starch content from A to PM. Starch content at A was non-significantly higher than at MGF but significantly ($p = 0,01$) higher than at PM. Starch content at MGF was not significantly higher than at PM.

Table 2.37 Mean whole stem starch content (g $stem^{-1}$) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
2,24	1,82	1,42

LSD (0,05) 0,55
LSD (0,01) 0,73

The interaction of hybrid with growth stage was non-significant (Figure 2.13). There were no significant components of the interaction either. However, there were apparent differences between hybrids in starch content levels in the whole stem during grain fill. Whole stem starch content ranged from a low of 0,68 g $stem^{-1}$ in PNR 473 at PM to 3,53 g $stem^{-1}$ in SR 52 at PM. Starch content increased from A to MGF in PNR 6427 and SA 60 and then declined from MGF to PM (Figure 2.13). In CG 4602, PNR 473 and HL 1 starch content declined from A to PM. In SR 52 starch content initially declined from A to MGF but then increased from MGF to PM with levels at PM higher than at A. Thus starch reserves were depleted in the latter phase of grain fill in PNR 6427 and SA 60, while utilization of starch reserves occurred continuously during grain fill in CG 4602, PNR 473 and HL 1. In SR 52 starch reserves were utilized during the first half of grain fill and then accumulated in the latter half.

The ratio of starch content to sucrose content at A (Table 2.33, Figure 2.14) indicates that sucrose exceeded starch in all hybrids particularly PNR 6427 and SA 60. As sucrose content

declined in the whole stems of all hybrids from A to MGF, the ratio of starch content to sucrose content increased in all hybrids over the same period. All hybrids except CG 4602, had more starch than sucrose at MGF. The ratio of starch content to sucrose content was particularly high for SA 60 at MGF. Sucrose content had declined markedly in SA 60 from A to MGF and at MGF, starch content and RS content were almost equal. In CG 4602 sucrose content had declined from A to MGF but sucrose content remained higher than starch content at MGF. In all hybrids except CG 4602 the ratio of starch content to sucrose content declined from MGF to PM. In CG 4602 the ratio increased from MGF to PM with starch exceeding sucrose at PM. Starch content also exceeded sucrose content in PNR 473 at PM. The other four hybrids had less starch content than sucrose content at PM.

It is noteworthy that for all hybrids over all growth stages starch content exceeded RS content only in PNR 473 at PM.

2.3.2.7 Total non-structural carbohydrate composition

The main effect for hybrid was significant (Table 2.38 and

Table 2.38 Mean whole stem total non-structural carbohydrate composition of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
14,6	15,2	16,6	23,0	9,9	11,8
LSD (0,05)	5,2				
LSD (0,01)	7,0				

Appendix 19.7). SR 52 had significantly (p = 0,05) higher TNC composition than CG 4602, and significantly (p = 0,01) higher TNC composition than all the other hybrids. CG 4602 and SA 60 had significantly (p = 0,05) higher TNC composition than PNR 473.

The main effect for growth stage was significant (Table 2.39). There was a significant negative linear decline in starch content from A to PM superimposed by a significant positive quadratic effect. This indicates that the decline in TNC composition from MGF to PM was much less marked than the initial decline from A to MGF. The TNC composition at A was significantly (p = 0,01) higher than that at MGF and PM, but TNC composition at MGF was non-significantly higher than at PM.

Table 2.39 Mean whole stem total non-structural carbohydrate composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
22,9	11,4	11,3
LSD (0,05) 3,7		
LSD (0,01) 4,9		

The interaction of hybrid with growth stage was non-significant (Figure 2.15). There were no significant components of the interaction either. However, there were apparent differences between hybrids in TNC composition levels in the whole stem during grain fill. The TNC composition ranged from a low of

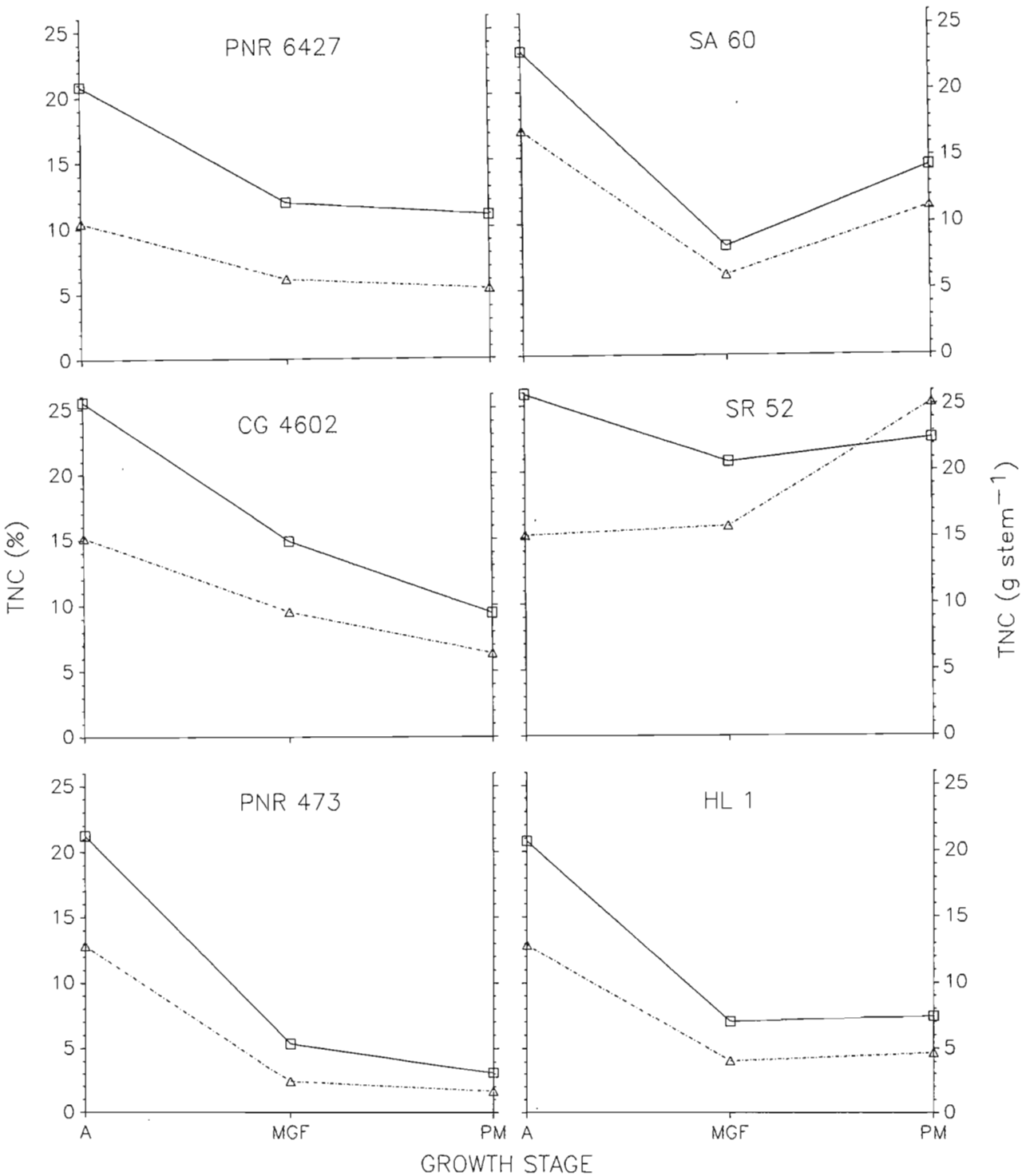


Figure 2.15 Fluctuation in total non-structural carbohydrate (TNC) composition (□——□) and content (△·····△) of whole stems of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

3,1 % in PNR 473 at PM to a high of 25,9 % in SR 52 at A. Whole stem TNC composition declined in all hybrids from A to MGF with the most substantial decline occurring in PNR 473, and SR 52 undergoing the least marked decline (Figure 2.15). Although the main effect means indicate that there was on average a further slight decline from MGF to PM, there were apparent exceptions to this trend. PNR 6427, CG 4602 and PNR 473 did decline in TNC composition from MGF to PM, but SA 60, SR 52 and HL 1 increased in TNC composition.

2.3.2.8 Total non-structural carbohydrate content, residual content and whole stem dry mass

Main effects for TNC content

The main effect for hybrid was significant (Table 2.40 and Appendix 19.8). SR 52 had significantly ($p = 0,01$) higher TNC content than all the other hybrids. Apart from SA 60 which had significantly ($p = 0,05$) higher TNC content than PNR 473; PNR 6427, SA 60, CG 4602, PNR 473 and HL 1 did not differ significantly from one another in TNC content.

Table 2.40 Mean whole stem total non-structural carbohydrate content (g stem^{-1}) of six maize hybrids during grain fill

			Hybrid		
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
7,27	11,45	10,32	18,72	5,63	7,20
LSD (0,05)	4,95				
LSD (0,01)	6,64				

The main effect for growth stage was significant (Table 2.41). There was a significant negative linear decline in TNC content from A to PM superimposed by a significant positive quadratic effect. This indicates that TNC content initially declined from A to MGF and then increased from MGF to PM. The TNC content at A was significantly ($p = 0,01$) higher than at MGF and PM, but TNC content at PM was not significantly higher than at MGF.

Table 2.41 Mean whole stem total non-structural carbohydrate content (g $stem^{-1}$) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
13,92	7,33	9,05
LSD (0,05) 3,50		
LSD (0,01) 4,70		

Main effects for residual content

The main effect for hybrid was non-significant and the main effect for growth stage was significant (Appendix 19.9). However, since the first order interaction of hybrid with growth stage was significant these main effects are of limited interest.

Main effects for whole stem dry mass

The main effect for hybrid was non-significant and the main effect for growth stage was significant (Appendix 19.10).

However, since the first order interaction of hybrid with growth stage was significant these main effects are of limited interest.

Interactions of hybrid with growth stage for TNC content, residual content and whole stem dry mass

The interaction of hybrid with growth stage for TNC content was non-significant (Figures 2.15 and 2.16). However, the hybrid x growth stage(linear) component of the interaction was significant. The interactions of hybrid with growth stage for residual content and dry mass were significant (Figure 2.16). The hybrid x growth stage(linear) components of the interactions were also significant.

The first order interactions for these three variates are presented together in Figure 2.16. The differences between hybrids in the fluctuations of residual content and dry mass over the growth stages constitute significant interactions for each variate and are discussed as such. However, the differences between hybrids in the fluctuations of TNC content over the growth stages do not constitute a significant interaction and are therefore discussed as apparent differences.

The ratio of TNC content to residual content was derived in order to more readily assess the amounts of TNC and residual components relative to one another (Table 2.42).

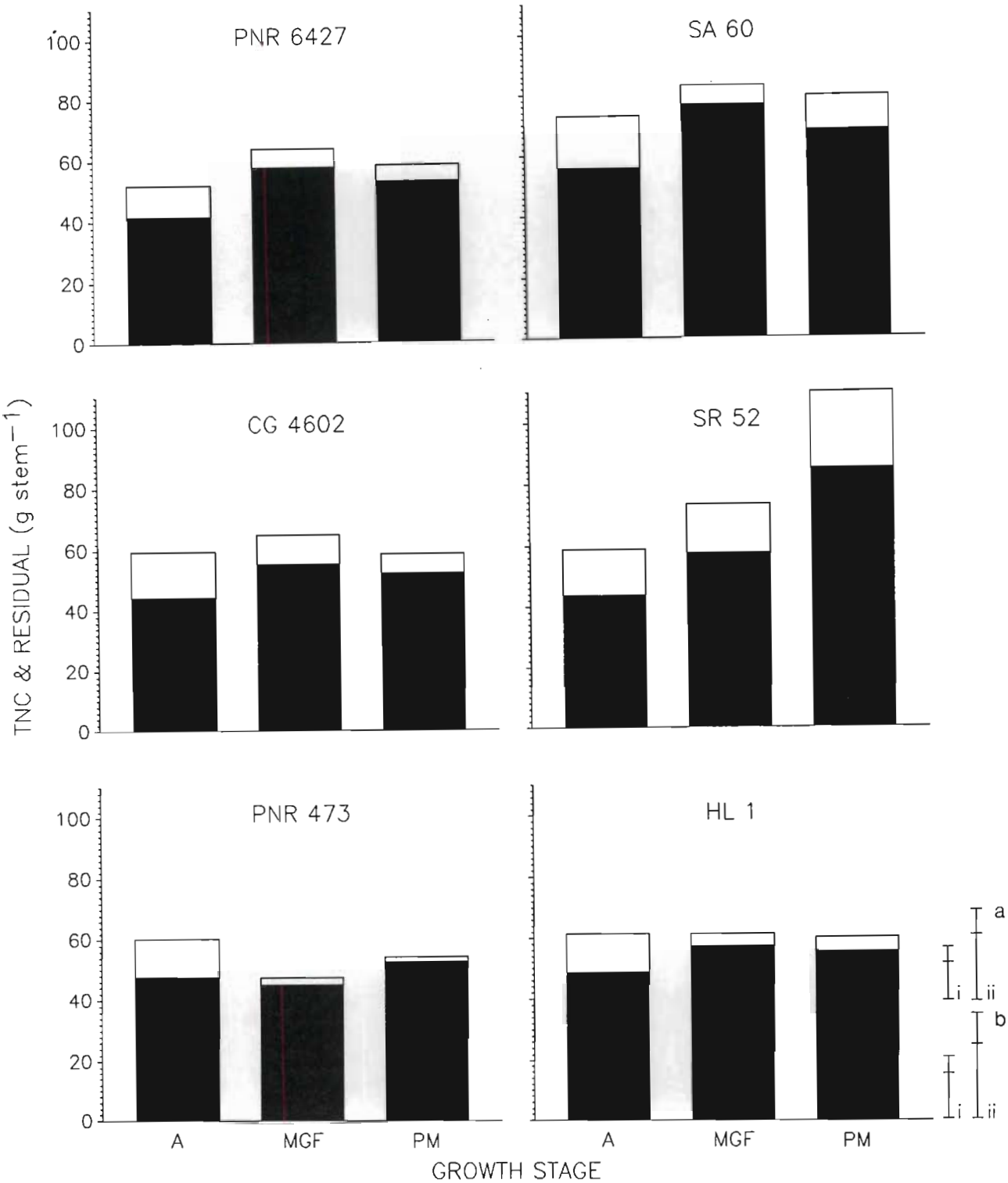


Figure 2.16 Fluctuation in total non-structural carbohydrate (TNC) (▭) and residual (▬) content, and dry mass (▬) of whole stems of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM).
Comparisons using LSD's of (a) residual content means and (b) dry mass means at the same level of (i) hybrid; and (ii) growth stage or with neither factor in common

Table 2.42 Ratio of total non-structural carbohydrate (TNC) content to residual content for the whole stem of six maize hybrids sampled at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	A	MGF	PM
	TNC:Residual	TNC:Residual	TNC:Residual
PNR 6427	0,266	0,142	0,127
SA 60	0,302	0,092	0,173
CG 4602	0,344	0,178	0,111
SR 52	0,350	0,279	0,308
PNR 473	0,270	0,057	0,032
HL 1	0,263	0,077	0,083
TNC : Residual ratio SE ($\bar{x}$)		0,045	

In PNR 6427 whole stem dry mass increased by 11,9 g stem^{-1} (NS) from A to MGF (Figure 2.16). Residual content increased by 16,2 g stem^{-1} ($p = 0,01$) from A to MGF. Thus the decline in TNC content from A to MGF may have been due to part of the TNC pool in the stem being converted to residual components. It must be emphasized that the level of TNC at any growth stage does not represent a static amount but there would be constant fluctuations in levels as the pool of TNC in the stem tissue is added to by current photosynthate or utilized by the various sinks in the plant. Thus the decline of 4,36 g stem^{-1} of TNC from A to MGF does not represent the total amount of TNC that has been utilized from stem pools when integrated over time (Figures 2.15 and 2.16). The increase in stem dry mass from A to MGF in PNR 6427 which occurred largely as a result of an increase in the residual content indicates that this hybrid continued to convert photosynthate to residual components during the first half of

grain fill. The lower levels of TNC content at MGF indicate that during peak grain filling there was little excess current photosynthate available to accumulate in the stem and maintain TNC content at the same levels from A to MGF. From MGF to PM stem dry mass declined by 5,7 g $stem^{-1}$ (NS), with residual content declining by 4,9 g $stem^{-1}$ (NS) and TNC content declining further by 0,76 g $stem^{-1}$. The water stress conditions that prevailed from MGF to PM may have enhanced the depletion of TNC pools in the stem to meet grain fill requirements, with residual components in the stem also being depleted possibly for grain fill requirements. The ratio of TNC content to residual content declined slightly from MGF to PM indicating that TNC declined by a slightly greater proportion than did the residual components (Table 2.42).

In SA 60 the stem dry mass increased by 9,8 g $stem^{-1}$ (NS) from A to MGF due to the 20,7 g $stem^{-1}$ ($p = 0,01$) increase in the residual content (Figure 2.16). SA 60 had the highest TNC content at A in comparison to the other hybrids and the decline in TNC content from A to MGF may have been due, in part, to conversion to residual components in the stem. The ratio of TNC content to residual content declined markedly from A to MGF (Table 2.42). Stem dry mass and residual content then declined by 3,4 (NS) and 8,5 g $stem^{-1}$ (NS) respectively, as the TNC content increased from MGF to PM. The increase in the ratio of TNC content to residual content from MGF to PM reflects this increase in TNC content as residual content declined. Thus it appears that SA 60 also converted photosynthate into residual components of the stem during the first half of grain fill. In addition,

supplying the carbohydrate requirements of the grain meant that there was little excess TNC left over to maintain constant levels of TNC in the stem from A to MGF. The water stress conditions that prevailed from MGF to PM may also have limited the supply of current photosynthate during peak grain fill. However, as physiological maturity was reached, continued photosynthetic capacity of the leaves apparently resulted in the reaccumulation of excess photosynthate as TNC in the stem. It appears, therefore, that the grain as a sink was limiting yield production in SA 60 since grain fill ceased when the leaves were still capable of producing photosynthate resulting in the stem serving as an alternative sink for photosynthate.

Dry mass increased slightly by 5,4 g $stem^{-1}$ (NS) in CG 4602 from A to MGF as the residual content increased by 11,0 g $stem^{-1}$ (NS) (Figure 2.16). Again since the increase in residual content exceeded the increase in dry mass, the TNC content declined from A to MGF. These changes are reflected in the decline in the ratio of TNC content to residual content (Table 2.42). As with PNR 6427 both the TNC content and residual content declined from MGF to PM resulting in an overall decline in stem dry mass. The ratio of TNC content to residual content declined from MGF to PM indicating that TNC content declined by a greater proportion than did the residual content. The depletion of TNC and residual components in the latter half of grain fill appears to indicate an undersupply of current photosynthate in CG 4602 which may have been exacerbated by the water stress conditions that prevailed from MGF to PM.

In SR 52 stem dry mass increased by 14,4 g stem^{-1} (NS) from A to MGF and by 36,6 g stem^{-1} ($p = 0,01$) from MGF to PM (Figure 2.16). The increases in dry mass from A to PM were as a result of increases in both TNC content and most markedly, residual content, with residual content increasing by 13,8 g stem^{-1} ($p = 0,01$) from A to MGF and by 27,3 g stem^{-1} ($p = 0,01$) from MGF to PM. These increases in dry mass in SR 52 were the most marked of all the hybrids. The decline in the ratio of TNC content to residual content from A to MGF reflects the greater proportional increase in residual content compared to that in TNC content (Table 2.42). The increase in the ratio from MGF to PM indicates that TNC content increased by a greater proportion than residual content. Stem dry mass at PM in SR 52 was significantly ($p = 0,01$) greater than that of any other hybrid at any of the growth stages. Since TNC content was at a maximum at PM in SR 52, it is clear that the carbohydrate requirements of the grain were low and thus the stem served as an alternative sink for photosynthate.

In comparison to all the other hybrids PNR 473 was the only one which had a marked decline of 12,9 g stem^{-1} (NS) in stem dry mass from A to MGF (Figure 2.16). However, residual content declined by only 2,5 g stem^{-1} (NS) with the decline in TNC content of 10,4 g stem^{-1} contributing the most to the decline in dry mass. The larger proportional decline in TNC content compared to residual content is reflected in their ratio (Table 2.42). From MGF to PM stem dry mass increased by 6,8 g stem^{-1} (NS) while residual content increased by a larger amount of 7,6 g stem^{-1} (NS) as a result of a further decline in TNC content from MGF to PM.

The decline in the TNC content from MGF to PM while the residual content increased is reflected in the decline in their ratio during the same period. Thus it appears that once anthesis was complete in PNR 473, the carbohydrate requirements of the grain were such that there was little excess photosynthate to maintain TNC content at A levels and so TNC content declined and remained at low levels throughout grain fill. The water stress conditions that prevailed from MGF to PM may have enhanced the depletion of TNC pools in the stem to supplement a reduced supply of current photosynthate during the latter half of grain fill. Nonetheless as grain fill ceased at PM, photosynthate was converted to residual components which indicates that the stem tissue was still an active sink, utilizing available photosynthate.

Stem dry mass in HL 1 remained remarkably constant at 61,5 g $stem^{-1}$ at A, 61,4 g $stem^{-1}$ at MGF and 60,3 g $stem^{-1}$ at PM (Figure 2.16). Residual content at A, MGF and PM was 48,6, 57,3 and 55,6 g $stem^{-1}$, respectively. As with all the other hybrids apart from SR 52, the residual content increased from A to MGF while TNC content declined. Part of the TNC pool may have been converted to residual components in the stem. The increase in residual content in association with the decrease in TNC content from A to MGF is reflected in the decline in the ratio of TNC content to residual content from A to MGF (Table 2.42). The decline in residual content in association with an increase in TNC content from MGF to PM is reflected in the increase in the ratio of TNC content to residual content from MGF to PM. The observation that stem dry mass did not increase in HL 1 from A to MGF, as happened in PNR 6427, SA 60 and CG 4602, may indicate

that most of the carbohydrate was partitioned to the grain with little excess left to accumulate in the stem. Equally, it may indicate that the stem tissue in HL 1 was not a very active sink creating demand for and utilizing carbohydrate.

2.3.3 Non-structural carbohydrate analysis of the cob

2.3.3.1 Reducing sugars composition

The main effect for hybrid was non-significant (Table 2.43 and Appendix 20.1). However, SR 52 and CG 4602 recorded the highest RS composition with HL 1 the lowest.

Table 2.43 Mean cob reducing sugars composition (%) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
5,41	5,2	8,2	8,6	5,7	5,0
LSD (0,05)	NS				
LSD (0,01)	NS				

The main effect for growth stage was significant (Table 2.44). There was a significant negative linear decline in RS composition from A to PM. The decline in RS composition was more marked from A to MGF, than from MGF to PM. The RS composition at A was significantly ($p = 0,01$) higher than at PM. The RS composition was significantly ($p = 0,01$) higher at MGF than at PM.

Table 2.44 Mean cob reducing sugars composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
11,4	5,6	2,1

LSD (0,05) 2,3

LSD (0,01) 3,0

The interaction of hybrid with growth stage was non-significant (Figure 2.17). There were no significant components of the interaction either. However, there were apparent differences between hybrids in RS composition levels in the cob during grain fill. The RS composition in the cob ranged from a low of 1,4 % in PNR 473 at PM to a high of 13,0 % in CG 4602 at A. The RS composition declined in all hybrids from A to MGF, most markedly in PNR 473 and least markedly in SR 52 (Figure 2.17). The RS composition declined further from MGF to PM in all hybrids. However, the decline from MGF to PM was more marked than the decline from A to MGF in CG 4602 and particularly SR 52. In PNR 6427 on the other hand, RS composition declined only slightly from MGF to PM. The fact that RS composition peaked in the cob at A in all hybrids is probably due to the small size of the cob with the residual components not yet making up a large component of the cob mass. The decline in RS composition in the cob of all hybrids from A to MGF was not accompanied by a decline in RS content and was therefore due to the 'dilution effect' of the large increase in cob dry mass during this period. The sharp decline in RS composition in the cob of all hybrids from MGF to PM was accompanied by a decline in RS content and is therefore

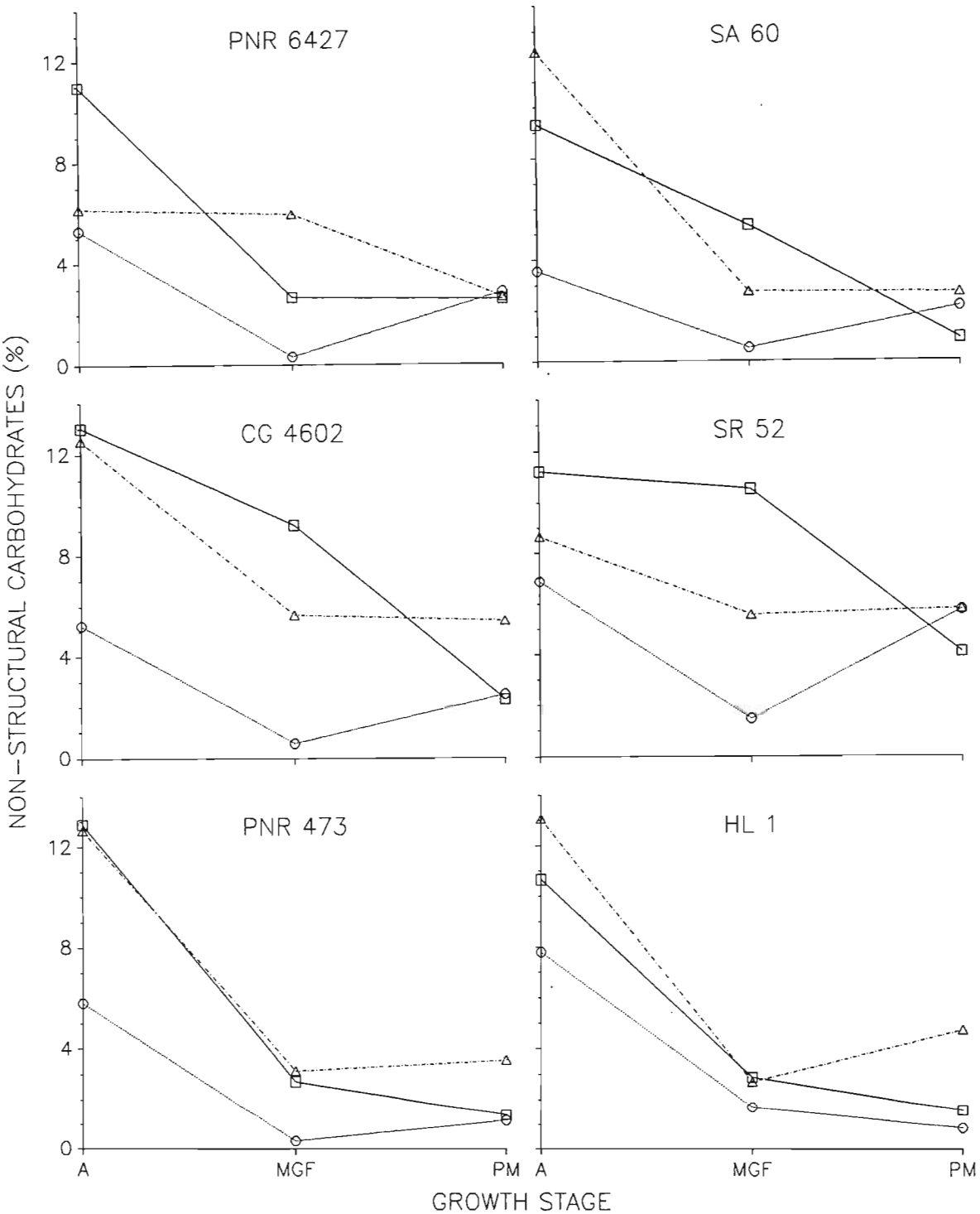


Figure 2.17 Fluctuation in reducing sugars (□——□), sucrose (○——○) and starch (△·····△) composition in cobs of the primary ears of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

indicative of a depletion of RS pools in the cob during this period.

2.3.3.2 Reducing sugars content

The main effect for hybrid was non-significant while the main effect for growth stage was significant (Appendix 20.2). However, since the first order interaction of hybrid with growth stage was significant these main effects are of limited interest.

The interaction of hybrid with growth stage was significant (Figure 2.18). The hybrid x growth stage(quadratic) component of the interaction was also significant. This indicates that the increase in RS content of the cob from A to MGF followed by the decline in RS content from MGF to PM was more marked in some of the hybrids than others. Cob RS content ranged from a low of 0,09 g cob^{-1} in PNR 473 at A to a high of 1,50 g cob^{-1} in SA 60 at MGF. Cob RS content increased by 0,35 (NS), 1,09 ($p = 0,01$), 1,18 ($p = 0,01$), 0,77 ($p = 0,01$), 0,13 (NS) and 0,27 g cob^{-1} (NS) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively (Figure 2.18). Thus the increase was particularly marked in CG 4602 and SR 52 and least marked in PNR 473. From MGF to PM RS content declined by 0,13 (NS), 1,22 ($p = 0,01$), 1,00 ($p = 0,01$), 0,26 (NS), 0,30 (NS) and 0,24 g cob^{-1} (NS) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. Thus the decline was most marked in SA 60 and least marked in HL 1.

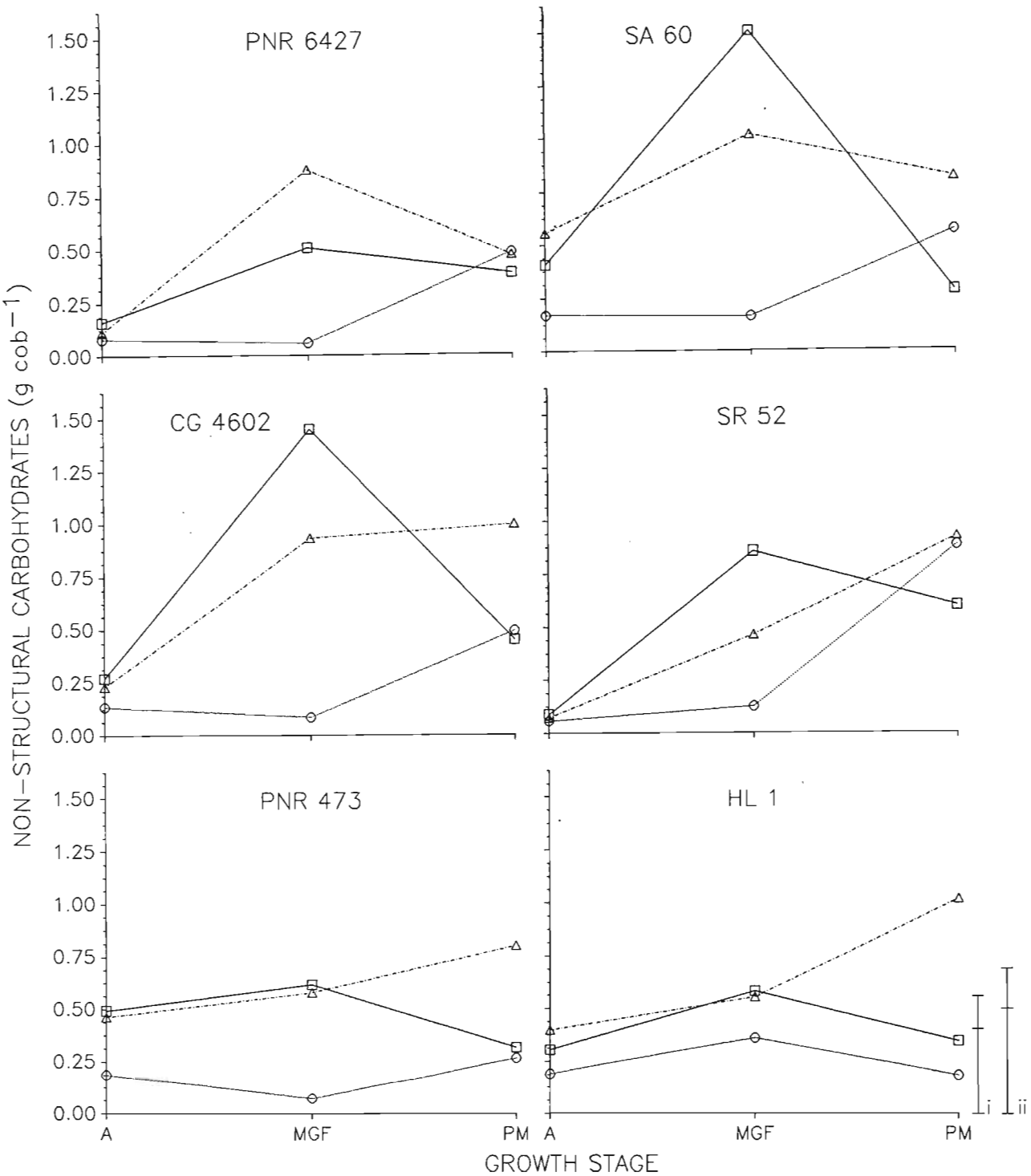


Figure 2.18 Fluctuation in reducing sugars (□——□), sucrose (○——○) and starch (△·····△) content in cobs of the primary ears of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM).

Comparisons using LSD's of reducing sugars content means at the same level of (i) hybrid; and (ii) growth stage or with neither factor in common

It is noteworthy that at A SR 52 had the lowest RS content in the cob of 0,09 g cob^{-1}, however, this was not significantly lower than any of the other hybrids at A. It appears then that the partitioning of photosynthate to the ear of SR 52 at A was limited in comparison to the other hybrids.

2.3.3.3 Sucrose composition

The main effect for hybrid was non-significant (Table 2.45 and Appendix 20.3). However, SR 52 followed by HL 1 recorded the highest sucrose composition while SA 60 recorded the lowest.

Table 2.45 Mean cob sucrose composition (%) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
2,8	2,1	2,8	4,7	2,4	3,5
LSD (0,05)	NS				
LSD (0,01)	NS				

The main effect for growth stage was significant (Table 2.46). There was a significant negative linear effect superimposed by a significant positive quadratic effect. This indicates that sucrose composition initially declined from A to MGF, and then increased from MGF to PM. Sucrose composition was significantly ($p = 0,01$) higher at A than at MGF and PM, but sucrose composition was significantly ($p = 0,05$) higher at PM than at MGF.

Table 2.46 Mean cob sucrose composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
5,8	0,8	2,5

LSD (0,05) 1,6

LSD (0,01) 2,1

The interaction of hybrid with growth stage was non-significant (Figure 2.17). There were no significant components of the interaction either. However, there were apparent differences between hybrids in sucrose composition levels in the cob during grain fill. Sucrose composition in the cob ranged from a low of 0,3 % in PNR 473 at MGF to a high of 5,7 % in SR 52 at PM. Sucrose composition in the cob declined in all hybrids from A to MGF (Figure 2.17). Sucrose composition was particularly low in PNR 6427, SA 60, CG 4602 and PNR 473 at MGF with levels less than 0,6 %. Sucrose composition was higher in SR 52 and HL 1 at 1,5 and 1,7 %, respectively. From MGF to PM sucrose composition increased in all hybrids except HL 1. The increase in sucrose composition was particularly marked in SR 52. In HL 1 sucrose composition declined from MGF to the lowest level of all the hybrids at PM.

2.3.3.4 Sucrose content

The main effect for hybrid was non-significant (Table 2.47 and Appendix 20.4). However, SR 52 followed by SA 60 recorded the

highest sucrose content while PNR 6427 and PNR 473 recorded the lowest.

Table 2.47 Mean cob sucrose content (g cob^{-1}) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
0,18	0,30	0,24	0,35	0,18	0,25
LSD (0,05)	NS				
LSD (0,01)	NS				

The main effect for growth stage was significant (Table 2.48). There was a significant positive linear increase in sucrose content from A to PM superimposed by a significant positive quadratic effect. This indicates that sucrose content remained constant from A to MGF and then increased markedly from MGF to PM. Sucrose content was significantly ($p = 0,01$) higher at PM than at A and MGF, while sucrose content at MGF was equal to that at A.

Table 2.48 Mean cob sucrose content (g cob^{-1}) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
0,14	0,14	0,47
LSD (0,05) 0,15		
LSD (0,01) 0,20		

The interaction of hybrid with growth stage was just non-significant (Figure 2.18). There were no significant components of the interaction either. However, there were apparent differences between hybrids in sucrose content levels in the cob during grain fill. Sucrose content in the cob ranged from a low of 0,07 g cob^{-1} in SR 52 at A to a high of 0,88 g cob^{-1} in SR 52 at PM. Sucrose content declined from A to MGF in PNR 6427, SA 60, CG 4602 and PNR 473 but increased from A to MGF in SR 52 and HL 1 (Figure 2.18). Sucrose content was lowest in PNR 6427 and highest in HL 1 at MGF. Except for HL 1, all hybrids then increased markedly in sucrose content from MGF to PM. The increase was particularly marked in SR 52. In HL 1 sucrose content declined to levels at PM lower than at A.

The ratio of sucrose content to RS content in the cob provides for an easier assessment of the relative proportions of the non-structural carbohydrates (Table 2.49). Also, by graphically expressing the component non-structural carbohydrate contents as a percentage of the total non-structural carbohydrate content, a summary of the changes in the relative proportions of the component carbohydrates is provided (Figure 2.19).

At A RS content exceeded sucrose content in all hybrids (Table 2.49, Figure 2.19). From A to MGF the ratio of sucrose to RS content declined markedly in all hybrids except HL 1. In HL 1 both sucrose content and RS content had increased by nearly the same proportion from A to MGF and so the ratio remained virtually the same from A to MGF. In the other hybrids RS content had

Table 2.49 Ratio of sucrose content to reducing sugars (RS) content and ratio of starch content to sucrose content for the primary cob of six maize hybrids sampled at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	A		MGF		PM	
	Sucrose : RS	Starch: sucrose	Sucrose : RS	Starch: sucrose	Sucrose : RS	Starch: sucrose
PNR 6427	0,50	1	0,18	26	1,00	2
SA 60	0,98	11	0,11	5	3,10	2
CG 4602	0,47	22	0,06	18	1,20	3
SR 52	0,70	1	0,12	27	1,44	1
PNR 473	0,62	275	0,12	20	0,79	5
HL 1	0,82	2	0,80	9	0,67	7
Sucrose : RS ratio			SE ($\bar{x}$)	0,42		
Starch : sucrose ratio			SE ($\bar{x}$)	66		

increased while sucrose content (except for SR 52) had declined from A to MGF thus the ratio declined markedly. In all hybrids, except HL 1, the ratio of sucrose content to RS content increased markedly from MGF to PM as a result of the marked increase in sucrose content during the same period. At PM sucrose content equalled RS content in PNR 6427, while in SA 60, CG 4602 and SR 52 sucrose content exceeded RS content. In HL 1 sucrose content declined by a greater proportion than RS content thus the ratio declined from MGF to PM.

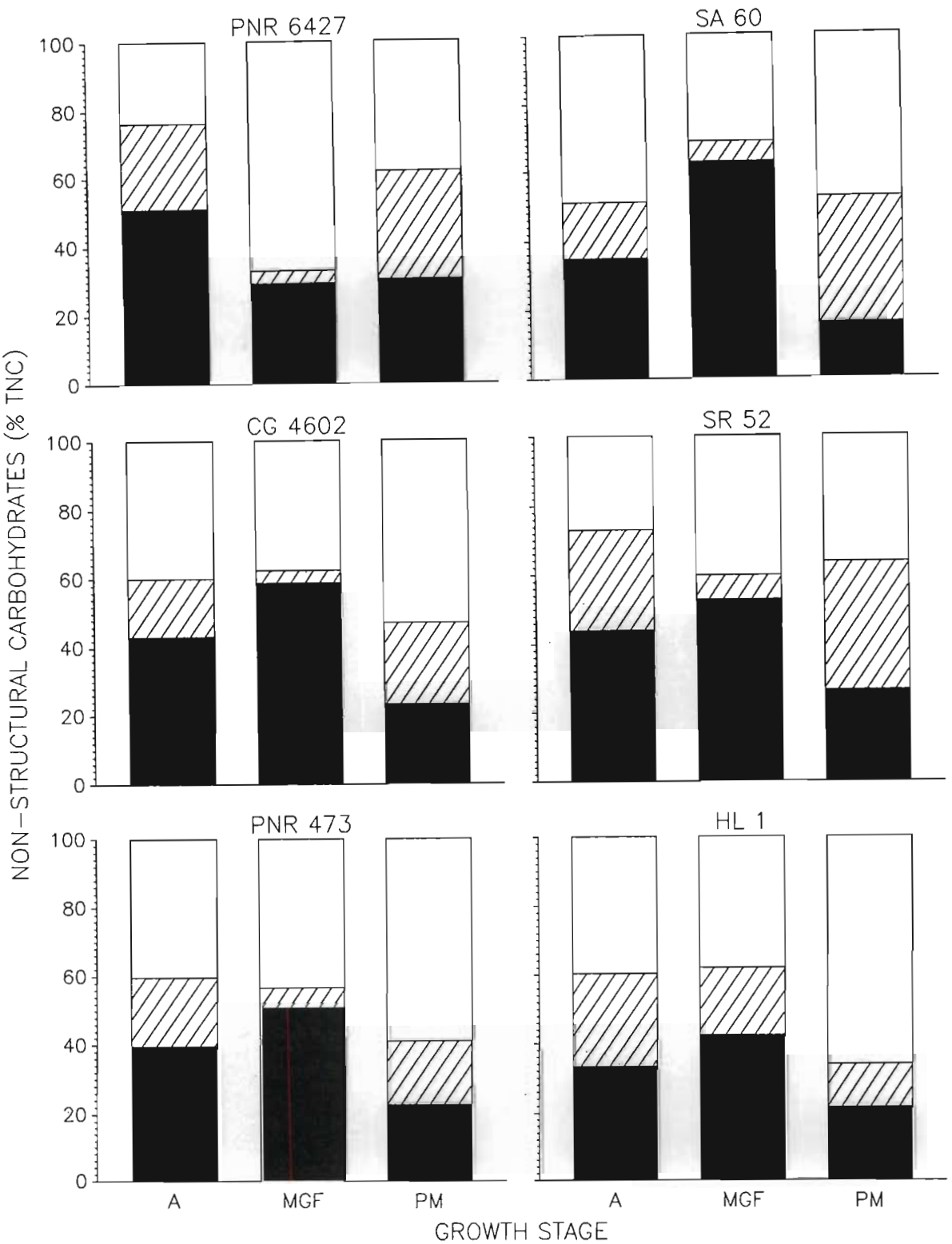


Figure 2.19 Fluctuation in component non-structural carbohydrate content expressed as a percentage of total non-structural carbohydrate (TNC) content in cobs of the primary ears of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

2.3.3.5 Starch composition

The main effect for hybrid was non-significant (Table 2.50 and Appendix 20.5). However, CG 4602 followed by HL 1 recorded the highest starch composition while PNR 6427 recorded the lowest.

Table 2.50 Mean cob starch composition (%) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
4,9	5,9	7,9	6,7	6,5	6,8
LSD (0,05)	NS				
LSD (0,01)	NS				

The main effect for growth stage was significant (Table 2.51). There was a significant negative linear decline in starch composition from A to PM, superimposed by a positive quadratic effect. This indicates that starch composition declined markedly from A to MGF and then only marginally declined from MGF to PM.

Table 2.51 Mean cob starch composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
10,9	4,3	4,1
LSD (0,05) 2,1		
LSD (0,01) 2,9		

Starch composition was significantly ($p = 0,01$) higher at A than at MGF and PM, but starch composition was not significantly higher at MGF than at PM.

The interaction of hybrid with growth stage was non-significant (Figure 2.17). There were no significant components of the interaction either. However, there were apparent differences between hybrids in starch composition levels in the cob during grain fill. Starch composition in the cob ranged from a low of 2,7 % in PNR 6427 at PM to a high of 13,1 % in HL 1 at A. Starch composition declined in all hybrids from A to MGF, most markedly in HL 1 and only marginally in PNR 6427 (Figure 2.17). From MGF to PM starch composition further decreased in PNR 6427, SA 60 and CG 4602 while starch composition increased in SR 52, PNR 473 and HL 1. The fact that starch composition in the cob peaked in all hybrids at A, while starch content increased from A to PM is again probably due to the small size of the cob, with the residual components making up a small proportion of the cob dry mass.

2.3.3.6 Starch content

The main effect for hybrid was non-significant (Table 2.52 and Appendix 20.6). However, SA 60 followed by CG 4602 recorded the highest starch content while PNR 6427 and SR 52 recorded the lowest.

Table 2.52 Mean cob starch content (g cob^{-1}) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
0,48	0,79	0,72	0,48	0,61	0,66
LSD (0,05)	NS				
LSD (0,01)	NS				

The main effect for growth stage was significant (Table 2.53). There was a significant positive linear increase in starch content from A to PM. The negative quadratic effect was almost significant which indicates that the increase in starch content tended to be more marked from A to MGF than from MGF to PM.

Table 2.53 Mean cob starch content (g cob^{-1}) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage			
A		MGF	PM
0,30		0,74	0,84
LSD (0,05)	0,21		
LSD (0,01)	0,28		

The interaction of hybrid with growth stage was non-significant (Figure 2.18). There were no significant components of the interaction either. However, there were apparent differences between hybrids in starch content levels in the cob during grain fill. Starch content in the cob ranged from a low of 0,07 g cob^{-1}

in SR 52 at A to a high of 1,02 g cob^{-1} in HL 1 at PM. Starch content increased in all hybrids from A to MGF, most markedly in PNR 6427 and least markedly in PNR 473 (Figure 2.18). From MGF to PM sucrose content further increased in CG 4602, SR 52, PNR 473 and HL 1 but declined in PNR 6427 and SA 60. The accumulation of starch from A to MGF in the cob of CG 4602, SR 52, PNR 473, and HL 1 may be interpreted as an accumulation of photosynthate surplus to grain requirements in the cob. However, since PNR 473 for example showed a decline in the TNC content of the stem from A to PM indicating an undersupply of photosynthate for grain requirements this interpretation is not necessarily the correct one. The decline in starch content in PNR 6427 and SA 60 from MGF to PM may indicate the utilization of starch reserves of the cob for continued grain fill in the latter half of grain fill. Whether or not this means that there was an undersupply of carbohydrate to the grain is not certain since SA 60, for example, showed a tendency to increase TNC content levels in the whole stem from MGF to PM.

The ratio of starch content to sucrose content (Table 2.49, Figure 2.19) was greater than one for all hybrids at all growth stages, indicating starch content exceeded sucrose content in all hybrids at all growth stages. PNR 473 at A recorded an extreme ratio value with starch content 275 times greater than sucrose content. As with the shank, RS content and starch content in the cob were higher than sucrose content at MGF. The lower sucrose content relative to starch content at MGF i.e. peak grain fill may be indicative of sucrose in the phloem tissue of the cob with very little stored in parenchyma cell vacuoles (Giaquinta, 1983).

The starch in the cob may serve as an emergency buffer supply for grain carbohydrate requirements (Franceschi, 1986), while the high RS content at MGF may be indicative of the high metabolic activity that may be expected to occur in the cob during peak grain fill.

2.3.3.7 Total non-structural carbohydrate composition

The main effect for hybrid was significant (Table 2.54 and Appendix 20.7). SR 52 recorded the highest TNC composition in the cob followed by CG 4602, however, these two hybrids were not significantly different from one another. SR 52 was significantly ($p = 0,01$) higher in TNC composition than PNR 6427 and SA 60, and significantly ($p = 0,05$) higher in TNC composition than PNR 473 and HL 1. SA 60 was significantly ($p = 0,05$) higher in TNC composition than PNR 6427 and SA 60. PNR 6427, SA 60, PNR 473 and HL 1 were not significantly different from one another.

Table 2.54 Mean cob total non-structural carbohydrate composition (%) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
13,2	13,1	18,8	20,0	14,6	15,3
LSD (0,05)	4,3				
LSD (0,01)	5,8				

The main effect for growth stage was significant (Table 2.55). There was a significant negative linear decline in TNC

composition from A to PM superimposed by a significant positive quadratic effect. This indicates that the decline in TNC composition from MGF to PM was much less marked than the initial decline from A to MGF. The TNC composition at A was significantly ($p = 0,01$) higher than at MGF and PM, but TNC composition at MGF was not significantly higher than at PM.

Table 2.55 Mean cob total non-structural carbohydrate composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage		
A	MGF	PM
28,0	10,7	8,8
LSD (0,05) 3,1		
LSD (0,01) 4,1		

The interaction of hybrid with growth stage was non-significant (Figure 2.20). There were no significant components of the interaction either. However, there were apparent differences between hybrids in TNC composition levels in the cob during grain fill. Cob TNC composition ranged from a low of 5,7 % in SA 60 at PM to a high of 31,5 % in PNR 473 at A. Cob TNC composition declined markedly in all hybrids from A to MGF with the most substantial declines occurring in PNR 473 and HL 1, and SR 52 undergoing the least marked decline (Figure 2.20). Cob TNC composition then declined marginally in all hybrids from MGF to PM, however, the decline was more marked in CG 4602.

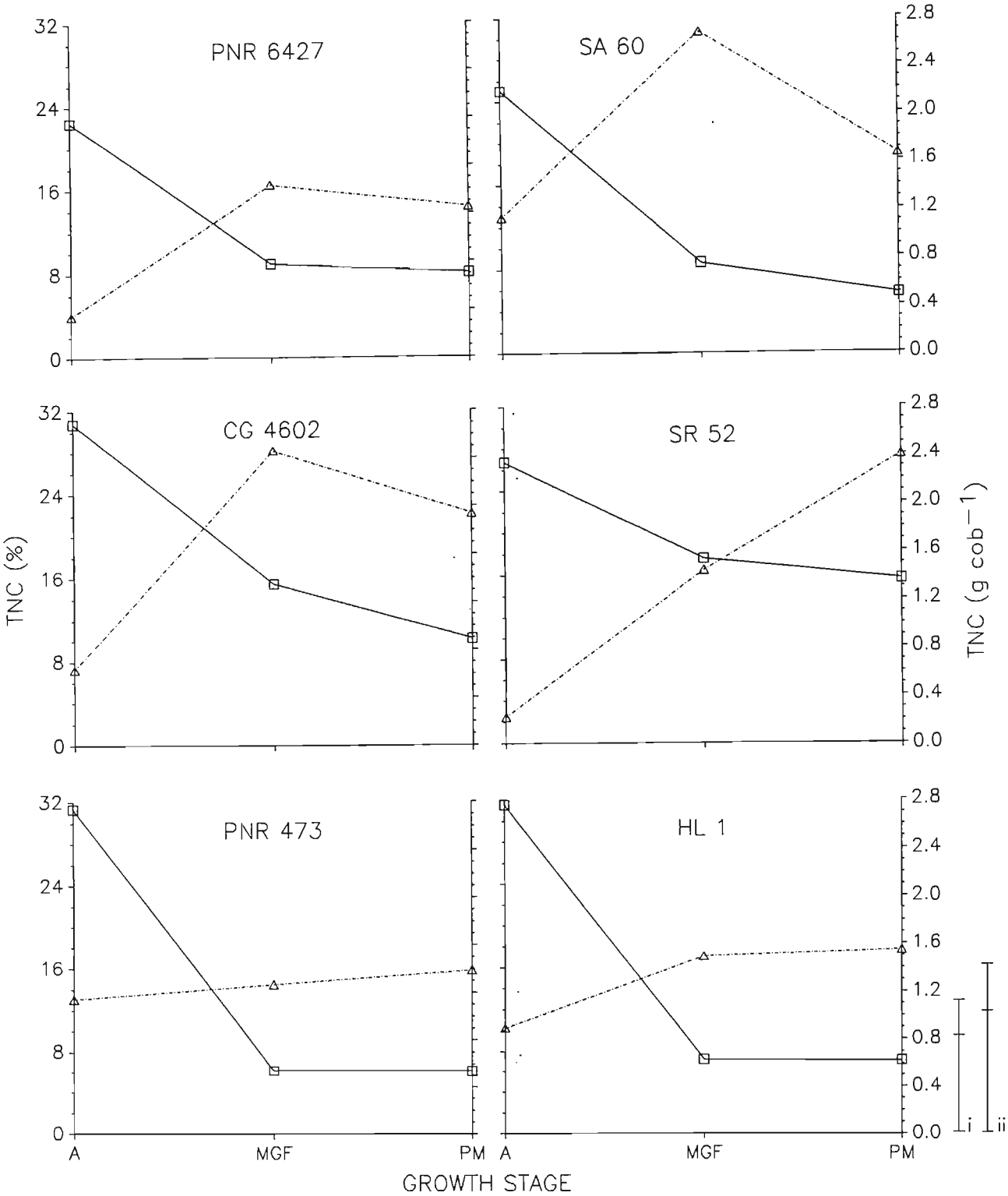


Figure 2.20 Fluctuation in total non-structural carbohydrate (TNC) composition (□——□) and content (△·····△) in cobs of the primary ears of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM).

Comparisons using LSD's of TNC content means at the same level of (i) hybrid; and (ii) growth stage or with neither factor in common

2.3.3.8 Total non-structural carbohydrate content, residual content and cob dry mass

Main effects for TNC content, residual content and cob dry mass

The main effect for hybrid was non-significant for TNC content (Appendix 20.8) and significant for residual content (Appendix 20.9) and cob dry mass (Appendix 20.10), while the main effect for growth stage was significant for all three variates. However, since the first order interactions of hybrid with growth stage were significant these main effects are of limited interest.

Interactions of hybrid with growth stage for TNC content, residual content and cob dry mass

The interactions of hybrid with growth stage for TNC and residual content and cob dry mass were significant (Figures 2.20 and 2.21). The hybrid x growth stage(linear) components of the TNC and residual content interactions and the hybrid x growth stage(quadratic) components of the residual content and cob dry mass interactions were also significant.

The ratio of TNC content to residual content was derived in order to more readily assess the amounts of TNC and residual components relative to one another (Table 2.56).

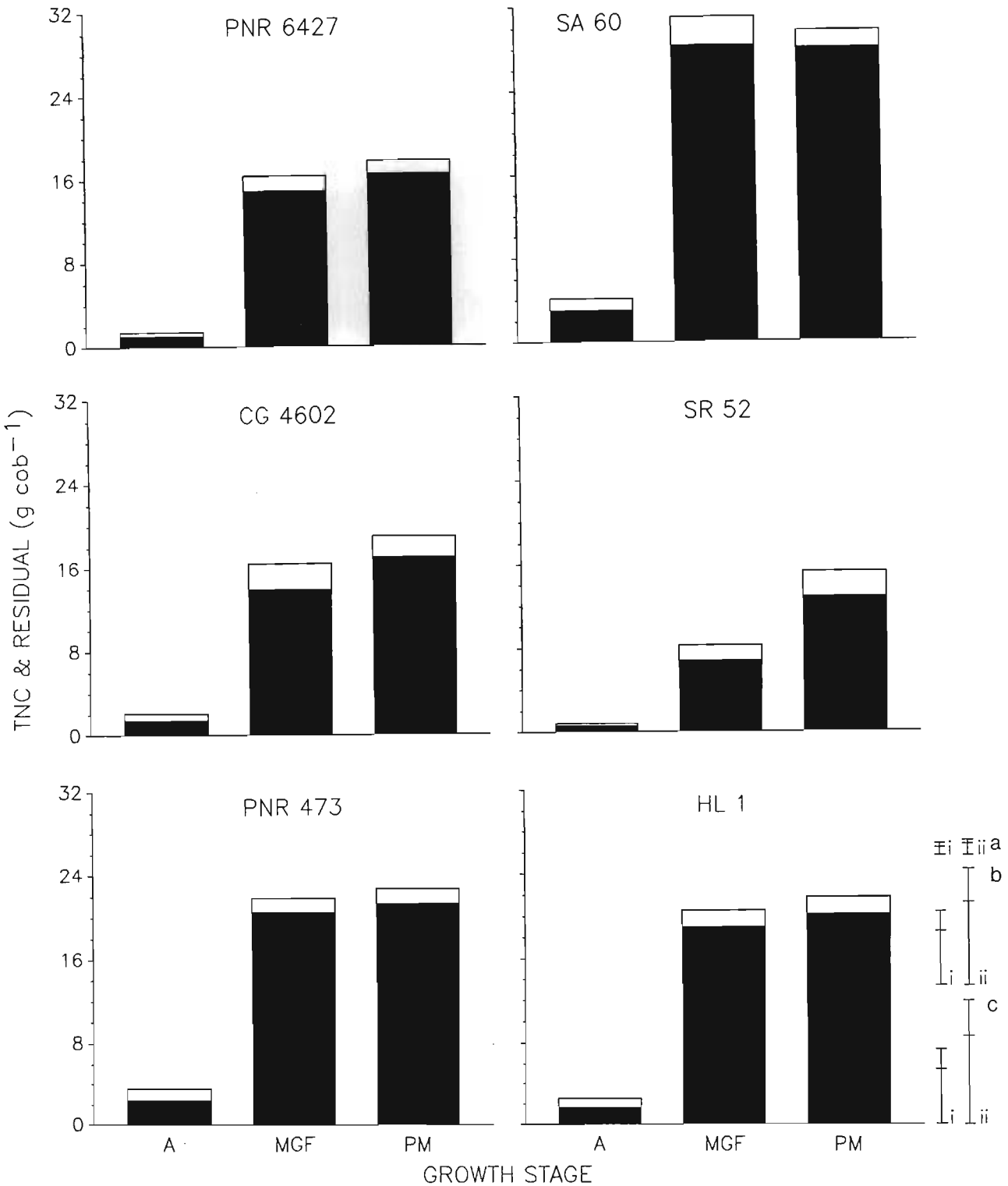


Figure 2.21 Fluctuation in total non-structural carbohydrate (TNC) (▭) and residual (▬) content, and dry mass (▭▬) of cobs of the primary ears of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM). Comparisons using LSD's of (a) TNC content means; (b) residual content means and (c) dry mass means at the same level of (i) hybrid; and (ii) growth stage or with neither factor in common

Table 2.56 Ratio of total non-structural carbohydrate (TNC) content to residual content for the primary cob of six maize hybrids sampled at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	A	MGF	PM
	TNC:Residual	TNC:Residual	TNC:Residual
PNR 6427	0,295	0,099	0,089
SA 60	0,339	0,094	0,060
CG 4602	0,447	0,184	0,114
SR 52	0,383	0,217	0,185
PNR 473	0,461	0,066	0,065
HL 1	0,482	0,079	0,077
TNC : Residual ratio SE ($\bar{x}$)		0,047	

All hybrids, except SA 60, increased in cob dry mass from A to PM. In SA 60 dry mass declined by 1,4 g cob^{-1} (NS) from MGF to PM. Dry mass increased from A to MGF by 15,0 ($p = 0,01$), 26,8 ($p = 0,01$), 14,3 ($p = 0,01$), 7,4 ($p = 0,01$), 18,2 ($p = 0,01$) and 18,0 g cob^{-1} ($p = 0,01$) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. Dry mass then further increased from MGF to PM by 1,3 (NS), 2,6 (NS), 7,0 ($p = 0,05$), 0,9 (NS) and 1,3 g cob^{-1} (NS) in PNR 6427, CG 4602, SR 52, PNR 473 and HL 1, respectively. Cob dry mass in SA 60 on the other hand, declined by 1,4 g cob^{-1} (NS) (Figure 2.21). Thus it is clear that there were major differences between hybrids in the changes in cob dry mass over the growth stages. In all hybrids the cob dry mass increased the most from A to MGF with SA 60 showing a particularly marked increase. In fact, SA 60 had significantly ($p = 0,05$) the highest cob dry mass at MGF than any of the other hybrids at MGF. Although the increase (decrease in SA 60) in cob dry mass from MGF to PM was less marked than from A to MGF for all hybrids, SR 52 dry mass almost increased by the same amount from MGF to PM, as from A to MGF. Although it is expected that

substantial increases in the size of the cob would occur from A to MGF none of the hybrids showed as marked an increase in cob dry mass as did SA 60 from A to MGF. It appears that SA 60 partitioned more than adequate amounts of photosynthate for the growth of the cob rather than the grain. SR 52 on the other hand did not, in comparison to the other hybrids, partition enough photosynthate for the growth of the cob.

As expected virtually all the dry mass gain in the cob was due to increases in the residual content of the cob (Figure 2.21). The patterns of residual content changes in the cob were thus much the same as discussed for dry mass changes. SA 60 showed a substantial increase in residual content of 25,3 g cob^{-1} ($p = 0,01$) from A to MGF.

Before grain fill commenced, TNC content levels were at their lowest in the cobs of all hybrids at A (Figures 2.20 and 2.21). From A to MGF TNC content increased by 1,09 ($p = 0,05$), 1,55 ($p = 0,01$), 1,83 ($p = 0,01$), 1,22 ($p = 0,01$), 0,12 (NS) and 0,59 g cob^{-1} (NS) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1. Thus CG 4602 showed the most substantial increase in TNC content from A to MGF, although SA 60 had the highest TNC content at MGF. The increase in TNC content from A to MGF in the cob of all hybrids probably reflects the translocation of photosynthate through the cob to the grain with excess photosynthate being temporarily stored in the cob. From MGF to PM TNC content declined by 0,19 (NS), 1,03 ($p = 0,05$) and 0,53 g cob^{-1} (NS) in PNR 6427, SA 60 and CG 4602 respectively, while in SR 52, PNR 473 and HL 1 it increased by 0,96 ($p = 0,05$), 0,12 (NS) and

0,06 g cob^{-1} (NS), respectively. In PNR 6427 and CG 4602 the decline in TNC content from MGF to PM was associated with an increase in residual content and an overall increase in cob dry mass. On the other hand, in SA 60 the decline in TNC content from MGF to PM was associated with a slight decline in residual content and an overall decline in cob dry mass. In SR 52, PNR 473 and HL 1 the increase in TNC content from A to MGF was associated with an increase in the residual content and an overall increase in cob dry mass. Whether or not the decline in TNC content of the cob in SA 60 from MGF to PM is indicative of a shortage of photosynthate, exacerbated by water stress, for grain requirements during the last phase of grain fill is not certain, since TNC content increased in the whole stem of SA 60 from MGF to PM.

The ratio of TNC content to residual content reflects these changes discussed above (Table 2.56).

2.3.4 Non-structural carbohydrate analysis of the grain

2.3.4.1 Reducing sugars composition

The main effect for hybrid was non-significant while the main effect for growth stage was significant (Appendix 21.1). However, since the first order interaction of hybrid with growth stage was significant these main effects are of limited interest.

The interaction of hybrid with growth stage was significant (Figure 2.22). The hybrid x growth stage(linear and quadratic)

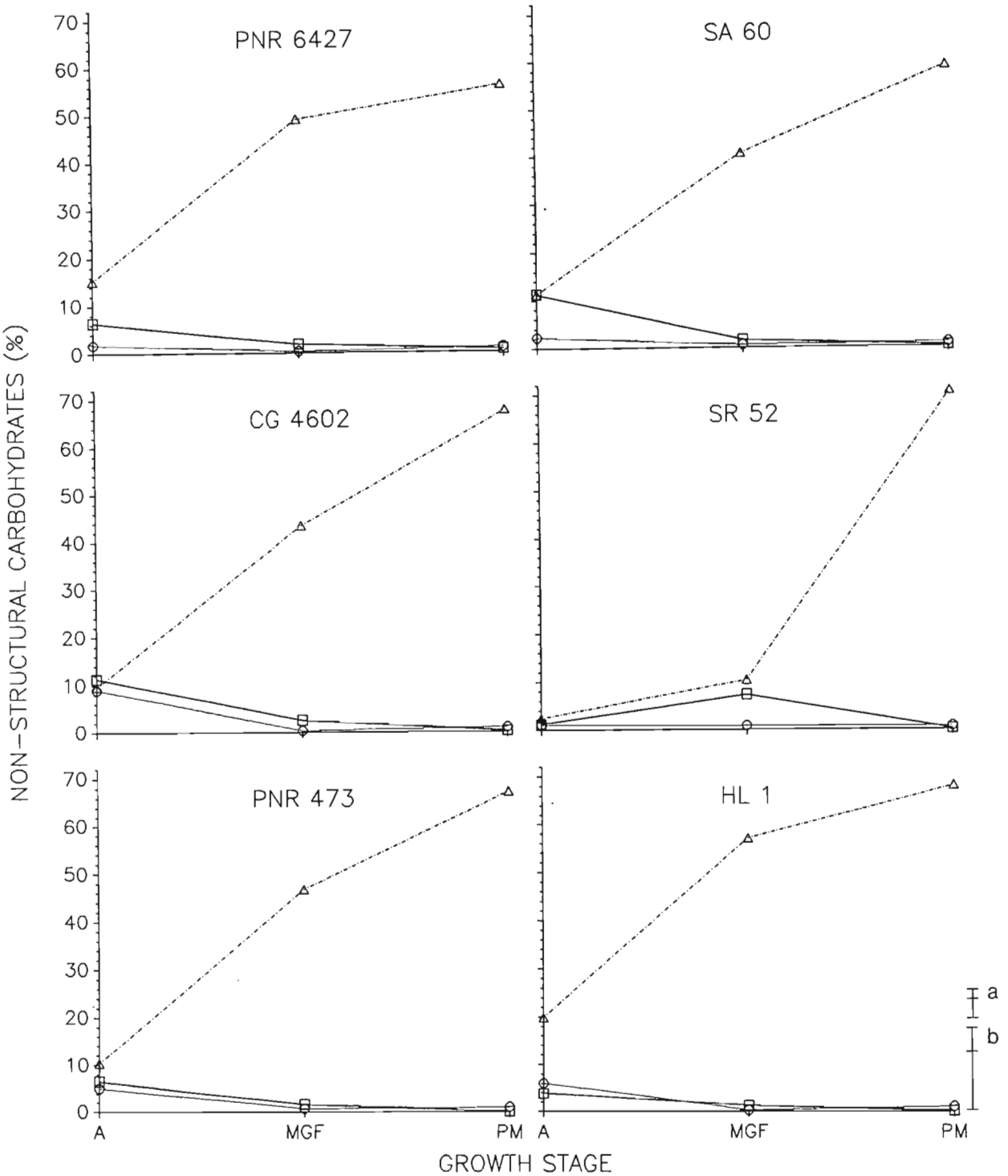


Figure 2.22 Fluctuation in reducing sugars (□—□), sucrose (○—○) and starch (△·····△) composition in grain of the primary ears of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM).

Comparisons using LSD's of (a) reducing sugars composition means and (b) starch composition means at the same levels of hybrid and growth stage

components of the interaction were also significant. Grain RS composition ranged from a high of 11,3 % in SA 60 and CG 4602 at A to a low of 0,1 % in SR 52 and HL 1 at PM. From A to MGF RS composition declined by 4,5 ($p = 0,05$), 9,7 ($p = 0,01$), 8,7 ($p = 0,01$), 5,0 ($p = 0,05$) and 2,7 % (NS) in PNR 6427, SA 60, CG 4602, PNR 473 and HL 1 respectively, while in SR 52 it increased by 6,1 %. From MGF to PM RS composition declined by 1,3 (NS), 1,3 (NS), 2,4 (NS), 7,2 ($p = 0,01$), 1,4 (NS) and 1,1 % (NS) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively (Figure 2.22). The fact that RS composition peaked in the grain of all hybrids at A, except SR 52, is probably due to the small size of the grain as endosperm cell division was presumably still being completed and starch deposition had not fully commenced. The decline in RS composition in the grain of all hybrids, except SR 52, from A to MGF was not accompanied by a decline in RS content and was therefore due to the dilution effect of the large increase in grain dry mass during this period. The slight decline in RS composition in the grain of all hybrids from MGF to PM was accompanied by a sharp decline in RS content and is therefore indicative of the depletion of RS in the grain during this period.

2.3.4.2 Reducing sugars content

The main effect for hybrid was non-significant (Table 2.57 and Appendix 21.2). However, CG 4602 followed by PNR 473 recorded the highest RS content while SR 52 recorded the lowest.

Table 2.57 Mean grain reducing sugars content (g grain^{-1}) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
0,46	0,62	0,86	0,30	0,68	0,51
LSD (0,05)	NS				
LSD (0,01)	NS				

The main effect for growth stage was significant (Table 2.58). There was a significant negative quadratic change in RS content from A to PM. This indicates that RS content initially increased from A to MGF and then declined from MGF to PM. The RS content at MGF was significantly ($p = 0,01$) higher than at A and PM, but RS content at PM was not significantly higher than at A.

Table 2.58 Mean grain reducing sugars content (g grain^{-1}) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage			
A		MGF	PM
0,15		1,34	0,22
LSD (0,05)	0,28		
LSD (0,01)	0,38		

The interaction of hybrid with growth stage was non-significant (Figure 2.23). There were no significant components of the interaction either. However, there were apparent differences between hybrids in RS content levels in the grain during grain

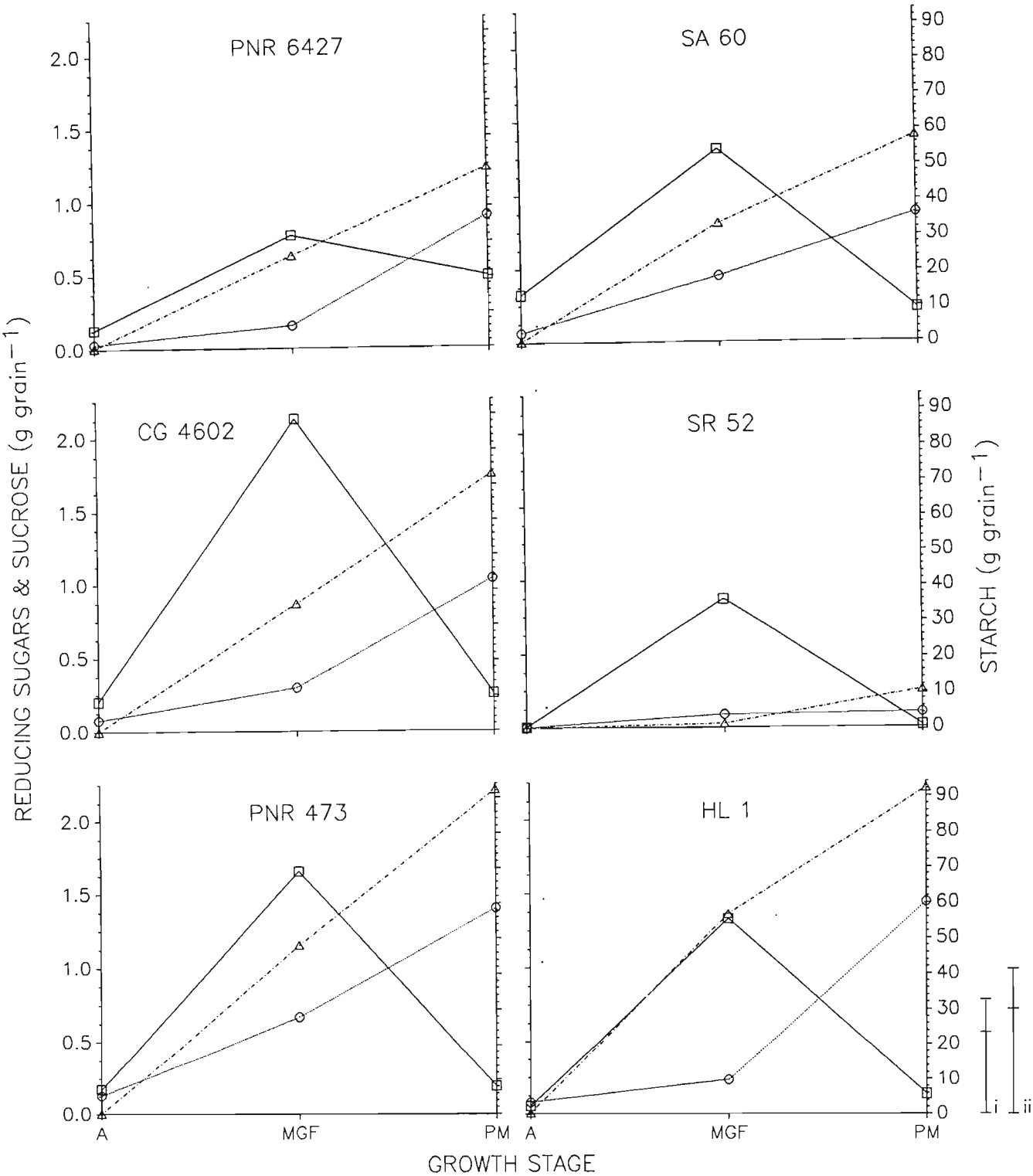


Figure 2.23 Fluctuation in reducing sugars (□—□), sucrose (○—○) and starch (△·····△) content in grain of the primary ears of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM).

Comparisons using LSD's of starch content means at the same level of (i) hybrid; and (ii) growth stage or with neither factor in common

fill. The RS content in the grain ranged from a low of 0,01 g grain^{-1} in SR 52 at PM to a high of 2,13 g grain^{-1} in CG 4602 at MGF. The RS content increased from A to MGF in the grain of all hybrids, the most marked increase occurred in CG 4602 followed by PNR 473, while the least marked increase occurred in SR 52 (Figure 2.23). The RS content then declined from MGF to PM, with levels at PM greater than those at A in all hybrids except SA 60. The most marked decline occurred in CG 4602 followed by PNR 473, with the smallest decline occurring in PNR 6427.

It is noteworthy that although RS composition generally declined from A to PM, RS content peaked in all hybrids at MGF. Obviously at MGF the size of the kernels has increased and although RS content has also increased, starch content now makes up a greater percentage of grain dry mass. The high RS content levels at MGF i.e. peak grain fill in all hybrids is possibly associated with a number of physiological phenomena, namely: (i) the inversion of sucrose to glucose and fructose prior to uptake from the apoplast by the basal endosperm transfer cells (Shannon, Porter and Knievel, 1986); (ii) 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); and (iii) utilization for various metabolic processes such as respiration and amino acid and lipid synthesis (Duffus and Duffus, 1984).

2.3.4.3 Sucrose composition

The main effect for hybrid was non-significant (Table 2.59 and Appendix 21.3). However, CG 4602 followed by HL 1 recorded the highest sucrose composition with SR 52 the lowest.

Table 2.59 Mean sucrose composition (%) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
1,1	1,3	3,4	0,8	2,3	2,5
LSD (0,05)	NS				
LSD (0,01)	NS				

The main effect for growth stage was significant (Table 2.60). There was a significant negative linear decline in sucrose composition from A to PM superimposed with a significant positive quadratic effect. This indicates that sucrose composition initially declined markedly from A to MGF and then increased from MGF to PM. Sucrose composition at A was significantly

Table 2.60 Mean sucrose composition (%) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage			
A		MGF	PM
4,2		0,5	0,9
LSD (0,05)	2,2		
LSD (0,01)	2,9		

(p = 0,01) higher at A than at MGF and PM, but sucrose composition at PM was not significantly higher than at MGF.

The interaction of hybrid with growth stage was non-significant (Figure 2.22). There were no significant components of the interaction either. However, there were apparent differences between hybrids in sucrose composition levels in the grain during grain fill. Sucrose composition in the grain ranged from a low of 0,3 % in HL 1 at MGF to a high of 9,0 % in CG 4602 at A. Sucrose composition declined from A to MGF in the grain of all hybrids, the most marked decline occurred in CG 4602 while the least marked decline occurred in PNR 6427 (Figure 2.22). Sucrose composition then increased in all hybrids except SR 52 from MGF to PM. The most marked increase occurred in HL 1. SR 52 declined marginally in sucrose composition from MGF to PM. As with RS composition, the fact that sucrose composition peaked in the grain of all hybrids at A is probably due to the small size of the kernels as endosperm cell division was presumably still being completed and starch deposition had not fully commenced.

2.3.4.4 Sucrose content

The main effect for hybrid was significant (Table 2.61 and Appendix 21.4). PNR 473 recorded the highest sucrose content followed by HL 1, however, the two hybrids were not significantly different from one another. PNR 473 was significantly (p = 0,05) higher in sucrose content than PNR 6427 and significantly (p = 0,01) higher in sucrose content than SR 52. PNR 473 was not significantly higher in sucrose content than SA 60 and CG 4602.

HL 1 had significantly ($p = 0,01$) higher sucrose content than SR 52, while SA 60 and CG 4602 had significantly ($p = 0,05$) higher sucrose content than SR 52. PNR 6427, SA 60, CG 4602 and HL 1 were not significantly different from one another in sucrose content. PNR 6427 and SR 52 were not significantly different from one another in sucrose content.

Table 2.61 Mean grain sucrose content (g grain^{-1}) of six maize hybrids during grain fill

Hybrid					
PNR 6427	SA 60	CG 4602	SR 52	PNR 473	HL 1
0,36	0,46	0,47	0,07	0,73	0,59
LSD (0,05)	0,34				
LSD (0,01)	0,48				

The main effect for growth stage was significant (Table 2.62). There was a significant positive linear increase in sucrose content from A to PM superimposed with a significant positive quadratic effect. This indicates that the initial increase in

Table 2.62 Mean grain sucrose content (g grain^{-1}) at three growth stages, anthesis (A), mid-grain fill (MGF) and physiological maturity (PM), from six maize hybrids

Growth stage			
A		MGF	PM
0,07		0,32	0,96
LSD (0,05)	0,20		
LSD (0,01)	0,27		

sucrose content from A to MGF was not as marked as that from MGF to PM. Sucrose content at PM was significantly ($p = 0,01$) higher than at A and MGF. Sucrose content at MGF was significantly ($p = 0,05$) higher than at A.

The interaction of hybrid with growth stage was just non-significant (Figure 2.23). However, the hybrid x growth stage(linear) component of the interaction was significant. This indicates that the fluctuations in grain sucrose content over the growth stages were different for each hybrid. Sucrose content in the grain ranged from 0,01 g grain^{-1} in SR 52 at A to a high of 1,44 g grain^{-1} in HL 1 at PM. Sucrose content increased from A to MGF in all hybrids, most markedly in PNR 473 and least markedly in SR 52 (Figure 2.23). The increase in sucrose content from MGF to PM was, however, more marked than the increase from A to MGF for all hybrids except SR 52. The most marked increase occurred in PNR 6427 and CG 4602 while SR 52 increased least markedly.

The ratio of sucrose content to RS content in the grain provides for an easier assessment of the relative proportions of the non-structural carbohydrate (Table 2.63). Also, by graphically expressing the component non-structural carbohydrate contents as a percentage of the total non-structural carbohydrate content, a summary of the changes in the relative proportions of the component carbohydrates is provided (Figure 2.24).

At A RS content exceeded sucrose content in PNR 6427, SA 60, SR 52 and PNR 473 while in CG 4602 and HL 1 the opposite is true

Table 2.63 Ratio of sucrose content to reducing sugars (RS) content and ratio of starch content to sucrose content for the grain of six maize hybrids sampled at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	A		MGF		PM	
	Sucrose : RS	Starch: sucrose	Sucrose : RS	Starch: sucrose	Sucrose : RS	Starch: sucrose
PNR 6427	0,32	58,1	0,20	148,5	2,16	61,0
SA 60	0,21	5,4	0,36	85,7	4,81	64,3
CG 4602	1,45	76,5	0,14	121,2	5,31	76,2
SR 52	0,85	2,6	0,12	25,8	6,90	102,2
PNR 473	0,80	4,1	0,47	80,6	8,43	67,9
HL 1	1,51	4,2	0,26	235,4	10,40	71,6
Sucrose : RS ratio			SE ($\bar{x}$)	1,07		
Starch : sucrose ratio			SE ($\bar{x}$)	28,5		

(Table 2.63, Figure 2.24). From A to MGF both RS and sucrose content increased in all hybrids. However, sucrose content increased by a smaller proportion than did RS content in PNR 6427, CG 4602, SR 52, PNR 473 and HL 1 as the ratio declined in these hybrids from A to MGF. In SA 60 sucrose content increased by a greater proportion than did RS content as the ratio increased from A to MGF. From MGF to PM sucrose content further increased while RS content declined and this is reflected in the increase in the ratio to greater than one in all hybrids. Sucrose content was markedly greater than RS content in HL 1 as shown by the ratio value of 10,40.

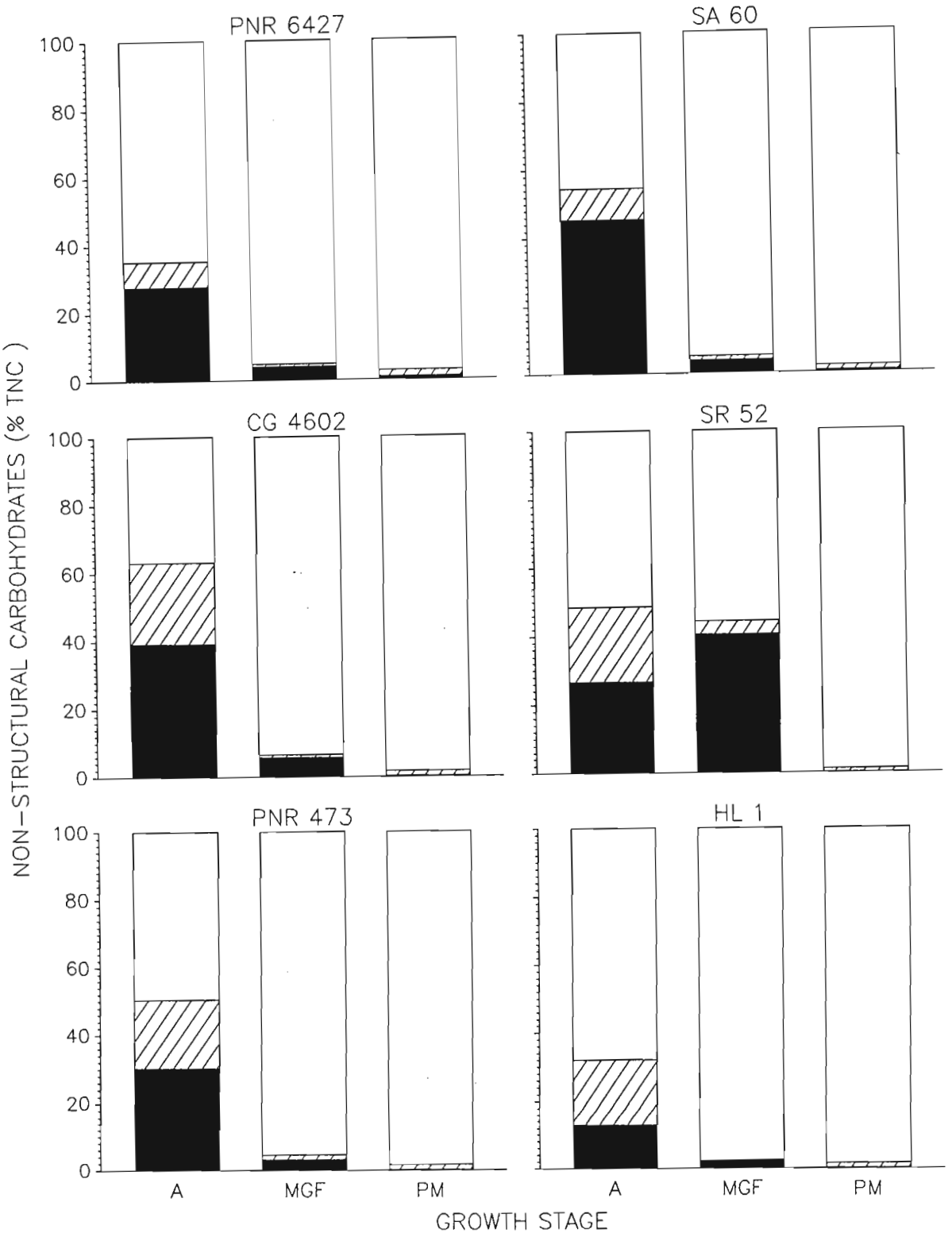


Figure 2.24 Fluctuation in component non-structural carbohydrate content expressed as a percentage of total non-structural carbohydrate (TNC) content in grain of the primary ears of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

It appears that sucrose content did not increase to a maximum at MGF as did RS content because it is continually converted to starch, lipids and amino acids, and after being broken down to glucose and fructose utilized for respiration in the grain (Shannon, 1968). According to Jenner (1970), during grain fill in wheat the pool of sucrose for starch synthesis in the grain never exceeds a day's requirements for synthesis. However, as the rate of grain fill slowed and then ceased at PM, sucrose content increased in the grain of all six hybrids while RS content declined. The decline in RS content is an indication of the decline in metabolic activity in the grain. It is, however, not easy to provide a physiologically based reason for why sucrose continued to be translocated to the grain as grain fill ceased. It is possible that an amount of sucrose is stored in the grain of the maize plant to provide for immediate respiration requirements before and during germination.

2.3.4.5 Starch composition

The main effects for hybrid and growth stage were significant (Appendix 21.5). However, since the first order interaction of hybrid with growth stage was significant these main effects are of limited interest.

The interaction of hybrid with growth stage was significant (Figure 2.22). The hybrid x growth stage(quadratic) component of the interaction was also significant. Starch composition in the grain ranged from a low of 2,4 % in SR 52 at A to a high of 70,5 % in SR 52 at PM. Starch composition increased from A to

MGF by 33,8 (p = 0,01), 29,3 (p = 0,01), 33,8 (p = 0,01), 7,9 (NS), 36,4 (p = 0,01) and 37,2 % (p = 0,01) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. What is notable here is that PNR 6427, CG 4602, PNR 473 and HL 1 showed remarkably similar increases in starch composition from A to MGF. Starch composition further increased from MGF to PM by 6,9 (NS), 18,1 (p = 0,01), 24,1 (p = 0,01), 60,2 (p = 0,01), 20,4 (p = 0,01) and 11,0 % (NS) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1 (Figure 2.22). Clearly the increase in starch composition from MGF to PM was most marked in SR 52 while PNR 6427 and HL 1 showed much smaller increases compared to the hybrids.

The increase in starch composition from A to MGF was 4,9 times more than that from MGF to PM in PNR 6427, 1,6 times more in SA 60, 1,4 times more in CG 4602, 1,8 times more in PNR 473 and 3,4 times more in HL 1. Although starch composition peaked at PM, the proportion of starch in the grain increased the most from A to MGF in these hybrids. On the other hand, in SR 52 the increase in starch composition from MGF to PM was 7,6 times more than that from A to MGF. Thus the proportion of starch in the grain increased more from MGF to PM in SR 52.

2.3.4.6 Starch content

The main effects for hybrid and growth stage were significant (Appendix 21.6). However, since the first order interaction of hybrid with growth stage was significant these main effects are of limited interest.

The interaction of hybrid with growth stage was significant (Figure 2.23). The hybrid x growth stage(linear) component of the interaction was also significant. Starch content ranged from a low of 0,0 g grain^{-1} in SR 52 at A to a high of 92,4 g grain^{-1} in both PNR 473 and HL 1 at PM. Starch content in the grain increased from A to MGF by 26,0 ($p = 0,05$), 33,3 ($p = 0,01$), 36,2 ($p = 0,01$), 1,0 (NS), 48,0 ($p = 0,01$) and 56,5 g grain^{-1} ($p = 0,01$) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. Starch content in the grain further increased from MGF to PM by 24,7 ($p = 0,05$), 24,4 ($p = 0,05$), 36,8 ($p = 0,01$), 9,6 (NS), 44,2 ($p = 0,01$) and 35,6 g grain^{-1} ($p = 0,01$), in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively (Figure 2.23). Thus the increase in starch content from A to MGF was most marked in PNR 473 and particularly HL 1, and least marked in SR 52. The increase in starch content from MGF to PM was most marked in CG 4602 and particularly PNR 473 and again less marked in SR 52.

The increase in starch content from A to MGF was 1,1 times more than that from MGF to PM in PNR 6427, 1,4 times more in SA 60, 1,1 times more in PNR 473 and 1,6 times more in HL 1. On the other hand, the increase in starch content from MGF to PM was 1,0 times more than that from A to MGF in CG 4602 and 9,6 times more in SR 52. By MGF PNR 6427 had attained 51,6 % of its final starch content, SA 60 had attained 57,9 %, CG 4602 had attained 49,7 %, SR 52 had attained 9,4 %, PNR 473 had attained 52,2 % and HL 1 had attained 61,5 %. These data clearly demonstrate the variation that existed among the hybrids in the rate of starch deposition in the grain under the influence of water stress

conditions that occurred during the latter half of grain fill. SR 52 accumulated the bulk of its grain starch content from MGF to PM while starch accumulation in the grain of HL 1 was proportionately less than that in the other hybrids in the latter half of grain fill. This may indicate a greater sensitivity of the grain filling process in HL 1 to the water stress conditions that prevailed from MGF to PM, on a relative basis, compared to the other hybrids, even though HL 1 recorded the highest final grain yield.

The ratio of starch content to sucrose content (Table 2.63, Figure 2.24) was greater than one for all hybrids at all growth stages indicating that starch content exceeded sucrose content in all hybrids at all growth stages. All hybrids except SR 52 recorded their highest starch to sucrose ratio at MGF and the ratio declined from MGF to PM. This reflects the greater proportional increase in sucrose content compared to starch content from MGF to PM.

2.3.4.7 Total non-structural carbohydrate composition

The main effects for hybrid and growth stage were significant (Appendix 21.7). However, since the first order interaction of hybrid with growth stage was significant these main effects are of limited interest.

The interaction of hybrid with growth stage was significant (Figure 2.25). The hybrid x growth stage(linear and quadratic) components of the interaction were also significant. Grain TNC

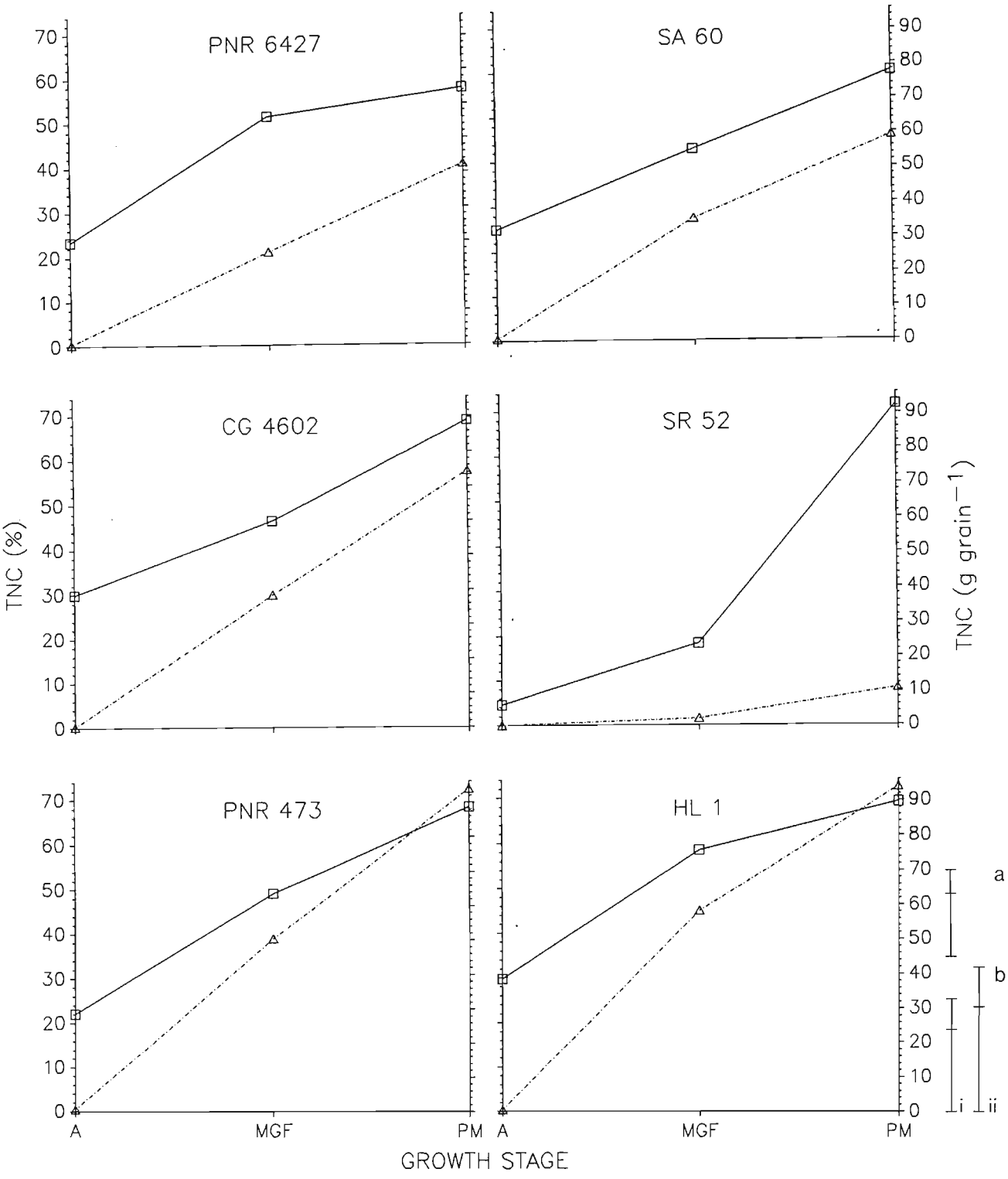


Figure 2.25 Fluctuation in total non-structural carbohydrate (TNC) composition (□——□) and content (△·····△) in grain of the primary ears of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM).
Comparisons using LSD's of (a) TNC composition means at the same levels of hybrid and growth stage and (b) TNC content means at the same level of (i) hybrid; and (ii) growth stage or with neither factor in common

composition ranged from a low of 4,6 % in SR 52 at A to a high of 71,3 % in SR 52 at PM. The TNC composition increased from A to MGF by 27,9 ($p = 0,01$), 17,7 ($p = 0,05$), 16,5 ($p = 0,05$), 13,7 (NS), 27,0 ($p = 0,01$) and 28,7 % ($p = 0,01$) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. The TNC composition further increased from MGF to PM by 6,3 (NS), 17,2 ($p = 0,05$), 22,3 ($p = 0,01$), 53,0 ($p = 0,01$), 19,2 ($p = 0,01$) and 10,6 % (NS) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively (Figure 2.25). Thus the increase in TNC composition from A to MGF was most marked in PNR 6427 and particularly in HL 1, and least marked in SR 52. From MGF to PM the increase in TNC composition was most marked in SR 52 and least marked in PNR 6427.

The increase in TNC composition from A to MGF was 4,5 times more than that from MGF to PM in PNR 6427, 1,0 times more in SA 60, 1,4 times more in PNR 473 and 2,7 times more in HL 1. On the other hand, the increase in TNC composition from MGF to PM was 1,4 times more than that from A to MGF in CG 4602 and 3,9 times more in SR 52. It appears that TNC only began to make up a greater proportion of the grain dry mass in the latter half of the grain filling period in CG 4602 and particularly in SR 52.

2.3.4.8 Total non-structural carbohydrate content, residual content and grain dry mass

Main effects for TNC content, residual content and grain dry mass

The main effects for hybrid and growth stage for TNC (Appendix 21.8) and residual content (Appendix 21.9) and grain dry mass (Appendix 21.10) were significant. However, since the first order interactions of hybrid with growth stage were significant these main effects are of limited interest.

Interactions of hybrid with growth stage for TNC content, residual content and grain dry mass

The interactions of hybrid with growth stage for TNC and residual content and grain dry mass were significant (Figures 2.25 and 2.26). The hybrid x growth stage(linear) components of the interactions for all three variates and the hybrid x growth stage(quadratic) components of the TNC and residual content interactions were also significant.

The ratio of TNC content to residual content was derived in order to more readily assess the amounts of TNC and residual components relative to one another (Table 2.64).

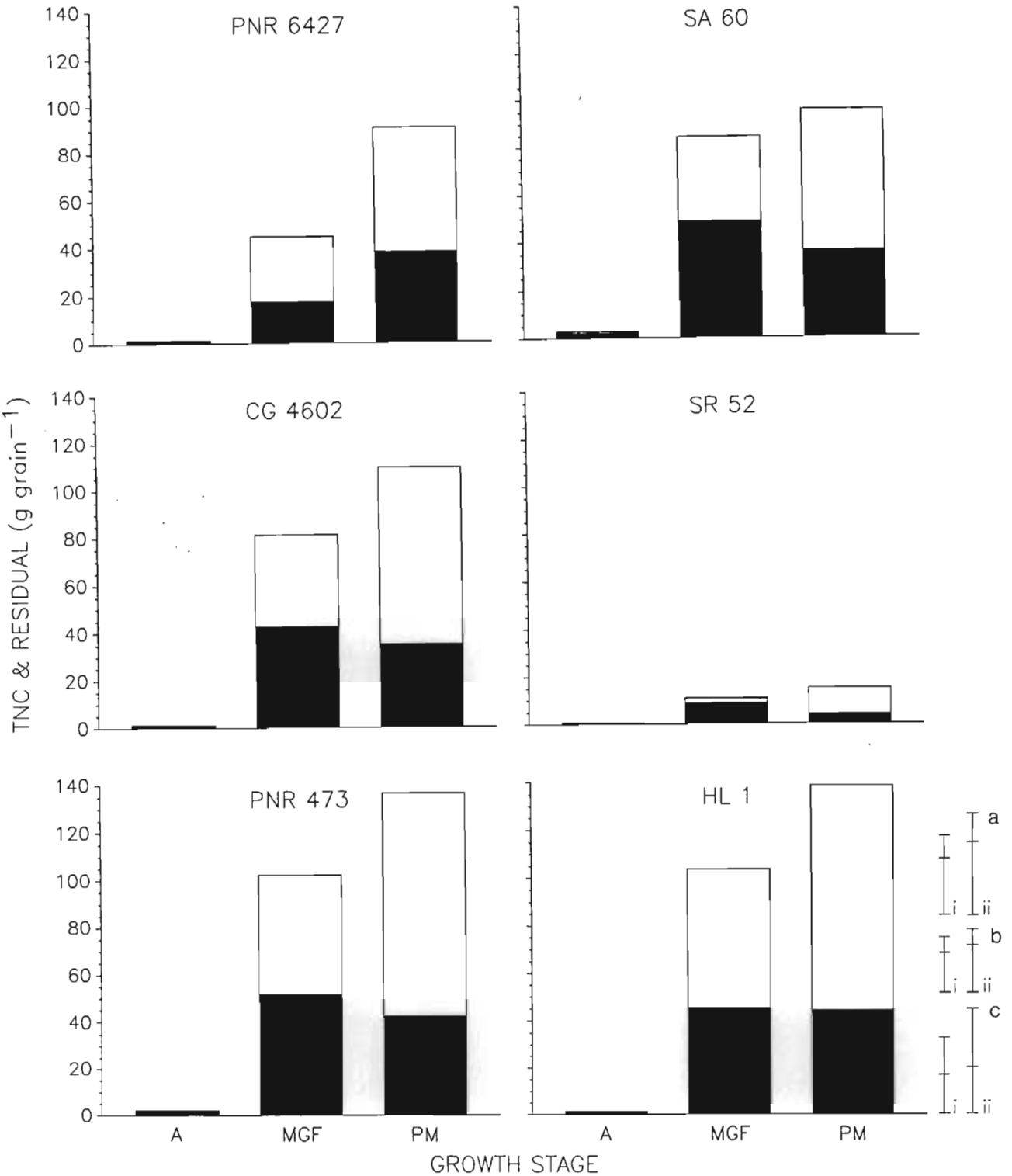


Figure 2.26 Fluctuation in total non-structural carbohydrate (TNC) (▭) and residual (▬) content, and dry mass (▭▬) of grain of the primary ears of six maize hybrids at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM). Comparisons using LSD's of (a) TNC content means; (b) residual content means and (c) dry mass means at the same level of (i) hybrid; and (ii) growth stage or with neither factor in common

Table 2.64 Ratio of total non-structural carbohydrate (TNC) content to residual content for the grain of six maize hybrids sampled at anthesis (A), mid-grain fill (MGF) and physiological maturity (PM)

Hybrid	A	MGF	PM
	TNC:Residual	TNC:Residual	TNC:Residual
PNR 6427	0,317	1,235	1,399
SA 60	0,333	0,775	1,667
CG 4602	0,453	0,912	2,377
SR 52	0,049	0,226	2,505
PNR 473	0,294	0,966	2,184
HL 1	0,433	1,546	2,311
TNC : Residual ratio SE ($\bar{x}$)		0,281	

All hybrids increased in grain dry mass from A to PM. From A to MGF grain dry mass increased by 42,9 ($p = 0,05$), 81,1 ($p = 0,01$), 80,0 ($p = 0,01$), 10,3 (NS), 100,1 ($p = 0,01$) and 102,3 g grain^{-1} ($p = 0,01$) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively (Figure 2.26). Grain dry mass further increased from MGF to PM by 45,7 ($p = 0,01$), 11,2 (NS), 28,3 (NS), 4,1 (NS), 34,1 ($p = 0,05$) and 34,5 g grain^{-1} ($p = 0,05$) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. Thus the increase in grain dry mass from A to MGF was most marked in PNR 473 and particularly HL 1 and least marked in SR 52. The increase in grain dry mass from MGF to PM was most marked in PNR 6427 followed by HL 1 and PNR 473, and least marked again in SR 52. By MGF PNR 6427 had attained 49,4 % of its final grain dry mass, SA 60 had attained 88,2 %, CG 4602 had attained 74,2 %, SR 52 had attained 72,7 %, PNR 473 had attained 75,0 % and HL 1 had attained 75,0 %. It may have been expected that each hybrid would have shown an approximate doubling of its grain dry mass from MGF to PM (Aldrich et al., 1975; Tollenaar, 1977), however, the water stress conditions that prevailed during the latter half

of grain fill apparently reduced the supply of photosynthate to the grain thus limiting the gain in grain dry mass during this period. Additionally water stress may have hastened the formation of grain black layer (Westgate and Boyer, 1985a). It appears that SA 60 was the most sensitive to water stress during the latter half of grain fill while PNR 6427 was the least sensitive in terms of the proportion of final grain dry mass accumulated from MGF to PM.

If the ratio of grain dry mass at PM to cob dry mass at PM is calculated, an indication is obtained of the relative amount of photosynthate partitioned to each organ for each of the hybrids. The ratio values thus obtained are 5,1, 3,2, 5,8, 1,0, 6,0 and 6,3 in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. Thus it appears that PNR 473 and HL 1 partitioned the most amount of photosynthate to the grain relative to that partitioned to the cob. SR 52 partitioned equal amounts to the grain and the cob while SA 60 partitioned the next lowest amount of photosynthate to the grain relative to the cob.

As expected most of the increase in grain dry mass from A to PM was due to increases in the TNC content of the grain. However, it is important to point out that at MGF (ignoring the data for SR 52) the residual fraction had made up as much as 47,3 % (SA 60) of the grain dry mass (Figure 2.26). Residual content increased from A to MGF by 16,1 (NS), 46,4 ($p = 0,01$), 41,8 ($p = 0,01$), 8,4 (NS), 50,1 ($p = 0,01$) and 44,4 g grain^{-1} ($p = 0,01$) in PNR 6427, SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. From MGF to PM residual content increased by

20,5 g grain^{-1} ($p = 0,01$) in PNR 6427 but declined non-significantly by 12,5, 7,5, 4,8, 9,4 and 1,2 g grain^{-1} in SA 60, CG 4602, SR 52, PNR 473 and HL 1, respectively. It would appear that the residual components have either been utilized in respiration or converted to TNC in the grain of those hybrids in which the residual content declined from MGF to PM.

Grain TNC content ranged from a low of 0,0 g grain^{-1} in SR 52 at A to a high of 94,0 g grain^{-1} in HL 1 at PM. The TNC content increased from A to PM in all hybrids (Figures 2.25 and 2.26). The increases of 49,9 ($p = 0,01$) and 58,0 g grain^{-1} ($p = 0,01$) in PNR 473 and HL 1 respectively, from A to MGF were most marked while the increase of 2,0 g grain^{-1} in SR 52 was the least marked. From MGF to PM the most marked increases of 43,4 ($p = 0,01$) and 35,6 g grain^{-1} ($p = 0,01$) occurred in PNR 473 and HL 1 respectively, while the least marked increase of 8,7 g grain^{-1} again occurred in SR 52. The ratio of TNC content to residual content reflects these changes discussed (Table 2.64).

The changes in TNC content from A to MGF and from MGF to PM are compared to the changes in grain dry mass from A to MGF and from MGF to PM in Table 2.65. It becomes apparent from Table 2.65 that the increase in TNC content from MGF to PM exceeded the increase in dry mass from MGF to PM by the same amount that residual content declined by in SA 60, CG 4602, SR 52, PNR 473 and HL 1. This provides support for the suggestion made earlier

that either the residual components declined through respiration or there was conversion to TNC components.

Table 2.65 Comparison of the changes (Δ) in primary grain total non-structural carbohydrate (TNC) content (g grain^{-1}) to changes in primary grain dry mass (g grain^{-1}) from anthesis (A) to mid-grain fill (MGF), and MGF to physiological maturity (PM)

Hybrid	From A to MGF		From MGF to PM	
	+Δ TNC	+Δ Dry mass	+Δ TNC	+Δ Dry mass
PNR 6427	26,7	42,9	25,2	45,7
SA 60	34,7	81,1	23,7	11,2
CG 4602	38,3	80,0	35,7	28,3
SR 52	2,0	10,3	8,7	4,1
PNR 473	49,9	100,1	43,4	34,1
HL 1	58,0	102,3	35,6	34,5

2.3.5 Leaf area index

The main effect for hybrid LAI was significant (Figure 2.27 and Appendix 22). At peak canopy (ca. two weeks after anthesis) HL 1 recorded the highest leaf area index of 3,78 which was significantly ($p = 0,01$) higher than that of SR 52 and significantly ($p = 0,05$) higher than that of PNR 6427, SA 60 and CG 4602. HL 1 and PNR 473 were, however, not significantly different in LAI. PNR 473 recorded the next highest leaf area index of 3,59 which was significantly ($p = 0,05$) higher than that of SR 52 but non-significantly higher than that of PNR 6427,

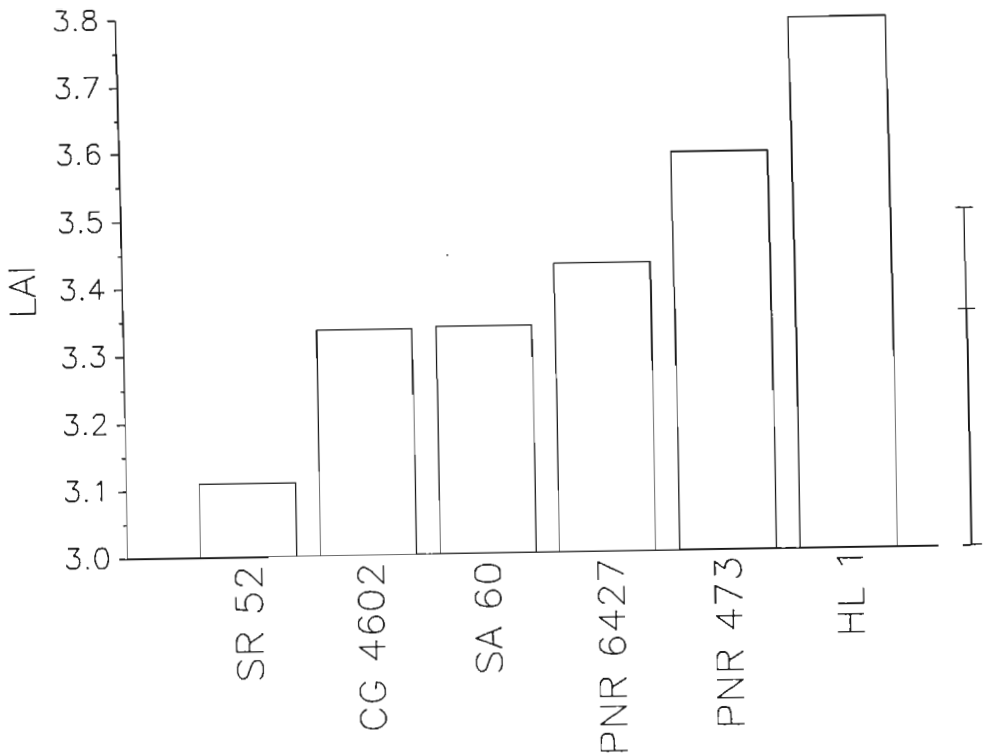


Figure 2.27 Leaf area index (LAI) at peak canopy (ca. two weeks after anthesis) of six maize hybrids

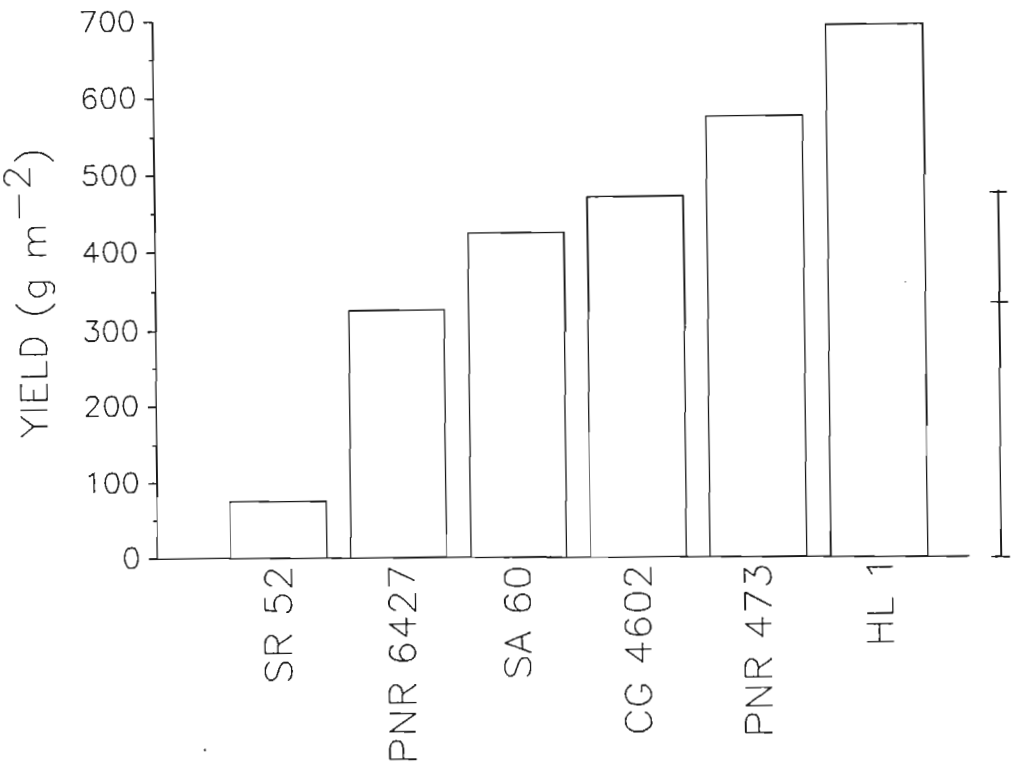


Figure 2.28 Grain yield at harvest maturity (primary plus secondary ears) for six maize hybrids

SA 60 and CG 4602. PNR 6427, SA 60, CG 4602 and SR 52 were non-significantly different to one another in LAI.

2.3.6 Yield and yield components

Grain yield

The main effect for hybrid final grain yield (primary plus secondary ear grain) was significant (Figure 2.28 and Appendix 23). The investment of HL 1 in larger leaf area returned the highest yield of 688 g m^{-2}. However, HL 1 only significantly ($p = 0,01$) out-yielded SR 52 and significantly ($p = 0,05$) out-yielded PNR 6427. PNR 473 recorded the next highest yield but only significantly ($p = 0,01$) out-yielded SR 52. SA 60 and CG 4602 also only significantly ($p = 0,05$) out-yielded SR 52 while PNR 6427 did not significantly out-yield SR 52.

It is noteworthy that the rank order of hybrids for LAI was not entirely the same as for final grain yield as, for example, PNR 6427 recorded the third highest LAI but the second lowest final grain yield. SR 52, on the other hand, recorded the lowest LAI and final grain yield.

It was pointed out earlier that SA 60 and SR 52 had low grain dry mass to cob dry mass ratios of 3,2 and 1,0, respectively. It is worth pointing out that SA 60 yielded the highest primary cob dry mass at harvest maturity of 147,0 g m^{-2} (Table 2.66). If this is added to the grain yield of 422 g m^{-2} it amounts to 569 g m^{-2} of

total ear dry mass which is still lower than the 688 g m^{-2} of grain dry mass yielded by HL 1.

Yield components and agronomic characteristics

The main effect for hybrid was significant for all the yield components (Table 2.66 and Appendix 24).

HL 1 recorded the highest and PNR 473 recorded the second highest primary ear yield components (Table 2.66). If the following calculation is performed - kernels row^{-1} x rows ear^{-1} x mass $kernel^{-1}$, PNR 473 records 134,8 g $plant^{-1}$ and HL 1 123,0 g $plant^{-1}$

Table 2.66 Yield components (primary ears only) and primary ear cob production at harvest maturity for six maize hybrids grown under semi-arid environmental conditions

Maize hybrid	Kernels[a] ear^{-1}	Kernels[a] row^{-1}	Rows[a] ear^{-1}	Mass[b] $kernel^{-1}$ (g)	Cob production[a] (g m^{-2})
PNR 6427	238	20,3	11,6	0,327	87,0
SA 60	325	25,1	12,8	0,366	147,0
CG 4602	340	27,6	12,3	0,455	129,0
SR 52	45	7,6	6,9	0,207	54,0
PNR 473	439	33,4	13,1	0,308	107,5
HL 1	447	35,4	12,5	0,278	96,0
LSD (0,05)	170	14,0	1,9	0,108	54,0
LSD (0,01)	242	19,9	2,7	0,154	76,8

a Average of five plants sub-sampled from plants harvested from two inner rows at harvest maturity

b Average of 50 kernels per five plants sub-sampled from plants harvested from two inner rows at harvest maturity

yield for the primary ear only. However, in HL 1 the primary ear contributed only 95,4 % of the final grain yield (Table 2.67 and Appendix 25) whereas in PNR 473 there was no contribution by secondary ears to final grain yield. Also, PNR 473 recorded a

Table 2.67 Agronomic characteristics at harvest maturity for six maize hybrids grown under semi-arid environmental conditions[a]

Maize hybrid	Stand %	% Barren plants	% Runt ears	% of final yield from 1° ear
PNR 6427	93,1	0,0	53,7	98,9
SA 60	92,2	4,8	59,1	100,0
CG 4602	91,2	4,8	32,8	100,0
SR 52	87,3	3,7	98,7	99,7
PNR 473	94,1	0,0	19,4	100,0
HL 1	95,1	0,0	17,1	95,4
LSD (0,05)	NS	NS	37,3	NS
LSD (0,01)	NS	NS	53,1	NS

a All data estimated from two inner rows harvested at harvest maturity

1,0 % lower stand percentage than HL 1 as well as a non-significantly higher runt percentage (Table 2.67 and Appendix 25). SR 52 recorded the lowest yield components and the highest runt percentage (Tables 2.66 and 2.67).

CHAPTER 3

1986/87 MAIZE SINGLE CROSS HYBRID RAIN-OUT SHELTER TRIAL

3.1 Introduction

In the 1985/86 maize inbred rain-out shelter trial (data in press) changes in the stem non-structural carbohydrates levels during grain fill as influenced by water stress were monitored in two inbred parent lines, M37W and M162W. However, in conducting experiments with inbred lines one deals with the whole syndrome of 'inbreeding depression'. Inbred plants tend to be small with a greatly reduced yield potential. Thus a strong sink capacity necessary to force the utilization of stem reserves is not available. The major objective of this study was of course to obtain an indication of the extent to which maize plants resort to utilising stem non-structural carbohydrates for continued grain fill under environmental conditions, specifically water deficits, that inhibit photosynthesis. On the other hand, in the 1985/86 maize hybrid rain grown trial (Chapter 2), three way and double cross hybrids were used which resulted in large plant to plant variability occurring. This then resulted in high C.V.'s being recorded for the data of each component non-structural carbohydrate, with possible significant interactions in analysis of variance tests consequently being masked by the high variance of the data. For these reasons it was decided to use single cross maize hybrids for a second rain-out shelter trial for the 1986/87 season. As these plants are hybrids they are robust with good yield potentials, but since they are

developed from single crosses they are genetically uniform providing ideal material for statistically designed trials. Also, uniform plant material is essential for studies of a physiological nature since metabolic pathways and compounds are dramatically influenced by small environmental changes.

In the 1985/86 maize hybrid rain grown trial entire plants were sampled and analyzed for non-structural carbohydrates. However, whole plant sampling generated a large amount of material and so considering manpower availability, time and cost factors, it was decided to cut down on the amount of plant material by sampling only the pair of internodes above and below the primary ear. These internodes reflect the accumulation and utilization patterns of non-structural carbohydrates in the entire stem, and their rôle in supplying carbohydrates to the developing grain has already been demonstrated in the 1985/86 maize hybrid rain grown trial. Importantly, by sampling only the pair of internodes above and below the primary ear the frequency of sampling could be increased thus providing a more comprehensive picture of the fluctuation in non-structural carbohydrate levels during the reproductive phase.

3.2 Methods and materials

A site description for the rain-out shelter at Ukulinga is provided in Appendix 2.

Field trial cultural and sampling procedures

Two maize single cross hybrids SA 6 and K78Y x I137TN, were planted under a rain-out shelter in a randomised blocks design at the University of Natal experimental farm, Ukulinga, on 8 November 1986 (Appendix 15). 'Hand-jabbers' were used to plant seed spaced 0,25 m apart in 0,8 m rows in plots at a uniform depth of 10 cm. Two seeds were planted per hill and later thinned to a single plant. The spacing provided five rows per plot and a final stand of 50 000 plants ha^{-1}. In accordance with soil analysis conducted by Cedara Fertilizer Advisory Service (Appendix 12), fertilizer was applied at the following rates: nitrogen applied as LAN (28) at 50 kg N ha^{-1} at planting, and a top dressing of 50 kg N ha^{-1} was applied when the plants were ca. 0,5 m in height. Phosphorus was applied as single superphosphate (10,5) at 40 kg P ha^{-1} before planting; and potassium was applied as KCl (50) at 60 kg K ha-1 before planting. Seed was dusted with molybdenum before planting. Insect and weed control was conducted as described for the 1985/86 maize hybrid rain grown trial. The trial was drip irrigated until one week after anthesis whereupon the respective treatments were subjected to water deficient conditions (stress) by complete withdrawal of drip irrigation or provided with adequate water (non-stress) by continued drip irrigation.

Whole plants from the replicated plots were sampled eight times at weekly intervals from one week after anthesis (1 WAA) to PM (8 WAA). Sampling procedure was identical to the 1985/86 maize hybrid rain grown trial except that only the first pair of

internodes immediately above (A1) and below (B1) the primary ear were taken for carbohydrate analysis (Figure 2.1). All other segments were discarded. Samples were oven dried, weighed, milled and stored as for the 1985/86 maize hybrid rain grown trial.

Leaf area

In the 1985/86 maize hybrid rain grown trial, leaf area was determined for plants from one of the two inner rows. A portable hand-held leaf area machine was used to determine leaf area at peak canopy (approximately two weeks after anthesis). Due to the difficulty experienced in obtaining consistent leaf area readings using the leaf area machine in the field, it was decided to adopt another method for determining leaf area in this trial. A bell punch was used to randomly cut discs of known area (4 cm^2) from stacks of leaf laminae stripped from plants sampled for carbohydrate analysis on a weekly basis. By determining the total area and total dry mass of leaf discs and the total dry mass of the leaves plus leaf discs the leaf area per plant could be calculated by simple proportions. Data was expressed as LAI.

Leaf water potential readings

Pre-dawn leaf Ψw readings were taken from the two plants per plot sampled for carbohydrate analysis using a Scholander pressure chamber (PMS Instrument Co., Corvallis). A single layer of moist tissue paper was placed on each surface of the third leaf from the top to be sampled for leaf Ψw readings. A rectangular

section of leaf approximately 20 x 70 mm was stripped from the mid-section of the leaf with one side of the leaf section being the leaf margin. Humidification of the chamber was ensured by placing a pad of tissue kept constantly moist in the chamber. Gaseous nitrogen was used to pressurise the chamber at a rate of 100 kPa.s^{-1}. Data was expressed in kPa.

Yield analysis

Yield and yield components as for the 1985/86 maize hybrid rain grown trial were determined per nett plot consisting of the four inner rows. All values were corrected to 12,5 % moisture content and expressed in grain mass (g) per square metre (m^2) ground area. Neither hybrid produced secondary ears.

Laboratory analytical procedures

The Modified Weinmann method (Weinmann, 1947) described by Smith (1981) was used to analyze samples for non-structural carbohydrates (Section 2.2.2).

Statistical analysis and presentation of data

The design of the experiment was set out as a 2^2 factorial in the field with two single cross hybrids subjected to water deficits (stress) and adequate water supply (non-stress) from 1 WAA to PM. In order to compare carbohydrate levels for internodal position for each sampling date the trial was analyzed as a factorial split for WAA, and split further for the two stem segments. Thus

the single cross hybrids and stress treatment factors were the whole-plot factor, WAA the sub-plot factor and stem segment the subsub-plot factor.

All biometrical analysis was conducted using the GENSTAT Version 4.04 statistical computer package. As mentioned in the methods and materials in Chapter 2, the split plot in time will usually estimate growth curves imprecisely, and the F-test for the treatment x sampling occasion will likely produce too many significant results (Greenhouse and Geisser, 1959; Gill, 1978). 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 WAA (sampling occasions). Additionally since the EMS for the stem segments (subsub-plot factor; this subdivision is not relevant to the leaf Ψw and LAI data) is calculated over sampling occasions the stem segments were treated as two 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 stem segments. However, since there were only two stem segments the epsilon factor for the stem segment EMS was one and the results of the original F-tests remain unchanged. In the analysis of variance of the RS content data and the leaf Ψw data, the EMS for WAA was larger than the EMS for water stress treatment. In this situation a weighted pooling of the two EMS's was conducted, i.e. the RS content data was analyzed as a split plot factorial design with hybrid x water stress treatment x WAA (eight sampling occasions) as the whole-plot factor and stem segments now as the sub-plot

factor; for the leaf Ψw data the split for stem segment is obviously not relevant. The epsilon factor was then multiplied by the degrees of freedom (DF1 and DF2 (pooled EMS)) of those F-tests that would have involved the EMS for WAA before pooling was done.

In the analysis of variance the sum of squares for WAA was partitioned into linear, quadratic and cubic regression effects and deviations from regression providing a description of the changes in non-structural carbohydrate levels, leaf Ψw and LAI as a function of WAA. 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. The highest order interaction for each component non-structural carbohydrate data, and for the leaf Ψw and LAI data was non-significant. However, the data of the highest order interactions are graphically presented and physiological trends shown by the data are discussed. Since none of the highest order interactions for each component non-structural carbohydrate data and for the leaf Ψw and LAI data was significant, LSD's are not presented on the graphs.

Polynomial regression equations were fitted to the component non-structural carbohydrate data and to the leaf Ψw and LAI data. Fourth and fifth order polynomial equations were necessary to adequately describe these variates. The polynomial equations were only derived for curve smoothing purposes and since the

y-intercept values generated by the equations predicting the variate value at 0 WAA (anthesis) were often unrealistic, the equations must not be use to predict variate values outside of the range 1 WAA to 8 WAA.

3.3 Results and discussion

3.3.1 Leaf water potential

Main effects

The main effect for hybrid was non-significant (Table 3.1 and Appendix 26). K78Y x I137TN recorded a marginally lower mean leaf Ψw than SA 6.

Table 3.1 Leaf water potential (kPa) of two maize hybrids meaned over water stress treatments during grain fill

Hybrid	
SA 6	K78Y x I137TN
-690	-744
LSD (0,05) NS	
LSD (0,01) NS	

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

First order interactions

The interactions of hybrid with stress treatment and hybrid with WAA were non-significant. There were no significant components of the latter interaction either.

The interaction of stress treatment with WAA was significant (Table 3.2). The stress treatment x WAA(linear, quadratic and cubic) components of the interaction were also significant. As is expected leaf Ψw declined more markedly under stress conditions from 1 WAA to PM. In particular leaf Ψw under stress conditions declined at a more rapid rate from 6 WAA to PM.

Table 3.2 Effect of water stress (S) and lack of water stress (NS) on mean maize hybrid leaf water potential (kPa) from one week after anthesis to physiological maturity

Stress treatment	Weeks after anthesis								Stress treatment means
	1	2	3	4	5	6	7	8	
S	-367	-696	-740	-889	-802	-858	-1195	-1857	-925
NS	-372	-566	-580	-422	-561	-524	-399	-640	-508
WAA means	-370	-631	-660	-655	-682	-691	-797	-1248	

Body of table

	LSD 0,05	LSD 0,01
Comparison of means	-282	-374
Marginal means		
Comparison of stress treatment means	-100	-132
Comparison of WAA means	-200	-264

Leaf Ψw was non-significantly lower under stress conditions than under non-stress conditions at 2, 3 and 5 WAA. Leaf Ψw was significantly ($p = 0,05$) lower under stress conditions than under non-stress conditions at 6 WAA. Leaf Ψw was significantly ($p = 0,01$) lower under stress conditions than under non-stress conditions at 4 and 7 WAA and at PM.

Second order interaction

The interaction of hybrid, stress treatment and WAA was non-significant (Figure 3.1). There were no significant components of the interaction either. However, apparent trends in the changes in leaf Ψw of each hybrid under stress and non-stress conditions are discussed.

Under non-stress conditions leaf Ψw fluctuated mildly during grain fill in both hybrids. SA 6 did tend to maintain higher leaf Ψw from 2 to 4 WAA in comparison to K78Y x I137TN. At 7 WAA leaf Ψw in K78Y x I137TN increased unexpectedly. At PM K78Y x I137TN had marginally higher leaf Ψw than did SA 6.

Under stress conditions leaf Ψw in SA 6 initially declined from 1 to 4 WAA and then fluctuated mildly until 7 WAA and then declined dramatically at PM reaching -1 780 kPa. Under stress conditions leaf Ψw in K78Y x I137TN showed an initial decline from 1 to 4 WAA followed by a marginal increase at 5 WAA and then a marked decline from 5 WAA to PM with leaf Ψw at PM reaching -1 934 kPa. It would therefore appear that K78Y x I137TN showed greater sensitivity to water deficits from 6 WAA to PM in

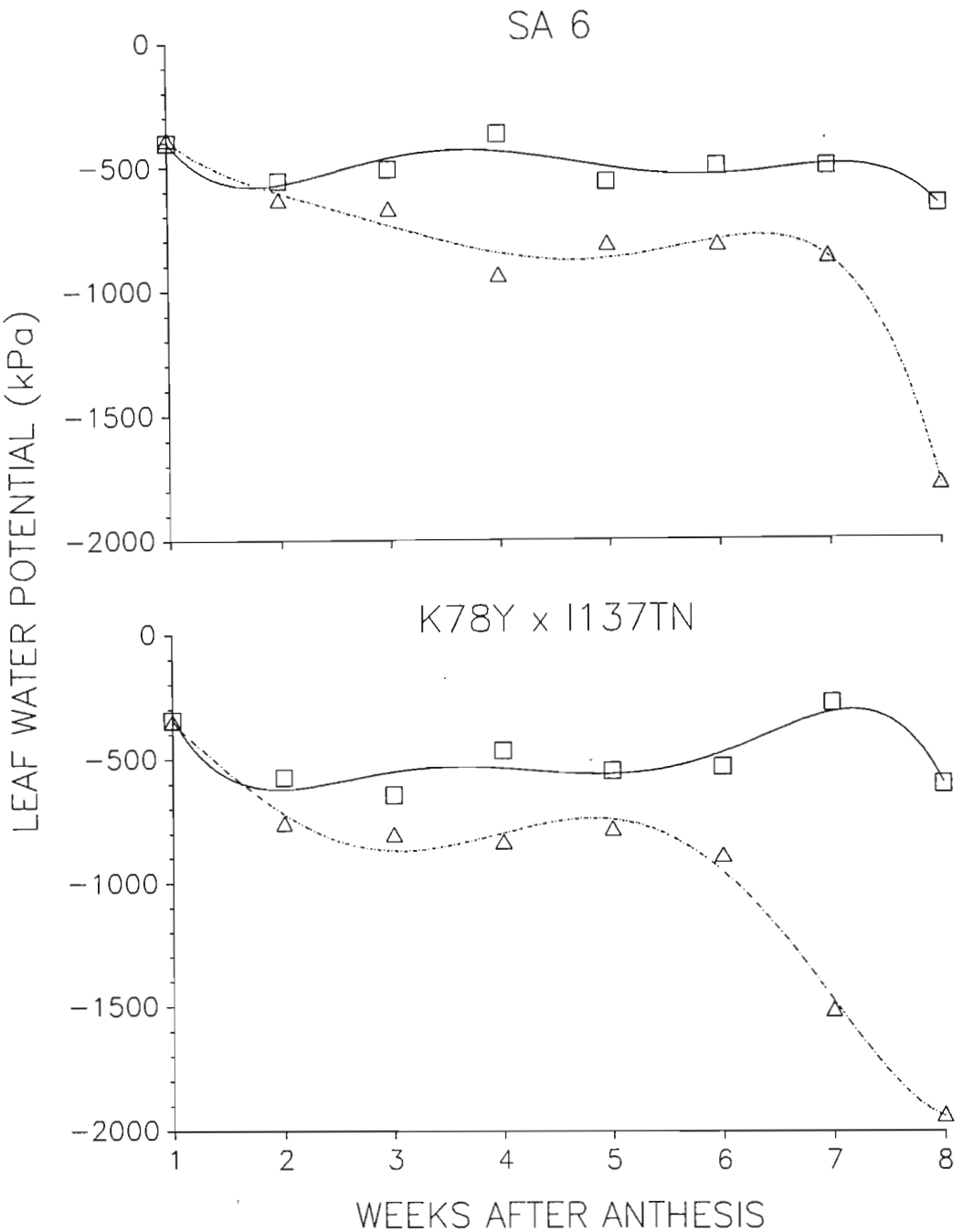


Figure 3.1 Effect of water stress (△——△) and lack of water stress (□——□) from one week after anthesis to physiological maturity on leaf water potential of two maize hybrids

Polynomial equations:

SA 6

Stress $284,3 - 1149,2x + 645,2x^2 - 198,6x^3 + 29,2x^4 - 1,6x^5$ $r^2=0,986$

Non-stress $998,8 - 2507,1x + 1435,1x^2 - 364,6x^3 + 42,4x^4 - 1,8x^5$ $r^2=0,805$

K78Y x I137TN

Stress $-205,3 + 258,6x - 620,1x^2 + 246,1x^3 - 36,3x^4 + 1,8x^5$ $r^2=0,992$

Non-stress $1456,0 - 3172,3x + 1791,6x^2 - 464,6x^3 + 56,1x^4 - 2,5x^5$ $r^2=0,817$

comparison to SA 6. SA 6 only showed a dramatic decline in leaf Ψw in the last week of grain fill.

Photosynthesis is often reported as being completely inhibited in maize leaves as leaf Ψw reaches -1 600 to -1 800 kPa (Westgate and Boyer, 1985a). It remains, however, to be shown whether or not a large range exists in the leaf Ψw readings at which complete inhibition of photosynthesis occurs depending on maize genotype. For instance Ackerson (1983) compared the photosynthetic rates of two hybrids as a function of leaf Ψw at the vegetative stage, tassel emergence and mid-grain fill and found that the one hybrid maintained higher photosynthetic rates than the other at leaf Ψw higher than -1 200 kPa. At leaf Ψw lower than -1 200 kPa photosynthetic rates of the two hybrids were similar. It is therefore quite possible for photosynthesis to be inhibited at varying leaf Ψw depending on genotype. In addition, the confounding influence of temperature will affect the relationship between leaf Ψw and photosynthetic activity. Unfortunately in this trial instrumentation to measure photosynthetic activity was not available. Thus it is not certain at what leaf Ψw photosynthesis was inhibited in each hybrid, if at all, for the range of leaf Ψw recorded.

3.3.2 Leaf area index

Main effects

The main effects for hybrid, stress treatment and WAA were significant (Appendix 27). However, since these factors were

involved in significant higher order interactions their main effects are of limited interest.

First order interactions

The interaction of hybrid with stress treatment was non-significant.

The interaction of hybrid with WAA was significant (Table 3.3). The hybrid x WAA(linear, quadratic and cubic) components of the interaction were also significant. In SA 6 LAI declined steadily from 2 WAA to PM. In K78Y x I137TN LAI declined less rapidly

Table 3.3 Influence of maize hybrid on leaf area index from one week after anthesis (WAA) to physiological maturity meaned over water stress treatments

Hybrid	Weeks after anthesis								Hybrid means
	1	2	3	4	5	6	7	8	
SA 6	2,12	2,08	1,92	1,73	1,47	1,01	0,75	0,44	1,44
K78Y x I137TN	2,14	2,13	2,07	1,95	1,84	1,62	1,08	0,62	1,68
WAA means	2,13	2,10	1,99	1,84	1,65	1,32	0,91	0,53	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,16	0,21
Comparison of means at the same level of WAA or with neither factor in common	0,16	0,22
Marginal means		
Comparison of hybrid means	0,07	0,09
Comparison of WAA means	0,11	0,15

from 2 to 5 WAA and then declined rapidly from 5 WAA to PM. The LAI of K78Y x I137TN was non-significantly higher than that of SA 6 from 1 to 4 WAA, significantly ($p = 0,01$) higher from 5 to 7 WAA and significantly ($p = 0,05$) higher at PM. The LAI for both hybrids at PM was significantly ($p = 0,01$) less than at 1 WAA, with the difference being the greatest in SA 6.

The interaction of stress treatment with WAA was significant (Table 3.4). The stress treatment x WAA(linear, cubic and deviations) components of the interaction were also significant. Under stress conditions LAI declined significantly ($p = 0,01$) from 1 to 2 WAA, whereas under non-stress conditions it increased

Table 3.4 Effect of water stress (S) and lack of water stress (NS) on mean hybrid leaf area index from one week after anthesis (WAA) to physiological maturity

Stress treatment	Weeks after anthesis								Stress treatment means
	1	2	3	4	5	6	7	8	
S	2,13	1,82	1,83	1,68	1,43	1,18	0,67	0,29	1,38
NS	2,13	2,39	2,16	1,99	1,88	1,46	1,16	0,77	1,74
WAA means	2,13	2,10	1,99	1,84	1,65	1,32	0,91	0,53	

Body of table

	LSD 0,05	LSD 0,01
Comparison of means at the same level of stress treatment	0,16	0,21
Comparison of means at the same level of WAA or with neither factor in common	0,16	0,22
Marginal means		
Comparison of stress treatment means	0,07	0,09
Comparison of WAA means	0,11	0,15

significantly (p = 0,01) during the same period. From 2 to 5 WAA LAI under stress conditions generally declined at the same rate as under non-stress conditions. From 5 to 6 WAA the rate of decline in LAI was more rapid in non-stressed plants than stressed plants. From 6 WAA to PM LAI declined more markedly in stressed than non-stressed plants. The LAI was significantly (p = 0,01) higher under non-stress conditions than stress conditions from 2 WAA to PM.

Second order interaction

The interaction of hybrid, stress treatment and WAA was non-significant (Figure 3.2). There were no significant components of the interaction either. However, there were apparent differences between hybrids in the changes in LAI during grain fill under stress and non-stress conditions.

At 1 WAA SA 6 and K78Y x I137TN stressed and non-stressed plants had similar LAI values. Induction of water stress commenced at 1 WAA and the most apparent decline in LAI in response to water deficits occurred immediately in both hybrids from 1 to 2 WAA. From 2 WAA to PM LAI of SA 6 declined steadily and at a similar rate under stress and non-stress conditions. In K78Y x I137TN LAI declined marginally from 2 WAA to 5 WAA, but the rate of decline was similar under stress and non-stress conditions. However, from 5 WAA to PM LAI declined more rapidly in K78Y x I137TN than in SA 6 during the same period, with the rate of decline similar under stess and non-stress conditions. At PM SA 6 had a smaller LAI under stress and non-stress conditions

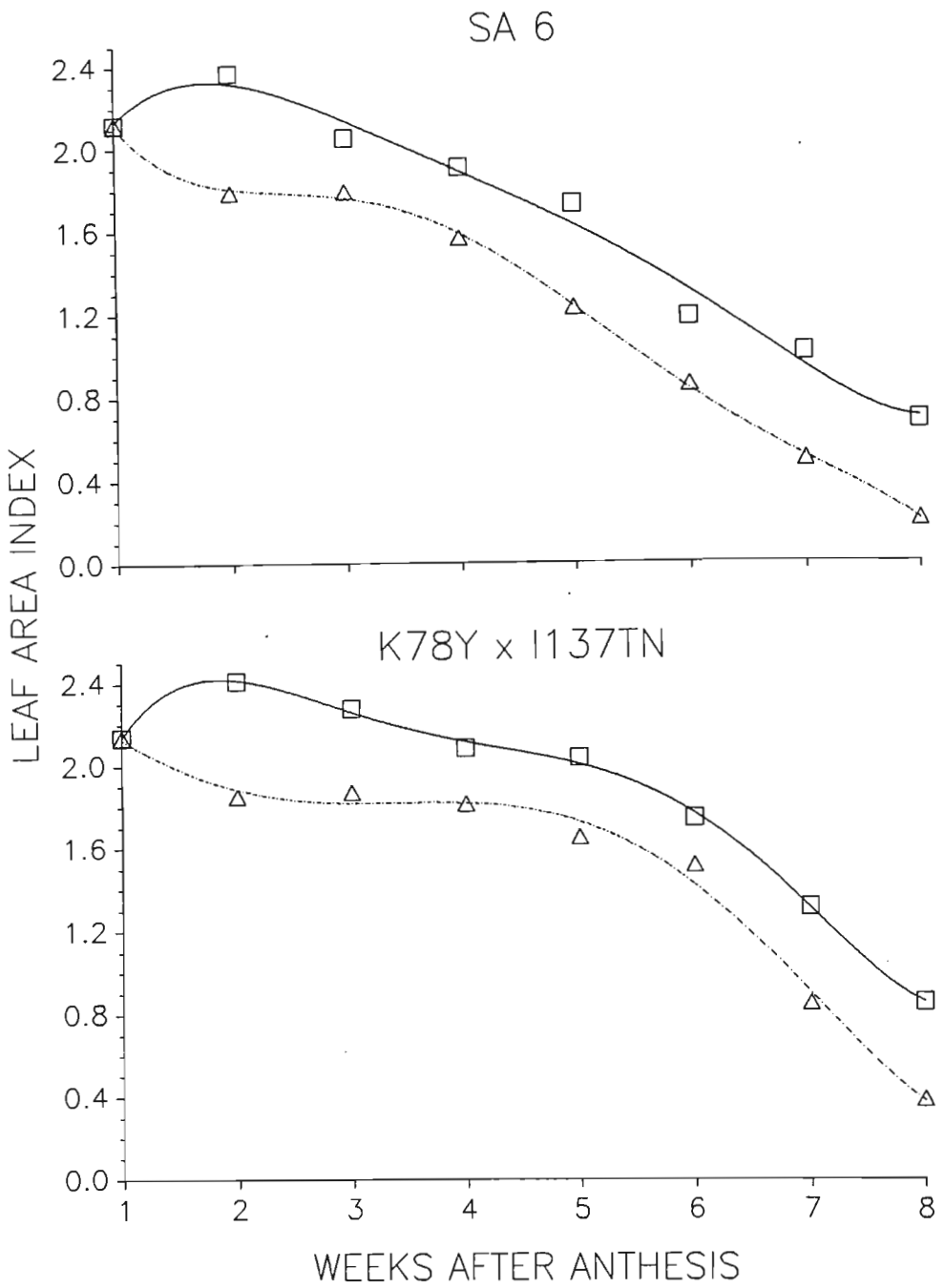


Figure 3.2 Effect of water stress (△----△) and lack of water stress (□——□) from one week after anthesis to physiological maturity on leaf area index of two maize hybrids

Polynomial equations:

SA 6

Stress 3,623 -2,571x +1,366x^2 -0,335x^3 +0,036x^4 -0,001x^5 r^2=0,999

Non-stress 0,887 +2,126x -1,110x^2 +0,253x^3 -0,028x^4 +0,001x^5 r^2=0,984

K78Y x I137TN

Stress 2,533 -0,428x -0,025x^2 +0,061x^3 -0,013x^4 +0,001x^5 r^2=0,991

Non-stress 0,291 +3,230x -1,769x^2 +0,433x^3 -0,049x^4 +0,002x^5 r^2=0,999

namely 0,20 and 0,68 in comparison to 0,39 and 0,85 for K78Y x I137TN respectively treated plants. In relative terms, this means that the LAI of stressed SA 6 plants was 29,41 % of that of non-stressed plants while the LAI of stressed K78Y x I137TN plants was 45,88 % of that of non-stressed plants at PM. Thus the possible advantage for increased yield afforded by higher leaf Ψw under stress and non-stress conditions was lost as a result of the greater leaf senescence in SA 6 plants during grain fill compared to K78Y x I137TN plants (Section 3.3.4).

3.3.3 Non-structural carbohydrate analysis for stem segments A1 and B1

3.3.3.1 Reducing sugars composition

Main effects

The main effects for hybrid and stress treatment were non-significant, while the main effects for WAA and stem segment were significant (Appendix 28.1). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

First order interactions

The interaction of hybrid with stress treatment was non-significant.

The interaction of hybrid with WAA was significant (Table 3.5). The hybrid x WAA(linear) component of the interaction was also significant. SA 6 had non-significantly higher RS composition at 1 WAA than did K78Y x I137TN. However, at 2 WAA both hybrids had similar RS composition levels. From 2 WAA to PM, RS composition declined more steadily and more rapidly in SA 6 than in K78Y x I137TN. At PM RS composition in K78Y x I137TN was significantly (p = 0,01) higher than in SA 6.

Table 3.5 Influence of maize hybrid on mean stem segment reducing sugars composition (%) from one week after anthesis (WAA) to physiological maturity meaned over water stress treatments

Hybrid	Weeks after anthesis								Hybrid means
	1	2	3	4	5	6	7	8	
SA 6	15,6	16,7	14,8	14,0	12,4	9,4	5,4	5,3	11,7
K78Y x I137TN	14,3	16,1	15,2	13,3	15,0	12,1	8,5	9,1	12,9
WAA means	15,0	16,4	15,0	13,6	13,7	10,7	6,9	7,2	

Body of table	LSD 0,05	LSD 0,01
Comparison of means at the same level of hybrid	2,4	3,2
Comparison of means at the same level of WAA or with neither factor in common	2,7	3,7
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of WAA means	1,7	2,3

The interaction of stress treatment with WAA was non-significant. However, the stress treatment x WAA(linear) component of the interaction was significant (Table 3.6). Water deficits caused a more marked decline in RS composition from 4 WAA to PM, although RS composition was only significantly (p = 0,05) higher under non-stress conditions than under stress conditions at PM.

Table 3.6 Effect of water stress (S) and lack of water stress (NS) on mean stem segment reducing sugars composition (%) from one week after anthesis (WAA) to physiological maturity meaned over maize hybrids

Stress treatment	Weeks after anthesis								Stress treatment means
	1	2	3	4	5	6	7	8	
S	14,8	16,3	15,5	13,0	13,1	10,0	5,8	5,8	11,8
NS	15,1	16,6	14,6	14,3	14,2	11,5	8,0	8,6	12,9
WAA means	15,0	16,4	15,0	13,6	13,7	10,7	6,9	7,2	

Body of table	LSD 0,05	LSD 0,01
Comparison of means at the same level of stress treatment	2,4	3,2
Comparison of means at the same level of WAA or with neither factor in common	2,7	3,7
Marginal means		
Comparison of stress treatment means	NS	NS
Comparison of WAA means	1,7	2,3

The interaction of hybrid with stem segment was significant (Table 3.7). While RS composition in SA 6 decreased significantly (p = 0,05) from the A1 to the B1 segment, in

K78Y x I137TN RS composition increased significantly (p = 0,01) from the A1 to the B1 segment.

Table 3.7 Influence of maize hybrid on stem segment reducing sugars composition (%) meaned over water stress treatments during grain fill

Hybrid	Stem segment		Hybrid means
	A1	B1	
SA 6	12,0	11,5	11,7
K78Y x I137TN	12,0	13,8	12,9
Stem segment means	12,0	12,6	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,5	0,7
Comparison of means at the same level of stem segment or with neither factor in common	1,5	2,2
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of stem segment means	0,3	0,5

The interaction of stress treatment with stem segment was non-significant.

The interaction of WAA with stem segment was non-significant. However, the WAA(linear) x stem segment component of the interaction was significant (Table 3.8). The RS composition in the B1 segment was significantly (p = 0,01) higher than that in the A1 segment at 1, 3 and 4 WAA; and non-significantly higher

at 2, 5, 6 and 7 WAA. At 8 WAA RS composition in the A1 segment was non-significantly higher than that in the B1 segment. Both segments showed a non-significant increase in RS composition from 1 to 2 WAA and then a decline in RS composition from 2 WAA to PM. The RS composition in both segments was significantly ($p = 0,01$) higher at PM than at 1 WAA. The decline in RS composition from 2 WAA to PM was more marked in the B1 segment as evidenced by the

Table 3.8 Influence of weeks after anthesis (WAA) on stem segment reducing sugars composition (%) meaned over maize hybrids and water stress treatments

WAA	Stem segment		WAA means
	A1	B1	
1	14,4	15,6	15,0
2	15,9	16,9	16,4
3	14,4	15,6	15,0
4	13,0	14,2	13,6
5	13,4	13,9	13,7
6	10,5	11,0	10,7
7	6,9	7,0	6,9
8	7,4	7,0	7,2
Stem segment means	12,0	12,7	

Body of table	LSD 0,05	LSD 0,01
Comparison of means at the same level of WAA	1,0	1,3
Comparison of means at the same level of stem segment or with neither factor in common	1,9	2,5
Marginal means		
Comparison of WAA means	1,7	2,3
Comparison of stem segment means	0,3	0,5

increasingly smaller difference in RS composition between it and the A1 segment as PM approached.

Second order interactions

The interactions of hybrid, stress treatment and WAA; hybrid, stress treatment and stem segment; hybrid, WAA and stem segment; stress treatment, WAA and stem segment were all non-significant. There were no significant components of the interactions involving WAA either.

Third order interaction

The interaction of hybrid, stress treatment, WAA and stem segment was non-significant (Figure 3.3). There were no significant components of the interaction either. However, there were apparent differences between hybrids in the changes in RS composition levels in the stem segments during grain fill under stress and non-stress conditions.

The RS composition ranged from a low of 3,9 % in the B1 segment of SA 6 at PM under stress conditions to a high of 18,3 % in the A1 segment of SA 6 at 2 WAA under non-stress conditions.

SA 6 under stress conditions underwent a smooth decline in RS composition from 2 WAA to PM. At 4 WAA and through to PM RS composition in SA 6 was marginally less in the B1 segment than the A1 segment. Whether RS made up a larger proportion of the dry mass of the A1 segment than the B1 segment, as a result of

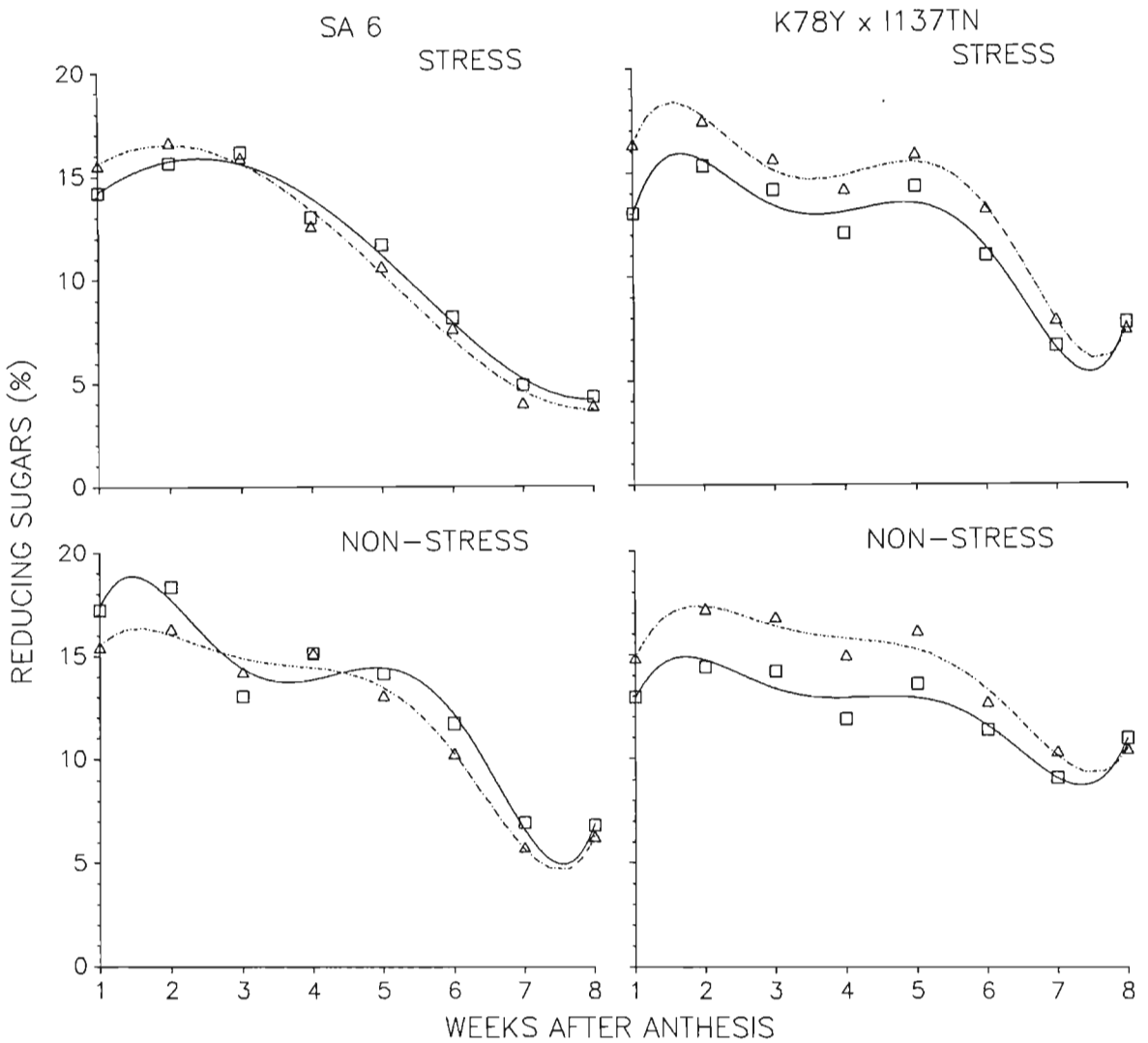


Figure 3.3 Effect of water stress from one week after anthesis to physiological maturity on reducing sugars composition in the first pair of internodes above (A1 □—□) and below (B1 △—△) the primary ear of two maize hybrids

Polynomial equations:

SA 6

Stress A1 $11,236 + 3,630x - 0,552x^2 - 0,092x^3 + 0,011x^4$ $r^2=0,990$

B1 $12,633 + 4,101x - 1,139x^2 + 0,018x^3 + 0,005x^4$ $r^2=0,992$

Non-stress A1 $-6,955 + 47,689x - 30,928x^2 + 8,557x^3 - 1,064x^4 + 0,048x^5$ $r^2=0,967$

B1 $4,272 + 21,876x - 14,201x^2 + 4,067x^3 - 0,534x^4 + 0,026x^5$ $r^2=0,990$

K78Y x I137TN

Stress A1 $-14,105 + 50,336x - 30,442x^2 + 8,174x^3 - 1,003x^4 + 0,046x^5$ $r^2=0,965$

B1 $-8,581 + 47,524x - 29,827x^2 + 8,146x^3 - 1,006x^4 + 0,046x^5$ $r^2=0,991$

Non-stress A1 $-4,188 + 31,369x - 18,642x^2 + 4,943x^3 - 0,604x^4 + 0,027x^5$ $r^2=0,899$

B1 $-1,831 + 29,648x - 16,843x^2 + 4,366x^3 - 0,529x^4 + 0,024x^5$ $r^2=0,960$

greater metabolic activity in the A1 segment is not clear. Under non-stress conditions RS composition in the A1 and B1 segments of SA 6 peaked at 2 WAA then declined to lower levels at 3 WAA, remained fairly constant until 5 WAA thereafter declining sharply through to 7 WAA. At PM there was a slight increase in RS composition. The B1 segment, as with stressed SA 6 plants, generally had less RS composition than the A1 segment. The RS composition in the A1 and B1 segments of SA 6 was higher at PM under non-stress conditions than under stress conditions.

The pattern of RS composition decline in the A1 and B1 segments of K78Y x I137TN under stress conditions in many ways resembled the pattern in SA 6 under non-stress conditions. There was one difference, however, and that was the B1 segment in K78Y x I137TN had higher RS composition levels than the A1 segment throughout grain fill. The RS composition peaked at 2 WAA then declined to lower levels from 3 to 6 WAA coinciding with mid-grain fill and then fell sharply to the lowest levels at 7 WAA. However, in contrast to SA 6 under stress conditions, levels of RS composition in the A1 and B1 segments of K78Y x I137TN under stress conditions increased slightly from 7 to 8 WAA. The RS composition at PM was higher in stressed K78Y x I137TN plants than stressed SA 6 plants.

Apart from more marked fluctuations under stress conditions, the overall patterns of RS composition changes in the A1 and B1 segments of K78Y x I137TN under non-stress conditions were similar to those under stress conditions. In contrast to SA 6 stem segments under non-stress conditions, K78Y x I137TN stem

segments under non-stress conditions did not undergo the same marked decline in RS composition from 5 to 7 WAA.

3.3.3.2 Reducing sugars content

Main effects

The main effect for hybrid was non-significant while the main effects for stress treatment, WAA and stem segment were significant (Appendix 28.2). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

First order interactions

The interaction of hybrid with stress treatment was non-significant.

The interaction of hybrid with WAA was non-significant. However, the hybrid x WAA(linear) component of the interaction was significant (Table 3.9). Initially from 1 to 2 WAA RS content in SA 6 was non-significantly higher than that in K78Y x I137TN. However, from 3 WAA to PM SA 6 showed a more marked decline in RS content from 1 WAA to PM compared to K78Y x I137TN. The RS content in K78Y x I137TN was non-significantly higher than that in SA 6 at 3, 5, and 7 WAA and at PM; and significantly ($p = 0,05$) higher at 6 WAA.

Table 3.9 Influence of maize hybrid on mean stem segment reducing sugars content (g segment^{-1}) from one week after anthesis (WAA) to physiological maturity meaned over water stress treatments

Hybrid	Weeks after anthesis								Hybrid means
	1	2	3	4	5	6	7	8	
SA 6	0,97	1,03	0,90	1,07	0,75	0,49	0,29	0,27	0,72
K78Y x I137TN	0,83	0,98	1,02	0,92	0,90	0,72	0,42	0,42	0,78
WAA means	0,90	1,00	0,96	0,99	0,83	0,61	0,35	0,35	

Body of table	LSD	
	0,05	0,01
Comparison of means	0,19	0,26
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of WAA means	0,14	0,18

The interaction of stress treatment with WAA was non-significant. However, the stress treatment x WAA(linear) component of the interaction was significant (Table 3.10). Water stress caused a more rapid decline in RS content from 2 WAA to PM. Under non-stress conditions RS content was non-significantly higher than under stress conditions at 2 and 3 WAA, but significantly higher at 4 WAA ($p = 0,01$), 5 WAA ($p = 0,05$), 6 WAA ($p = 0,05$), 7 WAA ($p = 0,05$) and at PM ($p = 0,01$).

Table 3.10 Effect of water stress (S) and lack of water stress (NS) on mean stem segment reducing sugars content (g segment^{-1}) from one week after anthesis (WAA) to physiological maturity meaned over maize hybrids

Stress treatment	Weeks after anthesis								Stress treatment means
	1	2	3	4	5	6	7	8	
S	0,90	0,97	0,92	0,84	0,71	0,51	0,24	0,22	0,66
NS	0,90	1,03	1,00	1,15	0,94	0,71	0,47	0,48	0,83
WAA means	0,90	1,00	0,96	0,99	0,83	0,61	0,35	0,35	

Body of table	LSD	
	0,05	0,01
Comparison of means	0,19	0,26
Marginal means		
Comparison of stress treatment means	0,07	0,09
Comparison of WAA means	0,14	0,18

The interaction of hybrid with stem segment was non-significant.

The interaction of stress treatment with stem segment was significant (Table 3.11). Whereas under non-stress conditions the B1 segment had 0,35 g segment^{-1} ($p = 0,01$) more RS content than the A1 segment, under stress conditions the B1 segment had 0,27 g segment^{-1} ($p = 0,01$) more RS content than the A1 segment. Under non-stress conditions the A1 and B1 segments had significantly ($p = 0,01$) more RS content than under stress conditions.

Table 3.11 Effect of water stress (S) and lack of water stress (NS) on stem segment reducing sugars content (g segment^{-1}) meaned over maize hybrids during grain fill

Stress treatment	Stem segment		Stress treatment means
	A1	B1	
S	0,53	0,80	0,66
NS	0,66	1,01	0,83
Stem segment means	0,59	0,90	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of stress treatment	0,05	0,07
Comparison of means at the same level of stem segment or with neither factor in common	0,08	0,10
Marginal means		
Comparison of stress means	0,07	0,09
Comparison of stem segment means	0,04	0,05

The interaction of WAA with stem segment was significant (Table 3.12). The WAA(linear, quadratic and cubic) x stem segment components of the interaction were also significant. The RS content in the B1 segment was significantly ($p = 0,01$) higher than that in the A1 segment from 1 to 6 WAA, but was non-significantly higher at 7 and 8 WAA. Both segments showed an increase in RS content from 1 to 2 WAA and then a decline in RS content from 2 WAA to PM. However, the decline in RS content was more marked in the B1 segment as evidenced by the increasingly smaller difference in RS content between these segments as PM was approached.

Table 3.12 Influence of weeks after anthesis (WAA) on stem segment reducing sugars content (g segment^{-1}) meaned over maize hybrids and water stress treatments

WAA	Stem segment		WAA means
	A1	B1	
1	0,69	1,12	0,90
2	0,75	1,26	1,00
3	0,72	1,20	0,96
4	0,78	1,21	0,99
5	0,68	0,97	0,83
6	0,51	0,70	0,61
7	0,31	0,40	0,35
8	0,31	0,38	0,35
Stem segment means	0,59	0,90	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of WAA	0,11	0,14
Comparison of means at the same level of stem segment or with neither factor in common	0,16	0,21
Marginal means		
Comparison of WAA means	0,14	0,18
Comparison of stem segment means	0,04	0,05

Second order interactions

The interactions of hybrid, stress treatment and WAA; hybrid, stress treatment and stem segment; hybrid, WAA and stem segment; stress treatment, WAA and stem segment were all non-significant.

There were no significant components of the interactions involving WAA either.

Third order interaction

The interaction of hybrid, stress treatment, WAA and stem segment was non-significant (Figure 3.4). There were no significant components of the interaction either. However, there were apparent differences between hybrids in the changes in RS content levels in the stem segments during grain fill under stress and non-stress conditions.

The RS content ranged from a low of 0,15 g segment^{-1} in the A1 segment of SA 6 at PM under stress conditions to a high of 1,58 g segment^{-1} in the B1 segment of SA 6 at 4 WAA under non-stress conditions.

As with RS composition, RS content declined steadily from 3 to 7 WAA and then remained constant from 7 to 8 WAA in SA 6 segments under stress conditions. Unlike RS composition however, RS content in the B1 segment exceeded that in the A1 segment from 1 WAA to PM. The B1 segment declined in RS content at a more rapid rate than the A1 segment from 1 WAA to PM. It would appear that the larger pool of RS in the B1 segment was rapidly depleted for sink requirements during grain fill. It is, however, not clear at this point what sinks are utilizing the RS pool in the stem segments. In direct contrast to RS composition under non-stress conditions, RS content in the stem segments of SA 6 increased from 1 to 4 WAA before declining sharply to 7 WAA. It

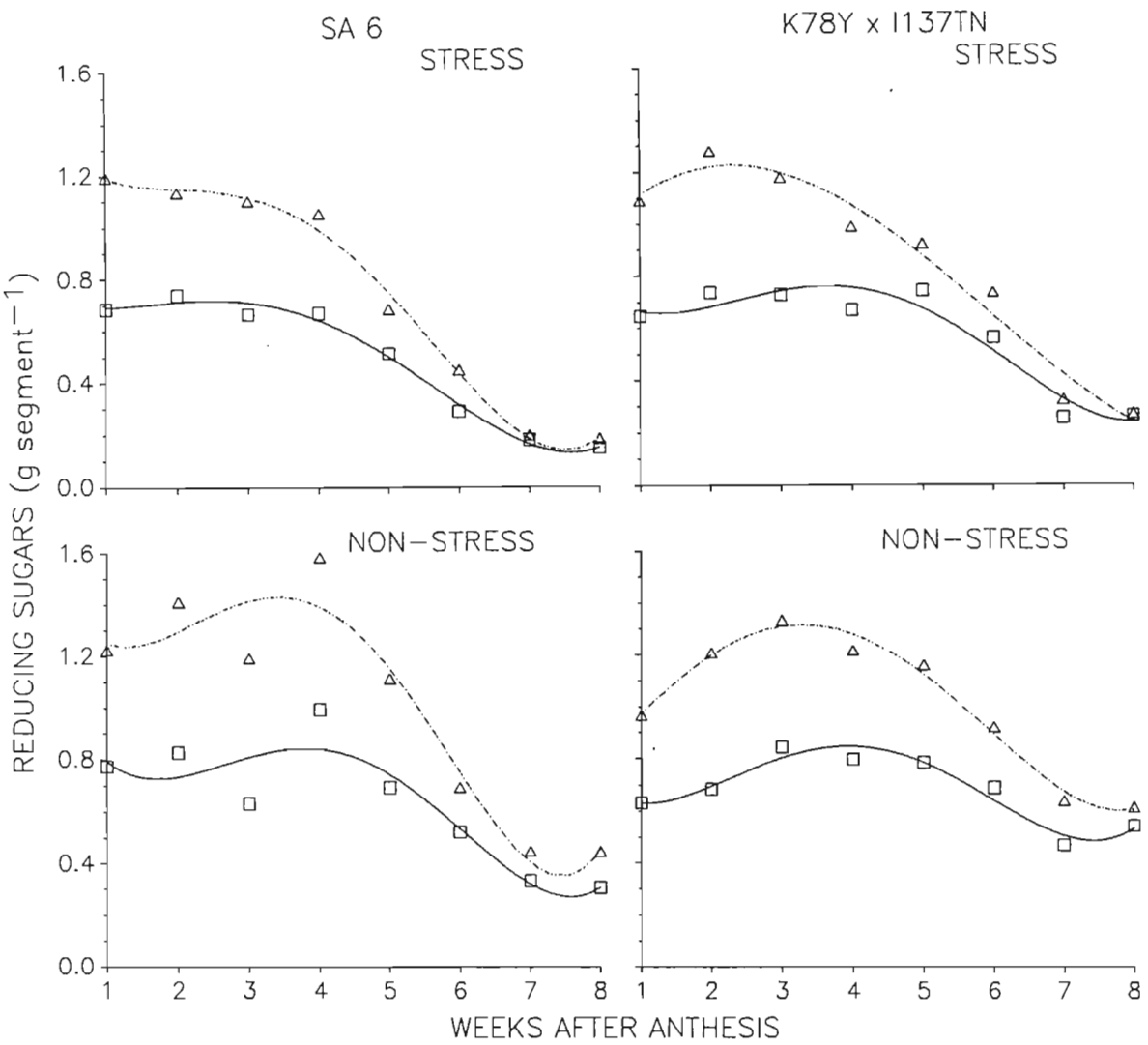


Figure 3.4 Effect of water stress from one week after anthesis to physiological maturity on reducing sugars content in the first pair of internodes above (A1 □—□) and below (B1 △----△) the primary ear of two maize hybrids

Polynomial equations:

SA 6

Stress	A1	$0{,}730 - 0{,}104x + 0{,}088x^2 - 0{,}023x^3 + 0{,}002x^4$	$r^2=0{,}989$
	B1	$1{,}408 - 0{,}385x + 0{,}210x^2 - 0{,}047x^3 + 0{,}003x^4$	$r^2=0{,}993$
Non-stress	A1	$1{,}257 - 0{,}781x + 0{,}382x^2 - 0{,}069x^3 + 0{,}004x^4$	$r^2=0{,}836$
	B1	$1{,}631 - 0{,}752x + 0{,}458x^2 - 0{,}095x^3 + 0{,}006x^4$	$r^2=0{,}919$

K78Y x I137TN

Stress	A1	$0{,}845 - 0{,}338x + 0{,}195x^2 - 0{,}038x^3 + 0{,}002x^4$	$r^2=0{,}917$
	B1	$0{,}842 + 0{,}358x - 0{,}093x^2 + 0{,}004x^3 + 0{,}0001x^4$	$r^2=0{,}968$
Non-stress	A1	$0{,}783 - 0{,}333x + 0{,}224x^2 - 0{,}045x^3 + 0{,}003x^4$	$r^2=0{,}932$
	B1	$0{,}691 + 0{,}279x + 0{,}020x^2 - 0{,}020x^3 + 0{,}002x^4$	$r^2=0{,}984$

will be recalled that RS composition declined from 2 WAA to a constant level from 3 to 5 WAA before declining further. Thus it would appear that other components contributing to stem segment dry mass accumulated from 1 to 5 WAA. It will also be recalled that RS composition in the B1 segment of SA 6 was generally lower than that in the A1 segment. However, RS content was higher in the B1 segment than in the A1 segment of SA 6. Thus it would appear that in the B1 segment, components contributing to segment dry mass other than RS make up a greater proportion of the dry mass. The RS content in the A1 and B1 segments of SA 6 was higher at PM under non-stress conditions than under stress conditions.

Under stress conditions RS content in the B1 segment of K78Y x I137TN increased to a maximum at 2 WAA and then declined markedly until 7 WAA and then remained constant from 7 to 8 WAA. The RS content in the A1 segment fluctuated within narrow limits from 1 to 5 WAA, then declined sharply until 7 WAA before increasing slightly at PM. It appears that stress developed in both SA 6 and K78Y x I137TN from 3 to 4 WAA. Under non-stress conditions RS content in the A1 and B1 segments of K78Y x I137TN increased from 1 to 3-4 WAA and then decreased until PM. The A1 segment increased slightly in RS content from 7 WAA to PM. The initial increase and final decrease in RS content was more marked in the B1 segment. Both segments of K78Y x I137TN under non-stress conditions had higher RS content levels at PM than did the segments of SA 6 at PM.

It is noteworthy that under stress and non-stress conditions both hybrids had greater levels of RS content in the B1 segment than the A1 segment during the first 4 WAA and that RS content declined more markedly in the B1 segment in the subsequent weeks until PM. At PM the A1 and B1 segments had similar amounts of RS content. Thus it appears that there was a greater depletion of RS pools in the B1 segment under stress and non-stress conditions in both hybrids. Which sinks utilized these pools of RS remains unclear at this stage.

It is also noteworthy that RS content declined in both hybrids under non-stress conditions between 4 to 5 WAA until PM. However, water deficits resulted in lower overall RS content levels for both hybrids during grain fill and a more marked decline in RS content to lower levels at PM compared to the levels under non-stress conditions.

3.3.3.3 Sucrose composition

Main effects

The main effects for hybrid and stress treatment were non-significant, while the main effect for WAA was significant (Appendix 28.3). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The main effect for stem segment was significant (Table 3.13). Sucrose composition in the A1 segment was significantly ($p = 0,05$) higher than that in the B1 segment.

Table 3.13 Mean sucrose composition (%) of stem segments during grain fill from maize hybrids subject to water stress treatments

Stem segment	
A1	B1
11,8	11,2
LSD (0,05) 0,6	
LSD (0,01) 0,7	

First order interactions

The interactions of hybrid with stress treatment; hybrid with stem segment; stress treatment with stem segment; WAA with stem segment were all non-significant. There were no significant components of the interactions involving WAA either.

The interaction of hybrid with WAA was significant (Table 3.14). The hybrid x WAA(linear and cubic) components of the interaction were also significant. Sucrose composition increased in both hybrids from 1 to 4 WAA, initially more markedly in SA 6 than K78Y x I137TN, and then declined until PM in both hybrids, again more markedly in SA 6 then K78Y x I137TN. There was a sharp decline in sucrose composition in K78Y x I137TN from 7 WAA to PM. At PM K78Y x I137TN had significantly ($p = 0,05$) higher sucrose composition than SA 6.

Table 3.14 Influence of maize hybrid on mean stem segment sucrose composition (%) from one week after anthesis (WAA) to physiological maturity meaned over water stress treatments

Hybrid	Weeks after anthesis								Hybrid means
	1	2	3	4	5	6	7	8	
SA 6	9,0	12,6	17,4	18,2	13,8	7,3	5,0	3,2	10,8
K78Y x I137TN	8,9	9,9	14,8	17,3	12,6	13,9	12,9	7,5	12,2
WAA means	8,95	11,3	16,1	17,8	13,2	10,6	8,9	5,4	

Body of table	LSD 0,05	LSD 0,01
Comparison of means at the same level of hybrid	3,3	4,4
Comparison of means at the same level of WAA or with neither factor in common	3,6	4,9
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of WAA means	2,3	3,1

The interaction of stress treatment with WAA was non-significant. However, the stress treatment x WAA(linear) component of the interaction was significant (Table 3.15). Initially sucrose composition increased in both stressed and non-stressed plants from 1 to 4 WAA, more markedly in stressed plants. In fact, sucrose composition in stressed plants non-significantly exceeded that in non-stressed plants from 2 to 4 WAA. Sucrose composition then declined from 4 WAA to PM more markedly in stressed plants particularly from 6 WAA to PM. Sucrose composition under non-stress conditions non-significantly exceeded that under stress

conditions at 1, 5 and 6 WAA and at PM, but significantly ($p = 0,05$) at 7 WAA.

Table 3.15 Effect of water stress (S) and lack of water stress (NS) on mean stem segment sucrose composition (%) from one week after anthesis (WAA) to physiological maturity meaned over maize hybrids

Stress treatment	Weeks after anthesis								Stress treatment means
	1	2	3	4	5	6	7	8	
S	8,5	11,8	17,2	18,8	12,6	10,6	7,1	4,0	11,3
NS	9,4	10,8	15,0	16,7	13,8	10,7	10,7	6,7	11,7
WAA means	9,0	11,3	16,1	17,8	13,2	10,6	8,9	5,4	

Body of table	LSD 0,05	LSD 0,01
Comparison of means at the same level of stress treatment	3,3	4,4
Comparison of means at the same level of WAA or with neither factor in common	3,6	4,9
Marginal means		
Comparison of stress treatment means	NS	NS
Comparison of WAA means	2,3	3,1

Second order interactions

The interactions of hybrid, stress treatment and WAA; hybrid, stress treatment and stem segment; hybrid, WAA and stem segment; stress treatment, WAA and stem segment were all non-significant. There were no significant components of the interactions involving WAA either.

Third order interaction

The interaction of hybrid, stress treatment, WAA and stem segment was non-significant (Figure 3.5). There were no significant components of the interaction either. However, there were apparent differences between hybrids in the changes in sucrose composition in the stem segments during the grain fill under stress and non-stress conditions.

Sucrose composition ranged from a low of 2,1 % in the B1 segment of SA 6 at PM under stress conditions to a high of 20,9 % in the B1 segment of SA 6 at 5 WAA under stress conditions.

The tendency for sucrose to make up a greater proportion of the dry mass of both stem segments in both hybrids under stress conditions from 2 to 4 WAA may indicate that there was less photosynthate available under stress conditions to be converted to other components contributing to stem dry mass. SA 6 under stress conditions had the highest sucrose composition during the period 2 to 4 WAA and this may indicate that there is a greater tendency for sucrose to accumulate in the stem of SA 6 under stress conditions perhaps due to reduced sink demand, particularly by the grain.

At PM K78Y x I137TN had higher sucrose composition in both stem segments under stress and non-stress conditions compared to the stem segments of the respectively treated SA 6 plants.

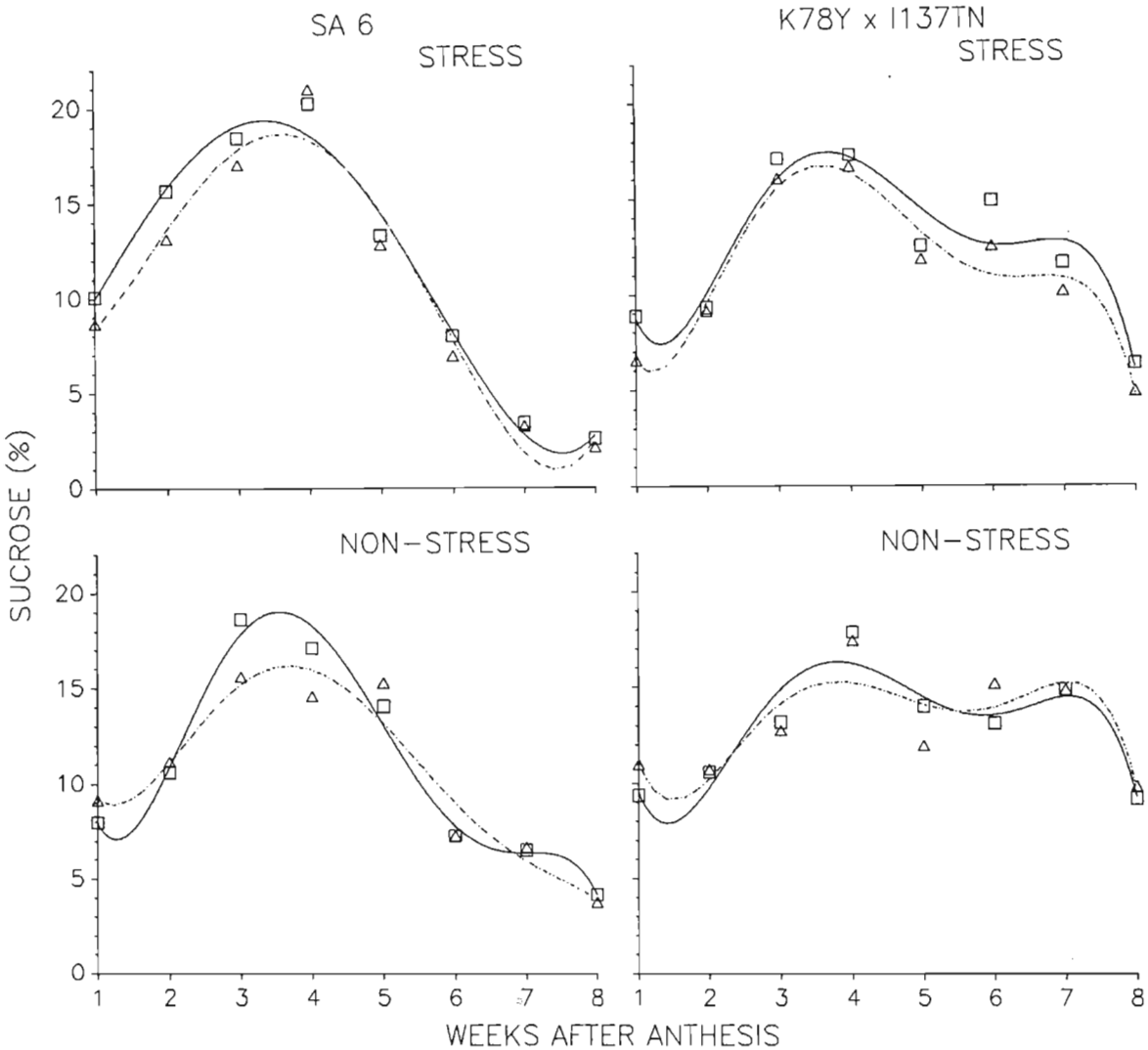


Figure 3.5 Effect of water stress from one week after anthesis to physiological maturity on sucrose composition in the first pair of internodes above (A1 □——□) and below (B1 △·····△) the primary ear of two maize hybrids

Polynomial equations:

SA 6

Stress	A1	$4{,}448 + 4{,}153x + 2{,}139x^2 - 0{,}812x^3 + 0{,}060x^4$	$r^2=0{,}984$
	B1	$7{,}242 - 2{,}998x + 5{,}438x^2 - 1{,}356x^3 + 0{,}089x^4$	$r^2=0{,}955$
Non-stress	A1	$37{,}325 - 60{,}873x + 41{,}375x^2 - 11{,}144x^3 + 1{,}296x^4 - 0{,}055x^5$	$r^2=0{,}983$
	B1	$22{,}135 - 27{,}172x + 18{,}461x^2 - 4{,}773x^3 + 0{,}523x^4 - 0{,}021x^5$	$r^2=0{,}926$

K78Y x I137TN

Stress	A1	$39{,}072 - 60{,}959x + 40{,}262x^2 - 10{,}902x^3 + 1{,}307x^4 - 0{,}058x^5$	$r^2=0{,}892$
	B1	$30{,}690 - 51{,}281x + 35{,}850x^2 - 9{,}946x^3 + 1{,}206x^4 - 0{,}054x^5$	$r^2=0{,}955$
Non-stress	A1	$38{,}202 - 56{,}286x + 36{,}154x^2 - 9{,}664x^3 + 1{,}154x^4 - 0{,}051x^5$	$r^2=0{,}888$
	B1	$37{,}900 - 51{,}519x + 32{,}277x^2 - 8{,}603x^3 + 1{,}035x^4 - 0{,}046x^5$	$r^2=0{,}727$

3.3.3.4 Sucrose content

Main effects

The main effects for hybrid and stress treatment were non-significant, while the main effects for WAA and stem segment were significant (Appendix 28.4). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

First order interactions

The interaction of hybrid with stress treatment was non-significant.

The interaction of hybrid with WAA was significant (Table 3.16). The hybrid x WAA(linear and cubic) components of the interaction were also significant. Sucrose content initially increased in both hybrids from 1 to 4 WAA but more markedly in SA 6 than K78Y x I137TN. In fact, from 2 to 4 WAA sucrose content was non-significantly higher in SA 6 than in K78Y x I137TN. From 4 WAA to PM sucrose content declined in both hybrids but more markedly in SA 6. From 7 WAA to PM sucrose content in K78Y x I137TN declined by a larger amount than in SA 6. At PM K78Y x I137TN had non-significantly higher sucrose content than SA 6.

Table 3.16 Influence of maize hybrid on mean stem segment sucrose content (g segment^{-1}) from one week after anthesis (WAA) to physiological maturity meaned over water stress treatments

Hybrid	Weeks after anthesis								Hybrid means
	1	2	3	4	5	6	7	8	
SA 6	0,54	0,79	1,03	1,39	0,86	0,38	0,31	0,16	0,68
K78Y x I137TN	0,54	0,62	0,96	1,19	0,79	0,86	0,66	0,37	0,75
WAA means	0,54	0,70	0,99	1,29	0,82	0,62	0,48	0,27	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,24	0,32
Comparison of means at the same level of WAA or with neither factor in common	0,31	0,42
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of WAA means	0,17	0,23

The interaction of stress treatment with WAA was non-significant. However, the stress treatment x WAA(linear) component of the interaction was significant (Table 3.17). Initially sucrose content increased in both stressed and non-stressed plants from 1 to 4 WAA but more markedly in stressed plants from 1 to 3 WAA, and then declined from 4 WAA to PM more markedly in stressed plants particularly from 6 WAA to PM. At no stage during grain fill did sucrose content in stressed plants exceed that in non-stressed plants. Sucrose content at PM in stressed plants was non-significantly less than that in non-stressed plants.

Table 3.17 Effect of water stress (S) and lack of water stress (NS) on mean stem segment sucrose content (g segment^{-1}) from one week after anthesis (WAA) to physiological maturity meaned over maize hybrids

Stress treatment	Weeks after anthesis								Stress treatment means
	1	2	3	4	5	6	7	8	
S	0,49	0,70	0,99	1,23	0,69	0,53	0,29	0,15	0,63
NS	0,58	0,71	1,00	1,35	0,96	0,70	0,68	0,38	0,80
WAA means	0,54	0,70	0,99	1,29	0,82	0,62	0,48	0,27	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of stress treatment	0,24	0,32
Comparison of means at the same level of WAA or with neither factor in common	0,31	0,42
Marginal means		
Comparison of stress treatment means	NS	NS
Comparison of WAA means	0,17	0,23

The interaction of hybrid with stem segment was significant (Table 3.18). Whereas sucrose content in the B1 segment of SA 6 exceeded that in the A1 segment by 0,28 g segment^{-1} ($p = 0,01$), sucrose content in the B1 segment of K78Y x I137TN exceeded that in the A1 segment by 0,16 g segment^{-1} ($p = 0,01$). Thus the difference between the A1 and B1 segments in sucrose content was more marked in SA 6 than K78Y x I137TN.

Table 3.18 Influence of maize hybrid on stem segment sucrose content (g segment^{-1}) meaned over water stress treatments during grain fill

Hybrid	Stem segment		Hybrid means
	A1	B1	
SA 6	0,54	0,82	0,68
K78Y x I137TN	0,67	0,83	0,75
Stem segment means	0,61	0,82	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,07	0,09
Comparison of means at the same level of stem segment or with neither factor in common	0,21	0,30
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of stem segment means	0,05	0,07

The interaction of stress treatment with stem segment was significant (Table 3.19). Under non-stress conditions the B1 segment exceeded the A1 segment in sucrose content by 0,29 g segment^{-1} ($p = 0,01$). However, under stress conditions the B1 segment exceeded the A1 segment in sucrose content by 0,14 g segment^{-1} ($p = 0,01$). It appears that under stress conditions the difference between the A1 and B1 segments in sucrose content was less marked than under non-stress conditions.

Table 3.19 Effect of water stress (S) and lack of water stress (NS) on stem segment sucrose content (g segment^{-1}) meaned over maize hybrids during grain fill

Stress treatment	Stem segment		Stress treatment means
	A1	B1	
S	0,56	0,70	0,63
NS	0,65	0,94	0,80
Stem segment means	0,61	0,82	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of stress treatment	0,07	0,09
Comparison of means at the same level of stem segment or with neither factor in common	0,21	0,30
Marginal means		
Comparison of stress treatment means	NS	NS
Comparison of stem segment means	0,05	0,07

The interaction of WAA with stem segment was significant (Table 3.20). The WAA(linear and quadratic) x stem segment components of the interaction were also significant. Sucrose content was significantly ($p \leq 0,05$) higher in the B1 segment than the A1 segment from 1 to 6 WAA, but was non-significantly higher at 7 and 8 WAA. Both segments showed an initial increase in sucrose content from 1 to 4 WAA but this was more marked in the B1 segment. From 4 WAA to PM sucrose content declined in both segments but this was more rapid in the B1 segment as evidenced by the increasingly smaller difference in sucrose content between these segments as PM approached.

Table 3.20 Influence of weeks after anthesis (WAA) on stem segment sucrose content (g segment^{-1}) meaned over maize hybrids and water stress treatments

WAA	Stem segment		WAA means
	A1	B1	
1	0,43	0,64	0,54
2	0,57	0,84	0,70
3	0,83	1,15	0,99
4	1,10	1,48	1,29
5	0,69	0,96	0,82
6	0,54	0,69	0,62
7	0,43	0,54	0,48
8	0,24	0,30	0,27
Stem segment means	0,61	0,82	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of WAA	0,14	0,19
Comparison of means at the same level of stem segment or with neither factor in common	0,20	0,26
Marginal means		
Comparison of WAA means	0,17	0,23
Comparison of stem segment means	0,05	0,07

Second order interactions

The interactions of hybrid, stress treatment and WAA; hybrid, stress treatment and stem segment; hybrid, WAA and stem segment; stress treatment, WAA and stem segment were all non-significant.

There were no significant components of the interactions involving WAA either.

Third order interaction

The interaction of hybrid, stress treatment, WAA and stem segment was non-significant (Figure 3.6). There were no significant components of the interaction either. However, there were apparent differences between hybrids in the changes in sucrose content levels in the stem segments during grain fill under stress and non-stress conditions.

Sucrose content ranged from a low of 0,09 g segment^{-1} in the A1 segment of SA 6 at PM under stress conditions to a high of 1,77 g segment^{-1} in the B1 segment of SA 6 at 4 WAA under stress conditions.

It is apparent that under non-stress conditions both hybrids, in particular SA 6, had a tendency to show a marked increase in sucrose content in both stem segments from 1 to 4 WAA. Under stress conditions this tendency was apparently enhanced in SA 6 particularly in the B1 segment. The more rapid increase in sucrose content from 1 WAA to 3-4 WAA under stress conditions than under non-stress conditions is not easy to explain as it may be due to a number of different physiological responses to stress. It may indicate: (i) that water stress caused late abortion of developing kernels and so the stem served as an alternative sink for photosynthate; (ii) the occurrence of osmoregulation in the stem tissue; (iii) that the stressed plants

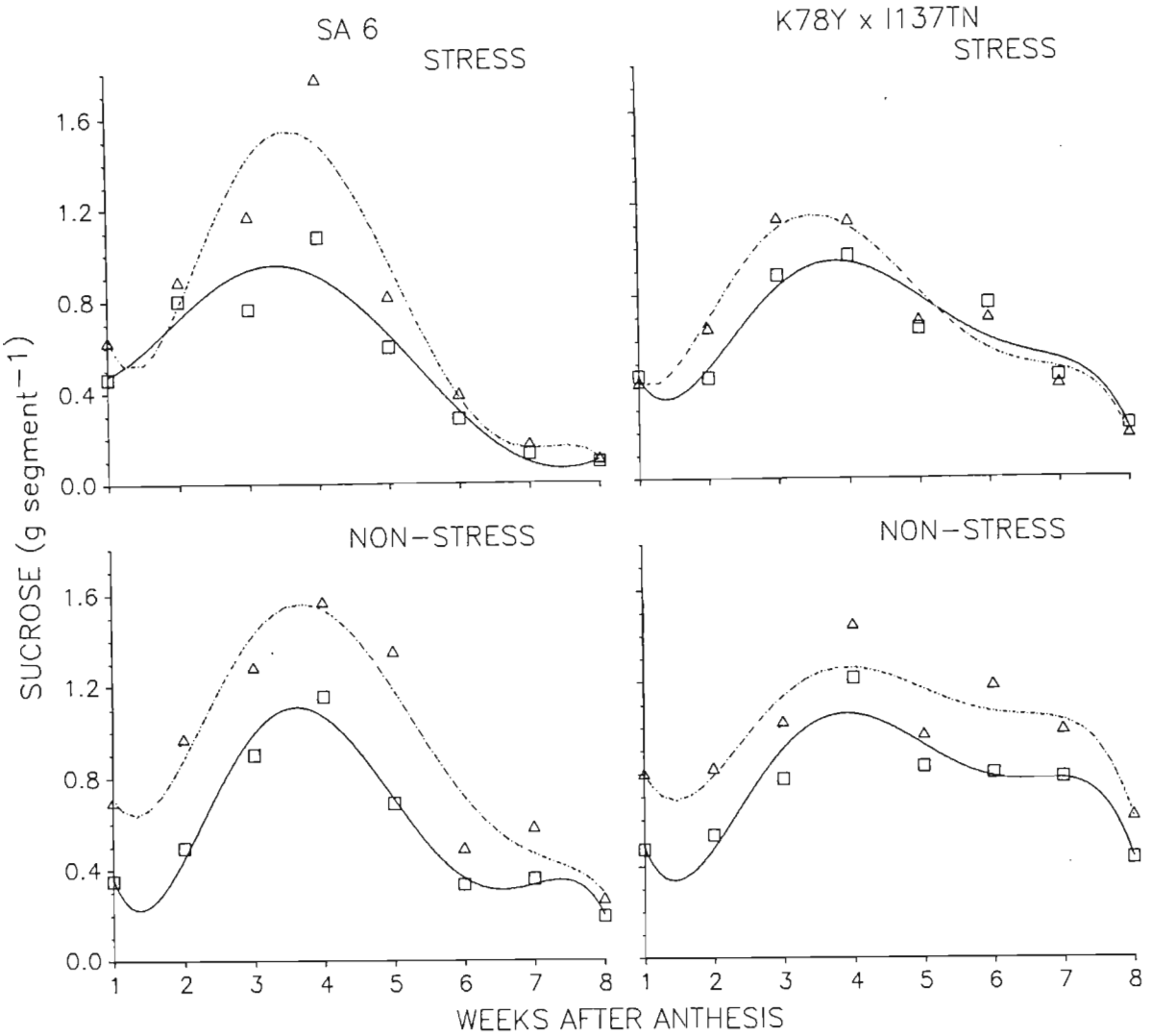


Figure 3.6 Effect of water stress from one week after anthesis to physiological maturity on sucrose content in the first pair of internodes above (A1 □—□) and below (B1 △---△) the primary ear of two maize hybrids

Polynomial equations:

SA 6

Stress	A1	0,728	-0,774x	+0,699x^2	-0,196x^3	+0,021x^4	-0,001x^5	r^2=0,918
	B1	3,748	-6,152x	+3,970x^2	-1,031x^3	+0,116x^4	-0,005x^5	r^2=0,916
Non-stress	A1	3,187	-5,605x	+3,629x^2	-0,958x^3	+0,111x^4	-0,005x^5	r^2=0,973
	B1	2,940	-4,471x	+2,923x^2	-0,756x^3	+0,084x^4	-0,003x^5	r^2=0,918

K78Y x I137TN

Stress	A1	2,160	-3,366x	+2,141x^2	-0,556x^3	+0,064x^4	-0,003x^5	r^2=0,883
	B1	1,742	-2,944x	+2,152x^2	-0,604x^3	+0,073x^4	-0,003x^5	r^2=0,943
Non-stress	A1	2,808	-4,484x	+2,810x^2	-0,730x^3	+0,085x^4	-0,004x^5	r^2=0,880
	B1	2,710	-3,660x	+2,291x^2	-0,597x^3	+0,070x^4	-0,003x^5	r^2=0,775

partitioned less sucrose for conversion to components of the residual fraction within the stem; and it may also indicate (iv) that the stressed plants function more efficiently under stress conditions, i.e. due to stomatal closure less H_2O is transpired as well as less CO_2 respired. The ratio of CO_2 assimilated through photosynthesis to H_2O transpired may have increased in stressed plants resulting in an initial increase in the sucrose pool in the stem segments studied (Stanhill, 1986).

Sucrose content in K78Y x I137TN fluctuated less markedly in stressed and non-stressed plants. At PM K78Y x I137TN had higher sucrose content in both stem segments under stress and non-stress conditions than that in the stem segments of the respectively treated SA 6 plants.

The ratio of sucrose content to RS content (Table 3.21, Figure 3.7) indicates that RS content exceeded sucrose content in both stem segments of SA 6 under non-stress conditions from 1 to 2 WAA. Sucrose content then increased and exceeded RS content from 3 to 5 WAA. Apart from the B1 segment at PM sucrose content then declined from 6 WAA to PM and was exceeded by RS content. Under stress conditions the pattern was fairly similar in SA 6 except that sucrose content exceeded RS content in the A1 segment at 2 WAA. Sucrose content in SA 6 under stress conditions exceeded RS content by a greater amount at 4 WAA compared to that under non-stress conditions.

Under non-stress conditions sucrose content in both stem segments of K78Y x I137TN only exceeded RS content from 4 WAA until PM,

Table 3.21 Ratio of sucrose content to reducing sugars (RS) content and ratio of starch content to sucrose content for the stem segments of two maize hybrids exposed to water stress (S) and lack of water stress (NS) from one week after anthesis (WAA) to physiological maturity

Hybrid	Stress treatment	WAA	Stem segment			
			A1		B1	
			Sucrose : RS	Starch: sucrose	Sucrose : RS	Starch: sucrose
SA 6	S	1	0,80	0,39	0,62	0,41
		2	1,10	0,35	0,85	0,40
		3	1,20	0,33	1,09	0,36
		4	1,61	0,27	1,74	0,24
		5	1,21	0,39	1,28	0,40
		6	0,97	0,34	0,92	0,38
		7	0,88	2,69	0,94	0,77
		8	0,65	1,19	0,58	1,69
	NS	1	0,48	0,48	0,64	0,36
		2	0,60	0,46	0,69	0,41
		3	1,54	0,32	1,12	0,34
		4	1,22	0,35	1,01	0,36
		5	1,00	0,43	1,17	0,30
		6	0,59	0,58	0,67	0,40
		7	0,89	0,93	1,10	0,40
		8	0,58	0,77	0,61	0,62
K78Y x I137TN	S	1	0,69	0,44	0,39	0,61
		2	0,62	0,53	0,53	0,44
		3	1,21	0,34	1,20	0,40
		4	1,47	0,32	1,18	0,33
		5	0,88	0,49	0,75	0,36
		6	1,35	0,29	0,95	0,26
		7	1,78	0,35	1,24	0,38
		8	1,10	0,46	0,83	0,43
	NS	1	0,79	0,56	0,84	0,40
		2	0,77	0,55	0,64	0,54
		3	0,97	0,46	0,78	0,42
		4	1,52	0,24	1,22	0,27
		5	1,07	0,44	0,81	0,74
		6	1,16	0,37	1,22	0,32
		7	1,65	0,26	1,48	0,25
		8	0,94	0,34	1,02	0,30
Sucrose : RS ratio			SE ($\bar{x}$)	0,13		
Starch : sucrose ratio			SE ($\bar{x}$)	0,24		

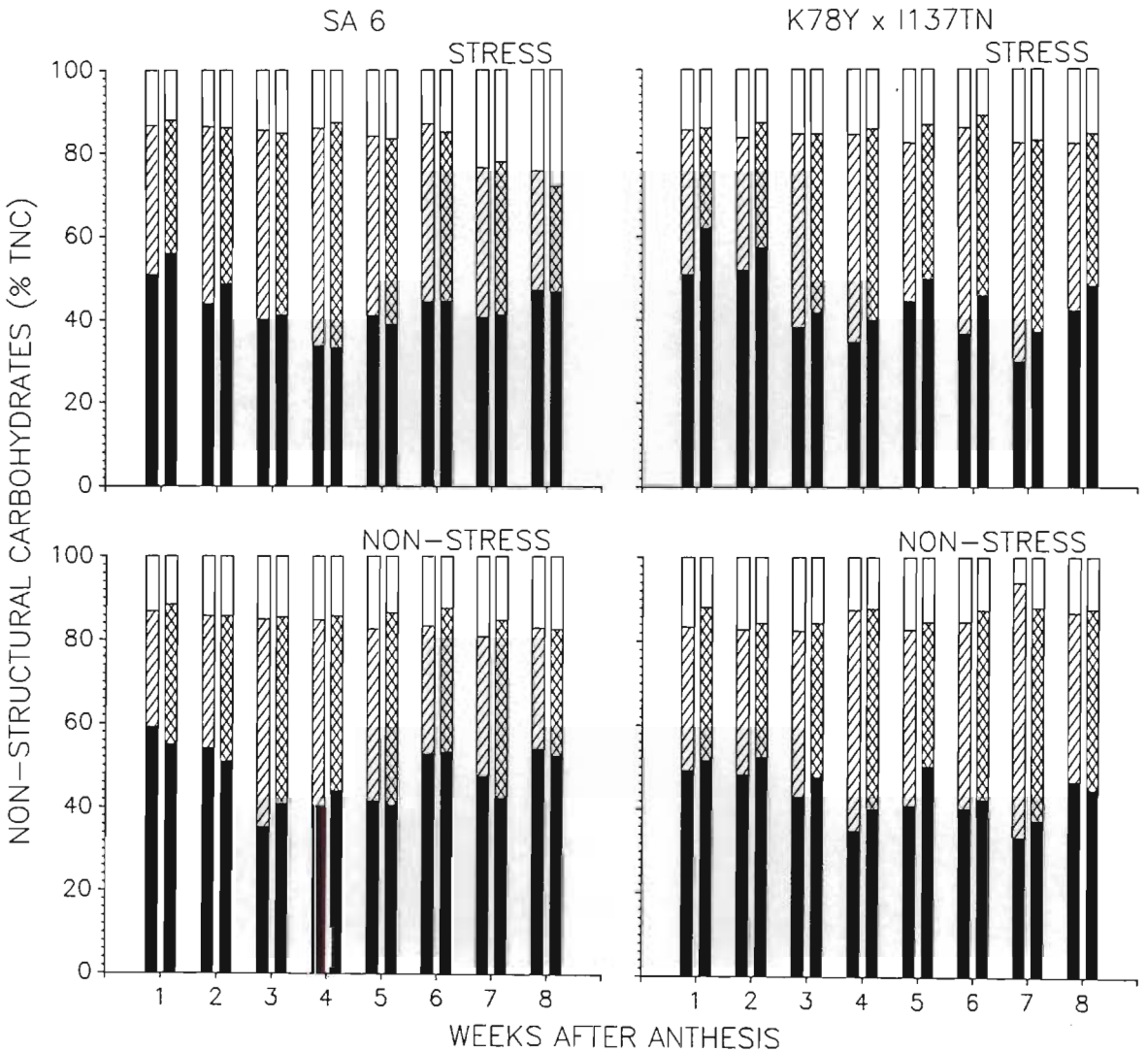


Figure 3.7 Effect of water stress from one week after anthesis to physiological maturity on component non-structural carbohydrate content expressed as a percentage of total non-structural carbohydrate (TNC) content in the first pair of internodes above (A1) and below (B1) the primary ear of two maize hybrids

except for the A1 segment at PM (Table 3.21, Figure 3.7). Under stress conditions sucrose content exceeded RS content at 3 WAA until 4 WAA and then fluctuated between being less than and greater than RS content in each segment until PM.

The periods during which the amount of sucrose in the stem was high relative to the amount of RS in the stem may provide an indication of the peak period of grain fill. It would appear that sucrose increased relative to RS one week later in K78Y x I137TN plants under non-stress conditions compared to SA 6 plants. However, sucrose content remained higher than RS content later into the grain filling period in K78Y x I137TN than SA 6 plants. These patterns were essentially retained under stress conditions (Table 3.21, Figure 3.7). Thus it appears that the synthesis of sucrose in the leaves and the partitioning of sucrose to the grain extends for a longer period in K78Y x I137TN plants under stress and non-stress conditions compared to SA 6 plants.

3.3.3.5 Starch composition

Main effects

The main effects for hybrid and WAA were significant while the main effects for stress treatment and stem segment were non-significant (Appendix 28.5). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

First order interactions

The interaction of hybrid with stress treatment was non-significant.

The interaction of hybrid with WAA was non-significant. However, the hybrid x WAA(linear and cubic) components of the interaction were significant (Table 3.22). SA 6 showed a more marked increase in starch composition from 1 to 3 WAA followed by a more marked decline in starch composition from 4 WAA to PM in comparison to K78Y x I137TN. Starch composition in K78Y x I137TN was non-significantly higher than that in SA 6 at 1, 3 and 5 WAA

Table 3.22 Influence of maize hybrid on mean stem segment starch composition (%) from one week after anthesis (WAA) to physiological maturity meaned over water stress treatments

Hybrid	Weeks after anthesis								Hybrid means
	1	2	3	4	5	6	7	8	
SA 6	3,5	4,8	5,6	5,3	4,9	2,6	2,7	2,1	3,9
K78Y x I137TN	3,8	4,7	5,7	4,8	5,1	3,8	3,5	2,7	4,3
WAA means	3,6	4,8	5,6	5,1	5,0	3,2	3,1	2,4	

Body of table	LSD 0,05	LSD 0,01
Comparison of means at the same level of hybrid	0,7	1,0
Comparison of means at the same level of WAA or with neither factor in common	0,8	1,0
Marginal means		
Comparison of hybrid means	0,3	0,5
Comparison of WAA means	0,5	0,7

and at PM, and significantly higher at 6 WAA ($p = 0,01$) and at 7 WAA ($p = 0,05$). At PM starch composition in both hybrids was significantly ($p = 0,01$) less than at 1 WAA.

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

The interaction of hybrid with stem segment was non-significant. Starch composition in the A1 segment exceeded that in the B1 segment by exactly the same amount of 0,5 % in both hybrids. However, this was not a consistent pattern under stress and non-stress conditions as the second order interaction of hybrid, stress treatment and stem segment was significant.

The interaction of stress treatment with stem segment was non-significant. This indicates that the A1 segment exceeded the B1 segment in starch composition by similar amounts under stress and non-stress conditions. However, this was not a consistent pattern for both hybrids as the second order interaction of hybrid, stress treatment and stem segment was significant.

The interaction of WAA with stem segment was non-significant. However, the WAA(cubic) x stem segment component of the interaction was significant (Table 3.23). Both the A1 and B1 segments generally increased in starch composition from 1 to 3 WAA. From 4 WAA to PM starch composition fluctuated somewhat in the A1 segment as it declined, while in the B1 segment starch composition declined steadily from 4 WAA to PM. Starch composition in the A1 segment was non-significantly higher

than that in the B1 segment at 2, 3 and 4 WAA and at PM, and significantly higher at 1 WAA ($p = 0,05$), 5 WAA ($p = 0,01$), 6 WAA ($p = 0,01$) and at 7 WAA ($p = 0,05$). Starch composition was significantly ($p = 0,01$) lower in both stem segments at PM than at 1 WAA.

Table 3.23 Influence of weeks after anthesis (WAA) on stem segment starch composition (%) meaned over maize hybrids and water stress treatments

WAA	Stem segment		WAA means
	A1	B1	
1	3,9	3,4	3,6
2	4,9	4,6	4,8
3	5,7	5,5	5,6
4	5,2	4,9	5,1
5	5,5	4,5	5,0
6	3,6	2,9	3,2
7	3,3	2,8	3,1
8	2,5	2,3	2,4
Stem segment means	4,3	3,9	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of WAA	0,4	0,6
Comparison of means at the same level of stem segment or with neither factor in common	0,6	0,8
Marginal means		
Comparison of WAA means	0,5	0,7
Comparison of stem segment means	NS	NS

Second order interactions

The interactions of hybrid, stress treatment and WAA; hybrid, WAA and stem segment; stress treatment, WAA and stem segment were all non-significant. There were no significant components of the interactions involving WAA either.

The interaction of hybrid, stress treatment and stem segment was significant (Table 3.24). Under non-stress conditions starch composition in the A1 segment of SA 6 exceeded that in the B1 segment by 0,8 % (p = 0,01). Starch composition in the A1 segment of K78Y x I137TN under non-stress conditions exceeded that in the B1 segment by 0,4 % (p = 0,01). Under stress conditions the A1 segment of SA 6 exceeded the B1 segment in

Table 3.24 Effect of water stress (S) and lack of water stress (NS) on starch composition (%) in stem segments of two maize hybrids meaned over grain fill

Stress treatment	Stem segment	Hybrid	
		SA 6	K78Y x I137TN
S	A1	4,0	4,5
	B1	3,8	3,9
NS	A1	4,3	4,5
	B1	3,5	4,1

Body of table

	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid and stress	0,3	0,4
Comparison of means at the same level of stem segment or with no factor in common	0,5	0,7

starch composition, by 0,2 % (NS). Starch composition in the A1 segment of K78Y x I137TN under stress conditions exceeded that in the B1 segment by 0,6 % ($p = 0,01$). Under stress conditions the B1 segment of SA 6 had non-significantly higher starch composition than under non-stress conditions. This is contrary to the trend of the A1 segment of SA 6 and both segments of K78Y x I137TN.

Third order interaction

The interaction of hybrid, stress treatment, WAA and stem segment was non-significant (Figure 3.8). There were no significant components of the interaction either. However, there were apparent differences between hybrids in the changes in starch composition levels in the stem segments during grain fill under stress and non-stress conditions.

Starch composition ranged from a low of 2,1 % in the A1 and B1 segments of SA 6 at PM under stress conditions to a high of 5,9 % in the A1 and B1 segments of SA 6 at 3 WAA under stress conditions.

The basis for the significant second order interaction of hybrid, stress treatment and stem segment becomes even clearer when data in Figure 3.8 is studied. Under stress conditions the A1 segment of SA 6 did not consistently have higher starch composition levels than the B1 segment as was generally the case under non-stress conditions and for K78Y x I137TN under stress and non-stress conditions.

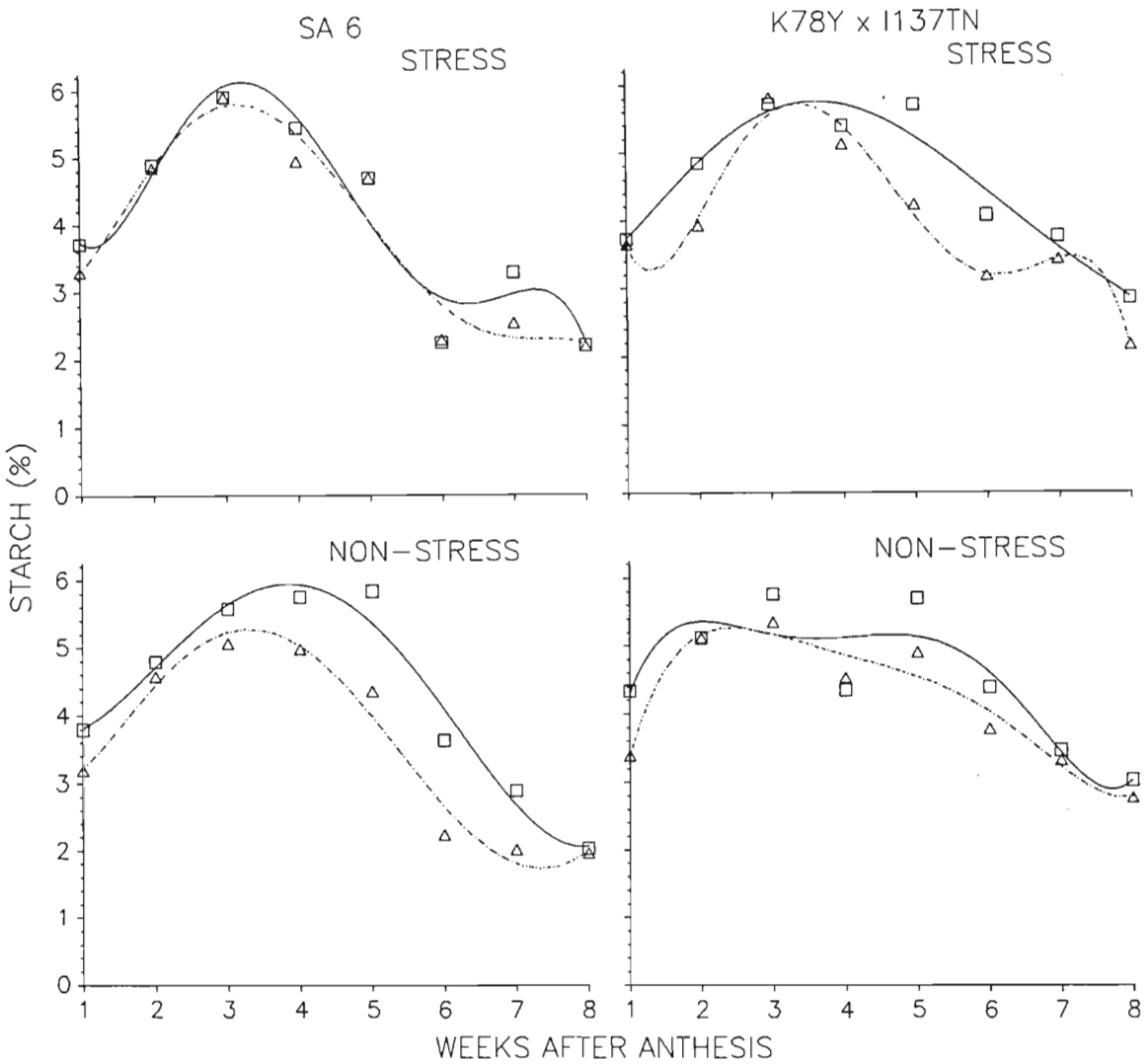


Figure 3.8 Effect of water stress from one week after anthesis to physiological maturity on starch composition in the first pair of internodes above (A1 □—□) and below (B1 △----△) the primary ear of two maize hybrids

Polynomial equations:

SA 6

Stress A1 $9,775 - 13,243x + 9,673x^2 - 2,775x^3 + 0,340x^4 - 0,015x^5$ $r^2=0,925$

B1 $3,911 - 3,241x + 3,669x^2 - 1,174x^3 + 0,146x^4 - 0,006x^5$ $r^2=0,937$

Non-stress A1 $4,010 - 1,225x + 1,299x^2 - 0,293x^3 + 0,019x^4 - 0,0001x^5$ $r^2=0,963$

B1 $3,104 - 1,270x + 1,912x^2 - 0,592x^3 + 0,065x^4 - 0,002x^5$ $r^2=0,967$

K78Y x I137TN

Stress A1 $3,102 - 0,059x + 0,979x^2 - 0,325x^3 + 0,037x^4 - 0,001x^5$ $r^2=0,938$

B1 $12,715 - 18,442x + 12,374x^2 - 3,416x^3 + 0,413x^4 - 0,018x^5$ $r^2=0,980$

Non-stress A1 $-1,907 + 10,900x - 6,078x^2 + 1,563x^3 - 0,187x^4 + 0,008x^5$ $r^2=0,794$

B1 $-3,378 + 10,888x - 5,157x^2 + 1,153x^3 - 0,125x^4 + 0,005x^5$ $r^2=0,946$

Meaned over weeks, K78Y x I137TN recorded higher starch composition in both segments under stress and non-stress conditions compared to the respectively treated SA 6 plants.

3.3.3.6 Starch content

Main effects

The main effect for hybrid was non-significant, while the main effects for WAA and stem segment were significant (Appendix 28.6). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

The main effect for stress treatment was significant (Table 3.25). Water stress resulted in a significant ($p = 0,01$) decline in starch content compared to non-stressed plants.

Table 3.25 Effect of water stress (S) and lack of water stress (NS) on mean stem segment starch content (g segment^{-1}) meaned over maize hybrids during grain fill

Stress	
S	NS
0,22	0,27
LSD (0,05) 0,03	
LSD (0,01) 0,05	

First order interactions

The interactions of hybrid with stress treatment; stress treatment with WAA; stress treatment with stem segment were all non-significant. There were no significant components of the interaction involving WAA either.

The interaction of hybrid with WAA was significant (Table 3.26). However, there were no significant components of the interaction. SA 6 showed a more marked increase in starch content from 1 to 4 WAA followed by a more marked decline in starch content from 4 WAA to PM in comparison to K78Y x I137TN. Starch content

Table 3.26 Influence of maize hybrid on mean stem segment starch content (g segment^{-1}) from one week after anthesis (WAA) to physiological maturity meaned over water stress treatments

Hybrid	Weeks after anthesis								Hybrid means
	1	2	3	4	5	6	7	8	
SA 6	0,21	0,29	0,34	0,41	0,29	0,13	0,13	0,10	0,24
K78Y x I137TN	0,22	0,28	0,37	0,33	0,31	0,23	0,17	0,12	0,25
WAA means	0,21	0,29	0,36	0,37	0,30	0,18	0,15	0,11	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,06	0,08
Comparison of means at the same level of WAA or with neither factor in common	0,07	0,09
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of WAA means	0,04	0,06

in SA 6 was non-significantly higher than that in K78Y x I137TN at 2 WAA and significantly ($p = 0,05$) higher at 4 WAA. Starch content in K78Y x I137TN was non-significantly higher than that in SA 6 at 1, 3, 5 and 7 WAA and at PM, but significantly ($p = 0,01$) higher at 6 WAA. Starch content at PM in both hybrids was significantly ($p = 0,01$) less than at 1 WAA.

The interaction of hybrid with stem segment was significant (Table 3.27). Whereas starch content in the B1 segment of SA 6 exceeded that in the A1 segment by 0,08 g segment^{-1} ($p = 0,01$), starch content in the B1 segment of K78Y x I137TN exceeded that

Table 3.27 Influence of maize hybrid on stem segment starch content (g segment^{-1}) meaned over water stress treatments during grain fill

Hybrid	Stem segment		Hybrid means
	A1	B1	
SA 6	0,20	0,28	0,24
K78Y x I137TN	0,24	0,27	0,25
Stem segment means	0,22	0,28	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,02	0,02
Comparison of means at the same level of stem segment or with neither factor in common	0,04	0,05
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of stem segment means	0,01	0,02

in the A1 segment by 0,03 g segment^{-1} ($p = 0,01$). Thus the difference between the A1 and B1 segments in starch content was more marked in SA 6 than K78Y x I137TN. While the A1 segment of K78Y x I137TN had significantly ($p = 0,05$) higher starch content than the A1 segment of SA 6, the B1 segment of SA 6 had non-significantly higher starch content than the B1 segment of K78Y x I137TN.

The interaction of WAA with stem segment was significant (Table 3.28). The WAA(linear, quadratic, cubic) x stem segment components of the interaction were also significant. Starch content was significantly ($p = 0,01$) higher in the B1 segment than the A1 segment from 1 to 4 WAA and significantly ($p = 0,05$) higher at 5 WAA. From 6 WAA to PM starch content was, however, non-significantly higher in the B1 segment than the A1 segment. Both segments showed an initial increase in starch content, from 1 to 4 WAA but this was more marked in the B1 segment. From 4 WAA to PM starch content declined in both segments but this was more rapid in the B1 segment as evidenced by an increasingly smaller difference in starch content between segments towards PM. Starch content at PM in both segments was significantly ($p = 0,01$) less than at 1 WAA, the difference being more marked in the B1 segment.

Table 3.28 Influence of weeks after anthesis (WAA) on stem segment starch content (g segment^{-1}) meaned over maize hybrids and water stress treatments

WAA	Stem segment		WAA means
	A1	B1	
1	0,18	0,24	0,21
2	0,23	0,34	0,29
3	0,29	0,42	0,36
4	0,32	0,42	0,37
5	0,28	0,32	0,30
6	0,18	0,18	0,18
7	0,14	0,16	0,15
8	0,10	0,12	0,11
Stem segment means	0,22	0,28	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of WAA	0,04	0,05
Comparison of means at the same level of stem segment or with neither factor in common	0,05	0,07
Marginal means		
Comparison of WAA means	0,04	0,06
Comparison of stem segment means	0,01	0,02

Second order interactions

The interactions of hybrid, stress treatment and WAA; hybrid, stress treatment and stem segment; hybrid, WAA and stem segment; stress treatment, WAA and stem segment were all non-significant.

There were no significant components of the interactions involving WAA either.

Third order interaction

The interaction of hybrid, stress treatment, WAA and stem segment was non-significant (Figure 3.9). There were no significant components of the interaction either. However, there were apparent differences between hybrids in the changes in starch content levels in the stem segments during grain fill under stress and non-stress conditions.

Starch content ranged from a low of 0,07 g segment^{-1} in the A1 segment of SA 6 at PM under stress conditions to a high of 0,53 g segment^{-1} in the B1 segment of SA 6 at 4 WAA under non-stress conditions.

Starch content levels followed a similar pattern to that of sucrose content levels in both hybrids under stress and non-stress conditions. Starch levels initially increased from 1 to 4 WAA, more markedly in SA 6, and then declined from 4 WAA to PM in both hybrids under stress and non-stress conditions. Stress did, however, reduce the amount of starch in each segment of both hybrids, generally by similar amounts. This may indicate some utilization of starch reserves in these stem segments as a result of the reduced photosynthetic capacity of the plants under stress conditions.

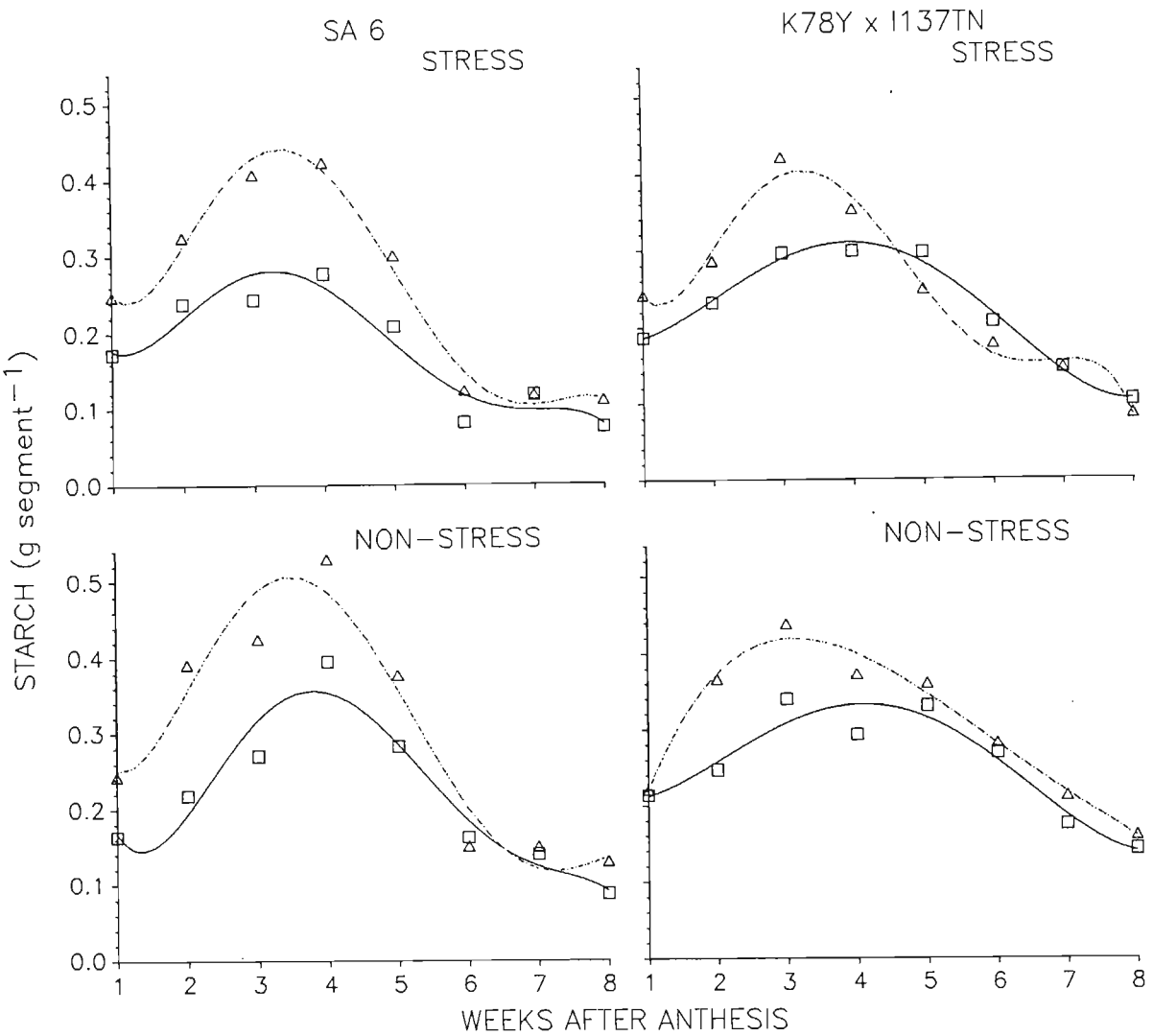


Figure 3.9 Effect of water stress from one week after anthesis to physiological maturity on starch content in the first pair of internodes above (A1 □—□) and below (B1 △···△) the primary ear of two maize hybrids

Polynomial equations:

SA 6

Stress	A1	$0,416 - 0,526x + 0,382x^2 - 0,108x^3 + 0,013x^4 - 0,001x^5$	$r^2=0,905$
	B1	$0,750 - 1,049x + 0,725x^2 - 0,196x^3 + 0,023x^4 - 0,001x^5$	$r^2=0,984$
Non-stress	A1	$0,682 - 1,101x + 0,646x^2 - 0,163x^3 + 0,018x^4 - 0,001x^5$	$r^2=0,921$
	B1	$0,585 - 0,775x + 0,581x^2 - 0,158x^3 + 0,018x^4 - 0,001x^5$	$r^2=0,930$

K78Y x I137TN

Stress	A1	$0,199 - 0,068x + 0,070x^2 - 0,015x^3 + 0,001x^4$	$r^2=0,986$
	B1	$0,744 - 1,072x + 0,757x^2 - 0,213x^3 + 0,026x^4 - 0,001x^5$	$r^2=0,985$
Non-stress	A1	$0,223 - 0,059x + 0,061x^2 - 0,013x^3 + 0,001x^4$	$r^2=0,912$
	B1	$-0,090 + 0,409x - 0,109x^2 + 0,011x^3 - 0,0004x^4$	$r^2=0,979$

The ratio of starch content to sucrose content (Table 3.21, Figure 3.7), indicates that only in the A1 segment at 8 WAA, and the A1 and B1 segments at PM in SA 6 under stress conditions did starch content exceed sucrose content. On average over the weeks during grain fill, SA 6 had a higher starch content to sucrose content ratio under both stress and non-stress conditions than did K78Y x I137TN. Also the starch content to sucrose content ratio was highest in SA 6 under stress conditions when averaged over weeks. The ratio averaged over weeks was generally the same for K78Y x I137TN under stress and non-stress conditions. The starch content to sucrose content ratio was generally higher in K78Y x I137TN from 1 to 4 WAA under stress and non-stress conditions compared to SA 6. From 4 WAA to PM the ratio was generally lower in K78Y x I137TN under stress and non-stress conditions compared to SA 6. In fact, while the ratio declined in K78Y x I137TN under stress and non-stress conditions from 4 WAA to PM, it increased markedly in SA 6 under stress and non-stress conditions during the same period and particularly from 5 WAA to PM. Thus it appears that sucrose content declined by a greater proportion than starch content in SA 6 under stress and non-stress conditions from 4 WAA to PM. The opposite was true in K78Y x I137TN. This again indicates that sucrose was moved through and/or accumulated in the stem of K78Y x I137TN until much later into the grain filling period compared to SA 6. Under stress conditions the starch content to sucrose content ratio was particularly high in SA 6 indicating, perhaps, reduced synthesis, translocation and/or storage of sucrose in the stem. This further indicates that in terms of sucrose partitioning patterns SA 6 was more sensitive to water deficits than K78Y x I137TN.

3.3.3.7 Total non-structural carbohydrate composition and residual composition

Main effects

The main effects for hybrid and WAA were significant, while the main effects for stress treatment and stem segment were non-significant (Appendix 28.7). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

First order interactions

The interaction of hybrid with stress treatment was non-significant. This indicates that stress resulted in a similar decline in TNC composition for both hybrids. However, this was not a consistent pattern for both segments as the second order interaction of hybrid, stress treatment and stem segment was significant.

The interaction of hybrid with WAA was significant (Table 3.29). The hybrid x WAA(linear and cubic) components of the interaction were also significant. SA 6 showed a more marked increase in TNC composition from 1 to 3 WAA followed by a more marked decline in TNC composition from 3 WAA to PM in comparison to K78Y x I137TN. Initially from 1 to 4 WAA TNC composition in SA 6 was non-significantly higher than that in K78Y x I137TN, but TNC composition was non-significantly higher in K78Y x I137TN than in SA 6 at 5 WAA and significantly ($p = 0,01$) higher from 6 WAA

to PM. At PM TNC composition in both hybrids was significantly ($p = 0,01$) less than at 1 WAA, with the difference more marked in SA 6 than in K78Y x I137TN. This is once again indicative of the capacity of K78Y x I137TN to maintain higher concentrations of non-structural carbohydrates in the stem segments later into grain fill than SA 6.

Table 3.29 Influence of maize hybrid on mean stem segment total non-structural carbohydrate composition (%) from one week after anthesis (WAA) to physiological maturity meaned over water stress treatments

Hybrid	Weeks after anthesis								Hybrid means
	1	2	3	4	5	6	7	8	
SA 6	28,1	34,2	37,9	37,4	31,1	19,4	13,0	10,6	26,4
K78Y x I137TN	27,0	30,8	35,6	35,4	32,7	29,8	24,8	19,4	29,4
WAA means	27,6	32,5	36,7	36,4	31,9	24,6	18,9	15,0	

Body of table	LSD 0,05	LSD 0,01
Comparison of means at the same level of hybrid	4,5	5,9
Comparison of means at the same level of WAA or with neither factor in common	4,6	6,2
Marginal means		
Comparison of hybrid means	2,0	2,9
Comparison of WAA means	3,1	4,2

The interaction of stress treatment with WAA was non-significant. However, the stress treatment x WAA(linear) component of the interaction was significant (Table 3.30). Stressed plants increased

Table 3.30 Effect of water stress (S) and lack of water stress (NS) on mean stem segment total non-structural carbohydrate composition (%) from one week after anthesis (WAA) to physiological maturity meaned over maize hybrids

Stress treatment	Weeks after anthesis								Stress treatment means
	1	2	3	4	5	6	7	8	
S	26,9	32,7	38,4	36,9	30,5	23,5	16,2	12,2	27,2
NS	28,2	32,2	35,0	35,9	33,2	25,7	21,6	17,8	28,7
WAA means	27,6	32,5	36,7	36,4	31,9	24,6	18,9	15,0	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of stress treatment	4,5	5,9
Comparison of means at the same level of WAA or with neither factor in common	4,6	6,2
Marginal means		
Comparison of stress treatment means	NS	NS
Comparison of WAA means	0,6	0,8

more rapidly in TNC composition levels from 1 to 3 WAA and then declined more rapidly in TNC composition from 3 WAA to PM in comparison to non-stressed plants. The TNC composition was non-significantly higher in stressed plants than in non-stressed plants from 2 to 4 WAA, but TNC composition was non-significantly higher in the non-stressed plants at 1, 5 and 6 WAA and significantly ($p = 0,05$) higher at 7 WAA and PM. At PM TNC composition in stressed and non-stressed plants was significantly ($p = 0,01$) less than at 1 WAA, however the difference was more marked in stressed plants than non-stressed plants. Thus it

appears that stressed plants were unable to maintain concentrations of non-structural carbohydrates in the stem segments at the same levels as the non-stressed plants, particularly from 5 WAA to PM.

The interaction of hybrid with stem segment was significant. Whereas TNC composition in the A1 segment of SA 6 exceeded that in the B1 segment by 1,5 % ($p = 0,01$), the B1 segment of K78Y x I137TN exceeded the A1 segment in TNC composition by 0,8 % ($p = 0,05$). However, this was not a consistent pattern under stress and non-stress conditions as the second order interaction of hybrid, stress treatment and stem segment was significant.

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

Second order interactions

The interactions of hybrid, stress treatment and WAA; hybrid, WAA and stem segment; stress treatment, WAA and stem segment were all non-significant. There were no significant components of the interactions involving WAA either.

The interaction of hybrid, stress treatment and stem segment was significant (Table 3.31). Under non-stress conditions TNC composition in the A1 segment of SA 6 exceeded that in the B1 segment by 2,0 % ($p = 0,01$), while TNC composition in the B1

segment of K78Y x I137TN exceeded that in the A1 segment by 1,6 % (p = 0,01). Under stress conditions the A1 segment of SA 6 exceeded the B1 segment in TNC composition by 1,2 % (p = 0,05). The TNC composition in the A1 segment of K78Y x I137TN under stress conditions exceeded that in the B1 segment by 0,1 % (NS). Thus the B1 segment of K78Y x I137TN exceeded the A1 segment in TNC composition under non-stress conditions but the opposite was true under stress conditions.

Table 3.31 Effect of water stress (S) and lack of water stress (NS) on total non-structural carbohydrate composition (%) in stem segments of two maize hybrids meaned over grain fill

Stress treatment	Stem segment	Hybrid	
		SA 6	K78Y x I137TN
S	A1	26,5	28,5
	B1	25,3	28,4
NS	A1	28,0	29,6
	B1	26,0	31,2

Body of table

	LSD 0,05	LSD 0,01
Comparison of means at the same level of hybrid and stress	1,2	1,6
Comparison of means at the same level of stem segment or with no factor in common	3,0	4,2

Third order interaction

The interaction of hybrid, stress treatment, WAA and stem segment was non-significant (Figure 3.10). There were no significant components of the interaction either. However, there were apparent differences between hybrids in the changes in TNC composition levels in the stem segments during grain fill under stress and non-stress conditions.

In both hybrids under stress and non-stress conditions, TNC made up an increasing proportion of the dry mass of both segments from 1 WAA to, and peaking at, 3 to 4 WAA. Under stress conditions the decline in TNC composition levels from 3 WAA to PM was more marked in both hybrids than under non-stress conditions. Stress resulted in a more marked decline in the TNC composition of the B1 segment than the A1 segment of K78Y x I137TN but at PM K78Y x I137TN had higher TNC composition levels in both stem segments under stress conditions than did SA 6. Under non-stress conditions K78Y x I137TN at PM also had higher TNC composition levels in both stem segments than did SA 6. This provides further evidence that K78Y x I137TN has a tendency to maintain higher TNC levels in the latter phase of grain fill under stress and non-stress conditions in comparison to SA 6.

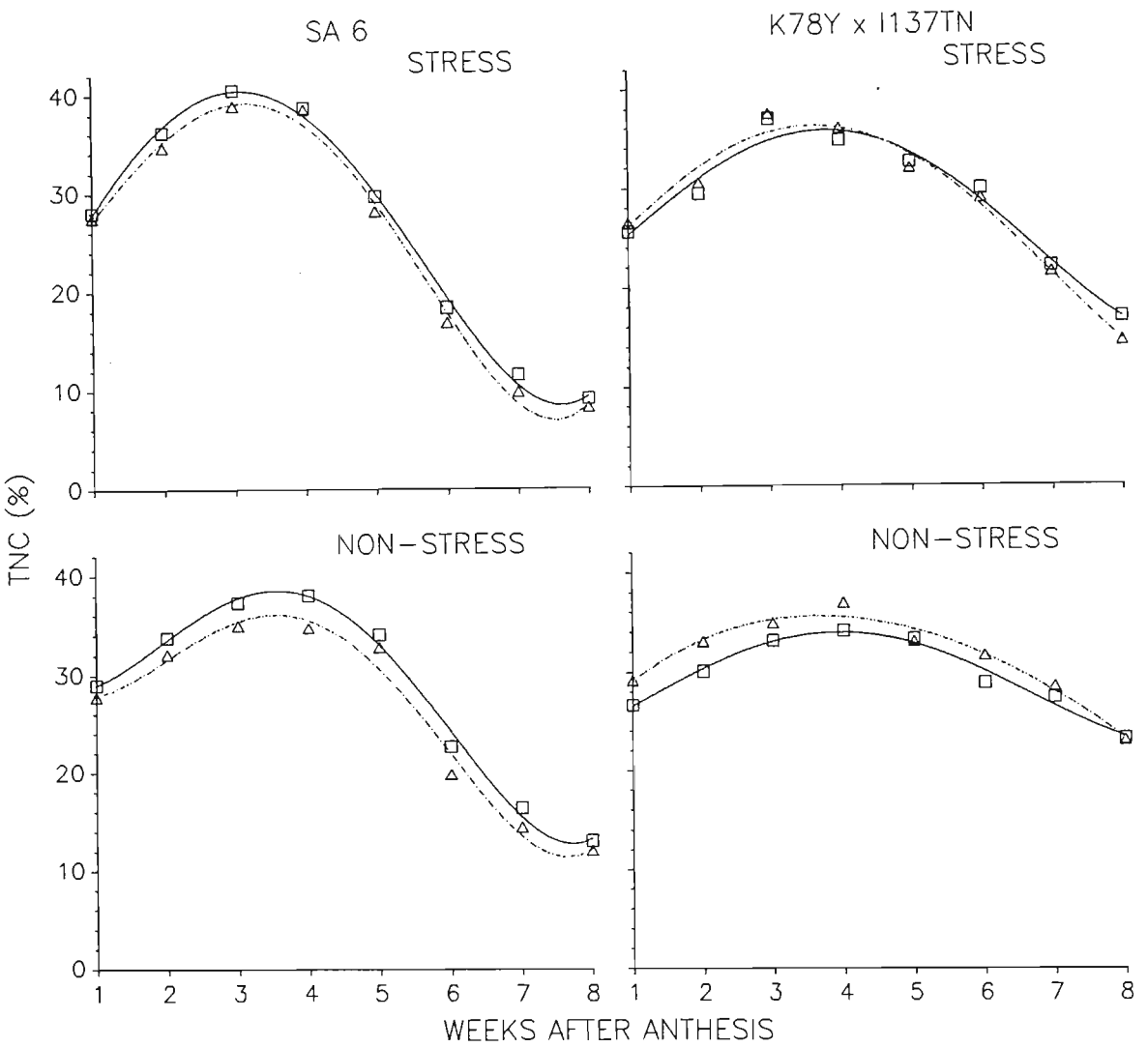


Figure 3.10 Effect of water stress from one week after anthesis to physiological maturity on total non-structural carbohydrate (TNC) composition in the first pair of internodes above (A1 □—□) and below (B1 △·····△) the primary ear of two maize hybrids

Polynomial equations:

SA 6

Stress	A1	$16,235 + 11,617x + 0,771x^2 - 0,873x^3 + 0,073x^4$	$r^2=0,997$
	B1	$19,946 + 4,989x + 3,585x^2 - 1,339x^3 + 0,099x^4$	$r^2=0,994$
Non-stress	A1	$30,371 - 6,982x + 7,188x^2 - 1,663x^3 + 0,105x^4$	$r^2=0,993$
	B1	$31,055 - 9,413x + 7,918x^2 - 1,765x^3 + 1,111x^4$	$r^2=0,982$

K78Y x I137TN

Stress	A1	$19,652 + 4,909x + 1,217x^2 - 0,487x^3 + 0,032x^4$	$r^2=0,966$
	B1	$18,710 + 7,653x + 0,059x^2 - 0,311x^3 + 0,022x^4$	$r^2=0,978$
Non-stress	A1	$22,803 + 3,234x + 0,827x^2 - 0,318x^3 + 0,021x^4$	$r^2=0,973$
	B1	$22,228 + 8,422x - 1,656x^2 + 0,111x^3 - 0,004x^4$	$r^2=0,970$

3.3.3.8 Total non-structural carbohydrate content, residual content and stem segment dry mass

Main effects for TNC content

The main effect for hybrid was non-significant, while the main effects for stress treatment, WAA and stem segment were significant (Appendix 28.8). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

First order interactions for TNC content

The interaction of hybrid with stress treatment was non-significant.

The interaction of hybrid with WAA was significant (Table 3.32). The hybrid x WAA(linear and cubic) components of the interaction were also significant. SA 6 showed a more marked increase in TNC content from 1 to 4 WAA, followed by a more marked decline in TNC content from 4 WAA to PM in comparison to K78Y x I137TN. The TNC content did, however, decline by greater amounts in K78Y x I137TN from 6 WAA to PM. Initially TNC content in SA 6 was non-significantly higher at 1, 2 and 4 WAA than in K78Y x I137TN. But TNC content in K78Y x I137TN was non-significantly higher than in SA 6 at 5 WAA and significantly higher at 6 WAA ($p = 0,01$) and 7 WAA ($p = 0,05$). At PM TNC content was non-significantly higher in K78Y x I137TN than in SA 6. At PM TNC content in both hybrids was significantly ($p = 0,01$) less than

at 1 WAA, with the difference being marked in SA 6. Thus it appears that initially from 1 to 4 WAA SA 6 accumulated higher amounts of non-structural carbohydrates in the A1 and B1 segments than K78Y x I137TN. However, perhaps as a result of greater leaf senescence under stress and non-stress conditions (Section 3.3.2), SA 6 was unable to produce enough current photosynthate to maintain the non-structural carbohydrates to the same levels as did K78Y x I137TN during the latter half of grain fill (Section 3.3.2). In fact, at PM SA 6 had depleted the TNC in the stem segments to a much greater extent than had K78Y x I137TN.

Table 3.32 Influence of maize hybrid on mean stem segment total non-structural carbohydrate content (g segment^{-1}) from one week after anthesis (WAA) to physiological maturity meaned over water stress treatments

Hybrid	Weeks after anthesis								Hybrid means
	1	2	3	4	5	6	7	8	
SA 6	1,71	2,11	2,26	2,87	1,91	0,99	0,73	0,53	1,64
K78Y x I137TN	1,59	1,88	2,35	2,43	1,99	1,82	1,25	0,91	1,78
WAA means	1,65	1,99	2,31	2,65	1,95	1,41	0,99	0,72	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,40	0,54
Comparison of means at the same level of WAA or with neither factor in common	0,46	0,63
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of WAA means	0,29	0,38

The interaction of stress treatment with WAA was non-significant. However, the stress treatment x WAA(linear) component of the interaction was significant (Table 3.33). Stressed plants increased less markedly in TNC content from 1 to 4 WAA compared to non-stressed plants, but declined more markedly in TNC content from 4 WAA to PM in comparison to non-stressed plants. The TNC content in non-stressed plants was non-significantly higher than that in stressed plants from 1 to 3 WAA and at 6 WAA but it was significantly higher in non-stressed plants than stressed plants at 4 WAA ($p = 0,05$), 5 WAA ($p = 0,05$), 7 WAA ($p = 0,01$) and at PM ($p = 0,05$). At PM TNC content in stressed and non-stressed

Table 3.33 Effect of water stress (S) and lack of water stress (NS) on mean stem segment total non-structural carbohydrate content (g segment^{-1}) from one week after anthesis (WAA) to physiological maturity meaned over maize hybrids

Stress treatment	Weeks after anthesis								Stress treatment means
	1	2	3	4	5	6	7	8	
S	1,61	1,94	2,25	2,41	1,66	1,19	0,66	0,46	1,52
NS	1,69	2,05	2,37	2,89	2,24	1,63	1,32	0,98	1,90
WAA means	1,65	1,99	2,31	2,65	1,95	1,41	0,99	0,72	

Body of table

	LSD 0,05	LSD 0,01
Comparison of means at the same level of stress treatment	0,40	0,54
Comparison of means at the same level of WAA or with neither factor in common	0,46	0,63
Marginal means		
Comparison of stress treatment means	0,27	0,38
Comparison of WAA means	0,29	0,38

plants was significantly (p = 0,01) less than at 1 WAA, with the difference being marked in stressed plants.

The interaction of hybrid with stem segment was significant (Table 3.34). Whereas TNC content in the B1 segment of SA 6 exceeded that in the A1 segment by 0,68 g segment^{-1} (p = 0,01), the B1 segment of K78Y x I137TN exceeded the A1 segment in TNC content by 0,49 g segment^{-1} (p = 0,01). Thus the difference between the A1 and B1 segments in TNC content was more marked in SA 6 than in K78Y x I137TN. The TNC content in the A1 segment of K78Y x I137TN was 0,23 g segment^{-1} (NS) more than that in the A1 segment of SA 6. The TNC content in the B1 segment of

Table 3.34 Influence of maize hybrid on stem segment total non-structural carbohydrate content (g segment^{-1}) meaned over water stress treatments during grain fill

Hybrid	Stem segment		Hybrid means
	A1	B1	
SA 6	1,30	1,98	1,64
K78Y x I137TN	1,53	2,02	1,78
Stem segment means	1,41	2,00	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,11	0,15
Comparison of means at the same level of stem segment or with neither factor in common	0,28	0,40
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of stem segment means	0,08	0,10

K78Y x I137TN was only 0,04 g segment-1 (NS) more than that in the B1 segment of SA 6.

The interaction of stress treatment with stem segment was significant (Table 3.35). Under non-stress conditions the B1 segment exceeded the A1 segment in TNC content by 0,71 g segment^{-1} ($p = 0,01$). Under stress conditions the B1 segment exceeded the A1 segment by 0,46 g segment^{-1} ($p = 0,01$). Thus the difference between the segments in TNC content was less marked under stress then under non-stress conditions. The A1 segment under non-stress conditions exceeded the A1 segment under stress conditions

Table 3.35 Effect of water stress (S) and lack of water stress (NS) on stem segment total non-structural carbohydrate content (g segment^{-1}) meaned over maize hybrids during grain fill

Stress treatment	Stem segment		Stress treatment means
	A1	B1	
S	1,29	1,75	1,52
NS	1,54	2,25	1,90
Stem segment means	1,41	2,00	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of stress treatment	0,11	0,15
Comparison of means at the same level of stem segment or with neither factor in common	0,28	0,40
Marginal means		
Comparison of stress treatment means	0,27	0,38
Comparison of stem segment means	0,08	0,10

in TNC content by 0,25 g segment^{-1} (NS). The B1 segment under non-stress conditions exceeded the B1 segment under stress conditions in TNC content by 0,50 g segment^{-1} ($p = 0,01$). Thus the difference in TNC content between the B1 segment under stress and non-stress conditions was more marked than for the A1 segment under stress and non-stress conditions. It therefore appears that water stress resulted in a greater depletion of the TNC in the B1 segment on an absolute basis in comparison to the A1 segment.

The interaction of WAA with stem segment was significant (Table 3.36). The WAA(linear, quadratic and cubic) x stem segment components of the interaction were also significant. The TNC content in the B1 segment significantly ($p = 0,01$) exceeded that in the A1 segment from 1 to 6 WAA, and significantly ($p = 0,05$) exceeded that in the A1 segment at 7 WAA. At PM, however, TNC content in the B1 segment non-significantly exceeded that in the A1 segment. Both segments showed an initial increase in TNC content from 1 to 4 WAA but this was more marked in the B1 segment. From 4 WAA to PM TNC content declined in both segments but this was more rapid in the B1 segment as evidenced by the increasingly smaller differences in TNC content between the segments as PM approached.

Table 3.36 Influence of weeks after anthesis (WAA) on stem segment total non-structural carbohydrate content (g segment^{-1}) meaned over maize hybrids and water stress treatments

WAA	Stem segment		WAA means
	A1	B1	
1	1,30	2,00	1,65
2	1,55	2,44	1,99
3	1,84	2,78	2,31
4	2,20	3,11	2,65
5	1,65	2,25	1,95
6	1,24	1,57	1,41
7	0,88	1,10	0,99
8	0,65	0,79	0,72
Stem segment means	1,41	2,00	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of WAA	0,22	0,29
Comparison of means at the same level of stem segment or with neither factor in common	0,33	0,43
Marginal means		
Comparison of WAA means	0,29	0,38
Comparison of stem segment means	0,08	0,10

Second order interactions for TNC content

The interactions of hybrid, stress treatment and WAA; hybrid, stress treatment and stem segment; hybrid, WAA and stem segment; stress treatment, WAA and stem segment were all non-significant.

There were no significant components of the interactions involving WAA either.

Main effects for residual content

The main effects for hybrid and WAA were non-significant, while the main effects for stress treatment and stem segment were significant (Appendix 28.9). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

First order interactions for residual content

The interactions of hybrid with stress treatment, hybrid with WAA, and stress treatment with WAA were all non-significant. There were no significant components of the interactions involving WAA either.

The interaction of hybrid with stem segment was significant (Table 3.37). Whereas residual content in the B1 segment of SA 6 exceeded that in the A1 segment by 2,10 g segment^{-1} ($p = 0,01$), in K78Y x I137TN the B1 segment exceeded the A1 segment by 0,96 g segment^{-1} ($p = 0,01$) in residual content. Thus the difference between the A1 and B1 segments in residual content was more marked in SA 6 than K78Y x I137TN. Residual content in the A1 segment of K78Y x I137TN was 0,40 g segment^{-1} (NS) more than that in A1 segment of SA 6. But residual content in the B1 segment of SA 6 was 0,74 g segment^{-1} ($p = 0,05$) more than that in B1 segment of K78Y x I137TN.

Table 3.37 Influence of maize hybrid on stem segment residual content (g segment^{-1}) meaned over water stress treatments during grain fill

Hybrid	Stem segment		Hybrid means
	A1	B1	
SA 6	3,24	5,34	4,29
K78Y x I137TN	3,64	4,60	4,12
Stem segment means	3,44	4,97	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,25	0,33
Comparison of means at the same level of stem segment or with neither factor in common	0,53	0,76
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of stem segment means	0,17	0,23

The interaction of stress treatment with stem segment was significant (Table 3.38). Under non-stress conditions the B1 segment exceeded the A1 segment in residual content by 1,74 g segment^{-1} ($p = 0,01$). Under stress conditions the B1 segment exceeded the A1 segment by 1,32 g segment^{-1} ($p = 0,01$) in residual content. Thus the difference between the segments in residual content was less marked under stress than under non-stress conditions. The A1 segment under non-stress conditions exceeded the A1 segment under stress conditions in residual content by 0,45 g segment^{-1} (NS). The B1 segment under non-stress conditions exceeded the B1 segment under stress conditions by

0,87 g segment^{-1} (p = 0,01). Thus the decline in residual content as a result of stress was more marked in the B1 segment than the A1 segment.

Table 3.38 Effect of water stress (S) and lack of water stress (NS) on stem segment residual content (g segment^{-1}) meaned over maize hybrids during grain fill

Stress treatment	Stem segment		Stress treatment means
	A1	B1	
S	3,21	4,53	3,87
NS	3,66	5,40	4,53
Stem segment means	3,44	4,97	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of stress treatment	0,25	0,33
Comparison of means at the same level of stem segment or with neither factor in common	0,53	0,76
Marginal means		
Comparison of stress means	0,50	0,72
Comparison of stem segment means	0,17	0,23

The interaction of WAA with stem segment was non-significant. However, the WAA(linear) x stem segment component of the interaction was significant (Table 3.39). Residual content in the B1 segment significantly (p = 0,01) exceeded that in the A1 segment from 1 WAA to PM. The B1 segment markedly exceeded the A1 segment in residual content from 1 to 4 WAA. From 4 WAA to PM residual content generally declined in both segments but this

was more rapid in the B1 segment, as evidenced by the increasingly smaller differences in residual content between the segments as PM approached.

Table 3.39 Influence of weeks after anthesis (WAA) on stem segment residual content (g segment^{-1}) meaned over maize hybrids and water stress treatments

WAA	Stem segment		WAA means
	A1	B1	
1	3,45	5,15	4,30
2	3,22	5,06	4,14
3	3,17	4,91	4,04
4	3,86	5,49	4,67
5	3,44	4,85	4,15
6	3,50	4,79	4,14
7	3,50	4,86	4,18
8	3,38	4,64	4,01
Stem segment means	3,44	4,97	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of WAA	0,49	0,65
Comparison of means at the same level of stem segment or with neither factor in common	0,60	0,80
Marginal means		
Comparison of WAA means	NS	NS
Comparison of stem segment means	0,17	0,23

Second order interactions for residual content

The interactions of hybrid, stress treatment and WAA; hybrid, stress treatment and stem segment; hybrid, WAA and stem segment; stress treatment, WAA and stem segment were all non-significant. There were no significant components of the interactions involving WAA either.

Main effects for stem segment dry mass

The main effect for hybrid was non-significant, while the main effects for stress treatment, WAA and stem segment were significant (Appendix 28.10). However, since these factors were involved in significant higher order interactions their main effects are of limited interest.

First order interactions for dry mass

The interaction of hybrid with stress treatment was non-significant. However, SA 6 showed a marginally greater reduction in dry mass due to water stress compared to K78Y x I137TN (Table 3.40). This infers that SA 6 has a tendency to utilize labile organic components that contribute to stem segment dry mass more than K78Y x I137TN during grain fill under stress conditions.

Table 3.40 Influence of maize hybrid and water stress (S) or lack of water stress (NS) on mean stem segment dry mass (g segment^{-1}) during grain fill

Hybrid	Stress treatment		Hybrid means
	S	NS	
SA 6	5,4	6,5	5,9
K78Y x I137TN	5,4	6,4	5,9
Stress treatment means	5,4	6,4	

Body of table	LSD 0,05	LSD 0,01
Comparison of means at the same level of hybrid	NS	NS
Comparison of means at the same level of stress treatment or with neither factor in common	NS	NS
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of stress treatment means	0,7	1,0

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

The interaction of stress treatment with WAA was non-significant. However, the stress treatment x WAA(linear) component of the interaction was significant (Table 3.41). Dry mass increased under stress and non-stress conditions from 1 to 4 WAA but much more markedly under non-stress conditions. From 4 WAA to PM dry mass declined but more markedly under non-stress conditions than under stress conditions. Stem segment dry mass was significantly ($p = 0,01$) higher under non-stress conditions than stress

conditions at 4 WAA, and significantly (p = 0,05) higher from 5 WAA to PM. At PM dry mass of stressed plants was significantly (p = 0,01) less than at 1 WAA, whereas dry mass of non-stressed plants at PM was non-significantly less than at 1 WAA. Thus it appears that under stress conditions the plants accumulated less dry mass in the stem segments from 1 to 4 WAA, and then from 4 WAA to PM depleted labile organic compounds which contribute to stem dry mass to lower levels than under non-stress conditions.

Table 3.41 Effect of water stress (S) and lack of water stress (NS) on mean stem segment dry mass (g segment^{-1}) from one week after anthesis (WAA) to physiological maturity meaned over maize hybrids

Stress treatment	Weeks after anthesis								Stress treatment means
	1	2	3	4	5	6	7	8	
S	5,9	5,9	5,9	6,5	5,5	4,9	4,5	4,1	5,4
NS	6,0	6,3	6,8	8,1	6,7	6,2	5,9	5,4	6,4
WAA means	5,9	6,1	6,3	7,3	6,1	5,5	5,2	4,7	

Body of table

	LSD 0,05	LSD 0,01
Comparison of means at the same level of stress treatment	0,9	1,3
Comparison of means at the same level of WAA or with neither factor in common	1,1	1,6
Marginal means		
Comparison of stress treatment means	0,7	1,0
Comparison of WAA means	0,7	0,9

The interaction of hybrid with stem segment was significant (Table 3.42). Whereas dry mass of the B1 segment of SA 6 exceeded that of the A1 segment by 2,8 g segment^{-1} (p = 0,01), in K78Y x I137TN dry mass of the B1 segment exceeded that of the A1 segment by 1,4 g segment^{-1} (p = 0,01). Thus the difference in dry mass between the A1 and B1 segments was more marked in SA 6 than K78Y x I137TN. The dry mass of the A1 segment of K78Y x I137TN was 0,7 g segment^{-1} (NS) more than that in the A1 segment of SA 6. But the dry mass of the B1 segment of SA 6 was 0,7 g segment^{-1} (NS) more than that of the B1 segment of K78Y x I137TN.

Table 3.42 Influence of maize hybrid on stem segment dry mass (g segment^{-1}) meaned over water stress treatments during grain fill

Hybrid	Stem segment		Hybrid means
	A1	B1	
SA 6	4,5	7,3	5,9
K78Y x I137TN	5,2	6,6	5,9
Stem segment means	4,9	7,0	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of hybrid	0,3	0,4
Comparison of means at the same level of stem segment or with neither factor in common	0,8	1,1
Marginal means		
Comparison of hybrid means	NS	NS
Comparison of stem segment means	0,2	0,3

The interaction of stress treatment with stem segment was significant (Table 3.43). Under non-stress conditions the dry mass of the B1 segment exceeded that of the A1 segment by 2,5 g segment^{-1} ($p = 0,01$). Under stress conditions the B1 segment exceeded the A1 segment by 1,8 g segment^{-1} ($p = 0,01$) in dry mass. Thus the difference between the segments in dry mass was less marked under stress than under non-stress conditions. The dry mass of the A1 segment under non-stress conditions was 0,7 g segment^{-1} (NS) more than that under stress conditions. The dry mass of the B1 segment under non-stress conditions was 1,4 g segment^{-1} ($p = 0,01$) more than that under stress conditions.

Table 3.43 Effect of water stress (S) and lack of water stress (NS) on stem segment dry mass (g segment^{-1}) meaned over maize hybrids during grain fill

Stress treatment	Stem segment		Stress treatment means
	A1	B1	
S	4,5	6,3	5,4
NS	5,2	7,7	6,4
Stem segment means	4,9	7,0	

Body of table

	LSD 0,05	LSD 0,01
Comparison of means at the same level of stress treatment	0,3	0,4
Comparison of means at the same level of stem segment or with neither factor in common	0,8	1,1
Marginal means		
Comparison of stress means	0,7	1,0
Comparison of stem segment means	0,2	0,3

Thus the decline in dry mass as a result of stress was more marked in the B1 segment than the A1 segment. Once again this is indicative of the greater depletion of labile organic compounds that contribute to dry mass in the B1 segment under stress conditions than was the case for the A1 segment.

The interaction of WAA with stem segment was significant (Table 3.44). The WAA(linear) x stem segment component of the

Table 3.44 Influence of weeks after anthesis (WAA) on stem segment dry mass (g segment^{-1}) meaned over maize hybrids and water stress treatments

WAA	Stem segment		WAA means
	A1	B1	
1	4,8	7,2	5,9
2	4,8	7,5	6,1
3	5,0	7,7	6,3
4	6,1	8,6	7,3
5	5,1	7,1	6,1
6	4,7	6,4	5,5
7	4,4	6,0	5,2
8	4,0	5,4	4,7
Stem segment means	4,9	7,0	

Body of table	LSD	
	0,05	0,01
Comparison of means at the same level of WAA	0,7	0,9
Comparison of means at the same level of stem segment or with neither factor in common	0,8	1,1
Marginal means		
Comparison of WAA means	0,7	0,9
Comparison of stem segment means	0,2	0,3

interaction was also significant. Dry mass of the B1 segment significantly ($p = 0,01$) exceeded that in the A1 segment from 1 WAA to PM. Both segments increased in dry mass from 1 to 4 WAA but the increase was more marked in the B1 segment than the A1 segment. From 4 WAA both segments declined in dry mass but this was more rapid in the B1 segment as evidenced by the increasingly smaller differences in dry mass between the segments as PM approached.

Second order interactions for dry mass

The interactions of hybrid, stress treatment and WAA; hybrid, stress treatment and stem segment; hybrid, WAA and stem segment; stress treatment, WAA and stem segment were all non-significant. There were no significant components of the interactions involving WAA either.

Third order interactions for TNC content, residual content and dry mass

The interactions of hybrid, stress treatment, WAA and stem segment for TNC and residual content and segment dry mass were all non-significant (Figures 3.11 and 3.12). There were no significant components of each interaction either. However, there were apparent differences between hybrids in the changes in TNC and residual content and dry mass of the stem segments during grain fill under stress and non-stress conditions.

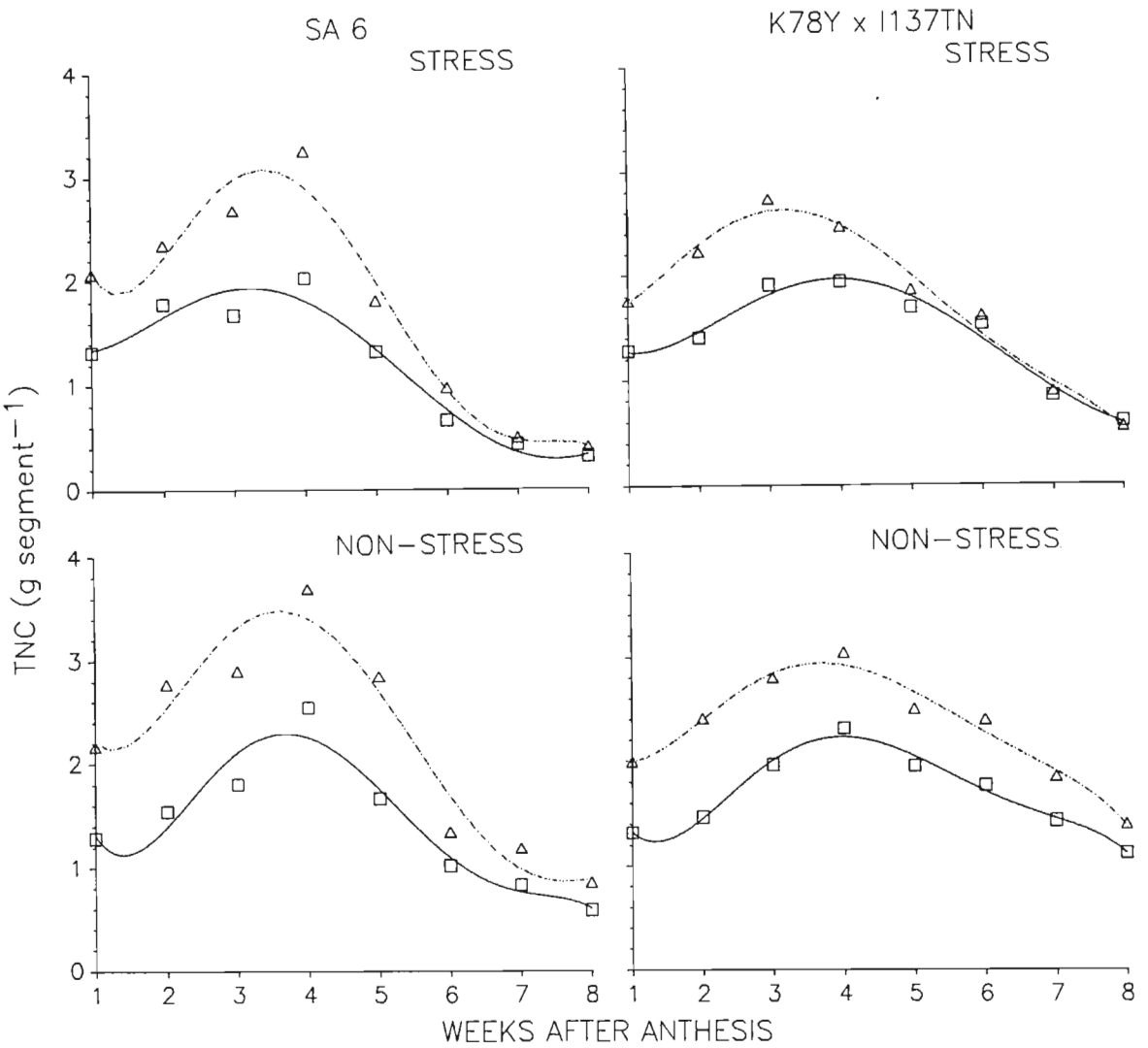


Figure 3.11 Effect of water stress from one week after anthesis to physiological maturity on total non-structural carbohydrate (TNC) content in the first pair of internodes above (A1 □—□) and below (B1 △····△) the primary ear of two maize hybrids

Polynomial equations:

SA 6

Stress	A1	1,806	-1,280x	+1,092x^2	-0,306x^3	+0,033x^4	-0,001x^5	r^2=0,952
	B1	6,333	-8,378x	+5,392x^2	-1,405x^3	+0,157x^4	-0,006x^5	r^2=0,966
Non-stress	A1	4,788	-6,774x	+4,273x^2	-1,088x^3	+0,120x^4	-0,005x^5	r^2=0,919
	B1	4,926	-5,574x	+3,701x^2	-0,938x^3	+0,099x^4	-0,004x^5	r^2=0,931

K78Y x I137TN

Stress	A1	1,925	-1,403x	+0,950x^2	-0,219x^3	+0,020x^4	-0,001x^5	r^2=0,970
	B1	1,813	-0,848x	+1,089x^2	-0,351x^3	+0,043x^4	-0,002x^5	r^2=0,980
Non-stress	A1	3,399	-4,108x	+2,623x^2	-0,662x^3	+0,073x^4	-0,003x^5	r^2=0,981
	B1	2,724	-1,884x	+1,533x^2	-0,427x^3	+0,049x^4	-0,002x^5	r^2=0,984

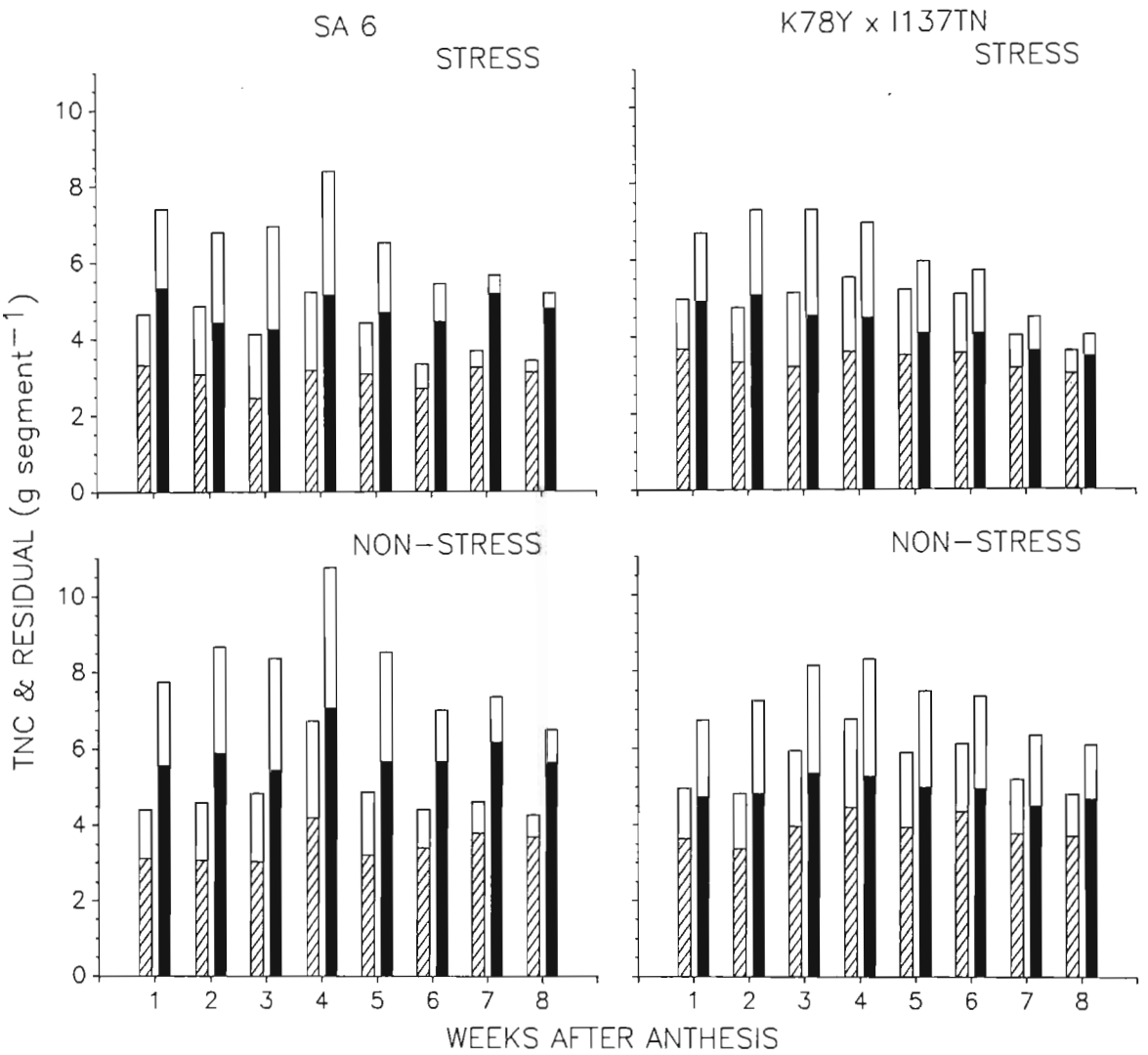


Figure 3.12 Effect of water stress from one week after anthesis to physiological maturity on total non-structural carbohydrate (TNC) and residual content, and dry mass of the first pair of internodes above (A1) and below (B1) the primary ear of two maize hybrids

Dry mass increased in both segments of both hybrids from 1 to 4 WAA under stress and non-stress conditions and then declined from 4 WAA to PM (Figure 3.12). Under non-stress conditions the initial increase in dry mass from 1 to 4 WAA was particularly marked in SA 6 in comparison to K78Y x I137TN. The B1 segment of SA 6 at 4 WAA under non-stress conditions recorded the highest dry mass of 10,8 g. Except for SA 6 at 7 WAA under stress and non-stress conditions the dry mass of the stem segments of both hybrids under stress and non-stress conditions generally declined from 4 WAA to PM. Water deficits resulted in a greater decline in dry mass during this period. This indicates that current photosynthate was limited as a result of grain requirements and increasing leaf senescence. Thus the TNC and residual components in the stem segments could not be maintained at their earlier levels. Under non-stress conditions SA 6 tended to more rapidly decline in stem dry mass from 4 WAA to PM in comparison to K78Y x I137TN. Over the entire grain filling period water deficits resulted in lower stem segment dry masses. It is therefore apparent that both hybrids, in particular SA 6, utilized labile organic components of the stem segments during grain fill.

Residual content of both the stem segments of both hybrids under stress and non-stress conditions did not change considerably during grain fill (Figure 3.12). From 1 to 5 WAA residual content levels fluctuated within narrow limits without consistently increasing or decreasing in both hybrids under non-stress conditions. However, under stress conditions residual content tended to decline in both hybrids from 1 to 3 WAA. From

3 WAA to PM the difference between the non-stressed and stressed segments in residual content was similar for both hybrids. Residual content under stress and non-stress conditions tended to increase in SA 6 from 6 WAA to PM, while it declined during the same period in K78Y x I137TN. Residual content in the A1 and B1 segments of SA 6 under stress conditions at PM was 85,05 %, and 84,57 % of that in the respective segments at PM under non-stress conditions. Residual content in the A1 and B1 segments of K78Y x I137TN under stress conditions at PM was 82,11 and 74,36 % of that in the respective segments at PM under non-stress conditions. It appears that under stress conditions, in comparison to SA 6, K78Y x I137TN tended to partition less photosynthate to components of the residual fraction during the last weeks of grain fill, which resulted in an overall decline in residual content.

In contrast to residual content, the TNC content of both segments of both hybrids under stress and non-stress conditions fluctuated considerably during grain fill (Figures 3.11 and 3.12). SA 6 tended to show a more marked increase in TNC content from 1 WAA to 3-4 WAA under stress and non-stress conditions in comparison to K78Y x I137TN. During this period SA 6 generally recorded higher TNC content levels under stress and non-stress conditions than did the respectively treated K78Y x I137TN plants. However, from 4 WAA to PM, TNC content declined more rapidly in SA 6 under stress and non-stress conditions compared to K78Y x I137TN. From 5 WAA to PM K78Y x I137TN generally recorded higher TNC content levels under stress and non-stress conditions than did SA 6. As with dry mass and residual content the difference in TNC content

between the stem segments of stressed and non-stressed plants was similar for both hybrids. This remarkably similar response to water deficits shown by both hybrids should, however, be viewed against the background of very different patterns in the partitioning of TNC for sink requirements. Total non-structural carbohydrates accumulated to a greater extent in the stem segments of SA 6 during the earlier part of grain fill i.e. from 1 WAA to 3-4 WAA. From 4 WAA to PM, however, SA 6 showed a more marked decline in TNC content levels in the stem segments. This was coupled to a tendency to increase the residual content of the stem segments from 6 WAA to PM. K78Y x I137TN, on the other hand, did not show as marked a decline in TNC content from 4 WAA to PM under stress and non-stress conditions, and in contrast to SA 6 from 6 WAA to PM the residual content in the stem segments declined. The TNC content in the A1 and B1 segments of SA 6 under stress conditions was 53,44 and 47,62 % of that in the respective segments at PM under non-stress conditions. The TNC content in the A1 and B1 segments of K78Y x I137TN under stress conditions at PM was 53,15 and 38,84 % of that in the respective segments at PM under non-stress conditions. The TNC content in the A1 and B1 segments of SA 6 under stress conditions at PM was 52,28 and 72,93 % of that in the respective segments of K78Y x I137TN at PM under stress conditions. The TNC content in the A1 and B1 segments of SA 6 under non-stress conditions at PM was 52,38 and 60,73 % of that in the respective segments of K78Y x I137TN at PM under non-stress conditions. It would appear that although K78Y x I137TN, on an absolute basis, maintained higher TNC content levels at PM under stress conditions than did SA 6, on a relative basis K78Y x I137TN had less TNC content in

the stem segments under stress conditions at PM than SA 6. Although TNC content in the stem segments of SA 6 declined by an overall greater amount from 4 WAA to PM under stress and non-stress conditions compared to K78Y x I137TN, the rate at which SA 6 declined in TNC content was less rapid from 7 WAA to PM in comparison to K78Y x I137TN. In fact, TNC content in K78Y x I137TN declined by greater amounts from 7 WAA to PM in comparison to SA 6 under stress and non-stress conditions. Under stress conditions the residual content of K78Y x I137TN also declined from 6 WAA to PM. Thus it would appear that under non-stress conditions K78Y x I137TN tended to deplete the TNC pool in the stem for grain fill and respiration requirements to a greater extent than SA 6 during the final week of grain fill. Under stress conditions K78Y x I137TN also depleted the TNC pool in the stem segments to a greater extent than did SA 6 during the final week of grain fill as well as depleting the residual components in the stem segments from 6 WAA to PM. The increased rate in leaf senescence from 5 WAA to PM under stress and non-stress conditions in K78Y x I137TN may explain the greater depletion of the TNC pool in the stem segments from 7 WAA to PM (Section 3.3.2). As photosynthetic leaf area declined there was less current photosynthate available to maintain TNC content levels in the stem segments of K78Y x I137TN. This resulted in a decline in TNC content as the various sink requirements were met.

The ratio of TNC content to residual content was derived in order to more readily assess the amounts of TNC and residual components relative to one another (Table 3.45). The ratio of TNC content

Table 3.45 Ratio of total non-structural carbohydrate (TNC) to residual content for the stem segments of two maize hybrids exposed to water stress (S) and lack of water stress (NS) from one week after anthesis (WAA) to physiological maturity

Hybrid	Stress treatment	WAA	Stem segment	
			A1	B1
			TNC : Residual	TNC : Residual
SA 6	S	1	0,39	0,38
		2	0,57	0,53
		3	0,68	0,64
		4	0,63	0,63
		5	0,43	0,39
		6	0,23	0,21
		7	0,13	0,11
		8	0,10	0,09
	NS	1	0,41	0,39
		2	0,51	0,47
		3	0,60	0,54
		4	0,62	0,54
		5	0,52	0,49
		6	0,32	0,27
		7	0,21	0,17
		8	0,15	0,14
K78Y x I137TN	S	1	0,35	0,37
		2	0,42	0,44
		3	0,59	0,60
		4	0,53	0,57
		5	0,49	0,47
		6	0,44	0,42
		7	0,29	0,29
		8	0,21	0,17
	NS	1	0,36	0,42
		2	0,43	0,49
		3	0,50	0,54
		4	0,52	0,59
		5	0,50	0,50
		6	0,41	0,48
		7	0,38	0,41
		8	0,30	0,30
TNC : Residual ratio		SE ($\bar{x}$)	0,03	

to residual content reflects the changes in TNC and residual content discussed above. The tendency for SA 6 to more markedly increase in TNC content from 1 to 4 WAA is reflected by the slightly higher ratio of TNC to residual content in comparison to K78Y x I137TN. The tendency for SA 6 to then more markedly decline in TNC content from 4 WAA to PM while the residual content increased from 6 WAA to PM is reflected by the decline in the ratio during the latter period. The tendency for K78Y x I137TN to maintain higher TNC content levels in the stem segments at PM is reflected by the higher ratio under stress and non-stress conditions in comparison to SA 6.

3.3.4 Yield and yield components

Grain yield

The main effect for hybrid was significant (Table 3.46 and Appendix 29). Grain yield for K78Y x I137TN was significantly ($p = 0,01$) higher than the mean yield for SA 6, by 77 g m^{-2}.

Table 3.46 Primary ear grain yield (g m^{-2}) at harvest maturity of two maize hybrids meaned over water stress treatments

Hybrid	
SA 6	K78Y x I137TN
236	313
LSD (0,05) 38	
LSD (0,01) 55	

The main effect for stress was significant (Table 3.47). Grain yield for the hybrids under stress conditions was significantly ($p = 0,01$) lower than that under non-stress conditions by 100 g m^{-2}. This amounted to a mean yield reduction of 31,0 %.

Table 3.47 Effect of water stress (S) and lack of water stress (NS) on primary ear grain yield (g m^{-2}) at harvest maturity meaned over maize hybrids

Stress treatment	
S	NS
224	324

LSD (0,05)	38
LSD (0,01)	55

The first order interaction of hybrid with stress treatment was non-significant (Figure 3.13). Yield for SA 6 of 291 g m^{-2} under non-stress conditions, was reduced by 38,0 % to 181 g m^{-2} under stress conditions. The yield reduction in K78Y x I137TN plants, from 357 g m^{-2} under non-stress conditions to 268 g m^{-2} under stress conditions, was 25,0 %.

Overall then, the capacity of K78Y x I137TN to maintain a larger viable leaf area later into the season, coupled with the capacity to maintain sucrose levels later into the season, as well as the tendency to maintain higher overall TNC levels in the stem until late grain fill, has afforded K78Y x I137TN with a higher yield capacity than SA 6 under stress and non-stress conditions. Both hybrids depleted the TNC pool in the stem from 4 WAA to PM to

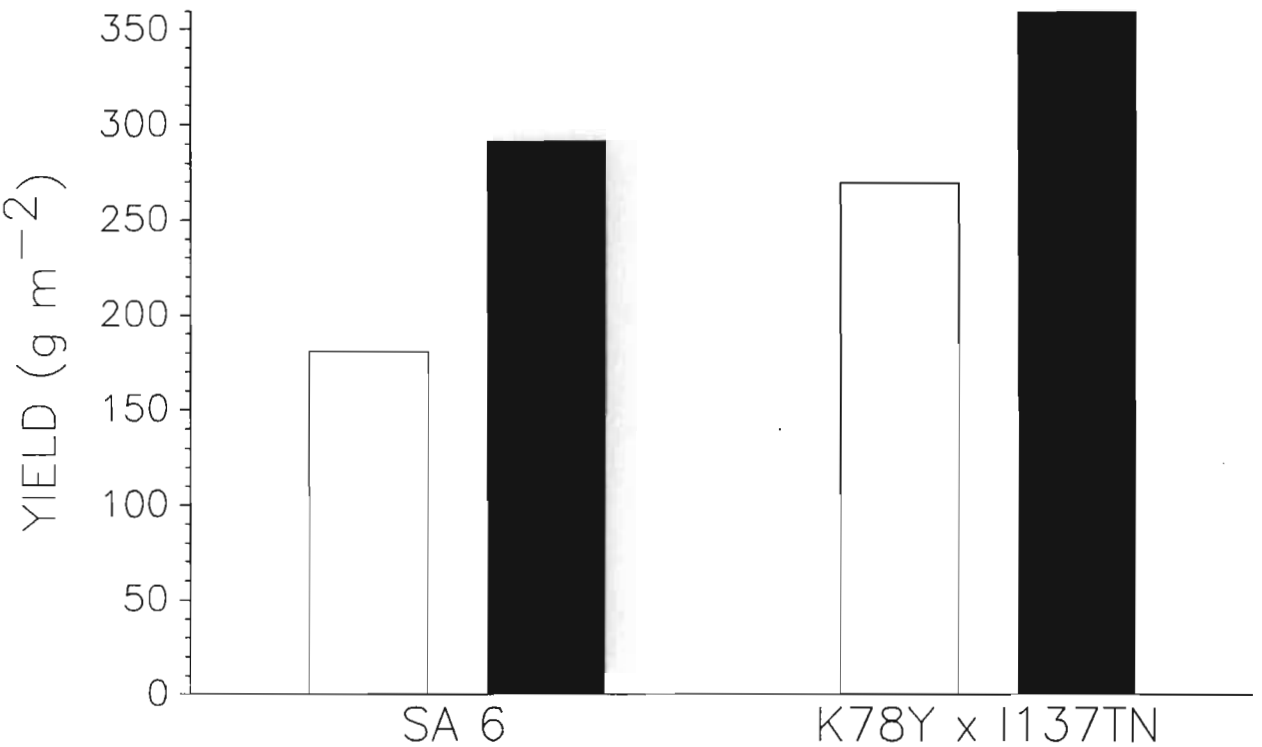


Figure 3.13 Effect of water stress (▭) and lack of water stress (▬) from one week after anthesis to physiological maturity on primary ear grain yield at harvest maturity of two maize hybrids

supplement the current photosynthate supply which was declining as a result of senescence (enhanced under stress conditions). However, SA 6 depleted the TNC pool in the stem segments more substantially from 4 WAA to PM than did K78Y x I137TN under stress and non-stress conditions. The rate at which SA 6 depleted the TNC pool was greater than that for K78Y x I137TN from 4 to 7 WAA under stress and non-stress conditions. However, the rate at which K78Y x I137TN depleted the TNC pool in the stem segments was greater than that for SA 6 from 7 WAA to PM under stress and non-stress conditions.

Yield components and agronomic characteristics

It is widely recognised that the time required for the induction of stress under field conditions is much longer than for controlled environment conditions (Clarke & Townley-Smith, 1984). For example a stress level which may develop in four to five weeks in the field may take only ten days in a controlled environment (Ludlow & Ng, 1976). It was expected that the development of stress would occur slowly in this trial. However, both kernel number (kernels ear^{-1}) and mass $kernel^{-1}$ (g) were reduced in magnitude for both SA 6 and K78Y x I137TN plants subjected to stress (Table 3.48). If severe stress had developed some weeks following water stress induction then it would be expected that mass $kernel^{-1}$ only, would be reduced. However, the decrease in both kernel mass and kernel number indicates that stress developed early enough in this trial to cause abortion of developing kernels. This probability is enhanced by the observed immediate decline in leaf area following induction of water

stress. The interaction of hybrid with stress treatment was non-significant for both kernels ear^{-1} and mass kernel^{-1}, indicating again the similar responses of the hybrids to water deficits (Table 3.48 and Appendix 30). Thus averaged over hybrids in response to water stress both kernels ear^{-1} and mass kernel^{-1} were respectively, significantly ($p = 0,05$) and non-significantly, reduced in magnitude. Averaged over stress treatments K78Y x I137TN recorded non-significantly higher kernels ear^{-1} and significantly ($p = 0,001$) higher mass kernel^{-1} than SA 6.

Table 3.48 Yield components and cob production for two single cross maize hybrids subjected to water stress (S) and lack of water stress (NS) during grain fill

Hybrid	Stress treat-ment	Kernels[a] ear^{-1}	Kernels[a] row^{-1}	Rows[a] ear^{-1}	Mass[b] kernel^{-1} (g)	Cob production[a] (g m^{-2})
SA 6	S	268	19,8	13,6	0,186	44,5
	NS	349	24,4	14,3	0,202	51,3
K78Y x I137TN	S	276	23,4	11,9	0,246	79,5
	NS	302	26,2	11,5	0,273	94,5
F-values						
Hybrid (H)		$0,785^{NS}$	$3,952^{NS}$	$24,339^{***}$	$14,839^{***}$	$38,728^{***}$
Stress treatment (S)		$5,826^{*}$	$7,440^{*}$	$0,151^{NS}$	$1,599^{NS}$	$2,992^{NS}$
H x S		$1,591^{NS}$	$0,407^{NS}$	$1,355^{NS}$	$0,125^{NS}$	$0,430^{NS}$

*,**,*** Significant at the 0,05, 0,01 and 0,001 probability levels respectively. NS = non-significant

a Average of five plants subsampled from plants harvested from inner furrows at harvest maturity

b Average of 50 kernels per five plants subsampled from plants harvested at harvest maturity

It is interesting to note that K78Y x I137TN partitioned more photosynthate to cob dry mass production under stress and non-

stress conditions in comparison to SA 6 (Table 3.48 and Appendix 30.5). The interaction of hybrid with stress treatment was non-significant indicating a similar decline in cob dry mass in response to water deficits for both hybrids. Thus, on average over stress treatments, cob production for K78Y x I137TN was significantly (p = 0,001) higher than that for SA 6 by 39,1 g m^{-2}.

K78Y x I137TN recorded a non-significantly higher percentage of barren plants under non-stress conditions than under stress conditions (Table 3.49 and Appendix 31.1). Averaged over stress treatments SA 6 had 18,7 % (p = 0,001) more barren plants than did K78Y x I137TN. Stress resulted in a significant (p = 0,01) 19,0 % increase in the percentage of runt ears averaged over hybrids (Table 3.49 and Appendix 31.2). SA 6 recorded a non-significantly higher runt percentage under stress and non-stress conditions than K78Y x I137TN.

Table 3.49 Agronomic characteristics at harvest maturity for two single cross maize hybrids subjected to water stress (S) and lack of water stress (NS) during grain fill

Hybrid	Stress treatment	Stand %	% Barren plants	% Runt ears
SA 6	S	100	26,6	47,5
	NS	100	21,1	28,6
K78Y x I137TN	S	100	2,3	41,1
	NS	100	7,8	22,1
F-values				
Hybrid (H)		-	$33,019^{***}$	$1,368^{NS}$
Stress treatment (S)		-	$0,000^{NS}$	$11,723^{**}$
H x S		-	$2,809^{NS}$	$0,000^{NS}$

*, **, *** Significant at the 0,05, 0,01 and 0,001 probability levels respectively. NS = non-significant