245 # MAIZE CROP GROWTH AND DEVELOPMENT RELATED TO SOLAR RADIATION

by

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I declare that this thesis has not been submitted to another University for degree purposes. Apart from discussions with my supervisor, Prof. J.M. de Jager, and the assistance acknowledged on pages 141 and 142, the work contained in this thesis was done by me.

HKaiser

JM. de Jager.

MAIZE CROP GROWTH AND DEVELOPMENT
RELATED TO SOLAR RADIATION

- H.W. Kaiser Ph.D. thesis

ERRATA

Page 32 - 1st line
"it can be concluded that maize in close rows"
should read
"it can be concluded that for maize in close rows"

Page 35 - last line
"log $\underline{I}'_v$ / $\underline{I}_v$ = 0,663 F"
should read
"log $\underline{I}'_v$ / $\underline{I}_v$ = -0,663 F"

Page 36 - in Fig 1.8
"Eqn. 1.19"
should read
"Eqn. 1.29"

Page 51 - Under the heading 'CO_2 uptake measurements'
the third sentence
"The plastic enclosure was 1,83m long and 3,35m high"
should read
"The plastic enclosure was 3,05m long, 1,83m wide and 3,35m high".

CONTENTS

ABSTRACT

The interception and reflection of solar radiant energy by maize crops was measured at Cedara using tube solarimeters. From the measured data the amount of *PHAR* that was intercepted was related to the $\underline{L}$ value of the crop. $\underline{K}_{\underline{v}}$, the extinction coefficient of *PHAR* thus obtained was found to vary with row spacing, plant population density and cultivar, whereas growth stage, time of day and weather conditions did not appear to effect the $\underline{K}_{\underline{v}}$ value markedly.

On clear days the albedo ($\underline{R}_{\underline{v}}$) of a maize crop was of the order of 0,05 to 0,08 during the middle of the day. However, at low sun angles in the early and late hours of the day, $\underline{R}_{\underline{v}}$ increased to values of the order of 0,2. On overcast days, the diurnal variation was considerably lower.

The rate of photosynthesis in a maize crop was measured using the plastic enclosure technique. The rate of CO_2 uptake was related to the amount of *PHAR* absorbed by the crop. A rectangular hyperbola (Eqn. 2.1) was found to describe this relationship well. The photosynthetic response of a crop to population density, plant spacing and temperature at different developmental stages is discussed.

The seasonal distribution of dry matter in the maize crop was studied using normal growth analysis techniques. From these data functions describing the partitioning of *DM* to the various plant organs (e.g. roots, leaves, grain) at different growth stages were developed.

The functions describing the absorption of light by the crop canopy, its photosynthetic rate and the partitioning of photosynthate were incorporated in a computer simulation model, which was used to estimate the growth of a maize crop from meteorological radiant flux density and temperature data. The functioning of the model and its possible use are discussed.

INTRODUCTION

Agriculturists have over the centuries been faced with the problem of judging the potential of an area for crop production. However, the many environmental factors involved have in the past made an accurate analysis of the potential of an area impossible. The advent and development of the computer has changed the situation considerably. Because of its speed, large masses of data can be analysed rapidly, a task which would previously have been monumental.

The analysis of environmental data, and in particular climatic data, with the object of establishing the potential of an area for crop production can, however, only be meaningful if it is based on a thorough understanding of the crop-environment interrelationship. Once the relationship between the crop and individual environmental factors can be quantitatively described by mathematical functions, these functions can be incorporated sequentially into a dynamic growth simulation model that estimates the daily growth of a crop. Computer models of this type have been developed by various researchers including 'ELCROS' by De Wit, Brouwer & Penning de Vries (1970) and 'PUTU' by De Jager (1974).

In addition to its use for determining the Agricultural potential of an area, the dynamic simulation model can be a powerful management or research tool. It can, for example, be used to predict the consequences of a management decision (e.g. when to plant the crop) or assist to identify those areas of research, including breeding, that will lead to most progress.

Approximately ten years ago a research programme was launched by the Agro-Meteorological section at the University of Natal, Pietermaritzburg, and the Agronomy Department at Cedara College of Agriculture, which has as one of its objectives the development of a dynamic computer simulation growth model that can be used in practice. Since maize is the Republic's foremost agronomic crop, and moisture the major limiting climatic factor, the response of maize to different moisture regimes was the first aspect considered in this programme. This work has been reported by Mallett (1972).

Photosynthesis is one of the basic processes governing the growth of a crop. During photosynthesis the crop converts solar radiant energy into chemical energy which is stored in the plant in the form of carbohydrates, proteins and other plant constituents. The rate of photosynthesis is therefore dependent on the level of incoming radiant energy that is available for conversion by the crop, and the efficiency with which this energy is intercepted and converted by the crop. To obtain a workable mathematical model for estimating the growth of the maize crop, a thorough understanding of the interrelationship between canopy density and energy interception, and its influence on crop photosynthesis is necessary. Hence, the second phase of the maize growth potential research programme, which was started in 1969/70, was concerned with (1) the interception of radiant energy by maize canopies of different age, plant population and spacing, and (2) the photosynthetic response of different canopies to changing solar radiant flux densities.

Instantaneous photosynthetic and light interception models are, however, not sufficient to simulate the day to day growth of a maize crop from climatic data. The size and composition of the crop changes from day to day and this in turn influences its capacity to intercept energy and, hence, its photosynthetic rate. Knowledge of the correct partitioning of the daily dry matter production to different plant tissues therefore becomes essential. Running concurrently with the light interception and photosynthetic studies, a series of growth analysis experiments were conducted to determine the composition of the maize crop at different growth stages.

In this dissertation the results from these studies are discussed. The instantaneous models that have been developed are incorporated in a dynamic growth simulation model. Many of the functions used are empiricial, whereas others have a sound theoretical basis. The development and use of the growth simulation model is discussed in Chapter 4. It is a comparatively simple model which is a prerequisite for the practical use of such models.

This phase of the overall research programme dealt specifically with the response of maize to solar radiant energy and, to a lesser extent, temperature. Every attempt was made to avoid growth limitations through moisture or nutrient stress.

Throughout this work, the yellow maize hybrid SA 60 was used as the standard crop. At the start of this programme, SA 60 was the most popular hybrid in Natal, but has in recent years largely been replaced by more productive ones. It was decided not to change the hybrid during the course of this programme, as this would have made comparisons between seasons and experiments difficult. At various stages, other newer hybrids were included for comparative purposes.

With the exception of the 1970/71 photosynthetic studies, which were done at the University of Natal, Pietermaritzburg, all the research work was conducted at Cedara College of Agriculture. Cedara has a reliable summer rainfall, but its climate is characterised by a high proportion of overcast and misty days during the summer months.

A large number of symbols and abbreviations are used in the text. These are listed below.

List of symbols and abbreviations

AI = absorbed radiant energy (W/m^2)

A_v = canopy absorption factor for PHAR

b = a canopy efficiency factor reducing LP_p', the maximum possible rate of photosynthesis at high light intensities

c = an efficiency factor of the canopy at low light intensities

CDM = dry mass of the total crop including roots (g)

C_r = transition coefficient from total radiation to NIRR

C_v = transition coefficient from total radiation to *PHAR*

C_t = maintenance respiration coefficient at temperature T

C_{30} = maintenance respiration coefficient at 30°C

D = number of days from emergence

d = change

d_i = difference in *IRGA* reading between the start and end of a recording period (division)

DL = rate of *DM* accumulation in the leaves relative to that in the total topgrowth

DM = dry matter

DMG_g = gross daily dry matter gain (g/m^2)

DMG_n = net daily dry matter gain (g/m^2)

DR = rate of *DM* accumulation in the roots relative to that of the total crop

D_r = number of days from silking

DY_m = *DM* yield at maturity (g/m^2)

DY_s = *DM* yield at silking (g/m^2)

F = accumulated *L* from the crop canopy surface to a horizontal plane within the canopy

f = corrected CO_2 flow rate (ml/s)

f_r = recorded CO_2 flow rate (ml/s)

GF = grain dry mass as a fraction of the total above ground DM produced after silking

GRY = grain dry matter yield (g/m^2)

HU = heat units (^oC)

I = total radiant flux density above the crop (W/m^2)

I' = total radiant flux density at a horizontal plane within the canopy (W/m^2)

IRGA = infra-red gas analyzer

I_v = radiant flux density of PHAR above the crop (W/m^2)

I'_v = radiant flux density of PHAR at a horizontal plane in the canopy (W/m^2)

K = extinction coefficient of a canopy for total radiant energy

k = construction respiration constant

K_v = extinction coefficient of a canopy for PHAR

L = leaf area index

l = index depend~~a~~ent on L

LA = leaf area (m^2)

LF = leaf dry mass as a proportion of dry mass of the topgrowth

LG = unsenesced LA after silking as a fraction of the maximum LA achieved

LM = leaf mass (g)

M = number of days over which HU are accumulated

m = the specific day for which HU are calculated

NIRR = near infra-red radiation (W/m^2)

P = net photosynthetic rate ($mgCO_2/m^2/s$)

P_d = total amount of CO_2 fixed during a day ($g/m^2/day$)

PHAR = photosynthetically active radiation (W/m^2)

P_o' = net photosynthetic rate of an individual leaf at light saturation ($mg/CO_2/m^2/s$)

P_{30} = net photosynthetic rate at 30°C ($mgCO_2/m^2/s$) ($mg\,CO_2/m^2\,s$)

Q = theoretical photochemical efficiency of the photosynthetic process for the middle of the PHAR wavelength range (approximately equal to 22×10^{-6} g CO_2/J)

R = canopy reflection factor for total radiant energy

RES = daily respiration ($g/m^2/day$) ($g/m^2\,d$)

RES_n = night respiration (g/m^2)

RF = root dry mass as a fraction of the total crop DM

RM = root dry mass (g)

R_r = canopy reflection factor for NIRR

R_v = canopy reflection factor for PHAR

S_r = sum of the reflection and transmission coefficients of the leaf for NIRR

S_v = sum of the reflection and transmission coefficients of the leaf for PHAR

T = ambient air temperature (^{o}C)

t = time (days)

T_i = mean temperature in the recording room (^{o}C)

TM = dry mass of topgrowth (g)

$Tmax$ = maximum day temperature (^{o}C)

$Tmin$ = minimum day temperature (^{o}C)

T_n = mean night time temperature (^{o}C)

T_r = canopy transmission factor for total radiant energy

t_r = length of recording period for measuring CO_2 uptake (s)

W = total dry biomass of a crop per unit area (g/m^2)

x = time interval (days)

Σ = sum

CHAPTER 1

ABSORPTION OF SOLAR RADIANT ENERGY BY MAIZE CANOPIES

Crop growth is largely governed by the rate of photosynthesis. During photosynthesis radiant energy is converted in the leaves into chemical energy, stored in the form of carbohydrates, proteins, fats and other chemical components. The rate of photosynthesis is therefore dependant on the amount of solar energy absorbed by the leaves of the crop. To describe or simulate the photosynthetic rate and hence the growth of a crop in terms of the prevailing solar radiation conditions, it is essential therefore to know what proportion of the incoming solar energy is actually absorbed by the crop.

Incoming solar radiant energy striking the crop surface follows one of three pathways. It can be

reflected from the crop surface;
transmitted through the crop; or
absorbed by the crop canopy.

Mathematically, the absorption factor, $\underline{A}$, the reflection factor, $\underline{R}$, and the transmission factor, $\underline{T}_r$, are related.

$$\underline{A} + \underline{R} + \underline{T}_r = 1 \qquad \text{...... Eqn. 1.1}$$

Monsi and Saeki (1953) showed that $\underline{I}'$, the radiant flux density at any horizontal plane at a given depth in the canopy follows approximately the Beer-Lambert law,

$$\underline{I}' = \underline{I}\,\exp(-\underline{KF}) \qquad \text{............ Eqn. 1.2}$$

where $\underline{K}$ = the extinction coefficient
$\underline{F}$ = accumulated $\underline{L}$ from the crop surface to a horizontal plane at the given depth, and
$\underline{I}$ = total radiant flux density above the crop (W/m^2).

For PHAR, photosynthetically active radiation, Eqn. 1.2 can be written as

$$\underline{I}_v' = \underline{I}_v \exp(-\underline{K}_v F) \quad \ldots\ldots\ldots\ldots\ldots\ldots \text{Eqn. } 1.3$$

Monsi & Saeki (1953) employed Eqn. 1.2 to predict dry matter production in relation to light interception. Their measurements gave $\underline{K}$ values that varied widely according to species from 0,3 to 2. In grass species the $\underline{K}$ value usually lay between 0,3 and 0,5. Davidson & Philip (1958) also used Eqn. 1.2 to model dry matter production from light interception.

Tooming (1966) showed that the interception of radiant energy in the photosynthetically active range (PHAR), viz. 0,38 to 0,71 microns, is far greater than that for near infra-red (NIRR) radiation (i.e. 0,71 to 4,0 microns). According to his data the transmission coefficient for PHAR is 0,074 as compared to 0,34 for NIRR. In other words, the extinction co-efficient, $\underline{K}_v$, for PHAR is considerably higher than for NIRR. In a maize crop with an $\underline{L}$ value of 4,3, Allen & Brown (1965) showed that energy transmission was highly wavelength dependant. They found that 0,07, 0,20 and 0,135 of the PHAR, NIRR and total radiation respectively was transmitted through the crop. Using a Weston illuminometer with a green correction-cosine filter, Loomis, Williams, Duncan, Dovrat & Nunez (1968) measured light profiles at different growth stages in maize planted in an equidistant pattern at three populations viz. 1,75; 4,87 and 12,5 plants/m^2. Fitting Eqn. 1.3 to their data they obtained $\underline{K}_v$ values ranging from 0,56 to 0,97. No definite pattern appeared from their data, except that for the intermediate population, the mean $\underline{K}_v$ value for three growth stages was 40% and 25% higher than at the highest and lowest population densities respectively.

The reflectivity of crop surfaces has been measured by various researchers. A summary of some of the findings reported in the literature is presented in Table 1.1.

It is clear that crop reflectivity is dependent on the solar elevation with low values at noon and high values for the early and late hours of the day (Monteith & Szeicz, 1961; Fritschen, 1967; Idso, Baker & Blad, 1969). These workers also showed that the type of surface will influence reflectivity. Monteith & Szeicz (1961) found that the R value for short grass was higher than for bare soil, whereas Idso et al. (1969) reported the opposite effect. Fritschen (1967) found variation in R values between wet and dry soils, young and fully developed crops, broadcast and row planted crops and between grasses and broad-leafed crops.

Table 1.1: A summary of R values found by various researchers.

Researchers	R	Description of conditions
Graham & King (1961)	0,12-0,21	Maize
Monteith & Szeicz (1961)	0,23 0,28 0,26	Solar elevation - 60^o; short grass Solar elevation - 20^o; short grass Daily mean for short grass
	0,16 0,19 0,17	Solar elevation - 60^o; bare soil Solar elevation - 20^o; bare soil Daily mean for bare soil
Allen & Brown (1965)	0,24	Maize
Fritschen (1967)	0,4 0,2 0,24 0,14 0,24	Approximate R value for the first & last hour of day Approx. R value at 12H00 Daily mean - average of a variety of crop surfaces Daily mean for wet soil Daily mean for dry soil
Idso et al. (1969)	0,4 0,23 0,26	At 17H00 over grass surface At 12H00 over grass surface Daily mean over grass surface

According to Chang (1974), cloud cover reduces the diurnal variation in $\underline{R}$ value, because of an increased proportion of diffuse radiation which is virtually independent of solar elevation.

As in the case of transmitted radiant energy, reflection is wavelength dependent. Tooming (1966) gives a mean $\underline{R}_v$ value (i.e. reflection factor for PHAR) as 0,10 compared to a $\underline{R}_r$ value (i.e. reflection factor for NIRR) of 0,47. Similar values were obtained by Yocum (1963). He measured $\underline{R}_v$ and $\underline{R}_r$ values of 0,07 and 0,40 respectively.

To determine what proportion of the incident PHAR is absorbed by the maize crop canopy, a series of four experiments were conducted at Cedara. In two of these, the transmission of energy through maize canopies of different age, plant population, spacing and hybrid was measured. In the other two trials the reflection from maize canopies of different age was recorded.

MATERIALS AND METHODS

Radiant energy interception by maize crops

Studies on the interception of radiant energy by maize canopies were conducted at Cedara during the 1969/70 and 1970/71 seasons. In 1969/70 energy interception by the yellow hybrid SA 60, growing in an equidistant planting pattern at two widely different populations, was measured at two different developmental stages. During 1970/71, SA 60 was again used as the test crop. It was grown at three population densities and at the intermediate population, three row spacings were compared. In addition a single spacing treatment with the white hybrid RO 1E, which is characterised by an upright leaf display, was included. On all plots the plant rows were orientated in a north-south direction to obtain maximum interception. The populations and spacings used for the different treatments in 1969/70 and 1970/71 are listed in Table 1.2. Experimental details regarding the establishment, production and harvesting of the crops are given in Table 3.1 and discussed under 'Materials and Methods' in Chapter 3.

Table 1.2: Cultivar, plant population and spacing of maize crops on which interception of radiant energy was measured.

Year	Treatment	Cultivar	Population density	Plant spacing
			plants/m^2	m
1969/70	1	SA 60	3,59	0,53 x 0,53
	2	SA 60	14,35	0,26 x 0,26
1970/71	3	SA 60	4,78	0,46 x 0,46
	4	SA 60	4,78	0,91 x 0,23
	5	SA 60	4,78	1,83 x 0,11
	6	SA 60	9,56	0,46 x 0,23
	7	SA 60	2,39	0,91 x 0,46
	8	RO 1E	4,78	0,91 x 0,23

The transmission of total radiant energy through the maize canopies was measured at different crop developmental stages using 15 tube solarimeters of a type similar to that described by Szeicz, Monteith & Dos Santos (1964). These are illustrated in Plate 1.1. The solarimeters were placed horizontally at different levels in the crop, with a number of solarimeters at each level and one above the crop measuring the total radiant flux density. Because of the low leaf area, sampling variation near the top of the maize canopy was greater than at the bottom, therefore more solarimeters were placed near the top than at the bottom of the crops. In 1969/70, when the plants were arranged in a square pattern, the solarimeters were placed at random in the crop, either in an east-west or north-south direction. With the north-south orientation of rows used in 1970/71, the solarimeters were placed in an east-west direction. The solarimeters were so positioned that the entire inter-row space was traversed at each recording level.

The e.m.f. generated by the thermopile of each solarimeter was measured and recorded by a 16 channel Kent potentiometer that had been adapted and fitted with counters which gave integrated hourly readings. The e.m.f. is directly related to the amount of radiant energy striking the thermopile. After calibration of the solarimeters, it was thus possible to relate the amount of energy trans-

Plate 1.1: Tube solarimeters used to measure incoming solar radiant energy.

mitted through the canopy to the level of each solarimeter, to the total amount of leaf area above each solarimeter (*F* in Eqn. 1.2). At the time that the transmission of energy was recorded in any specific treatment, seven plants chosen at random, were harvested from that treatment. The plants were cut horizontally into layers at the levels at which the solarimeters were situated. The leaves from each layer were traced on drawing paper of known density. From the mass of the drawing paper replicas the leaf area, *LA*, for each crop layer was calculated, as was *F*, the cummulative leaf area measured downwards from the top of the canopy to each recording level.

Calibration of solarimeters

Before the commencement of the trial, all 15 solarimeters were set to give near maximum deflection on the potentionmeter at mid-day. Variable potential dividers were included in the circuit to permit the desired setting to be made.

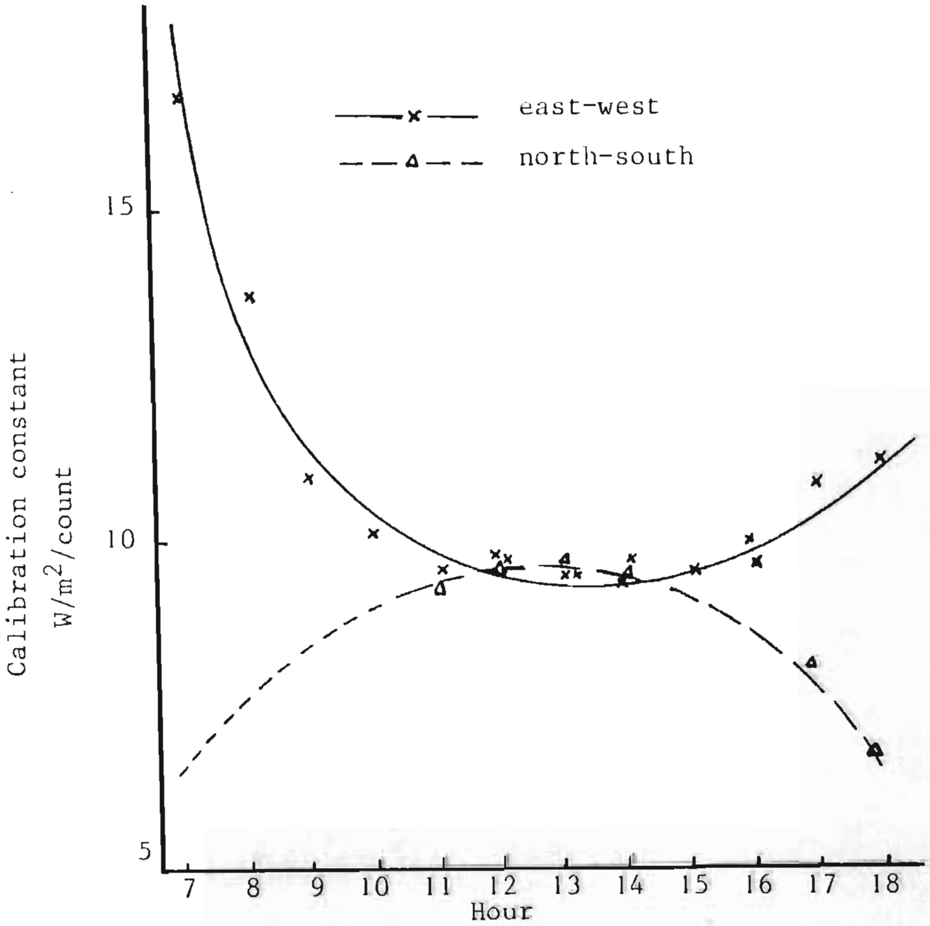

Fig. 1.1: Mean calibration constant of 15 solarimeters, orientated in an east-west and north-south direction, for the hours 7 to 18 (1969/70).

To calibrate the instruments, all the solarimeters were set up in an east-west direction and leveled. Readings were then taken throughout the day. At the same time, readings were taken with a standard Kipp solarimeter. These readings were taken on both clear and overcast days. The tube solarimeters were then turned through

90° (i.e. to a north-south direction) and the process repeated. On clear days, the relationship between the tube solarimeters and the Kipp readings did not remain constant throughout the day, but showed diurnal variation. This is illustrated in Fig. 1.1. For the hours 11 to 15 the calibration coefficients were virtually constant and equal for both the east-west and north-south orientation. However, during the earlier and later hours of the day, the calibration coefficients became progressively higher for the east-west orientated solarimeters and lower for a north-south orientation.

A single calibration constant was therefore used for each solarimeter for the hours 11 to 15 for both orientations. For the hours outside this range, the calibration coefficient was multiplied by the factors listed in Table 1.3. A comparison of overcast and clear day conditions showed that under cloudy conditions the calibration constant for hours 11 to 15 was on the average 7,3% higher for a clear day, and there was no diurnal variation.

Table 1.3: The factors used to adjust the calibration coefficients for hours 7 to 10 and 16 to 18.

Hour	Factor	
	N.S.	E.W.
7	0,635	1,746
8	0,786	1,427
9	0,885	1,138
10	0,947	1,055
16	0,911	1,000
17	0,843	1,104
18	0,729	1,168

The calibration constants of the individual solarimeters for 1969/70 and 1970/71 are listed in Table 1.4.

Table 1.4: Calibration constants of tube solarimeters.

Solarimeter No.	Calibration constant	
	1969/70	1970/71
	W/m^2/count	W/m^2/count
1	8,93	9,14
2	9,71	10,26
3	9,30	8,70
4	9,17	9,79
5	9,61	10,37
6	9,70	12,16
7	9,74	11,80
8	10,82	12,23
9	9,31	10,63
10	10,09	9,81
11	9,68	10,19
12	10,31	10,89
13	10,09	11,55
14	9,94	9,30
15	9,54	9,92

Calculation of the extinction coefficient

The amount of radiation recorded by each solarimeter in the crop was calculated as a fraction of the radiant energy recorded by the solarimeter above the crop (I'/I). The mean value of I'/I at each level in the crop was then determined. By substituting log I'/I and F, the cumulative leaf area index above the level at which I' was measured, into Eqn. 1.2, linear regression analyses were applied to the data from the different growth stages of the various treatments. The slope of the best fitting linear function gives the value of K. This K is the extinction coefficient for total radiant energy.

K_v, the extinction coefficient for PHAR, was determined from Eqn. 1.3. I'_v/I_v was calculated according to the method proposed by Tooming (1966) where for a given L value

$$I'/I = (S_v/2)^{\underline{1}} \cdot C_v + (S_r/2)^{\underline{1}} \cdot C_r \quad \ldots\ldots\ldots\ldots \text{ Eqn. 1.4}$$

and

$$I'_v/I_v = (S_v/2)^{\underline{1}} \quad \ldots\ldots\ldots\ldots \text{ Eqn. 1.5}$$

Values for $(S_v/2)$, C_v, $(S_r/2)$ and C_r given by Tooming (1966) are 0,087, 0,52, 0,405 and 0,48 respectively. By entering these values, together with the recorded values for I'/I into Eqn. 1.4, $(S_v/2)^{l}$ was determined by a process of iteration i.e. by successively entering increasing values of l into Eqn. 1.4 until Eqn. 1.4 becomes true.

Reflection of radiant energy from a maize crop

In 1973 the reflectance of radiant energy from a maize crop was measured over the periods 8 to 12 February and 20 to 26 March. The maize hybrid used was SA 60 growing at a plant spacing of 0,75m by 0,30m. At the time of measurement, this crop had a L value of 4,07. During the first recording period the crop was in the early tasseling stage, whereas in the second period the tassels had dried-off, and had a dull brown colour.

Two pairs of tube solarimeters were used for this study. Before installing the solarimeters above the crop, the two solarimeters from each pair were exposed to direct sunlight and set to give equal deflection on a millivolt recorder. One solarimeter from each pair was then placed facing upwards about 1m above the crop. The other solarimeter was placed at the same height above the crop, but inverted. A strip of aluminium foil approximately 1,5cm wide was attached to the back of the inverted solarimeter, to prevent heating of the back of the solarimeter element from direct sunlight. The first solarimeter thus measured incoming radiation and the second shortwave back radiation. The proportion of energy reflected off the crop canopy was then determined from integrated hourly readings taken throughout the day.

During 1973/74, reflection was measured over two SA 60 crops that had been planted four weeks apart on the 7/11/1973 and 5/12/1973. The plant spacing was 0,91m by 0,23m.

The reflectivity of the maize on the two plots was measured during the periods 8/1, 9/1, 10/1/1974; 31/1/1974; 14/2, 15/2/1974 and 9/3, 12/3, 13/3/1974. During the latter period measurements were limited to the November planted maize.

Six tube solarimeters connected to a six channel strip chart millivolt recorder were used in this experiment. Two (No. 2 and No. 6) of the six solarimeters were placed above the crops facing upwards and recording total incoming radiant energy. Of the remaining four solarimeters two were placed inverted 1m above each crop. The backs of the inverted solarimeters were again shielded with aluminium foil. Readings were taken on the half hour throughout the day by recording the deflection for each channel on the millivolt recorder.

The six solarimeters were calibrated against a standard Kipp solarimeter. Calibration was done on the half hour throughout a clear day by comparing the deflection produced on the millivolt recorder connected to the tube solarimeters with the deflection produced by the standard Kipp solarimeter. Similar comparisons were also made on an overcast day.

Incoming radiant energy was measured using solarimeters 2 and 6. The calibration constants used for these solarimeters depended on the weather conditions. Because the radiation reflected off the crop is diffuse, the calibration constants obtained during overcast conditions were used for those solarimeters measuring reflected energy. The calibration constants used are presented in Table 1.5.

Table 1.5: Calibration constants for tube solarimeters.

Solarimeter	Weather Conditions	Calibration constant
		$(W/m^2)/mV$
1	Overcast	84,8
3	Overcast	71,3
4	Overcast	76,6
5	Overcast	76,0
2	Overcast	87,8
6	Overcast	87,8
2	Clear	83,5
6	Clear	83,5

In addition to the reflectivity measurements described above, the $\underline{L}$ value and the proportion of plants with tassels were determined from 15 plants harvested at each recording period. Measurements of $\underline{L}$ were made according to the method described in Chapter 3. As when determining the interception of radiant energy, the reflection of PHAR was calculated from total reflection according to the method proposed by Tooming (1966) were

$$\underline{R} = \underline{R}_v^{1} \cdot \underline{C}_v + \underline{R}_r^{1} \cdot \underline{C}_r \quad \text{......... Eqn. 1.6}$$

Values for $\underline{R}_v$, $\underline{C}_v$, $\underline{R}_r$ and $\underline{C}_r$ listed by Tooming (1966) are 0,10, 0,52, 0,47 and 0,48. By inserting these values together with the recorded value for $\underline{R}$ in Eqn. 1.6, $\underline{R}_v^{1}$ was determined by a process of iteration.

RESULTS AND DISCUSSION

Interception of total radiation and PHAR

In general Eqns. 1.2 and 1.3 fitted well the data both for the measured total radiant energy and for the estimated PHAR respectively as calculated from the total radiant energy by Tooming's (1966) method. A comparison of the effect of cumulative leaf area index ($\underline{F}$) on the extinction coefficients for total radiant energy and PHAR is illustrated in Fig. 1.2. A linear regression equation was fitted to both the total radiant energy, as well as the PHAR data from clear days in 1969/70 for the period days 72 to 114. The best fitting function for the total radiation data was

$$\log \underline{I}'/\underline{I} = -0{,}0833 - 0{,}445\,\underline{F} \quad \text{........... Eqn. 1.7}$$

The regression was highly significant (P 0,01) and the S.E. for the regression function was 0,0135. The r value was -0,888. The best fitting linear regression equation for the PHAR data is Eqn. 1.10 given in Table 1.6. The $\underline{K}_v$ value for this equation was 0,874 ± 0,0207, which was almost twice as high as the $\underline{K}$ value for total radiation viz. 0,445 ± 0,0135, in Eqn. 1.7.

The relationship between K and K_v for the other recording periods was similar. In the remainder of this Chapter only the K_v values are listed and discussed.

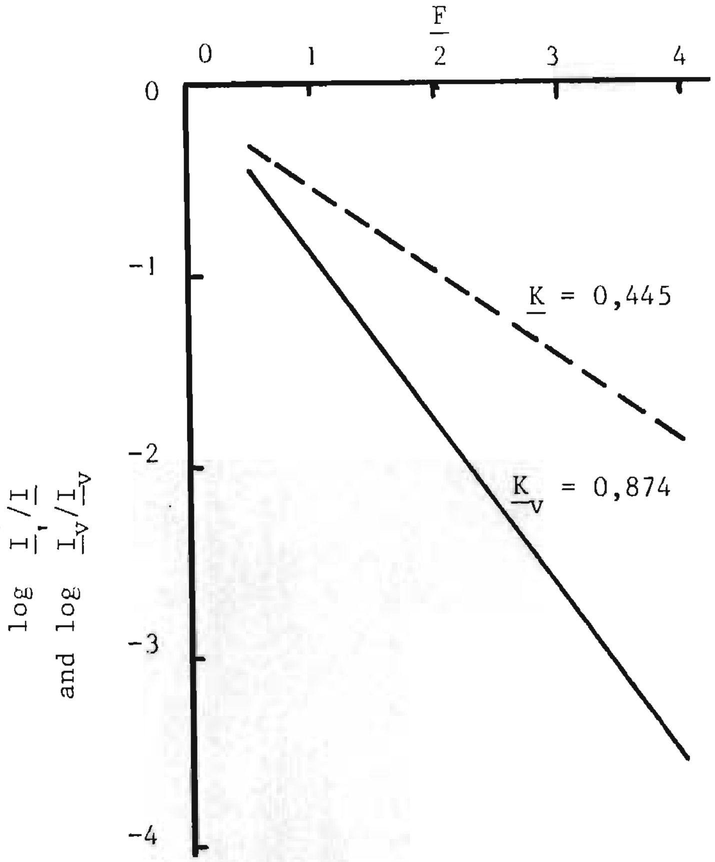

Fig. 1.2: Comparison of the extinction of total radiation and PHAR in a maize crop.

Diurnal Fluctuation

The effect of time of day on energy interception by the maize canopy was tested on the data from 13 days between day 72 and day 114 in 1969/70. Although fairly wide fluctuations in the hourly K_v values did occur, as shown in Fig. 1.3, no definite pattern could be established. Similar difficulties were reported by Stewart & Lemon

(1969). Their measurements also showed no definite and clear relationship between interception and sun angle.

The high S.E. values for the data from the early and late hours of the day, show that readings taken during these periods were less reliable than those from the middle of the day. This was to be expected as at low sun angles small inaccuracies in the leveling of the solarimeters will result in larger errors than at high sun angles.

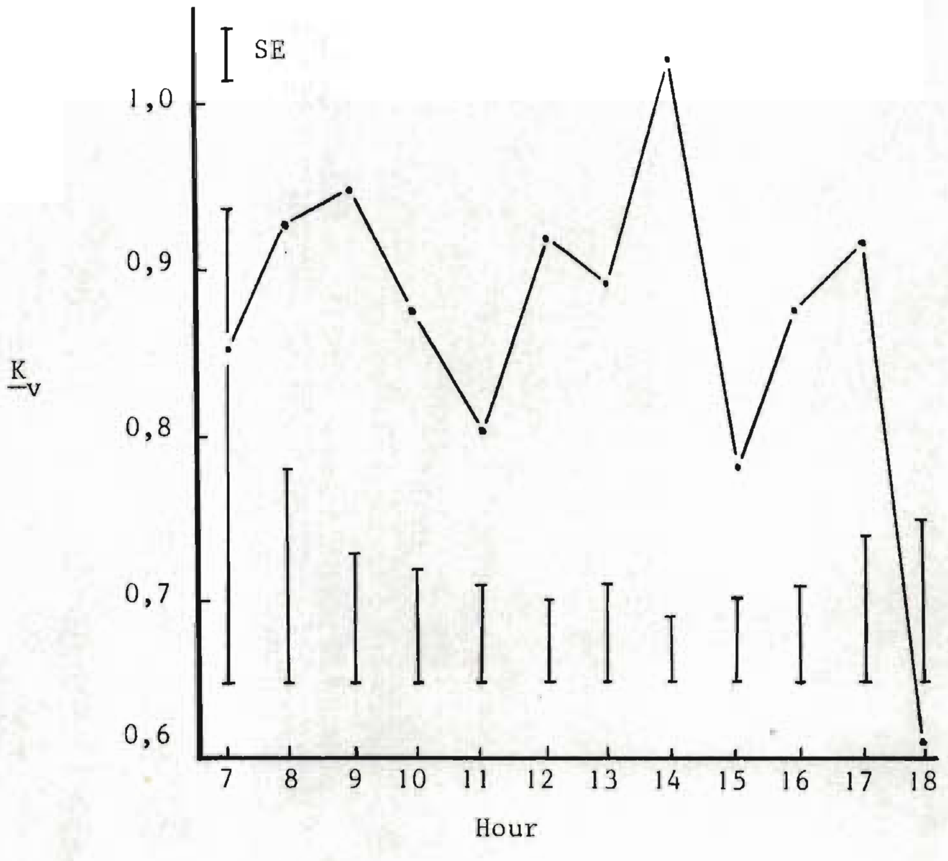

Fig. 1.3: Diurnal variation of the extinction coefficient ($\underline{K}_v$).

Furthermore, because of the low radiant flux densities at the extreme hours of the day, recording errors of equal magnitude have a far greater relative effect during these periods than at midday. For these reasons only readings taken from hours 10 to 16 were included in the calculation of the overall extinction co-efficient for a canopy. This is justified as by far the greater proportion of radiant energy for a normal day (approximately 75% on a clear February day at Cedara) reaches the crop canopy during that period of the day. In a simulation model therefore, discrepancies in the $\underline{K}_v$ value for the early and late hours of the day, although appreciable, should have little effect on the accuracy of the overall estimate of crop performance for a day and season.

General

Profile readings were made during the periods day 46 to day 114 in 1969/70, and day 44 to day 120 in 1970/71. The data for hours 10 to 16 were grouped according to stage of crop development, population density, row spacing, cultivar and weather conditions before fitting Eqn. 1.3. Details regarding the best fitting functions for the different sets of data are presented in Table 1.6.

The F, r and S.E. values obtained when testing the fit of the linear regression functions showed that Eqn. 1.3 adequately describes the relationship between radiant flux density in the canopy and $\underline{F}$. Of the best fitting functions, Eqn. 1.9 gave the highest r and F value, and the lowest S.E. for $\underline{K}_v$.

Eqn. 1.9 is illustrated in Fig. 1.4.

Table 1.6: The best fitting linear regression functions $\log \underline{I}'/\underline{I} = -\underline{K}_v F$, together with the S.E. of the slope and the r and F values, for maize growing at different populations and spacings, at different growth stages and weather conditions.

Year	Treat-ment (1)	Popula-tion	Recording Period	Growth Phase	Weather	$\underline{L}$	Intercept	$\underline{K}_v$	S.E.	r	F	n (4)	Eqn. No.
		plants/m^2	Days										
1969/70	1	3,59	57-59	Veg (2)	Clear	2,06	0,548	1,052	0,190	-0,705	31^{++}	33	1.8
		3,59	73-74	Tassel	Part.Cl (3)	3,56	0,0700	0,638	0,0157	-0,983	1641^{++}	58	1.9
		3.59	72-114	Tas/Rep	Clear	3,56	-0,0357	0,874	0,0207	-0,908	1781^{++}	379	1.10
		3,59	84-101	Rep	Overcast	3,56	-0,291	0,735	0,0355	-0,907	428^{++}	94	1.11
	2	14,35	46	Veg	Clear	5,40	-0,00222	0,513	0,0715	-0,855	52^{++}	21	1.12
		14,35	57-59	Veg	Clear	8,15	0,760	0,588	0,0415	-0,884	201^{++}	58	1.13
1970/71	3	4,78	44-45	Veg	Part.Cl	2,19	-0,311	0,625	0,0778	-0,835	65^{++}	30	1.14
		4,78	59-60	Veg	Part.Cl	4,32	-0,541	0,443	0,0942	-0,583	22^{++}	45	1.15
	4	4,78	51	Veg	Clear	3,00	1,269	0,899	0,277	-0,530	11^{++}	29	1.16
		4,78	64-66	Veg	Overcast	4,73	0,775	0,784	0,0330	-0,954	563^{++}	58	1.17
		4,78	87-120	Rep	Clear	4,47	0,149	0,887	0,0572	-0,887	241^{++}	67	1.18
		4,78	100	Rep	Part.Cl	4,47	-0,147	0,741	0,0876	-0,780	72^{++}	48	1.19
		4,78	116	Rep	Overcast	4,47	0,166	0,974	0,106	-0,972	85^{++}	7	1.20
	5	4,78	81-114	Rep	Clear	4,45	-0,229	0,594	0,0860	-0.718	48^{++}	47	1.21
		4,78	82	Rep	Overcast	4,45	0,0240	0,709	0,0387	-0,994	335^{++}	6	1.22
	6	9,56	46	Veg	Clear	4,25	-0,054	0,480	0,105	-0,689	21^{++}	25	1.23
		9,56	61	Veg	Part.Cl	5,95	0,269	0,768	0,0696	-0,887	122^{++}	35	1.24
		9,56	78-79	Silk	Part.Cl	8,28	-0,110	0,614	0,0245	-0,946	626^{++}	76	1.25
		9,56	80	Silk	Clear	8,28	-0,319	0,599	0,0338	-0,932	313^{++}	49	1.26
	7	2,39	54	Veg	Part.Cl	1,55	-0,0960	0,695	0,137	-0,661	26^{++}	35	1.27
		2,39	102	Rep	Clear	2,58	-0,0666	0,861	0,110	-0,752	61^{++}	49	1.28
	8	4,78	89	Rep	Clear	5,91	-0,367	0,515	0,120	-0,887	18^{++}	7	1.29

(1) Treatment details are given in Table 1.2; (2) Veg. = Vegetative, Rep = Reproductive; (3) Part.Cl = partly cloudy;
(4) n = No. of pairs ; ++ F value significant at the 1% level.

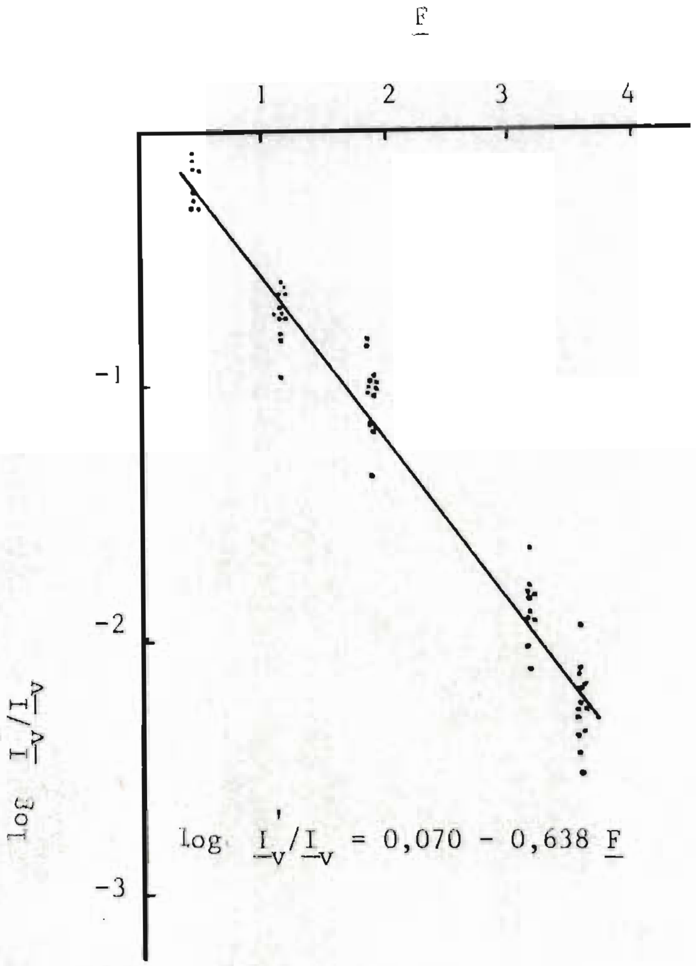

Fig. 1.4: Distribution of recorded values around the fitted regression line (Eqn. 1.9).

Weather

The effect of weather conditions on the interception of *PHAR* was tested by comparing Eqns. 1.9 and 1.10, Eqns. 1.18 and 1.20 and Eqns. 1.21 and 1.22. Each pair of equations is based on data recorded in the same crop with the same *L* value, but under different weather conditions.

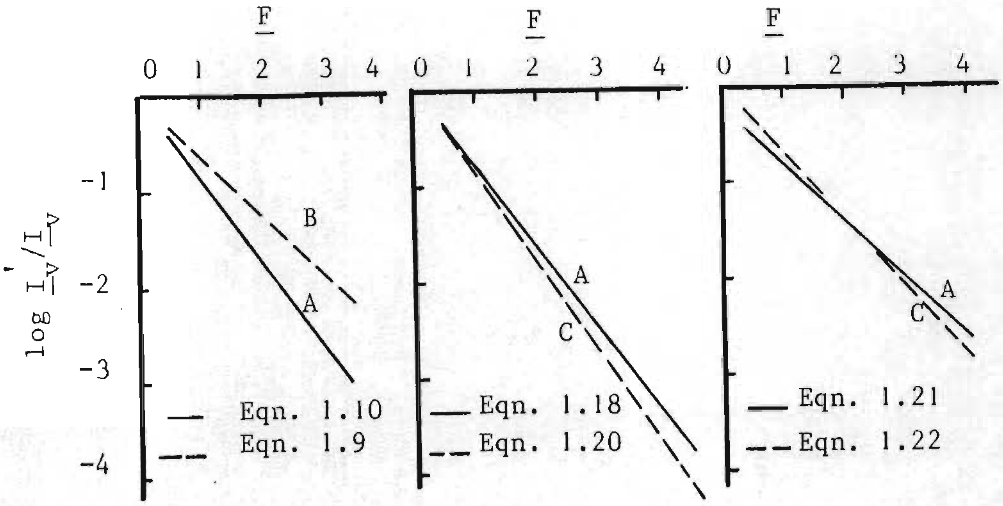

Fig. 1.5: Effect of weather on the extinction of *PHAR* in maize canopies (A = clear sky, B = partly cloudy, C = overcast conditions).

These comparisons are illustrated in Fig. 1.5. In the latter two comparisons weather conditions did not significantly change the K_v value obtained. However, in the first comparison based on the 1969/70 data, K_v was significantly affected by the weather ($P <,01.$)

The pattern was, however, inconsistant, the highest K_v being recorded for clear conditions and the lowest for partly cloudy skies, with an intermediate value for overcast conditions. (Table 1.6, Eqn. 1.9, 1.10 and 1.11). Furthermore, whereas in 1969/70 the K_v value was higher under clear sky than overcast conditions, the opposite trend was obtained in 1970/71, although the differences were not significant in the latter season.

Measurements by Stewart & Lemon (1969) also did not show a great deal of variation in $\underline{K}_v$ value for readings taken during clear days and overcast conditions.

Since no definite conclusions can be drawn from the above, the $\underline{K}_v$ value for clear sky conditions, when most of the photosynthetic activity occurs, will be used throughout in the simulation model.

Growth stage

To test whether or not the extinction coefficient ($\underline{K}_v$) varied with the growth stage of the crop, the following equations listed in Table 1.6 were compared: Eqns. 1.8 and 1.10, Eqns. 1.12 and 1.13, Eqns. 1.17 and 1.20, and Eqns. 1.27 and 1.28. Except for the second comparisons, where both sets of readings were taken during the vegetative growth stage, but two weeks apart, the other comparisons were always between readings from the second half of the vegetative period and the early part of the reproductive growth phase. With none of the above comparisons was a significant difference between the $\underline{K}_v$ values obtained. In the simulation model therefore, the $\underline{K}_v$ value of a crop will not be changed according to its growth stage.

Population density

The effect of population density on $\underline{K}_v$ during the reproductive growth phase was studied by comparing Eqns. 1.10, 1.18, 1.25 and 1.28. These equations covered a wide range of population densities from 2,39 plants/m^2 to 9,56 plants/m^2 planted in rows 0,91m apart or less. The $\underline{K}_v$ values for Eqns. 1.18 and 1.28 did not differ significantly, but the $\underline{K}_v$ for Eqn. 1.25 was significantly lower than the rest.

From these results, it can be concluded that maize in close rows (i.e. 0,91 m apart or less) the same $\underline{K}_v$ value can be used for population densities within the range 2,39 to 4,78 plants/m^2. Dense populations, as represented by the 9,56 plants/m^2 population, on the other hand, require a lower $\underline{K}_v$ value. The findings agree with those of Loomis _et al_. (1968) who obtained $\underline{K}_v$ values ranging from 0,78 to 0,97 and 0,56 to 0,66 for population densities of 4,78 and 12,5 plants/m^2 respectively. Associated with the lower $\underline{K}_v$ in high densities was a higher incidence of vertically orientated leaves near the top of the high density crop.

Most population densities used in practice fall within the range 2,39 plants/m^2 to 4,78 plants/m^2, whereas a common row spacing is 0,91m. Eqn. 1.18, modified to give zero intercept, was therefore used to determine the interception of visible energy by crops within the above population and row spacing range. The modified version of Eqn. 1.18 that gave the best fit of the data was

$$\log \underline{I}'_v/\underline{I}_v = -0{,}840\ \underline{F} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad \text{Eqn. } 1.30$$

For use in a simulation model an equation with zero intercept is essential, particularly in young crops where low $\underline{F}$ values can otherwise lead to erroneous interception values. The $\underline{K}_v$ values for Eqn. 1.18 and 1.30 are very similar. These equations are illustrated in Fig. 1.6.

The $\underline{K}_v$ values for different populations during two periods (viz. days 45 to 54 and 57 to 66) of the vegetative growth phase, were compared. For the early period Eqns. 1.27, 1.14, 1.23 and 1.12, representing the populations 2,39 plants/m^2, 4,78 plants/m^2, 9,56 plants/m^2 and 14,35 plants/m^2 respectively, were compared. The $\underline{K}_v$ values for these equations ranged from 0,480 for the population density 9,56 plants/m^2 to 0,695 for the 2,39 plants/m^2 population. The differences between the $\underline{K}_v$ values were not significant.

In the case of the second period (i.e. days 57 to 66 from emergence) Eqns. 1.18, 1.24 and 1.13 were compared. These equations were obtained from measurements made in crops with populations of 3,59 plants/m^2, 9,56 plants/m^2 and 14,35 plants/m^2 respectively. The $\underline{K}_v$ values differed significantly ($P < ,05$) with the higher values at lower populations and *vice versa*. However, these results must be treated with caution as in all three equations the intercepts were high.

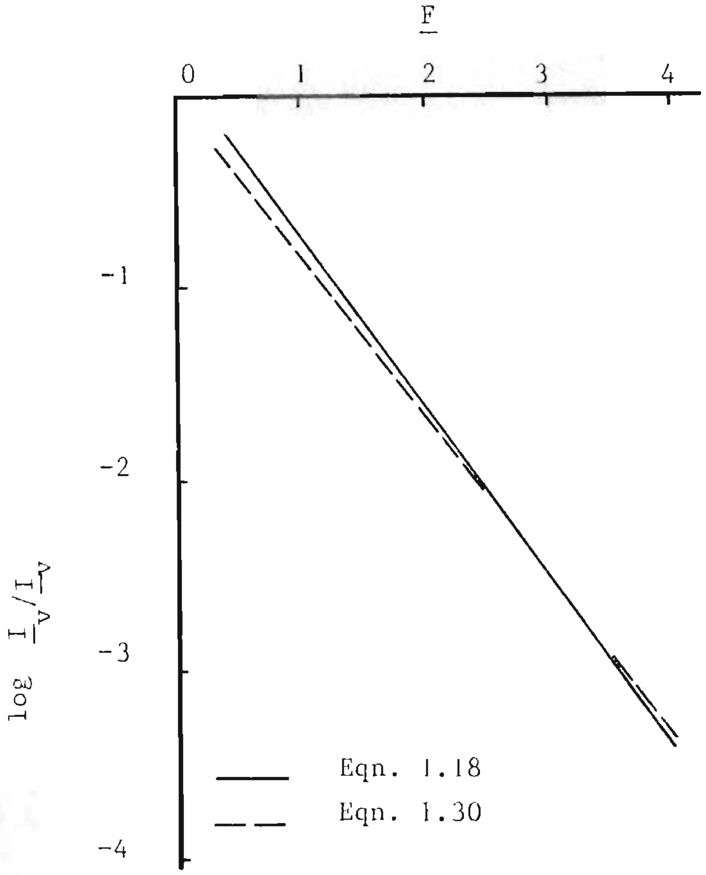

Fig. 1.6: Comparison of the overall best fitting regression line (Eqn. 1.18) and the best fitting line passing through the origin (Eqn. 1.30).

From the above results it can be concluded that after tasseling high populations (i.e. 9,56 plants/m^2) significantly reduce the $\underline{K}_v$ value of a crop. A possible reason for this is a more vertical orientation of the top leaves caused by high competition between plants. In younger plants the competition is less severe, hence no significant difference in the $\underline{K}_v$ value was observed at the earliest growth stage.

Row spacing

The effect of row spacing on the interception of visible radiant energy was studied by comparing the $\underline{K}_v$ value for maize growing at the same population density, viz. 4,78 plants/m^2, but arranged in different row spacings of 0,91m and 1,83m (Table 1.6, treatments 4 and 5 respectively). This was done both for clear (Eqn. 1.18 vs. Eqn. 1.21) and overcast conditions (Eqn. 1.20 vs 1.22). In both cases a significant difference (clear days $P < ,01$; overcast conditions $P < ,05$) between the two equations was obtained. Narrow rows had a higher $\underline{K}_v$ value than wide rows. This effect is illustrated in Fig. 1.7.

The above comparisons were made only during the reproductive growth phase. The solarimeters traversed the entire inter-row space. This meant that in the wide rows four solarimeters were placed next to each other, with two next to the plant rows being fairly well shaded, and two towards the centre of the inter-row space being almost totally exposed for long periods of the day. This resulted in wide variations in readings, especially under clear sky conditions, as shown by the comparatively low r value (-0,718) and high S.E. (0,086) for Eqn. 1.21.

Wide row spacings are popular in the drier parts of the Republic. Where the growth of maize in such rows is simulated, allowance must be made for the lower extinction coefficient. As in the case of population density, Eqn. 1.21 was modified by fitting a linear function to the data that passes through the origin. The best fitting

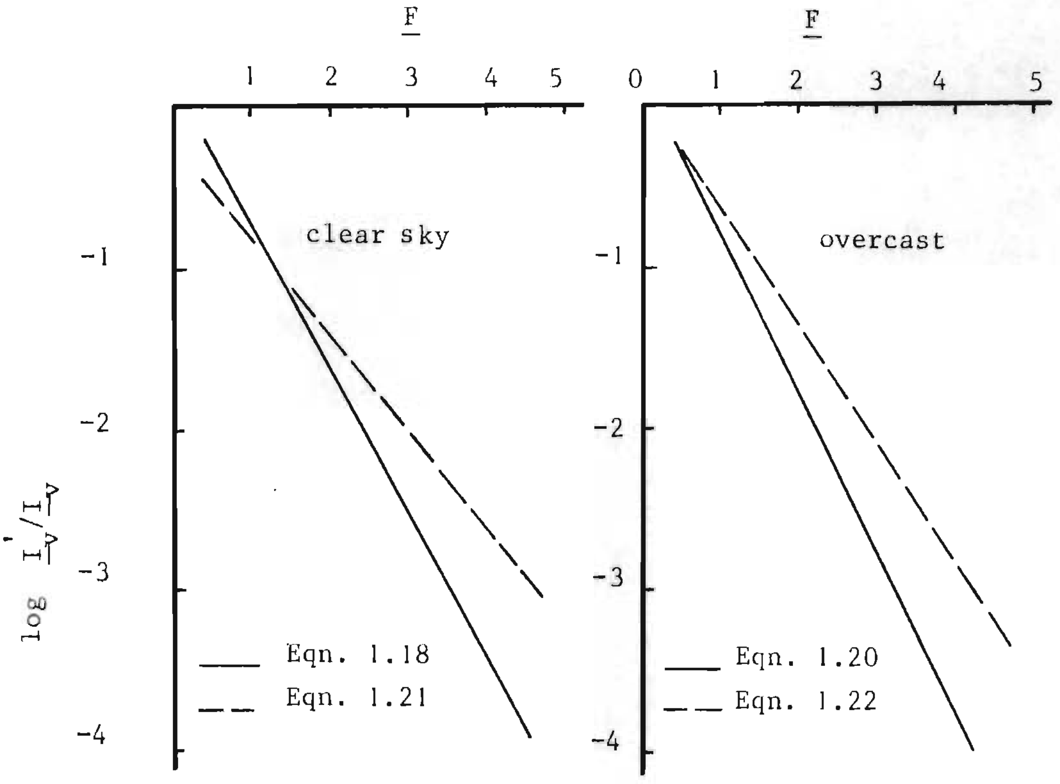

Fig. 1.7: Effect of row width on the interception of solar radiant energy by the maize canopy.

function of the data was

$$\log \underline{I}'_v/\underline{I}_v = 0{,}663\ \underline{F} \quad \ldots\ldots\ldots\ldots\ldots \quad \text{Eqn. 1.31}$$

Hybrid

An interesting comparison, which is illustrated in Fig. 1.8, is that between the two hybrids SA 60, which has a normal leaf display, and RO 1E, which has leaves that are more vertically orientated. Both these crops were planted in 0,91m rows at a population density of 4,78 plants/m^2.

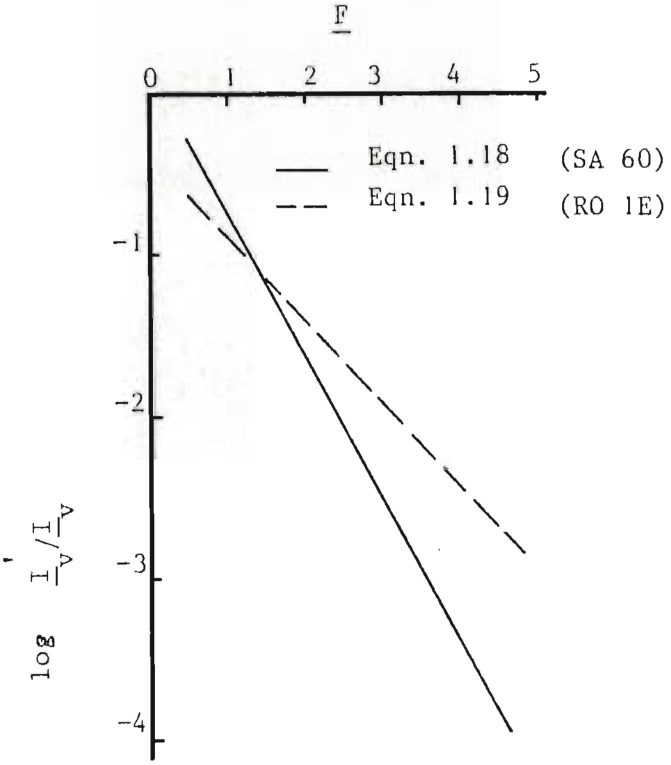

Fig. 1.8: Comparison of the interception of solar radiant energy by hybrids SA 60 and RO 1E.

Profile measurements were made when both crops were past the tasseling stage. Although the data from the RO 1E crop was limited, the best fitting linear regression function (Eqn. 1.29) gave a high correlation coefficient of -0,887 and an F value for the regression that was highly significant (P<,01). The $\underline{K}_{v}$ value was 0,515 as compared to 0,887 for SA 60 (Eqn. 1.18) growing at the same population density. This difference was significant (P<,05).

Conclusions

1. In general the Beer-Lambert Law (Eqn. 1.3) fitted the data adequately. Except in young crops, where the variability was high, correlation coefficients of the order of -0,7 to -0,9 were obtained.

2. No definite pattern in diurnal variation of energy interception was established, as readings taken at the extremes of the day were of doubtful accuracy. However, since the contribution of the early and late hours of the day to the total radiation is small, inaccuracies in the estimation of light interception during these periods will have little effect on the daily growth estimates. It was decided to use the relationship pertaining to the hours 10 to 16 as applicable for the entire day.

3. The effect of weather conditions on the $\underline{K}_v$ value was not clear. However, it did not appear to have a very marked effect. It was concluded that clear day relationships could be used under all conditions. Dull days should contribute less to growth. Hence, errors in estimates due to $\underline{K}_v$ for such days should have a small effect on total growth estimates for the season.

4. Where maize was planted in a square pattern or in 0,91m rows, population densities within the range 2,39 to 4,78 plants/m^2 gave similar $\underline{K}_v$ values. This range should cover most populations found in practice. For clear day conditions the $\underline{K}_v$ values obtained ranged from 0,86 to 0,89. The two high population densities used, viz. 14,35 and 9,56 plants/m^2, gave $\underline{K}_v$ values that were approximately 25% lower.

5. Maize in wide rows (e.g. 1,83m rows) has a lower extinction coefficient than maize in closer rows (e.g. 0,91m apart). Because of the clumping of leaves, readings in the 1,83m rows were more variable than those in closer rows. The $\underline{K}_v$ value for a crop in wide rows is therefore less reliable than that for closer spacings.

6. The effect of growth stage on $\underline{K}_v$ was variable. In 1969/70 the $\underline{K}_v$ value recorded for the vegetative stage was higher than that for reproductive growth, which agrees with the findings of Loomis *et al*. (1968). However, the 1970/71 results suggested the opposite. Since the tassel intercepts some radiant energy, but is not considered in determining the cumulative leaf area ($\underline{F}$), a higher $\underline{K}_v$ value could be expected after tasseling. No definite conclusions can be drawn from the results obtained. The same $\underline{K}_v$ value will therefore be used throughout the growing season.

Reflection of radiant energy from a maize crop

In Fig. 1.9 the reflectance of measured total radiation (R) and estimated PHAR ($\underline{R}_v$) for clear conditions during the period 8/2/73 to 12/2/73 are presented. The values for $\underline{R}$ were of the same order as those listed by Monteith & Szeicz (1961), Idso *et al*. (1969), Fritschen (1967) and Allen & Brown (1965), whereas the $\underline{R}_v$ values were similar to those presented by Yocum (1963) and Tooming (1966). The diurnal variation reported by a number of these researchers, with low values during the middle of the day and high values during the early and late hours, was also observed in this experiment.

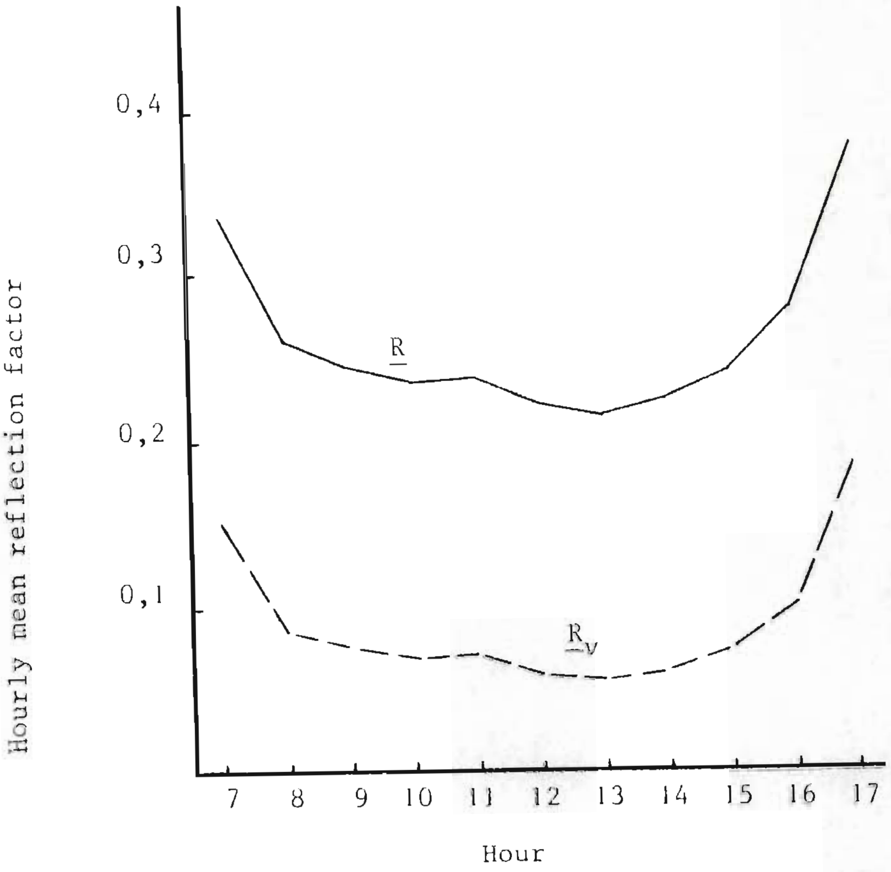

Fig. 1.9: Diurnal variation of measured $\underline{R}$ and estimated $\underline{R}_v$ values for maize in the reproductive growth stage and with an $\underline{L}$ value of 4,07 (1973).

Growth Stage

The effect of stage of crop development on the reflection factor was determined in 1974 by measuring reflectivity on the same day from both the November and December planted maize crops. The first recording was on days 8/1/1974, 9/1/1974 and 10/1/1974. At this stage the November planted maize had an L value of 1,57, whereas that for the December planted crop was equal to 0,32.

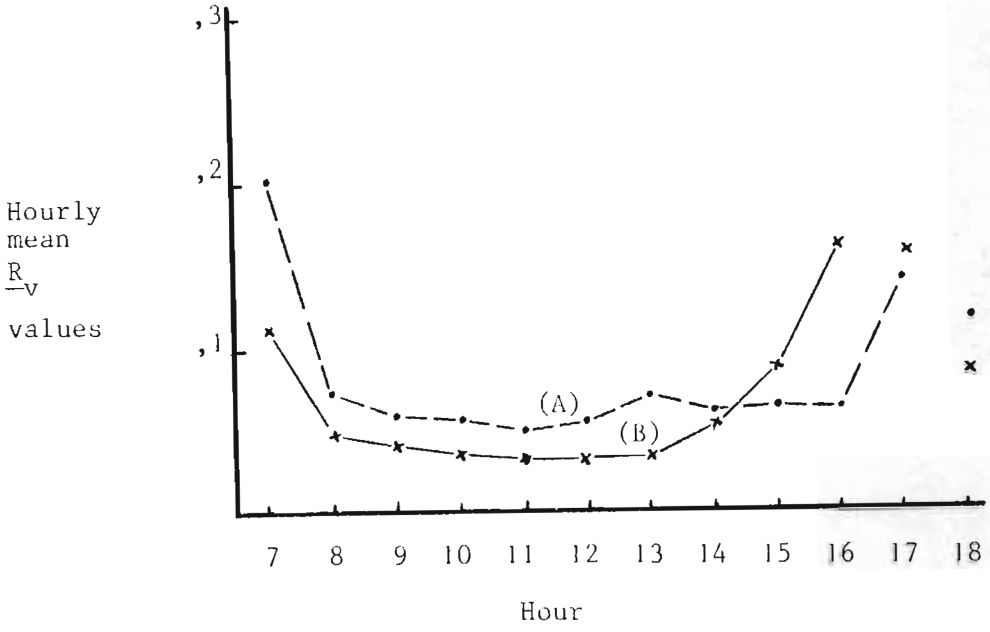

Fig. 1.10: $\underline{R}_v$ values for maize crops with L values of 0,32 (B) and 1,57 (A) (1974).

The mean hourly $\underline{R}_v$ values are presented in Fig. 1.10. Except for the hours 15 to 18, when the pattern was not clear the reflection factor for PHAR ($\underline{R}_v$) for the crop with an L value of 1,57 was higher than that with an L value of 0,32. The mean for the hours 8 to 14 were 0,060 for November and 0,039 for December planted maize, which support the findings of Fritschen (1967) that young crops have a lower reflectivity than older ones. This effect can be attributed to the large exposure of bare soil, with a low reflection value, in the young crop.

The effect of tassels on the reflectivity of the crop was measured on the 14/2/1974 and the results are presented in Fig. 1.11. At this stage the November planted maize was at 100 per cent tasseling and had an $\underline{L}$ value of 4,29 compared to the December planted crop with no tassels and an $\underline{L}$ value of 3,29. There was virtually no difference in the reflection factor between the two crops.

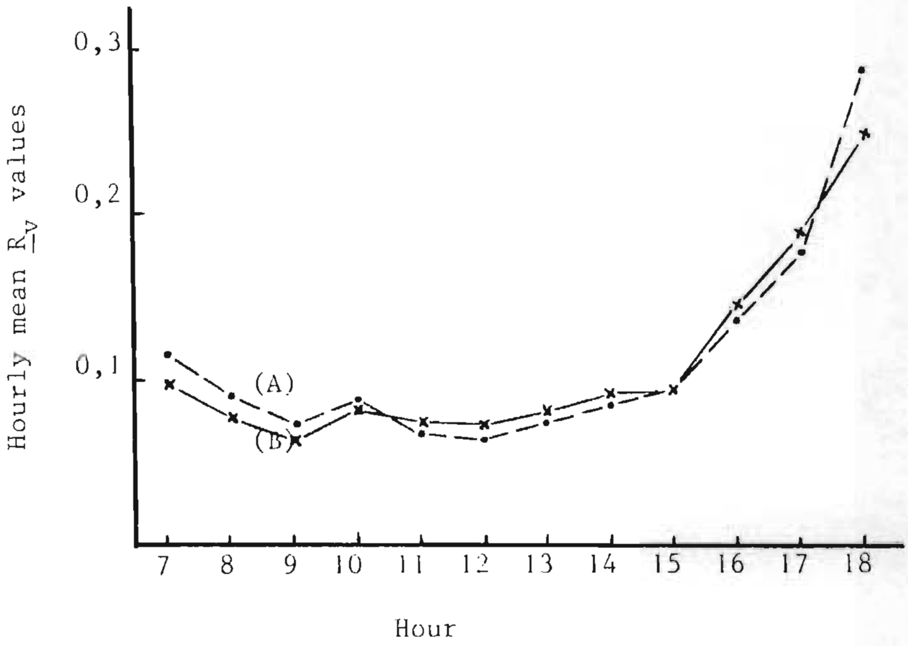

Fig. 1.11: A comparison of $\underline{R}_v$ values for the reproductive (A) and vegetative (B) growth stages (1974).

The mean values for hours 10 to 15 were 0,078 and 0,082 for the crops with and without tassels respectively. The whitish colour of the tassel therefore had no apparent effect on the reflectivity of the crop.

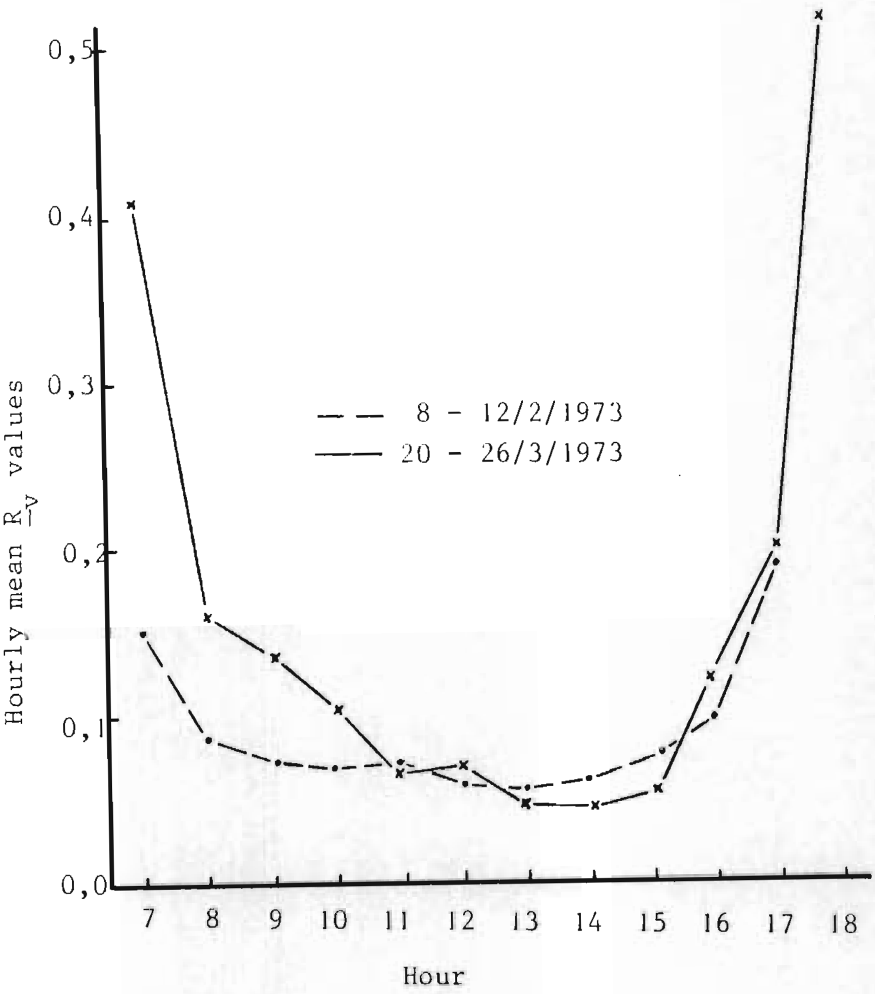

Fig. 1.12: Effect of time of year on $\underline{R}_v$ for a maize crop with an $\underline{L}$ value of 4,07 (1973).

Time of the year

From the data recorded it was also possible to test the effect of the time of the year. This was done by comparing the readings taken on 8/2/1973 to 12/2/1973 with those from the period 20/3/1973 to 23/3/1973 and the data from the 14/2/1974 and 15/2/1974 with the data from the 9/3/1974, 12/3/1974 and 13/3/1974. These results are presented in Fig. 1.12 and Fig. 1.13.

The diurnal response patterns were very similar for both years. There was very little difference in response pattern which can be ascribed to the difference in time of the year, except that in both cases $\underline{R}_v$ for the early hours of the day was higher later in the season. This can be ascribed to a lower sun angle during the later period. Why the effect was not as marked for the last hours of the day is not known.

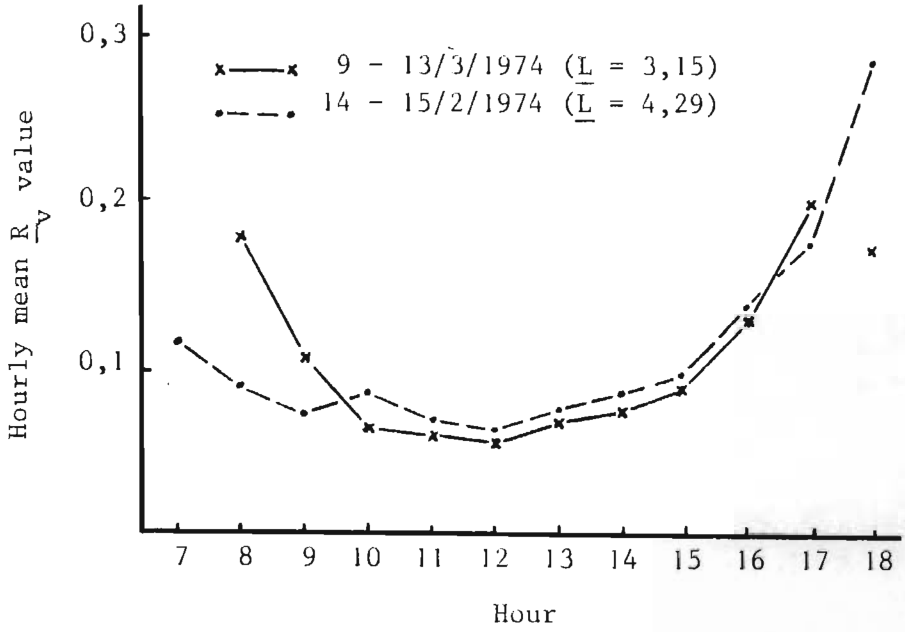

Fig. 1.13: Effect of time of year on $\underline{R}_v$ values for maize in the reproductive growth phase (1974).

Weather

During the recording period 9/3/1974, 12/3/1974 and 13/3/1974 readings were taken both during clear and overcast conditions. As shown in Fig. 1.14 the diurnal variation in $\underline{R}_v$ values was considerably less on overcast than on clear days, supporting Chang (1974) who stated that due to a larger proportion of diffuse light, which is independant of sun elevation, the diurnal variation on cloudy days is reduced in relation to clear skies.

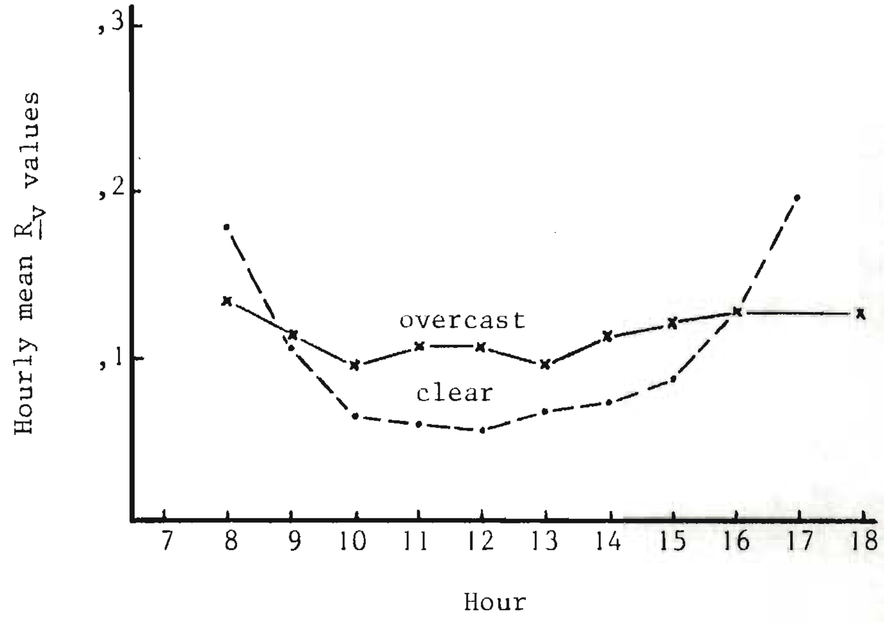

Fig. 1.14: Effect of weather on hourly $\underline{R}_v$ values during the reproductive growth phase (1974) (L = 3,15).

During the middle of the day, the $\underline{R}_v$ values for overcast conditions were higher than for clear periods. The mean for hours 10 to 15 was 0,068 for clear days and 0,106 for overcast conditions.

Conclusions regarding reflection

1. On clear days the reflection factor for PHAR ($\underline{R}_v$) during the middle portion of the day is low, and of the order of 0,05 to 0,08. However, during early and late hours, at low sun elevations, $\underline{R}_v$ increases to reach values of the order of 0,2 and higher.

2. Under overcast conditions $\underline{R}_v$ during the middle of the day is about a third higher than for clear conditions. The diurnal variation in $\underline{R}_v$ values is also lower for overcast conditions.

3. Except for an increase in $\underline{R}_v$ value with time for the early hours on clear days, the results from the reproductive phase show no obvious change in reflection with time of year. Readings of $\underline{R}$ were taken on days falling between 8 January and 26 March. This represents the most productive part of the maize growing season.

4. In young crops, growth stage has a significant effect on $\underline{R}_v$ due to the large portion of soil that is exposed.

General discussion

From the results obtained it becomes apparent that in calculating the absorption of visible radiant energy, reflectivity is small, but nevertheless plays a significant role. Except for the increased $\underline{R}_v$ values at the ends of the day, reflection remains fairly constant during the middle of the day, for different times of the growing season and crop development. In a simulation model a single set of hourly $\underline{R}_v$ values for clear conditions and a single daily mean for overcast days should provide sufficient accuracy in calculating energy absorption.

The transmission factor, on the otherhand, is far more variable. It is significantly affected by $\underline{L}$, plant spacing and population density. These relationships are, however, adequately described by the Beer-Lambert law (Eqn. 1.3).

CHAPTER 2

RELATIONSHIP BETWEEN MAIZE CROP PHOTOSYNTHESIS AND SOLAR RADIANT ENERGY AND TEMPERATURE

The basic biological process governing the growth of a crop is photosynthesis. During this process radiant energy is fixed by the plant and converted into a biological form and stored in the plant. Obviously the rate at which this process occurs is determined (1) by the amount of radiant energy that is available, and (2) the proportion of the available energy that is absorbed by the crop canopy. As shown in the previous Chapter, the second factor is, in turn, a function of the size of the canopy.

Various researchers, including Rabinowitch (1951), Hill & Wittingham (1957), Monteith (1963), De Wit (1965), Acock, Thornley & Warren Wilson (1971) and De Jager & King (1974), have used the hyperbolic relationship to describe the photosynthetic response of leaves to radiant energy.

De Jager & King (1974) extended their leaf model to the crop canopy. For this purpose they considered the crop canopy as a whole entity with a consistant distribution of "vegetative material which behaves in a characteristic manner when carrying out the photosynthetic process." Their photosynthetic model for a maize canopy is given in Eqn. 2.1.

$$\underline{P} = \frac{\underline{I}_v \cdot \underline{b} \cdot \underline{L} \cdot \underline{P}_o'}{\underline{b} \cdot \underline{L} \cdot \underline{P}_o' / \underline{A}_v \cdot \underline{c} \cdot \underline{Q} \cdot + \underline{I}_v} \qquad \text{............ Eqn. 2.1}$$

where

$\underline{P}$ = net photosynthetic rate ($mg/m^2/s$),

$\underline{P}_o'$ = net photosynthetic rate of an individual leaf at light saturation ($mg/m^2/s$),

$\underline{I}_v$ = incident PHAR (W/m^2),

$\underline{L}$ = leaf area index of the canopy,

$\underline{A}_v$ = absorption factor for PHAR,

$\underline{b}$ = a canopy efficiency factor reducing $\underline{LP}_o'$, the maximum possible rate of photosynthesis at high radiation intensity,

$\underline{Q}$ = theoretical photochemical efficiency of the photosynthetic process for the middle of the PHAR wavelength range (approximately equal to 22×10^{-6} g CO_2/J),

$\underline{c}$ = an efficiency factor of the canopy at low light intensities

Both $\underline{P}_o'$ and $\underline{c}$ are genetically controlled characters. $\underline{P}_o'$ is largely determined by the rate of CO_2 diffusion from the external air to the chloroplasts, whereas $\underline{c}$ is mainly dependant on the photochemical process resulting in the conversion of light energy. De Jager & King (1974) have presented values of 1,8 $mg/m^2/s$ and 0,84 for $\underline{P}_o'$ and $\underline{c}$ respectively, whereas their estimate of efficiency factor $\underline{b}$ was 0,5. These factors were based on results obtained in Canada by Totsuka & King (1970).

The photosynthetic response of a crop to temperature is less clear. Gates (1965), Idso (1968) and De Jager & King (1974) have calculated the relationship between net photosynthesis and temperature. For maize these workers have arrived at a peak photosynthetic rate at 30°C, which becomes progressively less at lower and higher temperatures.

According to De Jager & King (1974) the effect of temperature on maize crop photosynthesis can be mathematically described as

$$\underline{P} = \underline{P30} \ \exp \ (-0{,}0015 \ (30-\underline{T})^2) \quad \ldots\ldots\ldots \quad \text{Eqn. 2.2}$$

where $\underline{P30}$ = photosynthetic rate at 30°C ($mg/m^2/s$),

and $\underline{T}$ = ambient air temperature (°C).

Eqn. 2.2 was derived from data presented by Totsuka & King (1970). However, this data exhibited considerable scatter and the number of observations were small. Its reliability is therefore questionable.

Blackman (1970) working with several species found "that the effects of temperature on relative growth rate were more associated with effects on leaf area growth than on net assimilation rate." Similarly, Monteith & Elston (1971) concluded that in Britain the photosynthetic rate of a healthy crop is almost independent of foliage temperature, especially within the range 10°C to 25°C. Under dull conditions the photochemical process limits photosynthesis, whereas in bright sunshine the diffusion of CO_2 to the chloroplasts is limiting. These workers agree with Blackman (1970) that leaf growth is strongly temperature dependent.

In the case of maize, measurements on the effect of temperature on crop photosynthesis have given varying results. Moss, Musgrave & Lemon (1961) maintained an average temperature differential of 4,2°C between two enclosures. The temperature range studied ranged from 20°C to 44°C. On the average CO_2 assimilation was 8% higher in the warmer chamber. Over a similar air temperature range, viz. 24°C to 40°C, Hesketh and Musgrave (1962) could not detect a response in the rate of photosynthesis to changes in temperature.

Data presented by Hofstra & Hesketh (1969), on the otherhand, showed no difference in CO_2 uptake where leaf temperatures varied from 30°C to 42°C, but a marked decrease was recorded at temperatures beyond 42°C.

From the above results it can be concluded that under normal conditions temperature is likely to play only a minor direct role in photosynthesis. At high light intensities and high CO_2 concentrations, however, both the photochemical and the CO_2 diffusion processes may be non-limiting in which case the temperature dependant biochemical process may become the major limiting force. This was well demonstrated by Gaastra (1969) using cucumber leaves. At 0,03% CO_2 concentration, there was no difference in the rate of photosynthesis between leaves at 20°C and 30°C, but at a CO_2 concentration of 0,13% the leaves at 30°C had a photosynthetic rate approximately 40% higher than leaves at 20°C. In all cases the leaves were exposed to high radiation intensities. Through its effect on respiration, temperature does affect the daily CO_2 gain in the crop. This aspect is discussed in Chapter 4.

To study the relationship between the rate of photosynthesis of a maize crop and radiant energy and air temperature, the CO_2 uptake of maize, planted at different population densities, was measured at different growth stages during the 1971/72 seasons.

MATERIALS AND METHODS

In 1970/71 the yellow maize hybrid SA 60 was grown at a population density of 4,78 plants/m^2 at the University of Natal, Pietermaritzburg, whereas the following season (1971/72) the same hybrid was grown at three population densities at Cedara College of Agriculture.

Details regarding the population densities, plant spacings, planting and emergence dates and fertilizer applications are given in Table 2.1. To eliminate, as far as possible, nutrient and moisture deficiencies, high levels of fertilizer were applied and the crops were irrigated whenever necessary. The plant rows were also orientated in a north-south direction to allow for near maximum interception of solar radiant energy.

Table 2.1: Treatments and experimental details for the CO_2 uptake studies.

	Year	
	1970/71	1971/72
Population density (plants/m^2)	4,78	2,39; 4,78; 9,57
Plant spacing (m)	,91 x ,23	1,88 x ,23; ,91 x ,23; ,46 x ,23
Planting date	16/11/70	8/11/71
Emergence date	23/11/70	17/11/71
Fertilizer application (kg/ha)		
N	477	148
P	302	88
K	403	85
Agricultural lime	2118	2118
Gypsum	159	-
Borax	-	16
Zinc sulphate	-	16
Copper sulphate	-	16

In 1970/71 the net photosynthetic rate of the crop was measured during the grain filling period. After measuring the CO_2 exchange for four days, the population was reduced to 3,58 plants/m^2 by removing a number of plants from the plastic enclosure. After a further two days of CO_2 measurements, a number of plants were again removed to give a final population of 2,39 plants/m^2. It was thus possible to measure the photosynthetic rate of plants from the same original population growing at different population densities.

During the 1971/72 season the net photosynthetic rate of SA 60 growing at three population densities (viz. 2,39 plants/m^2; 4,78 plants/m^2

and 9,57 plants/m^2) was measured. In the case of the 4,78 plants/m^2 population readings were taken during both the vegetative and the reproductive growth phases, as well as at silking. The same plants were used for both growth stages. For the high and low populations CO_2 uptake was recorded in the vegetative and reproductive phases respectively.

CO_2 uptake measurements

The rate of CO_2 exchange in the maize crops was measured using a method similar to that described by Musgrave & Moss (1961) and Baker & Musgrave (1964). A number of plants near the center of the plot were enclosed in an airtight plastic tent. The plastic enclosure was 1,83m long and 3,35m high. The floor of the enclosure consisted of masonite sheeting placed on top of 0,05m by 0,08m by 1,83m poles. The floor was thus raised from the soil surface which allowed for the free movement of air below the enclosure and facilitated watering of the plants. The masonite was covered by 400 gauge plastic sheeting which was sealed around the plants with plastic adhesive tape. The frame was made of steel conduit and it was covered by 400 gauge plastic sheeting which was sealed to the plastic floor cover.

To control the temperature inside the tent, an air-conditioner was installed on the south side of the plastic enclosure above the crop surface. A fan was placed into the top north-western corner of the tent, which, together with the fan from the air conditioner facilitated air movement across the crop surface. The plastic enclosure is illustrated in Plate 2.1 and a diagramatic view of the tent from above is given in Fig. 2.1.

Plate 2.1: The plastic enclosure used for measuring crop photosynthesis. Top - A general view with the air conditioner on the left. Bottom - A close-up with the plastic sides rolled up.

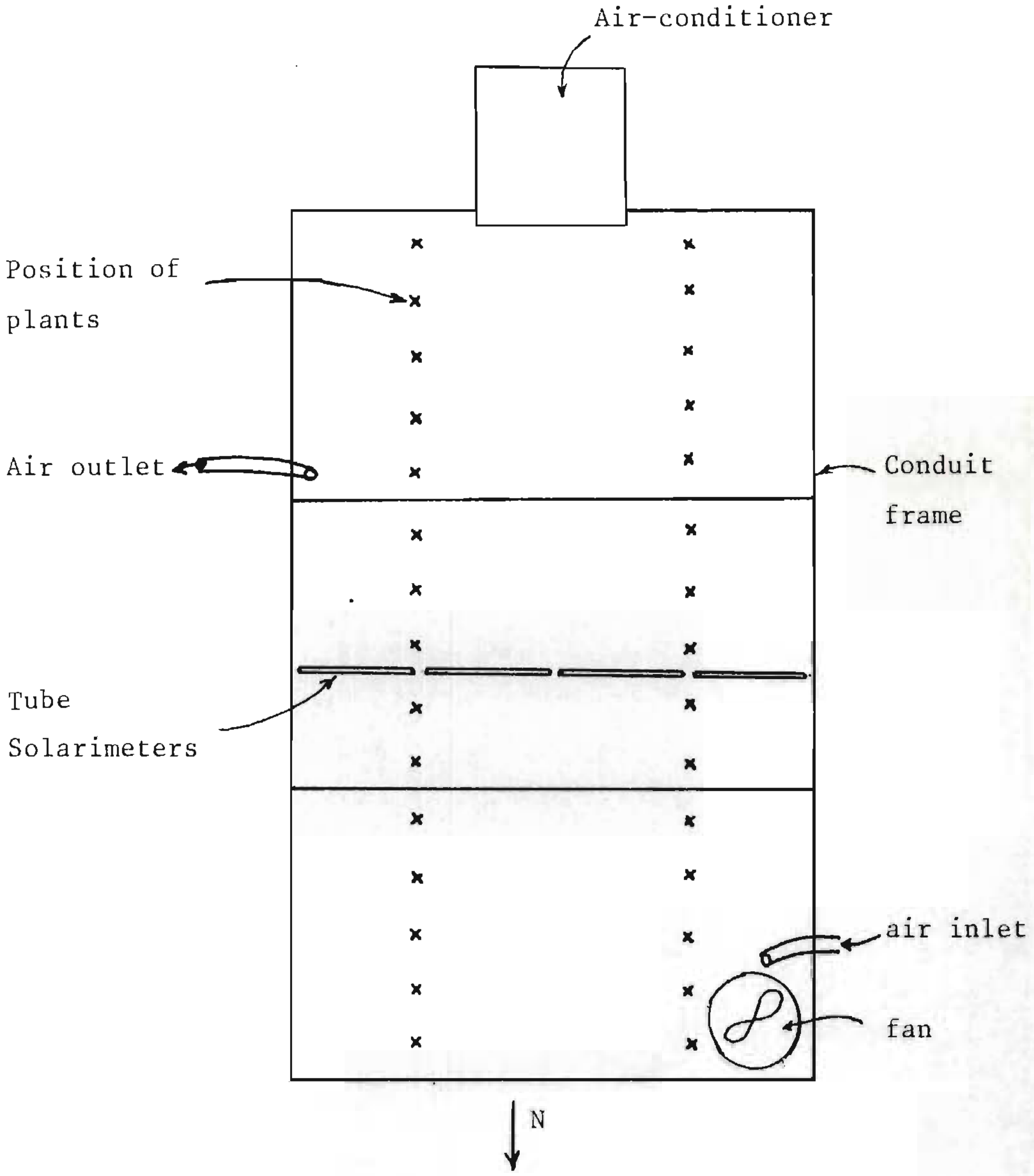

Fig. 2.1: A diagramatic view of the tent from above.

With the help of a vacuum pump, a stream of air was withdrawn from the tent, passed through 13mm (internal dimension) plastic tubing through a series of flow meters into a Grubb-Parsons infra-red gas analyser (IRGA) and back to the plastic enclosure. In 1971/72 a Beckman Model A IRGA was used. The point of withdrawal from the tent was on the eastern side, approximately 1,8m from the floor and 2m from the north wall of the enclosure. The inlet was directly over the fan in the north-western top corner, which allowed for the rapid circulation of air through the plastic pipes, the larger portion of the extracted air by-passed the IRGA and only a small fraction was actually passed through the IRGA. The flow rate of the air by-passing the IRGA was measured to be 166ml/s. By means of flow and pressure regulators the flow rate through the IRGA was kept constant at 15ml/s.

At the start of the experiment the sample and reference tubes of the IRGA were balanced at near ambient CO_2 level. This was achieved by passing a constant and equal stream of air obtained from about 5m above the ground through both IRGA cells and balancing the instrument to give a mid-scale deflection. Once stability had been reached the reference cell was closed-off by valves. To avoid a pressure build up in the reference cell, the valve controlling the flow into the reference cell was closed eight seconds before the valve which was connected to the outlet tube of the IRGA by a 3m long plastic tube. Air was then withdrawn from inside the plastic enclosure. As the CO_2 concentration in the tent decreased, so did the CO_2 concentration in the sample tube of the IRGA decrease, causing an imbalance between sample and reference cells producing a negative deflection of the meter needle. To replenish this deficiency, pure CO_2 from a cylinder was passed through a flow meter into the airstream. The CO_2 enriched air entered the plastic tent above the fan and was thus rapidly mixed with the atmosphere in the tent.

The amount of CO_2 required to maintain the CO_2 concentration inside the plastic enclosure at a constant level over a given time period could thus be determined. This equals the photosynthetic rate. A schematic layout of the monitoring equipment is given in Fig. 2.2

Radiant Energy

Six tube solarimeters of the type described by Szeicz et al. (1964) were used to measure the radiant flux density inside the tent. These solarimeters were orientated in an east-west direction and levelled. Two were positioned above the crop and four at ground level. The latter four were placed in such a way that they traversed the entire width of the enclosure (see Fig. 2.1). An integrated value of the solar energy transmitted through the canopy was thus obtained. The emf emitted by these solarimeters was recorded on a 6 channel strip-chart millivolt recorder.

Temperature

The temperature inside the tent and in the maize surrounding the tent, was continually monitored using suitably screened resistance thermometers placed at 0m, 1,5m and 3m from ground level inside and outside the tent.

Crop measurements

The procedure followed to determine the DM yield and L value of the crop at the time that CO_2 uptake measurements were made was the same as that described under 'Materials and Methods' in Chapter 3. In 1970/71, DM and L determinations were made on the plants removed from the enclosure when the population density was reduced. During the time that CO_2 uptake was recorded in 1971/72, ten plants were selected at random from the area around the tent, but not from the plants actually adjoining the enclosure, and used for DM and L determinations.

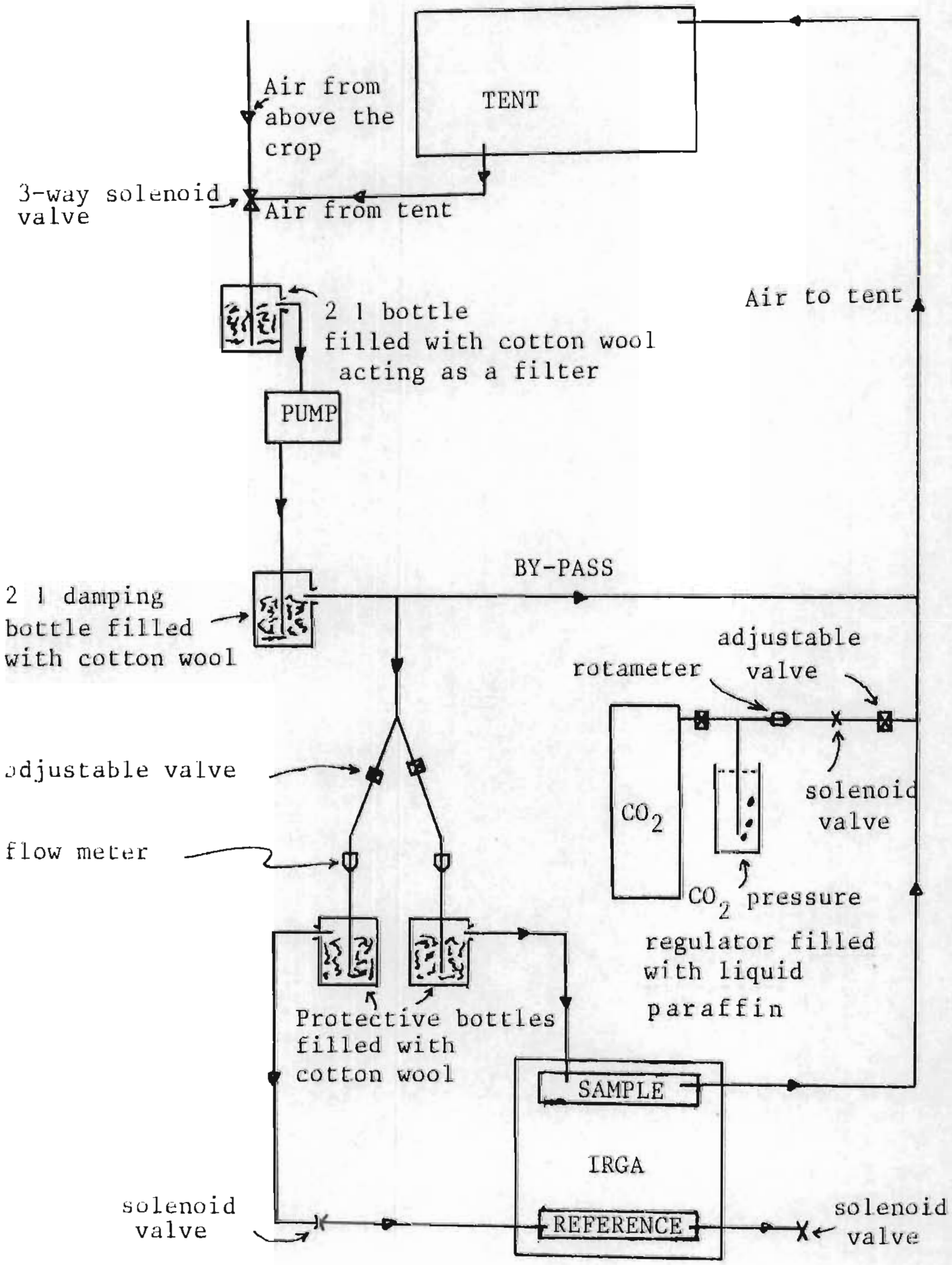

Fig. 2.2: A schematic layout of the CO$_2$ measuring system.

Calibration of instruments

1. Flow meters

The rotameter used for metering CO_2 was calibrated at room temperature (i.e. 22,5°C) by bubbling CO_2 into a 250ml measuring cylinder filled with liquid paraffin. Fifteen settings on the rotameter, ranging from 1,7 to 12,6 which covered the full range of values used in the experiment, were used. The amount of liquid paraffin displaced per unit time was determined for each setting. The linear regression function

$$\underline{f} = 0,768 + 0,898\ \underline{f}_r \quad \ldots\ldots\ldots\ldots \text{ Eqn. 2.3}$$

where $\underline{f}$ = corrected flow rate (ml/s)
$\underline{f}_r$ = recorded flow rate (ml/s)

fitted the data extremely accurately ($\underline{r}$ = 0,9996).

The function of the two manometers used to monitor the flow of air into the IRGA, was merely to ensure a constant air flow rate of 15ml/s. The same method as that described above for the rotameter was used to calibrate the manometers.

2. Tube solarimeters

The six solarimeters used in this experiment were calibrated according to the method described in Chapter 1. For the early and late hours of clear days the calibration constants were adjusted according to the factors listed in Table 1.3, whereas for overcast days they were increased by 7,3%. (See 'Calibration of solarimeters' under Materials and Methods' in Chapter 1.) The calibration constants used are listed in Table 2.2. In 1970/71 the four solarimeters installed at the base of the crop (solarimeters 2,3,5 and 6) had a higher sensitivity than those installed above the crop surface. In 1971/72 potential dividers were used to ensure that all solarimeters gave equal deflection on the strip chart recorder for the same incident radiant flux density.

Table 2.2: Calibration constants for the six solarimeters used.

Solarimeter	Calibration constant	
	1970/71	1971/72
	W/m^2 per m V	W/m^2 per m V
1	75,74	74,57
2	31,96	74,57
3	23,10	74,57
4	68,44	74,57
5	22,94	74,57
6	28,79	74,57

3. Resistance thermometers

The manufacturer's calibration constants were used to correct recorded temperatures.

4. IRGA

In this trial the IRGA was used merely as a null detector. A highly sensitive range of the IRGA, Gain 6, was utilized. The instrument was set at mid-scale when air equal to ambient CO_2 level was passing at 15ml/s through both the sample and reference cells. During the actual recording periods the readings were maintained as closely as possible to mid-scale deflection. Where the readings before and after a specific time period differed, the amount of CO_2 metered into the tent during that period was corrected according to the difference in IRGA reading, calculated using the manufacturer's calibration. This was considered accurate since errors in the calibration constant have only a minimal effect on the calculated amounts of CO_2 taken up by the crop. Consider the following example:

The capacity of tent $\simeq$ $19m^3$,
one division on IRGA scale = 2 v.p.m., and

one division difference $\simeq$ 38ml CO_2.
If CO_2 metered in during the entire period = 5 l, and
the difference in a IRGA reading = 10 divisions,
then the required correction = 7,6%.
Suppose the error in the manufacturer's calibration = 10%, then
the overall error due to inaccuracy in the IRGA calibration = 0,8%

Hence even at the relatively low CO_2 uptake of 5l, a big difference in IRGA readings of 10 divisions and a relatively large calibration error of 10%, only an estimated error of less than 1% in the calculated photosynthetic rate results.

Calculation of CO_2 uptake

The mass of CO_2 taken up by the crop during any specific time period was calculated according to Eqn. 2.4.

$$P = \frac{1{,}976 \cdot (f + d_i \cdot 38/t_r)}{5{,}574} \cdot \frac{(273)}{(273+T_i)} \qquad \text{..... Eqn. 2.4}$$

where

P = photosynthetic rate ($mg/m^2/s$),
f = CO_2 flow rate (ml/s),
1,976 = density of CO_2 at 0^oC (mg/ml),
5,574 = surface ground area in the tent (m^2),
d_i = difference in IRGA reading at the start and end of the specific recording period (divisions),
T_i = mean temperature in the recording room (^oC),
t_r = length of recording period (s),
273 = absolute temperature, and
38 = volume of CO_2 equivalent to one division on IRGA scale (ml).

Calculation of absorption factor (A_v) for PHAR

The difference in readings between the solarimeters above and at the base of the crop, gave the total amount of radiant energy intercepted by the crop. Using the method proposed by Tooming (1966), and described under 'Materials and Methods' in Chapter 1, the interception of PHAR was then estimated. To find the amount of PHAR absorbed by the crop, the reflected energy was subtracted. For this purpose hourly R_v values presented in Fig. 1.9 (Chapter 1) were used.

Discussion of the experimental procedure

1. The plastic enclosure technique

Measurements made at 12h00 showed that the plastic material used in the construction of the tent intercepted 16% of the total incoming solar energy on a clear day. The solar energy regime inside the tent was therefore lower than outside. In 1971/72 this difference was accentuated by the fact that this work was conducted under a hail shelter which also intercepted some of the incoming energy. It was therefore not possible to test the crop response under conditions of very high solar radiation.

It was not always possible to prevent a shadow of the conduit frame or hail shelter from falling onto one of the solarimeters installed above the crop. This problem was obviated by selecting the higher of the two readings as the true value for incoming solar energy.

Except in the first tent used in 1970/71, when the air conditioner was faulty, temperature control inside the tent was satisfactory, but it was not possible to maintain a temperature inside the tent of less than 20°C on hot days. No attempt was made to simulate the outside temperature inside the tent. The temperature inside the tent was set at a constant level while the radiation climate varied. In 1971/72 the temperature differential was approximately 1½°C around the mean.

A serious problem in this work was damage done and disturbance to the crop when installing the tents, particularly in dense and fully developed maize canopies. For this reason movement into the enclosure was kept to an absolute minimum. In 1970/71 some damage was unavoidable when some of the plants were removed from the tent. In 1971/72 damage to the plants inside the tent was minimal, even though the tent was removed between recording periods to allow the plants to develop under as near natural conditions as possible.

The recording room was a considerable distance away from the tent. This resulted in a time lag between the change in CO_2 climate inside the tent and its measurement by the IRGA. This lag was reduced by increasing the flow rate of air through the connecting pipes and bypassing the IRGA with the major portion of the air stream. In 1970/71 the time lag between change in CO_2 input and response on the IRGA was 2,75 minutes, which was insignificant since hourly CO_2 uptake values were recorded. In 1971/72 the lag was 3,75 minutes. The measurements, were corrected for this lag which was particularly important when the CO_2 uptake over 15 minute periods was determined.

Although all possible precautions were taken in sealing the tent, it is possible that in so big an enclosure small leaks did occur. However, since the CO_2 inside the enclosure was kept at the ambient level, there was no major gradient between the CO_2 concentration inside and outside the tent, and CO_2 exchange between the air in the tent and the outside atmosphere by diffusion should therefore have been insignificant. Furthermore, only a slight positive pressure was maintained inside the tent.

There was considerable turbulence of air above the crop inside the tent, resulting in marked vibration of the top leaves.

2. The maize crops

The reasons for chosing the hybrid SA 60 for this work were (a) it was the most popular and uniform hybrid in the Natal Midlands; (b) it had been widely used in other experiments; (c) it is well adapted to conditions at Cedara; (d) it has good standability; and (e) it is shorter and thus more manageable for this type of work than the more productive hybrids SR 52 and PNR 353. Since the start of the programme numerous new hybrids have appeared on the market which are proving more popular than SA 60.

In growing the crop all possible precautions were taken to eliminate fertilizer and moisture stress. Nevertheless, in 1971/72 four of the plants inside the plastic enclosure in the crop with a 4,78 plants/m^2 population did not form ears. This could have been due to competition for sunlight particularly as this maize was grown under hail shelter. However, it is possible that undetected moisture or nutrient stress played a role.

3. Harvesting and sampling techniques

The sampling technique used in 1970/71, when measurements were made on plants removed from the enclosure, made it possible to measure the effect of a changing L and energy absorption values on the CO_2 uptake of plants from the same original tent population. Furthermore, the sample taken was truly representative of the plants used for the CO_2 exchange determinations. However, it had two major disadvantages viz. (a) being destructive, the same plants could not be used at different developmental stages, and (b) repeated removal of plants from the tent caused some damage to the leaves of the remaining plants.

The sampling technique used in 1971/72, when 10 plants were selected at random from the area around the tent, had the advantage that the plants that were being monitored were left undisturbed and could be used at different growth stages. The major disadvantage was that the plants measured were not the ones actually used for the CO_2 uptake recordings. At times plants had to be selected that were a fair distance away from the tent. However, an earlier study on sample sizes for SA 60 growing at Cedara had shown that a sample of 5 plants gives an adequate estimate of the L value of the crop (Kaiser & Mallett, 1968). Since L was the most important attribute required, the 10 plant sample was more than sufficient for this purpose.

RESULTS AND DISCUSSION

Photosynthesis response to radiant flux density

The CO_2 exchange data was grouped according to the developmental stage of the crop, its population density and the year. The photosynthetic model of De Jager & King (1974), given in Eqn. 2.1, was then fitted to the different groups of data. The model fitted the data well as shown by the high correlation coefficients (r) presented in Table 2.3. With one exception, the r values exceeded 0,9. Eqn. 2.8 is illustrated in Fig. 2.3 as an example of the relationship between the fitted curve and the observed values.

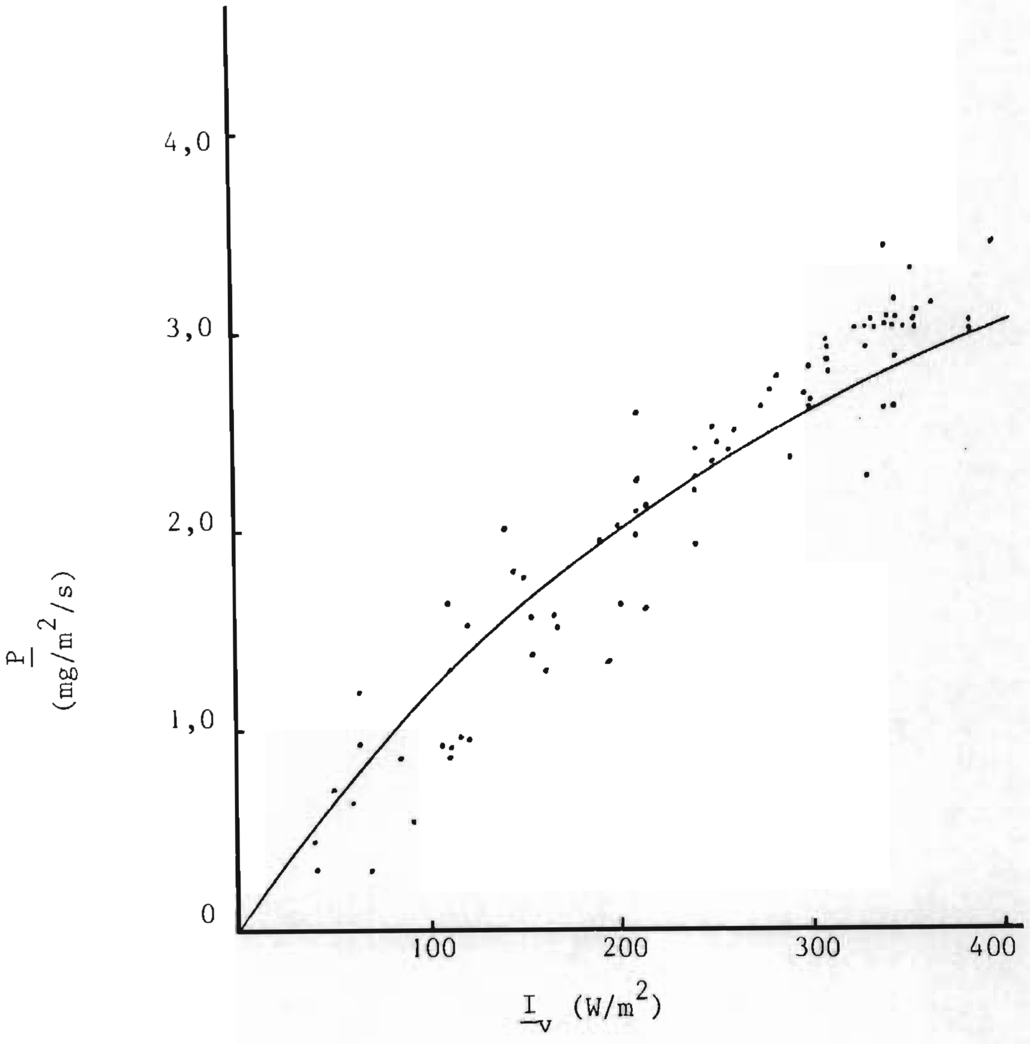

Fig. 2.3: Relationship between net photosynthesis at silking and PHAR (Eqn. 2.8) for maize with an $\underline{L}$ value of 4,32.

Table 2.3: The values for factors L, A_v, b and c giving the best fit of Eqn. 2.1, together with the r value obtained and the number of observations (n) for data from different growth stages and population densities.

Population density	Growth stage	Year	Days from Emergence	L	A_v	b	c	r	n	Eqn. no.
plants/m^2										
4,78	Vegetative	1971/72	50	1,96	,731	,878	1,139	,977	24	2.5
4,78	Vegetative	1971/72	63;64	3,93	,914	,812	1,005	,961	22	2.6
4,78	Vegetative	1971/72	70;71;72	4,62	,913	,843	,710	,958	65	2.7
4,78	Silking	1971/72	84,86	4,32	,895	,783	,765	,976	80	2.8
4,78	Reproductive	1971/72	106;107	4,17	,913	,473	,757	,957	50	2.9
4,78	Reproductive	1971/72	120	3,93	,928	,599	,633	,733	13	2.10
4,78	Reproductive	1970/71	88;89;90;92	4,84	,870	,627	,671	,903	20	2.11
3,58	Reproductive	1970/71	93;94	3,63	,822	,745	,677	,925	17	2.12
2,39	Reproductive	1970/71	95;96	2,50	,775	,791	,687	,964	10	2.13
2,39	Reproductive	1971/72	112	2,30	,792	,492	1,044	,951	23	2.14
2,39	Reproductive	1971/72	126;127	2,30	,844	,458	,928	,902	30	2.15
9,57	Vegetative	1971/72	55;58	6,19	,925	,723	,946	,953	15	2.16

In Table 2.3 the values for $\underline{L}$, $\underline{A}_v$, $\underline{b}$ and $\underline{c}$ for the best fit of Eqn. 2.1 of the different sets of data are presented, together with other crop details. $\underline{L}$ was determined from measurements made on the crop at the time of the CO_2 uptake readings and $\underline{A}_v$ from solarimeter readings taken above and below the crop. The $\underline{A}_v$ values presented are the means for the specific recording period. Using values of 1,8 mg/m^2/s and 22 x 10^{-6} g CO_2/J for $\underline{P}_o'$ and $\underline{Q}$ respectively, efficiency factors $\underline{b}$ and $\underline{c}$ for the best fitting rectangular hyperbola were determined by an iterative process. Estimated values of $\underline{b}$ and $\underline{c}$ were read into the computer program and the squared deviations from the mean calculated. By iteration the squared deviations from the mean were reduced until the improvement in the fit became less than one percent.

The calculated absorption factors ($\underline{A}_v$) ranged from 0,731 at an $\underline{L}$ of 1,96 (Eqn. 2.5) to 0,928 at an $\underline{L}$ reading of 3,93 (Eqn. 2.6). These figures compare favourably with those of Tooming (1966), who presented figures of 0,76 and 0,89 for maize with $\underline{L}$ values of 2 and 4 respectively. For a maize crop with an $\underline{L}$ of 4,3 Yocum, Allen & Lemon (1964) and Lemon (1967) give slightly lower $\underline{A}_v$ figures of 0,86 and 0,84 respectively. The $\underline{A}_v$ of 0,870 (Eqn. 2.11) obtained with an $\underline{L}$ of 4,84 in 1970/71 agrees closely with the latter two values.

The absorption of PHAR in the crop with a high population density of 9,57 plants/m^2 and an $\underline{L}$ of 6,19 (Eqn. 2.16) was no higher than the 4,78 plants/m^2 crop with an $\underline{L}$ of 3,93. This agrees with the findings of both Tooming (1966) and Duncan (1972) who showed that light interception in a maize crop appeared to reach a maximum at $\underline{L}$ equal to 4.

A comparison of Eqns. 2.5, 2.6 and 2.7 shows that the efficiency factor $\underline{b}$ remained more or less constant during the vegetative development of the maize crop grown at 4,78 plants/m^2. The mean for the three recording periods was 0,844. In the case of maize growing at 9,57 plants/m^2 the $\underline{b}$ factor was approximately 14% lower (Eqn. 2.16). Since $\underline{L}$ is required to calculate $\underline{b}$, the accuracy of the $\underline{b}$ value is dependent on the accuracy of the $\underline{L}$ measurement. It is possible that the L of 6,19 was slightly inflated by the inclusion of leaves with undetected senescence in the measured sample.

At silking the 4,78 plants/m^2 crop had a b value of 0,783 (Eqn. 2.8), which was approximately 7% lower than the mean for the vegetative phase.

After silking the efficiency factor b of the same crop was noticably lower viz. 0,473 (Eqn. 2.9). This reduction in efficiency is illustrated in Fig. 2.4, where Eqn. 2.6 and 2.9, representing the vegetative and reproductive growth phases respectively, are illustrated.

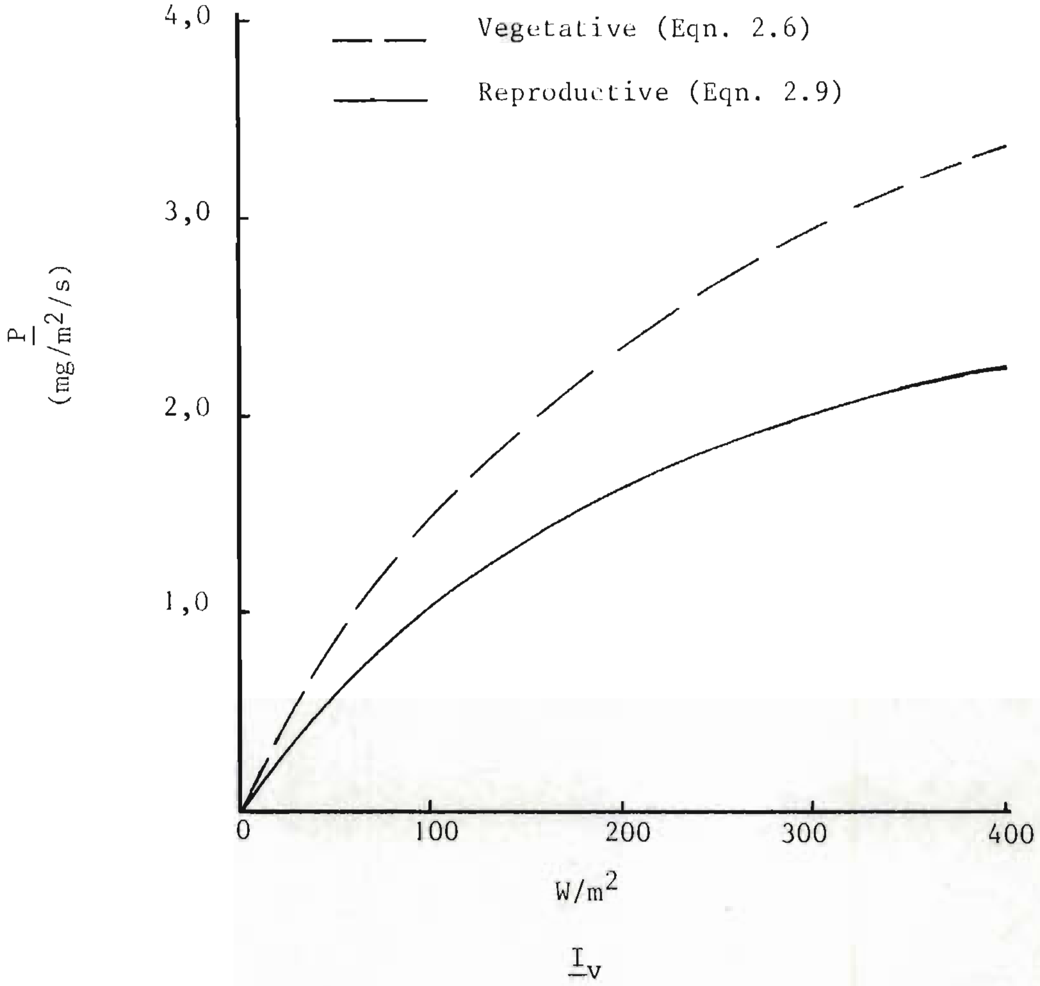

Fig. 2.4: Comparison of the net photosynthetic response of maize to PHAR during the vegetative and reproductive growth stages (1971/72).

In 1971/72 maize growing in wide rows at a population density of 2,39 plants/m^2 (Eqn. 2.14 and 2.15) gave b values, for the reproductive phase, that were similar to that of the crop grown at 4,78 plants/m^2.

The value of 0,473 for b agrees closely with the 0,5 calculated by De Jager & King (1974) from data obtained with maize in the reproductive growth phase at Elora, Canada, by Totsuka & King (1970). However, in 1970/71 SA 60 growing at the same population density of 4,78 plants/m^2 at the University of Natal, Pietermaritzburg, gave a value of 0,627 for efficiency factor b (Eqn. 2.11), which is higher than that recorded in 1971/72, but still lower than the b value recorded for the vegetative stage in that year.

The reduced photosynthetic efficiency of a crop at high light intensities after silking, relative to the vegetative stage, supports the earlier findings of the writer (Kaiser, 1972), that for the same L value the growth rate of SA 60 after silking was lower than that during the vegetative phase.

The reduction in the value of b with time can possibly be ascribed to one or more of the following causes:

(1) Shadows from the tassels will have resulted in a decrease of the radiant flux density at the surface of the crop's leaf canopy. According to figures presented by Duncan, Williams & Loomis (1967) a reduction in photosynthetic rate of 9% due to tassel shadows could be expected. In this experiment CO_2 uptake was related to the radiant flux density above the tassels. Since these values were slightly inflated, relative to the radiant energy striking the actual leaf canopy, this could have resulted in an apparent lower efficiency of the leaves at high light intensities.

(2) According to De Wit, Brouwer & Penning de Vries (1970) the photosynthetic rate of leaves is highly dependent on their age. A decrease in the photosynthetic efficiency of the canopy with time could therefore be expected. However, it appears unlikely that the abrupt decrease in b value after silking can be ascribed entirely to an ageing process.

(3) In a discussion of the relationship between the source and the sink in the plant, Beevers (1969) concludes that 'the photosynthetic rate of the source appears to be closely regulated by the demands of the sink.' After silking the greater proportion of the photosynthate produced by the maize plant is channelled to the ear. It is possible that the ear, with its comparatively limited storage capacity and confined location on the plant, has a lower sink demand than the developing leaf and stem tissues during the vegetative growth stage.

Saturation point is therefore reached at lower irradiances. Moss (1962) showed that the prevention of pollination or the removal of the ears resulted in a marked reduction in the photosynthetic rate of maize plants and an accumulation of sugars in the stem tissues. This represents an extreme case of the reduction in sink demand. At the other end of the scale would be a multi-eared plant with properly fertilized developing grain. It is logical to conclude that plants with different degrees of sink demand occur between these two extremes. This would explain the apparent anomaly between the b efficiency factors for the reproductive phase recorded in 1970/71 and 1971/72. In the first year all plants used for the CO_2 exchange measurements had well developed ears, whereas in 1971/72 four of the 25 plants inside the enclosure were barren. A further two plants had only poorly developed ears. Clearly the lower photosynthetic rate of these plants must have reduced the total CO_2 uptake of the crop at high light intensities.

The CO_2 uptake measurements made on day 120 on the 4,78 plants/m^2 crop showed considerable variation and have to be treated with reservation. The b value of 0,599 does indicate, however, that although the canopy operates at a lower efficiency after silking, the photosynthetic rate does not decrease rapidly during this growth stage.

The factor c in Eqn. 2.1 determines the efficiency of a canopy at low irradiance levels. For the crop planted at 4,78 plants/m^2 in 1971/72 the best fitting rectangular hyperbola gave c values of 1,139 (Eqn. 2.5) and 1,005 (Eqn. 2.6) at days 50 and 63-64 after emergence respectively. However, for the readings taken on days 70-72 from emergence, which coincided with the early tasseling stages, the c value had decreased to 0,710 (Eqn. 2.7). Similar values were obtained during the early reproductive phase (Eqn. 2.8, 2.9). In 1970/71 the c values obtained were slightly lower (Eqn. 2.11, 2.12, 2.13).

The sharp decline in the c value during the latter part of the season can be linked to the shading effect of the tassels. In this trial CO_2 uptake at low irradiances was measured at low sun angles. Duncan et al. (1967) showed that at low sun angles the rate of photosynthesis in a maize stand of 4,94 plants/m^2 can be reduced by up to 30% due to shading by tassels. The lower c value after silking does therefore not necessarily mean that the individual leaves of the plant are less efficient, but gives the efficiency of the crop as a whole. At low sun angles a considerable proportion of the absorbed energy is intercepted by the tassels and never reaches the leaves.

In the case of the high density maize (i.e. 9,57 plants/m^2), the c value during the vegetative growth period was 0,946 (Eqn. 2.16), a figure that is similar to those of the 4,78 plants/m^2 crop. However, in the case of the maize planted in 1,83m rows at 2,39 plants/m^2 (Eqns. 2.14 and 2.15), c values during the reproductive phase amounted to 1,044 and 0,928. These values were similar to those recorded for the vegetative phase of the higher density crops, but considerably higher than the c values for maize at a corresponding growth phase, but growing at 4,78 plants/m^2. A possible explanation for this apparent anomally can be found in the work of Duncan et al. (1967). They showed that at low populations the relative shading effect of the tassels is lower than at high population densities. For example, at low sun angles the reduction in photosynthetic rate due to shading was calculated approximately 12% for a population of 2,5 plants/m^2 compared to approximately 25% for double the population. It is likely that a further reduction in shading by tassels will occur where low populations are coupled with wide rows, as was the case for Eqns. 2.14 and 2.15.

Based on readings taken by Totsuka & King (1970) during the reproductive growth period, De Jager & King (1974) calculated a c value of 0,84. This figure is about 10% higher than was obtained for a similar growth phase at Cedara in 1971/72.

The lower efficiency of the maize canopy in the reproductive, compared to the vegetative phase, is illustrated in Fig. 2.4.

Photosynthesis response to temperature

The capacity of the air conditioner in relation to the size of the plastic enclosure, did not permit CO_2 uptake measurements at temperatures below 18°C.

The effect of changes in temperature within the range 20°C to 30°C on the net photosynthetic rate of maize growing at 4,78 plants/m^2 was measured in 1971/72 during the vegetative stage (days 70-72), at silking (days 84-86) and the reproductive phase (days 106 and 107). The data from these days was grouped into the temperature ranges 20°C ± 2,5°C; 25°C ± 2,5°C and 30°C ± 2,5°C. Eqn. 2.1 was then fitted to each group. The results are presented in Table 2.4.

Table 2.4: Effect of temperature on the basic parameters b and c of Eqn. 2.1 at different growth stages, and the correlation coefficient (r) and the number of observation in each group.

Growth stage	Days from emergence	Temperature °C	b	c	r	n
Vegetative	70 - 72	20 ± 2,5	,986	,641	,984	20
		25 ± 2,5	,901	,630	,963	29
		30 ± 2,5	,997	,639	,888	17
Silking	84 and 86	20 ± 2,5	-	-	-	-
		25 ± 2,5	,767	,717	,980	32
		30 ± 2,5	,733	,765	,968	30
Reproductive	106 and 107	20 ± 2,5	,476	,789	,944	14
		25 ± 2,5	,504	,650	,970	19
		30 ± 2,5	,527	,623	,939	16

The model of De Jager & King (1974) (Eqn. 2.1) fitted the data well. With the exception of the readings taken at 30°C on days 70-72, for which the correlation coefficient was 0,888, the r value for the other sets of data ranged from 0,939 to 0,984. As indicated by the

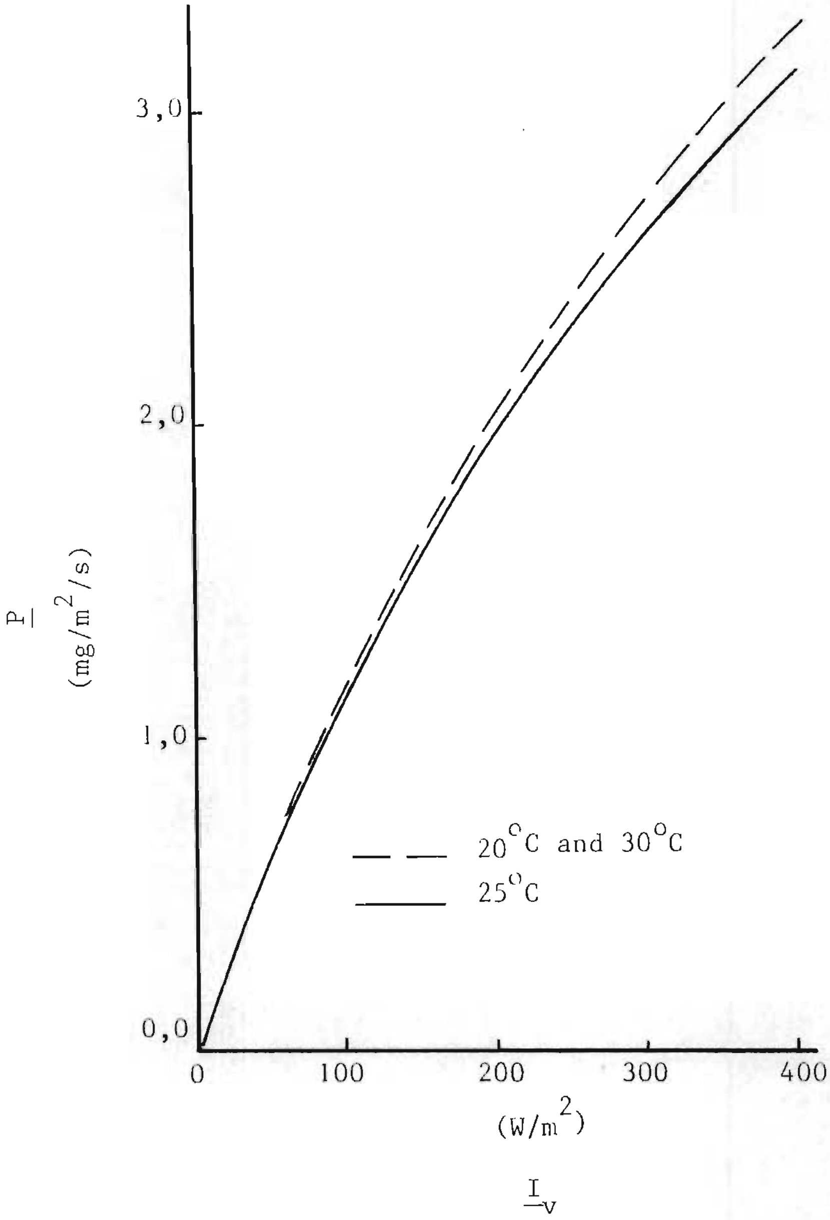

Fig. 2.5: Effect of temperature on the photosynthetic rate of maize during the vegetative growth period (1971/72).

efficiency factors $\underline{b}$ and $\underline{c}$, temperature changes had no definite and consistent effect on the rate of net photosynthesis at the three growth stages. This is illustrated in Figs. 2.5, 2.6 and 2.7. The results obtained therefore do not support the model of De Jager & King (1974), as given in Eqn. 2.2, or those of Gates (1965) and Idso (1968). However, they lend support to the findings and conclusions of Hesketh & Musgrave (1962), Hofstra & Hesketh (1969), Blackman (1970) and Monteith & Elston (1971) that fluctuations within the normal temperature range have little effect on the photosynthetic rate of a crop.

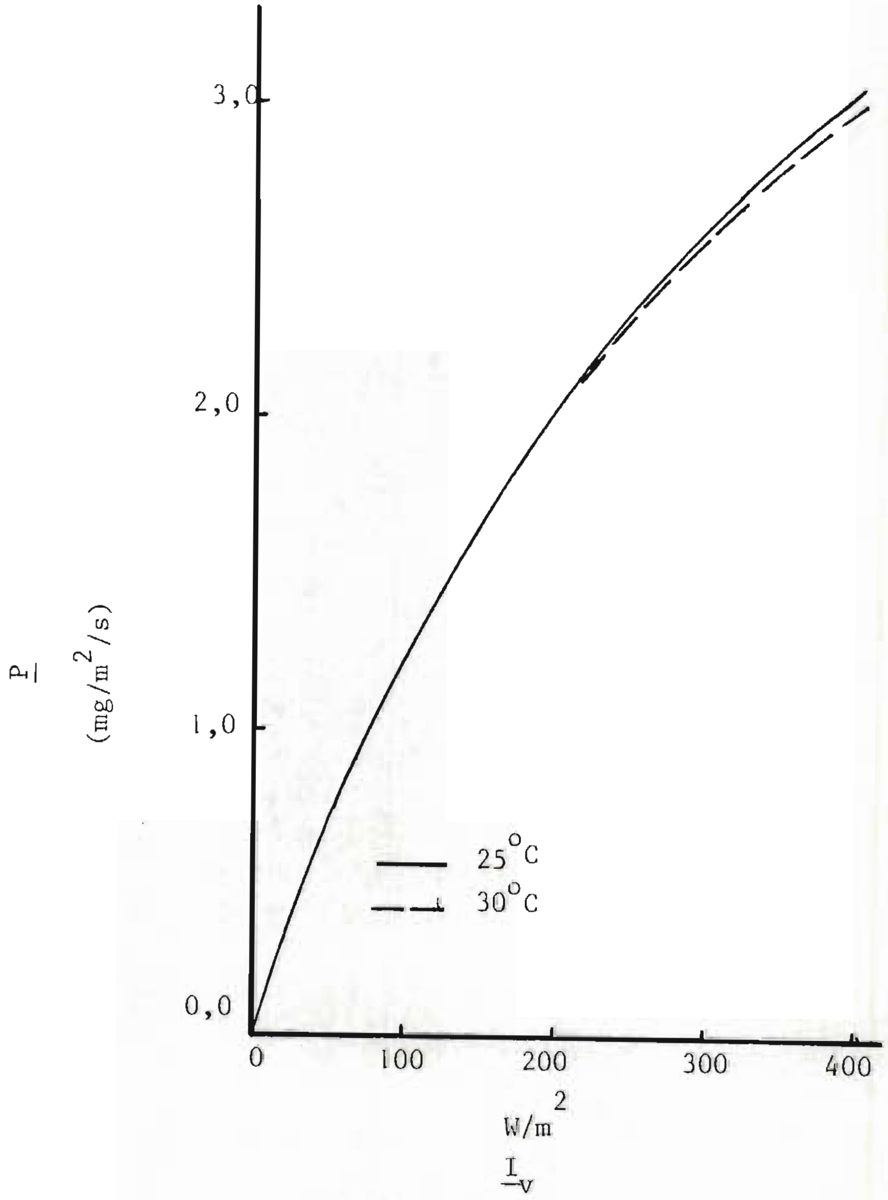

Fig. 2.6: Effect of temperature on the photosynthetic rate of maize at silking (1971/72).

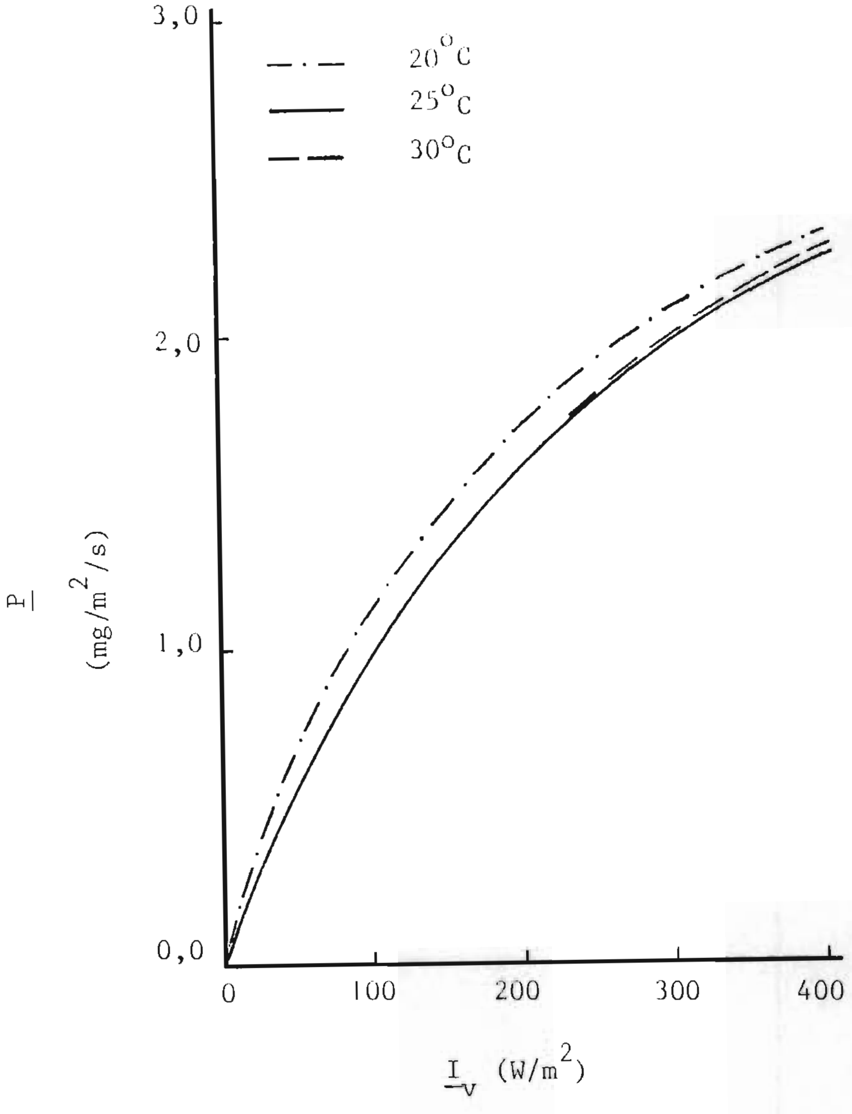

Fig. 2.7: Effect of temperature on the photosynthetic rate of maize during the reproductive growth stage (1971/72).

CONCLUSIONS

(1) The rectangular hyperbola proposed by De Jager & King (1974) (Eqn. 2.1) adequately describes the photosynthetic response of a maize crop to changes in PHAR. This model fitted the data from all three populations tested and from the different growth stages, well.

(2) The efficiency of the canopy is lower during the reproductive than the vegetative phase both at low and high radiant flux densities. At high levels of PHAR this appears to be mainly the result of a lower sink demand, whereas at low PHAR levels the shading of the tassels seems to play a major role.

(3) Maize spaced in 1,83 m rows makes more efficient use of the absorbed energy at low irradiances, but absorbs less PHAR than maize planted in 0,91 rows. At high PHAR levels the maize in closer rows appears to have a higher photosynthetic efficiency.

(4) For use in a practical growth simulation model temperature can, at this stage, be ignored as a direct factor in CO_2 uptake during the day. However, its effect on night time respiration can not be ignored. The latter aspect will be discussed in Chapter 4.

CHAPTER 3

SEASONAL DISTRIBUTION OF DRY MATTER IN THE MAIZE CROP

The growth of the maize plant can be divided into three main phases (1) planting to emergence, (2) emergence to silking, and (3) silking to maturity. During the first phase the developing seedling is totally dependent for its energy supply on the seed endosperm. Growth during this short period is therefore not directly influenced by solar radiation. This period was not considered in the present study.

The second phase, viz. emergence to silking, is the period during which the major part of the vegetative development occurs. During this period the canopy or 'factory' of the crop is formed. As it increases, greater quantities of solar energy are intercepted, which in turn affect the photosynthetic capacity of the crop. To accurately describe the growth of the crop during this period, it is essential therefore to calculate the portion of photosynthate that is used in the development of the different plant organs.

At silking 'factory' development is complete. The ensuing reproductive growth stage commences with an initial steady period. Later the photosynthetic capacity of the canopy decreases due to the senescence of leaves. During the reproductive phase, once the respiratory needs of the crop have been met, most of the photosynthate produced is absorbed in grain formation with a certain proportion used for the manufacture of the ear core and husks, and storage in the stem.

A series of growth studies covering the entire growth period were undertaken. The objective of these experiments was to quantitatively describe the allocation of photosynthate to the various plant tissues for the purpose of producing an effective growth simulation model.

The following relationships were determined:

(1) the proportion of photosynthate channelled to the roots during the vegetative growth period;

(2) the rate of dry matter accumulation, DM, in the leaves relative to the remainder of the topgrowth, during vegetative growth;

(3) the specific leaf area of the crop;

(4) the proportion of photosynthate produced after silking that is used in the manufacture of grain;

(5) the rate of decrease in L between silking and maturity; and

(6) the time of maturity of maize plants.

Investigations on the effect of population density, plant spacing, planting date and cultivar on the different developmental relationships in a maize crop were included. These factors have a marked influence on the interception of solar radiant energy.

All experiments reported were conducted at Cedara on a Doveton soil series and fertilizer and moisture limitations were eliminated by the application of heavy dressing of fertilizer and supplementary irrigation.

MATERIALS AND METHODS

The growth and development of the maize crop were studied through the period from 1968/69 to 1974/75. Treatments used and other experimental details are given in Table 3.1.

In all six seasons the yellow hybrid SA 60 was grown as the standard cultivar, but other cultivars were included at various stages for comparative purposes. Except for the second planting in 1973/74, the crop was always planted during the first half of November.

Table 3.1: Treatments and experimental details for the series of growth studies.

	Year					
	1968/69	1969/70	1970/71	1971/72	1973/74	1974/75
Population density (plants/m^2)						
1	0,90	3,59	2,39	2,39	2,39	2,39
2	3,59	14,35	4,78	4,78	4,78	4,78
3	7,18		9,56	9,56		
4	14,35					
Plant spacing (m)						
1	1,06x1,06	,53x,53	,91x,46	1,83x,23	1,83x,23	1,83x,23
2	,53x,53	,26x,26	,46x,46	,91x,23	,91x,23	1,83x,11
3	,37x,37		,91x,23	,46x,23		,91x,46
4	,26x,26		1,83x,11			,91x,23
5			,46x,23			,46x,46
Hybrid						
1	SA60	SA60	SA60	SA60	SA60	SA60
2	SR52		RO1E		SR52	RO1E
Planting date						
1	12/11	8/11	6/11	8/11	7/11	12/11
2					5/12	
Emergence date						
1	25/11	25/11	16/11	17/11	16/11	19/11
2					13/12	
Harvest Interval (days)	14	14	Varied	Varied	7	21
Fertilizer(kg/ha)						
N	197	410	620	148	140	140
P	85	254	320	88	60	66
K	113	339	430	85	80	88
Agricultural Lime	-	-	2120	2118	1300	-
Manure	-	32000	-	-	-	-
Trace Elements Used	Mo	Zn,Mo	Mo	B,Zn Cu,Mo	B,Zn Mo	Zn,B Mo
No. of plots/ treatment	3	3	1	1	1	4

Three seeds were planted per hill. The date on which approximately 80% of the seedlings had emerged was noted as the emergence date. When the plants had reached a height of about 0,1m the crop was thinned to its prescribed population.

At selected times during each stage of the entire growing season, a sample area was chosen at random in every plot. The plants from this sub-plot were severed at ground level and weighed. A sample of seven to ten plants were selected at random from the harvested plants. These plants were divided into their different components, i.e. leaf blades, stems (normally including leaf sheaths), tassels, husks and ears (again sub-divided into grain and core in some cases). The leaf blades were traced on drawing paper of consistent density and the drawing paper replicas weighed. From the mass of the drawing paper replicas, the area of the leaves was calculated. A random sub-sample was taken from each plant component, weighed, oven-dried at 90°C and re-weighed to determine the DM content. The size of the sample area harvested and the time interval between harvests for the different years are listed in Table 3.1.

In 1968/69 the roots of three of the five plants selected for plant measurements were also harvested. This was done by removing a column of soil 0,6m deep and subtended by the surface area representing the specific plant. The soil was rinsed away on a sieve and the roots (including the below-ground stem fraction) were oven-dried at 90°C and their dry mass determined. Practical difficulties prevented root measurements in all treatments. The root study was confined mainly to SA 60 planted at 3,59 plants/m^2.

The date on which 50% of the plants had silked was determined by making regular counts on 40 plants per plot over the silking period. In the 1973/74 season the silking date of a number of individual SA 60 and SR 52 plants growing at 4,78 plants/m^2 were noted. The DM accumulation in the kernels of these plants was measured from the late dough stage onwards using the method described by Duncan & Hatfield (1972). Kernels from near the centre of an individual row were carefully removed with a specially shaped wood chissel. Ten undamaged kernels were selected at random. These were weighed, oven-dried at 90°C and re-weighed. This procedure was repeated on alternate rows at two or three day intervals. At each sampling the number of kernels, from the tip of the cob down, which showed a black layer (as described by Daynard & Duncan, 1969; Baker, 1971) were counted and the amount of senescence on the husks was rated on a 0 to 5 scale, where 0 and 5 represented zero and complete senescence respectively.

The crop measurements were made either on individual plots to which a certain set of treatments had been applied, or where the treatments could be replicated three or four times, on plots in a randomised blocks design. The number of plots per treatment combination in each year are given in Table 3.1.

High levels of fertilizer were applied (See Table 3.1). Except for two-thirds of the N dressing, which was applied as a topdressing when the plants reached a height of 0,5m, the fertilizer was broadcast over the experimental site and disced into the soil prior to planting. Moisture stress was avoided by regular irrigation of the experiments. Weeds and insect pests were controlled by normal agronomic practices.

Calculation of accumulated heat units

The development of the crop was related to the accumulated HU (heat units), which were calculated according to the remainder index method as described in the literature review by Dijkhuis (1971) and given in Eqn. 3.1.

$$HU = \sum_{m=1}^{m=M} \frac{\underline{Tmax}_m + \underline{Tmin}_m}{2} - 10 \qquad \text{......... Eqn. 3.1}$$

where

on the mth day $\underline{Tmax}_m$ and $\underline{Tmin}_m$ are the maximum and minimum temperatures in $^{\circ}$C respectively, and
M is the number of days over which HU are accumulated.

Maximum temperatures above 30°C and minimum temperatures below 10°C are set equal to 30°C and 10°C respectively.

Calculation of root and leaf partitioning factors

The rate of DM accumulation in the roots (DR) relative to the total DM accumulated in the crop during a specific time interval (x) was calculated as follows:

$$DR = \frac{d\,RM}{dCDM}$$

$$= \frac{d\,RM}{dt} \Bigg/ \frac{dCDM}{dt}$$

$$= \frac{RM_{m} - RM_{m-x}}{CDM_{m} - CDM_{m-x}} \qquad \text{.......... Eqn. 3.2}$$

where RM = root dry mass (g), and

CDM = dry mass of the total crop including roots (g), and

t = time (days).

The rate of DM accumulation in the leaves (DL) relative to the DM accumulated in the topgrowth for a specific time interval (x) was calculated as

$$DL = \frac{d\,LM}{d\,TM}$$

$$= \frac{d\,LM}{dt} \Bigg/ \frac{d\,TM}{dt}$$

$$\frac{LM_{m} - LM_{m-x}}{TM_{m} - TM_{m-x}} \qquad \text{.......... Eqn. 3.3}$$

where LM = leaf dry mass (g), and

TM = dry mass of topgrowth (g).

RESULTS AND DISCUSSION

The developmental growth stages

The number of days and accumulated HU required by the maize crop to pass through different developmental stages in the Cedara experiments are presented in Table 3.2

Table 3.2: The number of days and HU accumulated during different growth stages.

Year	Hybrid	Planting date	Plant. to emergence		Emergence to silking		Silking to maturity	
			Days	HU	Days	HU	Days	HU
1969/70	SA 60	18/11	7	50	83	748	-	-
1970/71	SA 60	6/11	10	77	80	754	-	-
1971/72	SA 60	8/11	9	54	82	770	-	-
1973/74	SA 60	7/11	9	43	79	746	-	-
	SR 52	7/11	9	43	81	771	-	-
	SA 60	5/12	8	59	75	738	56	458
	SR 52	5/12	8	59	77	762	72	523
	SA 60	MEAN	9	57	80	751		
		SE	1	13	3	13		

Maize planted into a moist soil at Cedara took, on the average, between 8 to 10 days to emerge. Silking occurred 79 to 83 days later where SA 60 had been planted in November, and 75 days later where it was planted in 5/12 in 1973. The coefficient of variation in days to silking was 3,8%. In 1973/74 SR 52 silked two days after SA 60.

SA 60 required the accumulation of, on the average, 57 ± 13 HU between planting and emergence, whereas 751 ± 13 HU were accumulated during the crop development from emergence to silking. The C.V. in this case was 1,5% or less than half that for the day scale.

These results support the findings of Dijkhuis (1971,1972) that HU are a more reliable measure of the length of the growth period from emergence to silking than days. Data presented by Mallett (1974), obtained with five popular Natal hybrids grown at three sites, viz. Cedara, Kokstad and Dundee, gave a greater mean variation when a time scale was used, as opposed to the HU scale. The mean C.V. for the five cultivars was 4,4% and 8,2% for the HU and day scales respectively.

Over the vegetative growth period hybrid SR 52 required 24 HU (or 3,2%) more than hybrid SA 60.

Studies on the length of the reproductive growth period (i.e. silking to maturity) were limited to the December planted maize of the 1973/74 season, when the growth of kernels on five ears of hybrid SA 60 and seven ears of SR 52 were studied. DM accumulation in the kernels in relation to days and accumulated HU from silking for four and six ears of SA 60 and SR 52 respectively, are presented graphically in Fig. 3.1 and 3.2 respectively. Due to the small number of replications the scatter of points is fairly wide. Nevertheless, the time of maximum kernel mass was sufficiently consistent to estimate the time of maturity.

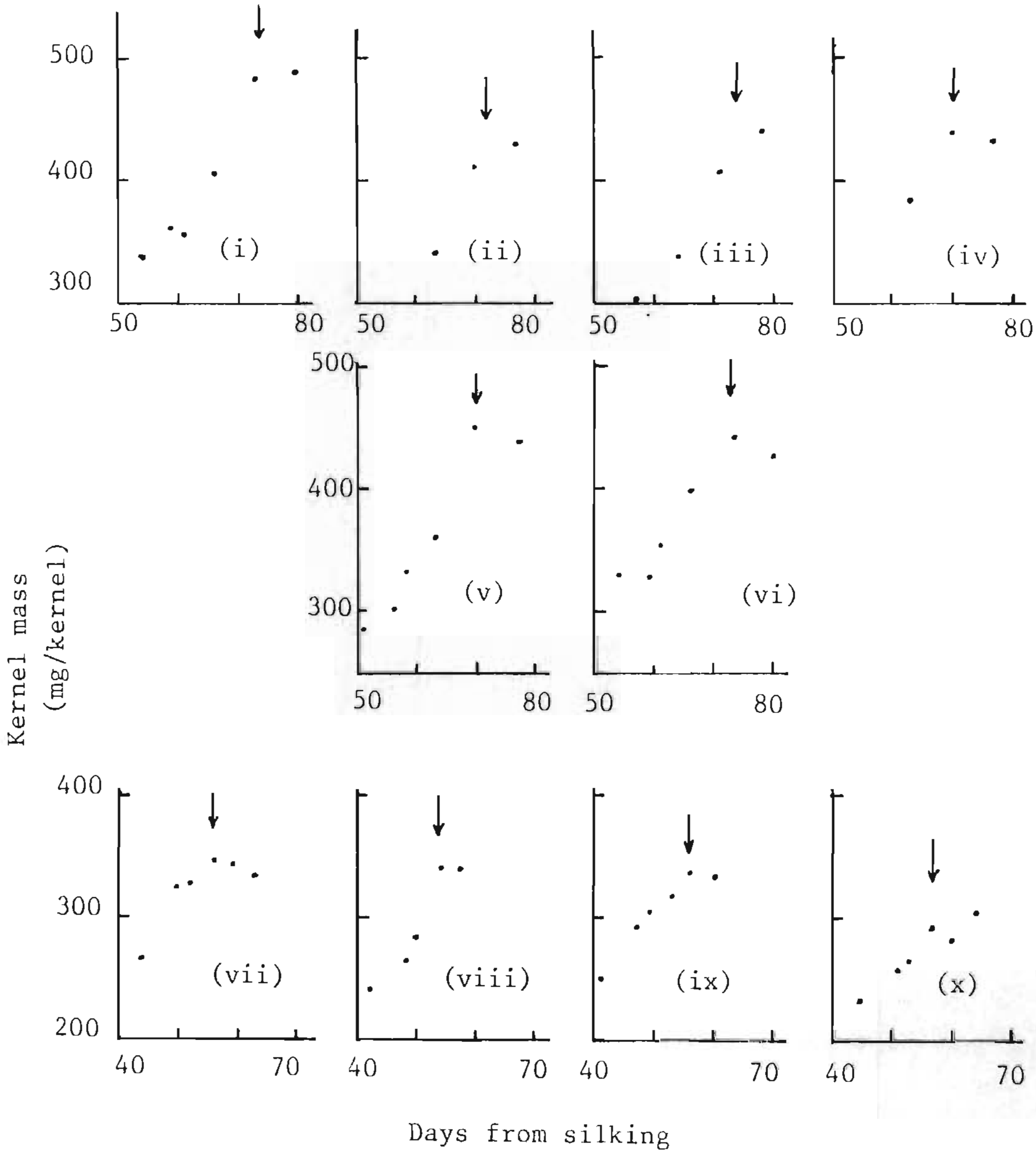

Fig. 3.1: Relationship between DM accumulation in the kernel and days from silking. Graphs numbered (i) to (vi) represent six SR 52 plants, whereas those numbered (vii) to (x) are four SA 60 plants. Arrows indicate the estimated maturity (1973/74).

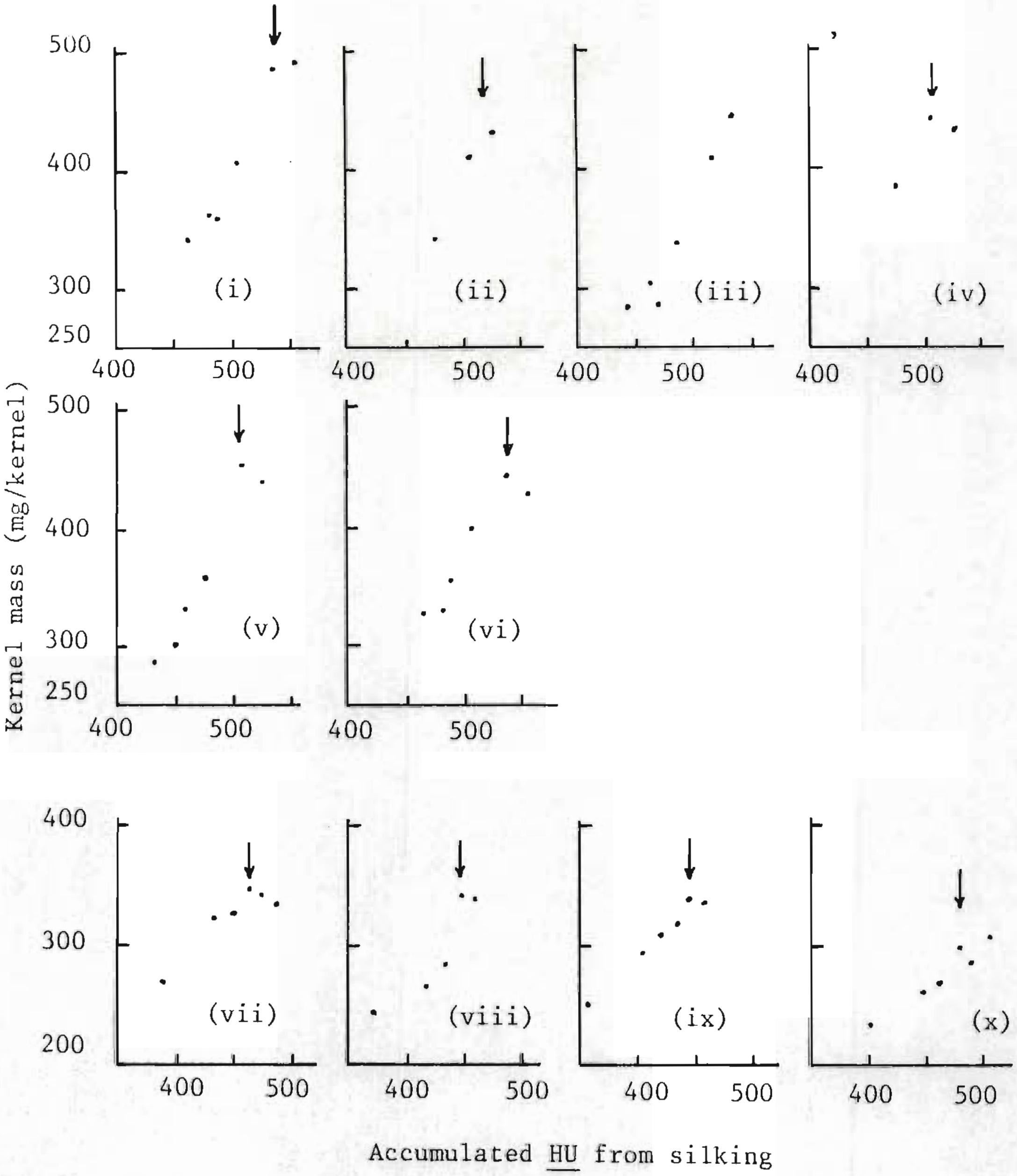

Fig. 3.2: Relationship between DM yield of the kernel and HU accumulated after silking. Graphs numbered (i) to (vi) represent six SR 52 plants, whereas those numbered (vii) to (x) are four SA 60 plants. Arrows indicate the estimated maturity (1973/74).

In the case of SA 60 estimated maturity was reached 56 ± 1 day or 458 ± 13HU from silking, whereas for SR 52 these figures were 72 ± 2 days or 523 ± 14 HU.

Researchers have for many years sought a method whereby maturity may be visually detected. Various methods have been tested. Of these the black layer technique has become the most widely accepted (see Daynard & Duncan, 1969; Baker, 1971). This method is based on the argument that when a kernel reaches maximum dry mass, the placenta tissue cells connecting the kernel to the core collapse and turn brown then black, thus sealing the kernel. Black layer formation starts with the grain at the tip and progresses along the cob. The generally accepted standard for date of maturity is when the kernels in the middle of the cob have a black layer. At Cedara senescence of the cob sheaths or husks has also been used as an indicator of maturity (Mallett, 1970).

At each harvest of kernels, the number of kernels from the tip of the cob down that showed a black layer were counted and the amount of husk senescence was rated. With the exception of two kernels on one SA 60 ear, not a single kernel with a black or even brown layer was found on any SA 60 or SR 52 cobs on the date that the kernels reached maximum DM yield. However, at that stage it was possible to break the kernel at the placenta without damaging it and a clear abscission layer was discernable. This was the case for all kernels down to the base of the ear. Black layer appeared on the center kernels approximately one week later. At the time of maximum DM the proportion of senesced husks had reached between 80% to 100%.

The results indicate that for local conditions, black or brown layer is not an acceptable indicator of physiological maturity. The black layer becomes apparent some considerable time after the placenta cells have collapsed and sealed the kernel. With experience it should be possible to recognise the appearance of the abscission layer. This is, however, not a simple method of detecting maturity. A simpler method would be the rating of the husks. However, whether or not this method has universal application requires further investigation.

Measurements on individual kernel growth were only done on the December 1973 planted maize. From those readings the conclusion was drawn that hybrid SA 60 reached physiological maturity 56 days or 458 accumulated HU from silking. Judging by the senescence of the husks and the overall growth curves obtained in 1973/74, and the other seasons, from the November planted SA 60 crops, it is clear that time gave a more consistant measure of maturity than a scale based on accumulated heat. Whereas the DM yield of early planted SA 60 reached a maximum at approximately 56 days, growth was still continuing at a rapid rate when 458 HU had accumulated from silking. It was therefore concluded that in a growth simulation model the development of the crop during the reproductive phase should be gauged using a time scale expressed in days.

The main difference between the development of the two maize hybrids SA 60 and SR 52 occured during the reproductive phase. On average SR 52 silked only two days later than SA 60, but its reproductive phase was estimated to be 16 days or 29% longer. The longer grain filling period gives SR 52 a greater yield potential. The 56 days reproductive period found for SA 60 agrees closely with the 55 day period used by Mallett (1972) in his model, which was based on readings taken with the same hybrid.

The distribution of DM to the roots

The relationship between DR, the root partitioning factor (Eqn. 3.2), and time during the vegetative growth period, as expressed in days from emergence (D), was described by Kaiser & De Jager (1975). Both the number and size of samples were small, because of practical limitations, with the result that the data showed high variability. Nevertheless, a highly significant linear relationship was obtained (See Eqn. 3.4 in Table 3.3, and Fig. 3.3). A quadratic function was also fitted, but yielded no significant improvement.

Table 3.3: The relationship between DR and D, HU and RF (1968/69).

Year	Regression Equation	S.E.	Correlation coefficient	F	n	Eqn. No
1968/69	DR = ,443 - ,00439 D	,000757	-,878	$33,7^{**}$	12	3.4
1968/69	DR = ,430 - ,000414 HU	,0000749	-,868	$30,5^{**}$	12	3.5
1968/69	DR = ,0376 + ,532 RF	,120	-,818	$14,2^{**}$	9	3.6

A similar linear regression was obtained between DR and accumulated HU (See Eqn. 3.5 in Table 3.3, and Fig. 3.4). Again no improvement was achieved by fitting a quadratic function.

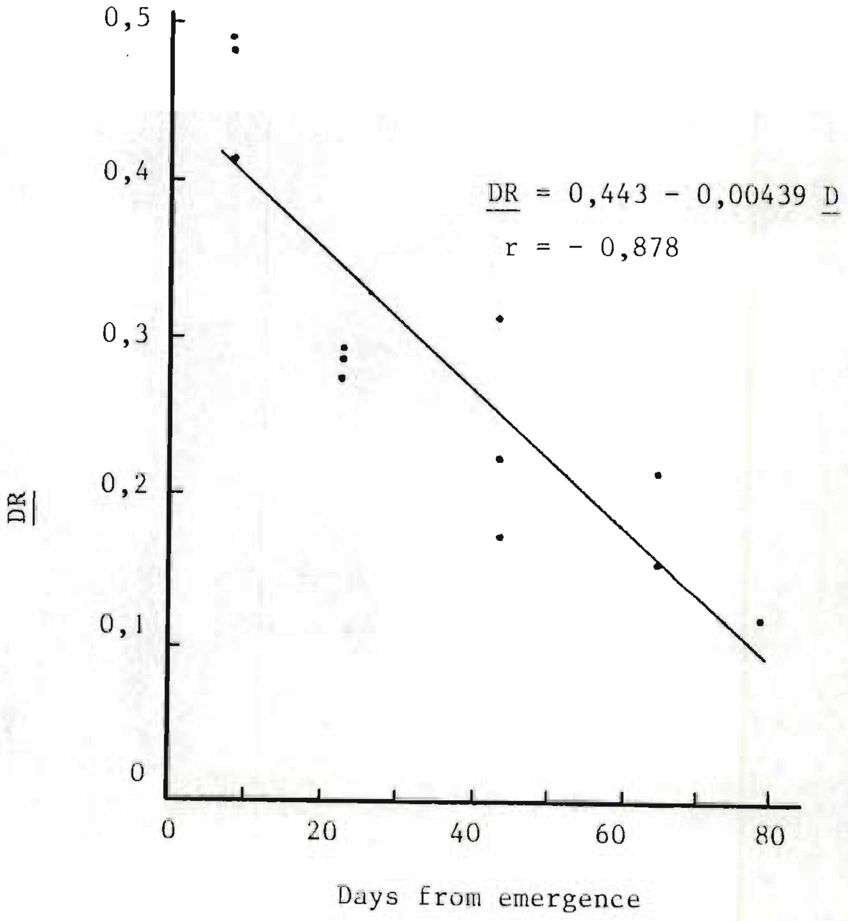

Fig. 3.3: Relationship between DR and time measured in days from emergence (Eqn. 3.4) (1968/69).

The above two relationships imply, that at emergence, just under half of the total DM produced is channeled to the roots, but that this figure decreases at a rate of approximately 1% and 0,1% per day or HU respectively thereafter.

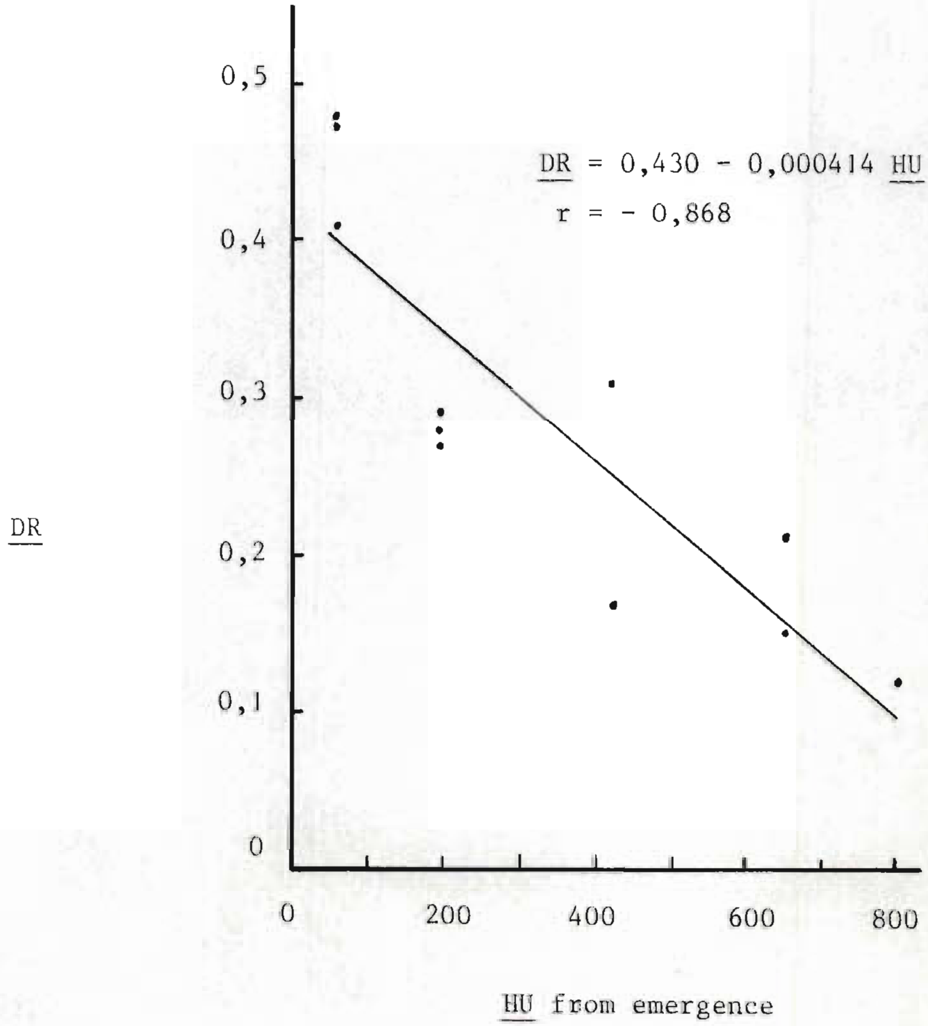

Fig. 3.4: Relationship between DR and HU accumulated after emergence (Eqn. 3.5) (1968/69).

The relationship between the root partitioning factor, DR, and RF, the amount of root DM relative to total DM, was also tested. The linear regression was again highly significant (See Eqn. 3.6 in Table 3.3 and Fig. 3.5), but the quadratic effect was not.

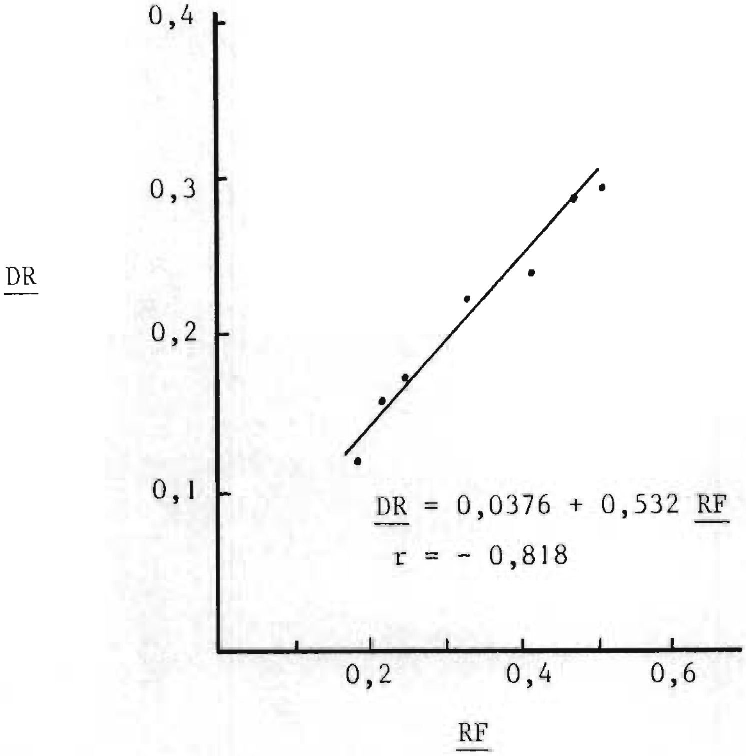

Fig. 3.5: Relationship between DR and RF (Eqn. 3.6) (1968/69).

Significant relationships were obtained between the growth of roots and (1) time, as expressed in days from emergence (D), (2) the heat unit accumulation from emergence (HU), and (3) the proportion of root dry matter in the total crop (RF). For a specific hybrid, grown at a specific site and planted in, say, November the first relationship should be adequate. However, as shown in the previous section, the rate of development of maize is dependent on the climatic conditions, and temperature in particular plays an important role. A function based on HU should therefore have greater general application than one simply related to days. Of the three relationships tested, the third, which is based on the proportion of roots in the total *DM*, appears to have most biological meaning. Under normal growing conditions the size and composition of the crop will determine its root requirements. This last relationship was therefore included in the simulation model when calculating the proportion of the daily *DM* production to be partitioned to the roots. Environmental factors could however, influence the above relationship. Monsi & Murata (1970), for example, showed for soybeans that *DR* increases during periods of drought stress. The roots of maize constitute a relatively small proportion of the total crop *DM*. It is doubtful therefore whether modifications due to climate will markedly affect the final production estimates.

Distribution of *DM* in the tops

Fig. 3.6 shows the distribution of *DM* in the tops of maize (hybrid SA 60) grown at 3,59 plants/m^2 at Cedara during the 1969/70 season. Graphs of a similar nature have been presented for hybrid SR 52 by Allison (1969).

The two components of the maize crops that are the most vital when modeling its growth are (1) the leaves, which intercept the radiant energy, and (2) the grain or salable product. In the case of the crop presented in Fig. 3.6 the contribution of the leaves to the total above ground *DM* at silking was 0,31 (See Table 3.4), whereas of the total *DM* accumulated in the tops after silking, 66% was found in the grain.

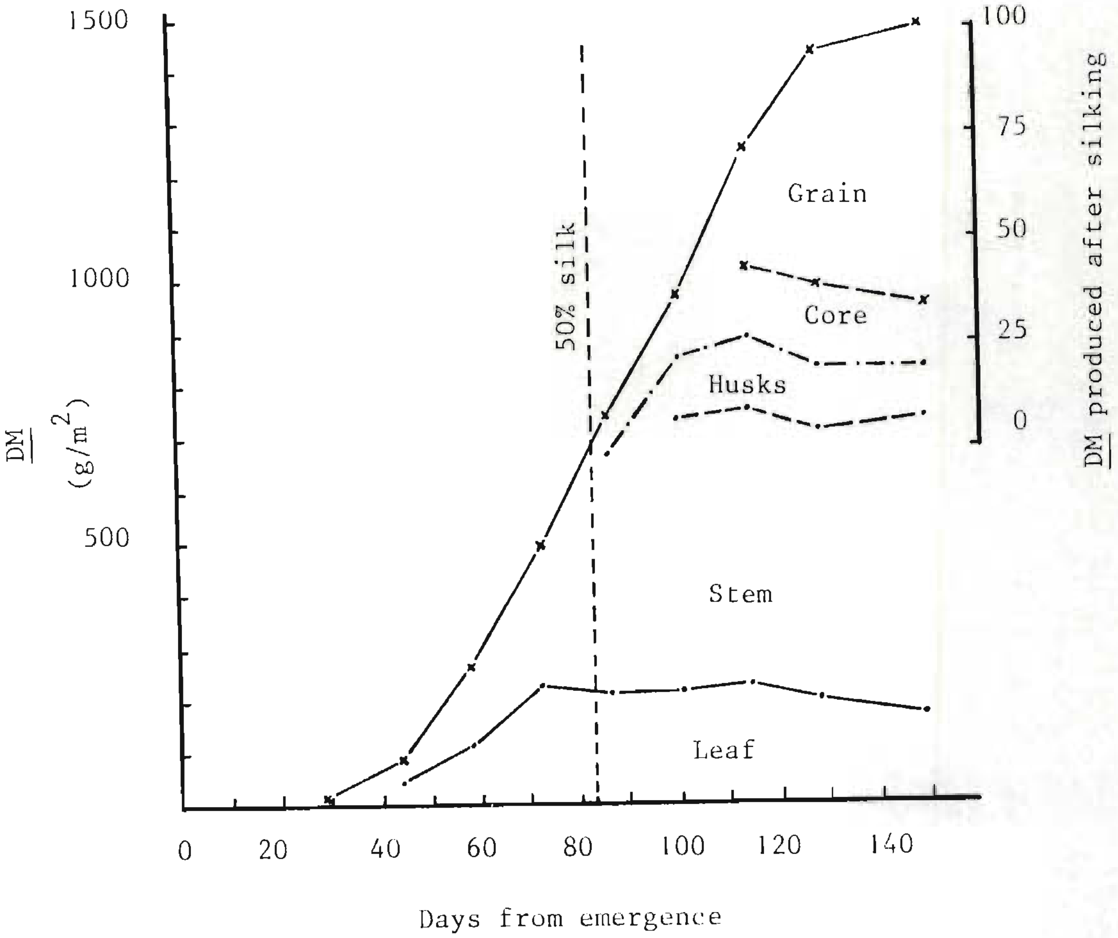

Fig. 3.6: DM yield of the various plant components at different growth stages of the hybrid SA 60 (1969/70) .

Leaf development

The mean LF value, the amount of leaf DM relative to the dry mass of the topgrowth, at silking in 1969/70 was 0,31. The question that arises is whether or not this value changes markedly from year to year and for different treatments. If the value LF at silking should prove to be sensitive to changes in growing conditions, it means that DL is a function of environment and for general use in a simulation model the DL function would have to include weather terms.

The LF values at silking for different treatment combinations were calculated from data obtained during all seasons except 1970/71. The results are presented in Table 3.4, 3.5 and 3.6. The statistical analysis of the data from 1968/69 showed that LF at silking differed between the two hybrids SA 60 and SR 52 as well as between populations. These results are presented in Table 3.4. The population differences were only significant at the extreme populations, which are unlikely to occur in practice. The two values, 0,297 and 0,330 obtained at 3,59 and 7,18 plants/m^2 are not significantly different at the 5% level.

Although the overall effect of hybrid on LF at silking was significant, the difference at the population density of 3,59 plants/m^2, which is representative of populations commonly used in the higher potential maize areas, was less than 6%.

Table 3.4: LF at silking for two hybrids and four population densities (1968/69).

Hybrid	Population density (plants/m^2)				Mean
	0,90	3,59	7,18	14,35	
SA 60	0,254	0,305	0,349	0,410	0,329
SR 52	0,247	0,288	0,311	0,383	0,308
Mean	0,250	0,297	0,330	0,396	0,318

Hybrid means			Population means		
S.E.		0,0071	S.E.		0,0180
L.S.D.	(0,05)	0,0217	L.S.D.	(0,05)	0,0385
	(0,01)	0,0301		(0,01)	0,0533

The LF values at silking for the three seasons 1969/70, 1971/72 and 1973/74 are presented in Table 3.5. These were not statistically analysed, but they are in close agreement with the mean value for 3,59 plants/m^2 obtained in 1968/69. With one exception the LF values for these years were between 0,30 and 0,32.

Table 3.5: LF, the proportion of DM in leaves at silking, GF, the proportion of dry matter accumulated after silking that is used in grain formation and DM yields at silking and maturity.

Year	Hybrid	Population	Plant time	LF at silk	GF	DM yield		No. of plots
						silk	maturity	
		plants/m^2				g/m^2	g/m^2	
1969/70	SA 60	3,59	18/11	0,31	0,66	674	1472	3
1971/72	SA 60	2,39	8/11	0,30	0,65	460	1097	1
		4,78	8/11	0,32	0,73	719	1419	1
1973/74	SA 60	4,78	7/11	0,32	0,72	705	1435	1
		4,78	7/11	0,30	0,78	667	1462	1
		4,78	5/12	0,32	0,64	650	1370	1
		4,78	5/12	0,36	0,53	486	1234	1
		2,39	7/11	0,31	0,70	415	947	1
		2,39	5/12	0,31	0,53	360	833	1
	SR 52	4,78	7/11	0,30	0,86	750	1717	1
		4,78	5/12	0,32	0,69	715	1482	1

The effect of plant population and spacing on LF was also studied in 1974/75. LF values at silking were not affected by the plant arrangement, but were significantly reduced by a lower plant population. These results are presented in Table 3.6 together with the DM yield at silking.

Table 3.6: Effect of population density on the LF value and DM yield at silking (1974/75) .

Plant population	LF at silking	DM at silking
plants/m^2		g/m^2
2,39	0,276	554
4,78	0,307	737
MEAN	0,292	646
S.E.	0,00696	12,8
L.S.D. (0,05)	0,0210	38,6
(0,01)	0,0290	53,3
C.V.	8,3%	6,9%

From the results obtained it can be concluded that, under conditions of adequate moisture and plant nutrient availability, the value for LF at silking is a constant which:

(1) is not a function of climate;

(2) although significantly affected by plant population density, does not vary by more than about 10% within the population range 2,39 to 4,78 plants/m^2, which covers most of the populations used in practice; and

(3) is not influenced by plant arrangement and planting date.

It may also be implied that hybrids SA 60 and SR 52 will flower when LF reaches a value of approximately 0,31.

Considering the above conclusions, it can further be deducted that DL should be a function of the instantaneous proportion of DM in the leaves (LF). In other words the distribution of DM to the leaves is a recipient controlled process.

Partitioning of DM to leaves during vegetative growth

In the previous section it has been shown that at silking the leaves constitute approximately 31% of the total above ground DM of a SA 60 crop growing at a high fertility and moisture level. The question is how the DM is partitioned, from emergence to silking and what factors control it.

Monsi & Murata (1970) showed that DL decreased with time to reach zero shortly after silking. The DL of Monsi & Murata (1970) is the DM accumulation in the leaves per unit DM increment for the total crop. Here DL is defined as the proportional growth of leaves relative to the topgrowth of the plant.

The change in DL during the vegetative growth period was studied using the data from 1969/70, 1970/71, 1973/74 and 1974/75. DL was related to: (1) the number of days from crop emergence (D); (2) the number of HU accumulated from emergence; and (3) the proportion of leaf to total above ground DM yield (LF).

Under the sub-heading 'The developmental periods' it was shown that the length of the vegetative growth period was best measured using a temperature (HU) rather than a time scale. For general application, therefore, a relationship describing DL in terms of accumulated HU could be expected to be more reliable than that between DL and D. However, the identification of a critical LF at silking implies that the partitioning of DM to the leaves is controlled by the actual state of the crop, in particular by the amount of leaf material present i.e. it is an internal recipient controlled process not greatly influenced by external influences, although external conditions (e.g. moisture stress) can modify the needs of the crop (See Monsi & Murata, 1970). Thus there is sound evidence to support the use of LF as the biological variable for describing and controlling the magnitude of DL.

The relationship between DL and D, HU and LF during the vegetative period was tested. The results are presented in Table 3.7

Table 3.7: Relationship between DL and D, HU and LF (Pooled data 1969/70, 1970/71, 1973/74, 1974/75).

Regression Equation	S.E.	Correlation Coefficient	F	n	Eqn. No.
DL = ,841 - ,00895 D	,000253	- ,939	1247,8**	170	3.7
DL = ,737 - ,00177 D - ,0000857 D^2		,956	64,4**	170	3.8
DL = ,830 - ,000973 HU	,0000255	- ,947	1453,1**	170	3.9
DL = ,757 - ,000419 HU - ,000000721 HU^2		,957	36,9**	170	3.10
DL = - ,464 + 1,631 LF	,0503	,945	1051,0**	127	3.11
DL = -1,072 + 4,088 LF - 2,368 LF^2		,955	26,1**	127	3.12

Highly significant (P<,01) linear relationships were found between DL and D, HU and LF (Eqn. 3.7, 3.9, 3.11). The linear and quadratic equations listed in Table 3.7 represent the best fits of the pooled data from all plots planted to SA 60 during the four seasons. The data was pooled after it had been established that changes in population density, plant spacing, planting time and season did not significantly alter the best fitting linear regression line. Neither did the linear regression equations for the two hybrids differ significantly.

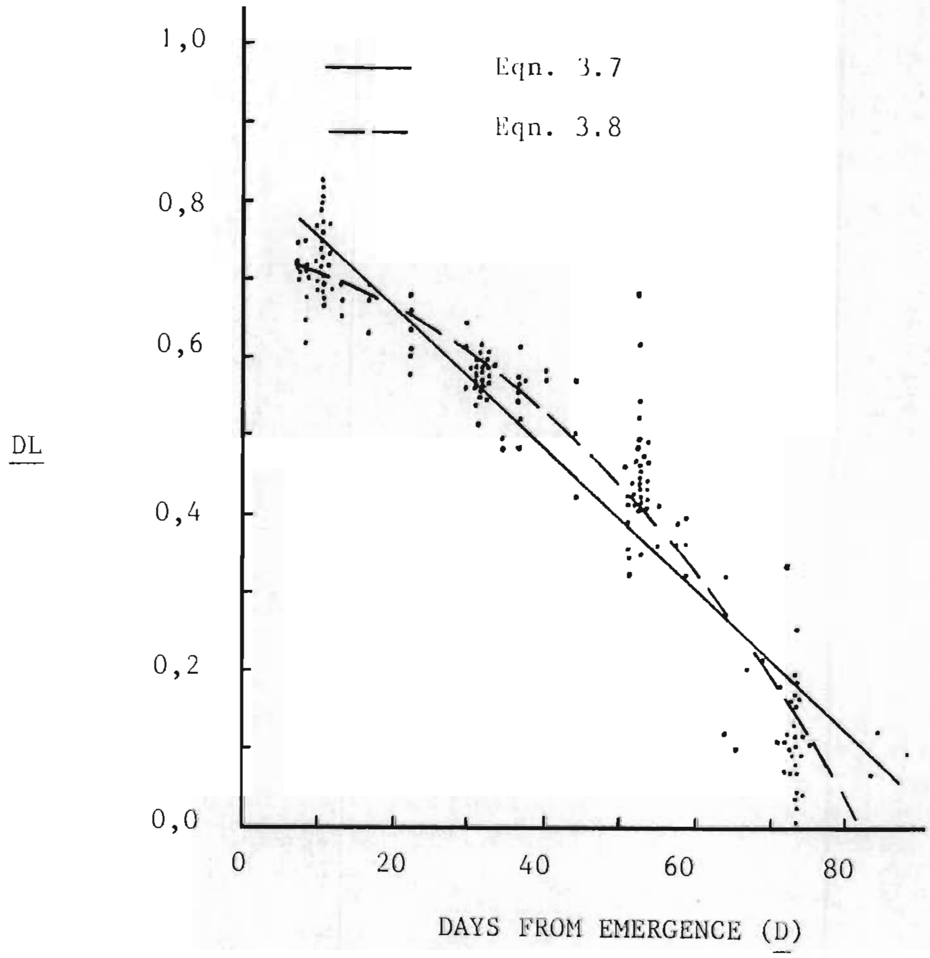

Fig. 3.7: Relationship between partitioning of DM to the leaves and time from emergence.

The equations presented in Table 3.7 are shown graphically, together with the measured points, in Figs. 3.7, 3.8 and 3.9. These show that in the very young seedling plant approximately three quarters of all the DM used for the development of the above ground parts is channelled to the leaves. As the plant develops DL decreases to zero at approximately the silking stage.

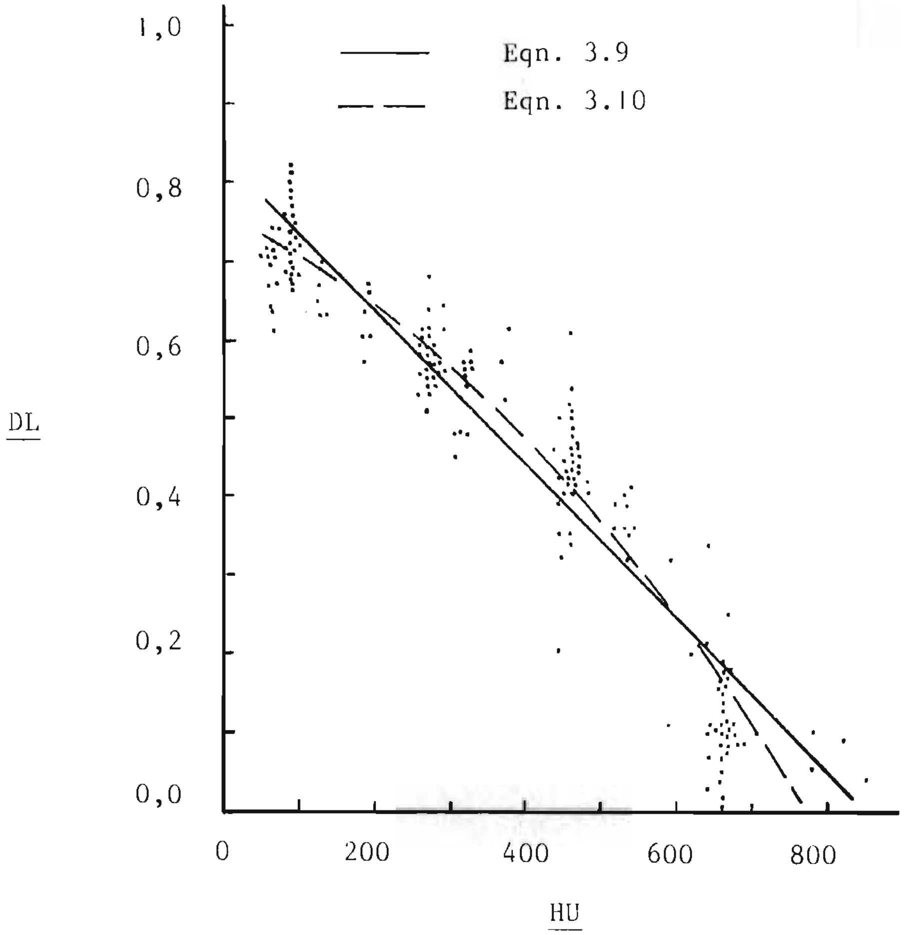

Fig. 3.8: Relationship between DM partitioning to the leaves and HU accumulated after emergence.

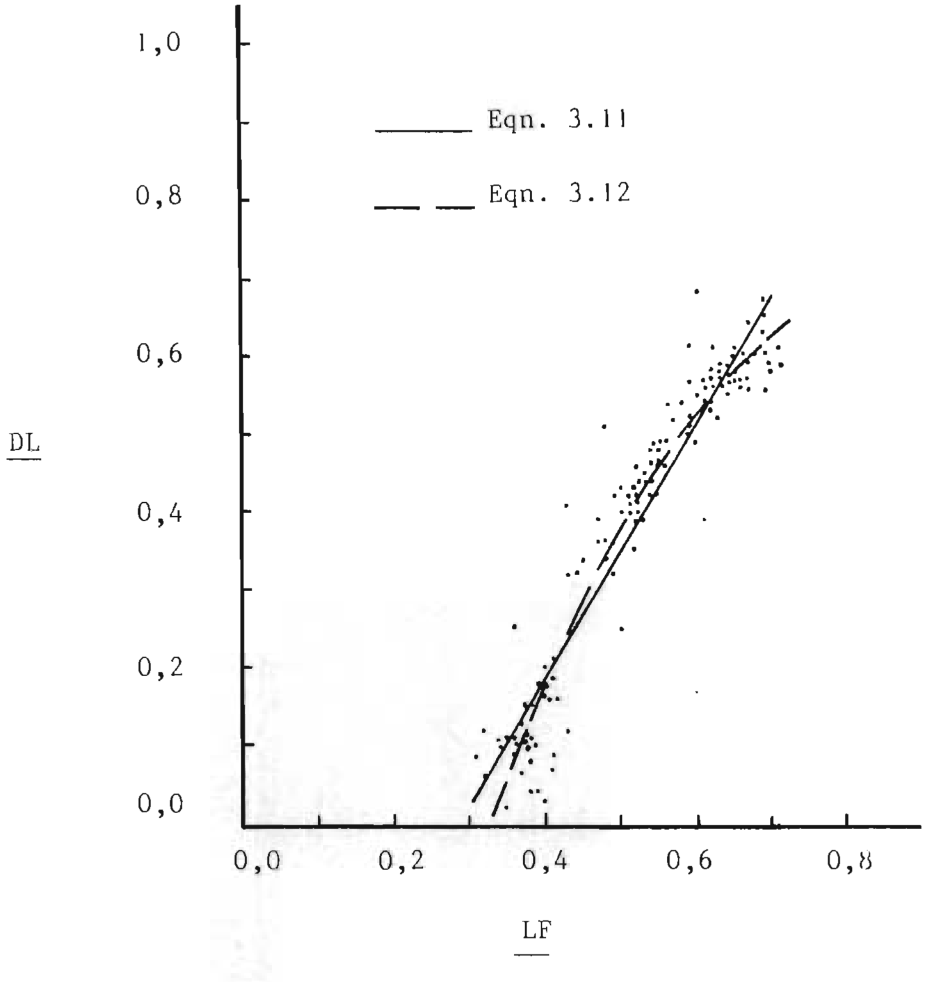

Fig. 3.9: Effect of changes in LF value on DM partitioning to the leaves.

Statistically there is little to choose between the three relationships tested. In all cases the correlation coefficient was very high and the F - test highly significant.

In the simulation model the empirically determined relationship between DL and LF will be used to partition DM to the leaves during the vegetative growth period, because, as stated earlier, this relationship is recipient controlled and has greater biological meaning than the relationship between DL and D, and DL and HU. This implies that the need for leaf relative to stem material is governed by the plant. Monsi & Murata (1970) have shown with soybeans, these needs can be modified by outside influences. They found that DL decreased and DR increased when the soybean plants were subjected to drought stress. However, a return to conditions of adequate moisture supply resulted in the opposite effect. In relating DL and D these workers could show no difference in this relationship between sites situated between 43^{o} 3'N. Lat. and 32^{o} 53' N. Lat. Where the simulation model is used to simulate the development of the crop under conditions that include drought stress, some modification to Eqns. 3.11 and 3.12 might be required. Further work on this aspect is indicated. Except under prolonged drought conditions, it is unlikely however that the use of Eqn. 3.11 and 3.12 will introduce grave errors. Possibly of greater significance will be nutritional stress. A study of the response of DL to sub-optimal nutritional levels would be most valuable.

In his model "PUTU", De Jager (1974) used LM instead of LF to determine DL. For a specific set of conditions the use of LM as the biological control in a growth simulation should be acceptable, however, for general application it has major limitations. From the DM and LF values at silking given in Tables 3.5 and 3.6, it is clear that LM at silking differed markedly for different treatments, in this case, mainly due to population. Yet the LF value at silking was very constant. In a simulation of growth if DL was calculated from LM it would yield very different LF values at silking for the listed treatments.

Specific leaf area

The relationship of leaf area to leaf mass was calculated from the 1973/74 data and has been reported on by Kaiser and De Jager (1975). Both linear and quadratic functions were fitted to this data. The linear regression was highly significant ($P<,01$) and there was no significant evidence that this relationship was affected by planting time, plant population density or hybrids used. Linear regression analysis was done on the pooled data from all the SA 60 plots. The linear relationship again was highly significant ($P<,01$), but an improved fit was obtained with a quadratic function ($P<,01$). The linear and quadratic equations that fitted the data best are presented in Table 3.8 (Eqn. 3.13 and 3.14 respectively).

The curvilinear relationship between *LA* and *LM* indicates that as the leaves mature, *LM* occupies less *LA*. The positive and negative emperical constants in Eqn. 3.13 and Eqn. 3.14 respectively, imply that at zero *LM* the *LA* is either positive or negative which is not possible. Neither Eqn. 3.13 nor Eqn. 3.14 can therefore be used to calculate *LA* from *LM* in a very young crop. It was also found that when simulating *LA* development in dense crops, the curvilinear relationship (Eqn. 3.14) resulted in negative leaf growth at *L* values considerably lower than the maximum recorded in practice. The best fitting linear equation (Eqn. 3.15) which passes through the origin was therefore calculated and is used in the simulation model. Eqn. 3.14 and 3.15 are illustrated graphically in Fig. 3.10.

Table 3.8: Relationships between *LA* and *LM*.

Regression Equation	S.E.	Correlation Coefficient	F	n	Eqn. No.
$LA = ,338 + ,0197\,LM$	,000717	,981	$757{,}8^{**}$	32	3.13
$LA = -\,,139 + ,0312\,LM - ,0000480\,LM^2$		,989	$19{,}6^{**}$	32	3.14
$LA = ,0218\,LM$				32	3.15

The specific leaf area in this experiment varied from about 225cm^2/g leaf DM in the very young crop to approximately 208cm^2/g leaf DM at silking. Williams, Loomis & Lepley (1965) also reported a decrease in specific leaf area with time from approximately 225cm^2/g leaf DM seven weeks after planting to about 190 cm^2/g leaf DM

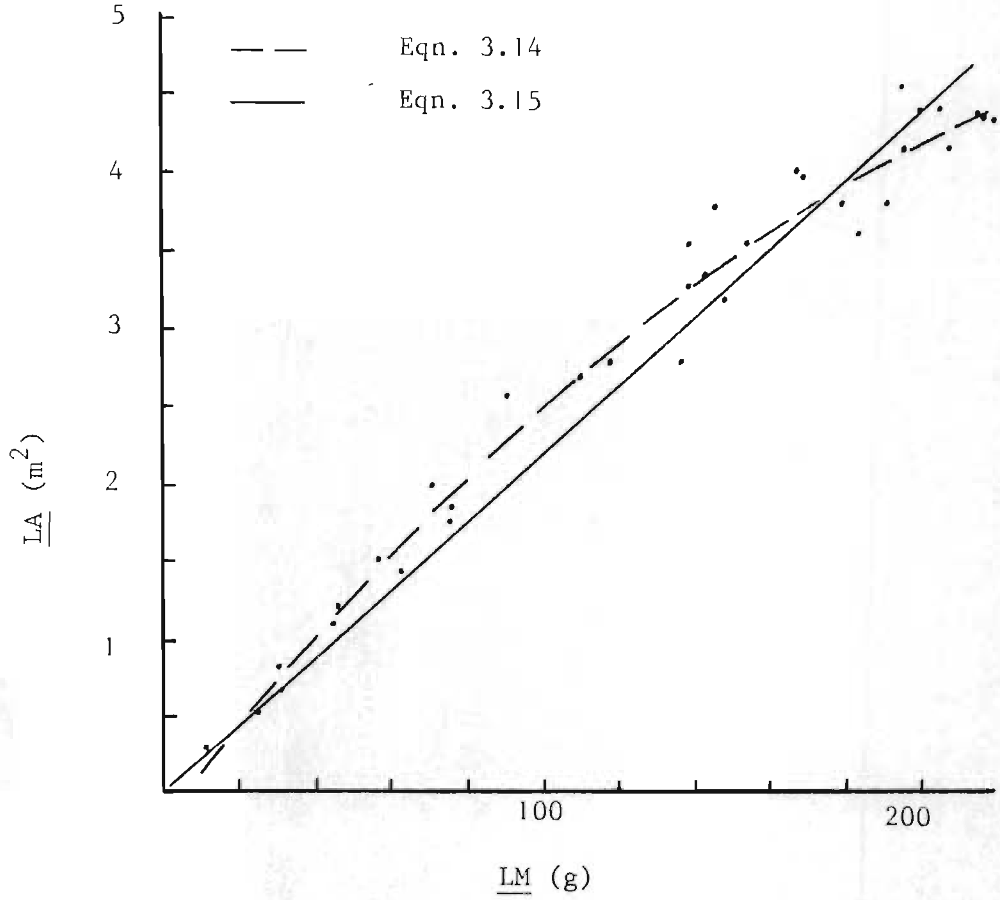

Fig. 3.10: Relationship between LA and LM for hybrid SA 60.

twelve days later when the tassels were appearing. These workers also showed an increase in specific leaf area with increases in population density. Similarly, Allison (1969) found that the specific leaf area at ten weeks from planting was increased from $156cm^2/g$ leaf DM at a population density of 2,3 plants/m^2 to $207cm^2/g$ leaf DM at 7,38 plants/m^2. Eddowes (1969) reported specific leaf area values at anthesis ranging from 172 to $189cm^2/g$ leaf DM with no clear response to population density. In the Cedara trial no difference in specific leaf area was found between the populations 2,39 and 4,78 plants/m^2. This population range is narrow compared to those used by the above workers, but covers the range normally encountered in practice.

Leaf senescence

LA measurements after silking were made during 1969/70, 1971/72, 1973/74 and 1974/75. In the latter three seasons these measurements were extended to beyond the maturity of the maize crop. The results agree with the findings of Allison (1964), Williams, Loomis, Duncan, Dovrat & Nunez (1968) and Allison (1969), who showed that the maximum L value for a maize crop remained constant for a period after silking, before declining due to leaf senescence.

A graphical analysis of the Cedara results showed that once leaf senescence had commenced, the decline in L with time, expressed in days from silking (D_r) appeared to be linear. Quadratic and logarithmic functions were, however, fitted to the data, but it was found that these produced fits no better than linear relationships. It was therefore decided to use a simple linear function to describe leaf senescence in the simulation model.

A highly significant linear relationship between leaf senescence and time (D_r) was established.

No significant differences between regression parameters resulted from comparisons of regression lines for different seasons, the populations 2,39 and 4,78 plants/m^2, the different plant spacings and the hybrids SA 60, SR 52 and RO 1E, although a graphical presentation of the results did suggest a delay of approximately four days in the commencement of senescence where a population density of 2,39 plants/m^2 instead of 4,78 plants/m^2 were used. The rate of senescence for both populations appeared to be equal. The results presented by Allison (1969) and Williams et al. (1968) indicate more rapid senescence in crops with a higher density. Though not significantly different, the late maturing hybrids SR 52 and RO 1E appeared to commence senescence about four days after SA 60.

For hybrid SA 60 the best fit of 99 comparisons was obtained from Eqn. 3.16.

$$\underline{LG} = 1,888 - 0,0208\ \underline{D}_r \quad \ldots\ldots\ \text{Eqn. 3.16}$$

Where LG is the unsenesced LA after silking as a fraction of the maximum LA achieved.

The statistical values S.E., r and F for this function were 0,000739, -0,944 and $793,0^{**}$ respectively.

Eqn. 3.16 is illustrated in Fig. 3.11

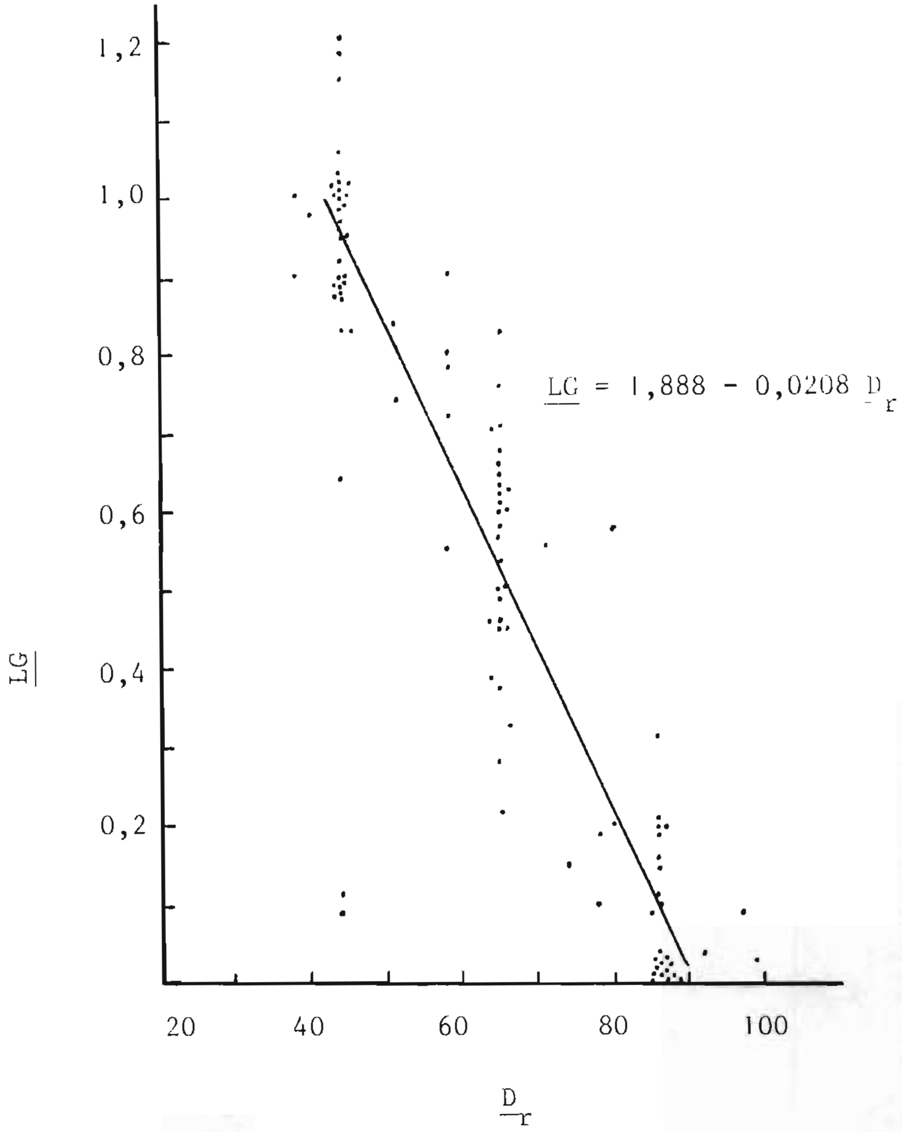

Fig. 3.11: Relationship between $\underline{LG}$ and the number of days from silking $\underline{D}_r$ (Eqn. 3.15).

Grain Formation

GF, the portion of the total DM accumulated after silking that was used in the manufacture of grain showed considerable variation. The data presented in Table 3.5 indicates that GF is affected by the hybrid grown, population density and planting time.

The GF value for SR 52 was on the average 17% higher than for SA 60. This can be ascribed to the longer grain filling period of SR 52.

The GF values for SR 52 planted on 15/12/74 and 7/11/74 were 0,69 and 0,86 respectively. These show close agreement with those reported by Allison (1969), who obtained values that varied between 0,73 and 0,82 with the same hybrid at Salisbury, Rhodesia. The increased GF reported by Allison (1969) was the response to an increase in population density from 2,30 to 7,40 plants/m^2.

The results presented in Table 3.5 reflect a similar response to population density. At 2,39 plants/m^2 the mean GF value for SA 60 was 0,63 whereas at 4,78 plants/m^2 it was 0,68, an increase of 8%. Although a statistical analysis of the 1974/75 data showed no significant difference in the GF values at these two population densities, the values were of the same order as those for November planted SA 60 presented in Table 3.5 and the difference was approaching significance at the 5% level. The 1974/75 GF values were 0,66 and 0,75 for the 2,39 plants/m^2 and 4,78 plants/m^2 populations respectively. Changes in plant spacing for the same population had no significant effect on the GF values.

Time of planting appeared to have a marked effect on the partitioning of DM to the grain. The mean GF value for all plots planted in November 1973 was 0,76 compared to 0,60 for the same treatments planted in December 1973, a decrease of 21%.

It is clear from the data obtained that of the total DM accumulated after silking, the proportion that is channeled to the grain is highly dependent on the cultivar and the growing conditions. In estimating grain yields from total DM production, great care will have to be exercised to take these factors into account. The GF values used in the simulation model are listed in Table 3.9.

Table 3.9: GF values used in the growth simulation model.

Hybrid	Planting time	Population	GF
		plants/m^2	
SA 60	Oct/Nov	4,78	0,73
SA 60	Dec	4,78	0,58
SA 60	Oct/Nov	2,39 - 3,59	0,68
SA 60	Dec	2,39 - 3,59	0,53
SR 52	Oct/Nov	4,78	0,86
SR 52	Dec	4,78	0,69

CHAPTER 4

SIMULATING THE GROWTH OF MAIZE FROM CLIMATIC SOLAR RADIATION AND TEMPERATURE DATA

INTRODUCTION

De Jager (1974) distinguishes between three simulation models, viz.

(1) the instantaneous model which describes mathematically the interaction between factors at a given instant;

(2) the dynamic model 'in which solutions from the instantaneous models are arranged sequentially to trace the development of a system'; and

(3) an operational model which 'is designed to produce a solution of practical use in guiding practice or decision making.'

The equations developed in the foregoing three chapters are instantaneous models. Here these are included in a dynamic simulation model which traces the growth of a maize crop throughout its growing season.

The approach in this model is similar to that followed by De Jager (1974) in the construction of his model 'PUTU'. However, this model deals specifically with the growth of the maize crop in relation to solar radiation and temperature. All other environmental factors, such as moisture and fertility are taken to be non-limiting. The functions used in this model can easily be incorporated into 'PUTU' which is the more general model.

DESCRIPTION OF THE MODEL STRUCTURE

The growth simulation was executed on an I.B.M. 1130 computer. A flow diagram of the computer model is given in Fig. 4.1, whereas the complete Fortran programme is listed in Appendix I.

Variable names used in the Fortran programme are presented in the text in capital letters and in brackets.

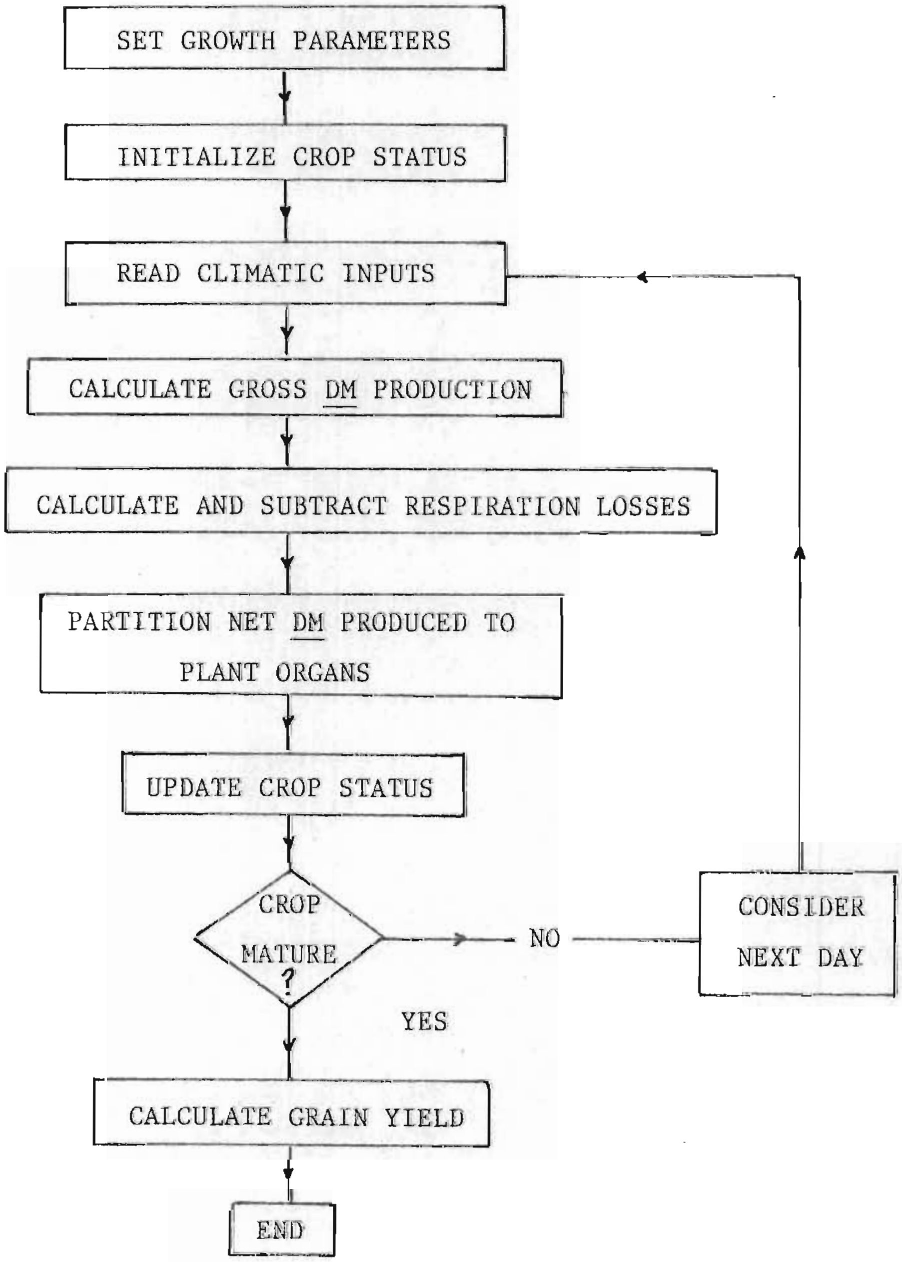

Fig. 4.1: Flow diagram of the dynamic computer model used to simulate the growth of a maize crop.

A detailed discussion of each component of the above flow diagram (Fig. 4.1) follows.

Growth Parameters

The instantaneous photosynthetic model of De Jager & King (1974) (Eqn. 2.1) is used to calculate the CO_2 uptake of the crop from the mean hourly radiant flux densities. To achieve this, values for I_v, b, L, P_o', A_v, c and Q are required. The calculation of values for I_v and L is discussed in later sections, whereas P_o' and Q are taken as 1,8mg/m^2/s and 22 x 10^{-6} gCO_2/J respectively, which are the values used by De Jager & King (1974).

The absorption factor A_v refers to the absorption of the vegetative crop material alone. If T_r is the transmission factor of the crop canopy, and R_v is the reflectivity of the crop vegetation alone, then the radiation balance of the vegetative cover may be written

$$I = A_v I + T_r I + R_v (I - T_r I) \quad \ldots\ldots\ldots\ldots\ 4.1$$

as only intercepted light can be reflected. From this expression, A_v may be calculated as follows:

$$A_v = 1 - T_r - R_v (1 - T_r) \quad \ldots\ldots\ldots\ldots\ 4.1.1$$

From the results presented in Chapter 1, T_r can be determined using Eqn. 1.3. Eqn. 4.1.1 may therefore be written as

$$A_v = 1 - \exp(-K_v L) - R_v (1 - \exp(-K_v L)) \quad \ldots\ldots\ 4.1.2$$

or

$$A_v = (1 - \exp(-K_v L) \,.\, (1 - R_v) \quad \ldots\ldots\ldots\ldots\ 4.1.3$$

K_v is a function of row spacing (See Chapter 1) and has values of 0,84 and 0,60 for row widths of 0,91m and 1,83m respectively. In Chapter 1 the R_v measurements made included both the reflection from the vegetative material and the soil. However, in a well developed dense maize crop the contribution of soil reflection to the total reflection is small. Except in the case of the crop with an $\underline{L}$ value of 0,32 (See Fig. 1.10), the $\underline{R}_v$ values presented in Chapter 1 therefore approximately equal the reflectivity of the vegetative material alone. Hence for the calculation of $\underline{A}_v$ in the computer simulation model the following assumptions were made:

(1) The $\underline{R}$ measurements made in 1974 over a maize crop in the vegetative growth period which had $\underline{L}$ values ranging from 1,57 to 3,29 and was spaced in 0,91 m rows, equals the reflection from the vegetative material alone. The mean hourly $\underline{R}_v$ values calculated from the $\underline{R}$ measurements are listed in Table 4.1.

(2) For all practical purposes, L, leaf arrangement and the growth stage of the crop do not effect $\underline{R}_v$ for the vegetative material.

As described in Chapter 1, however, $\underline{R}_v$ is markedly influenced by the sun angle during clear days. This is taken into consideration when calculating $\underline{A}_v$ (See Table 4.1).

Table 4.1: Hourly $\underline{R}_v$ values used in the simulation model.

Hour																
5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
,146	,146	,146	,075	,062	,058	,056	,058	,062	,069	,081	,100	,137	,215	,215	,215	,215

Of the total $\underline{PHAR}$ that is intercepted by the vegetative material only a small portion is reflected. At high sun angles when the photosynthetic activity is at its highest this should be less than 10%.

Errors introduced by the above assumptions will therefore have only a minor influence on the accuracy of the $\underline{A}_v$ estimate and, hence, should not introduce large errors in the calculation of crop growth using the simulation model.

Efficiency factors $\underline{b}$ and $\underline{c}$ vary with the status of the crop. From emergence to silking $\underline{b}$ is equal to 0,844, whereas after silking its value is reduced to 0,627. Similarly, $\underline{c}$ values of 1,072 and 0,726 are used before and after the crop tassels. (See Chapter 2)

In the computer programme the constants $\underline{K}_v$, $\underline{R}_v$, $\underline{b}$ and $\underline{c}$ are read in as (EXTK), (ALBE), (BVEG) and (CVEG) respectively. For the reproductive period $\underline{b}$ and $\underline{c}$ are given as (BREP) and (CREP).

Initial status of the crop and developmental details

The mechanics of the computer programme is such that growth simulation can commence at any stage during the period crop emergence to silking. The initial status of the crop has to be defined i.e.

(1) the number of $\underline{HU}$ that have accumulated from emergence to the start of the simulation (HUST);

(2) the total mean dry mass (g) of the plants (TPLDY);

(3) the proportion of root (FRT) in the total dry mass and leaf (FRL) in the top dry mass; and

(4) the population density of the crop (POP).

In the present research programme the first reliable growth measurements were made fifteen days after the emergence of the crop. Growth simulations were therefore not started before this time. The initial values used are listed in Table 4.2 and are based on measurements made on SA 60 in the 1968/69 and 1969/70 seasons.

Table 4.2: Dry mass of plants, the proportion of root and leaf material and the accumulated HU fifteen days after emergence for SA 60.

Mean total crop dry mass (g) (TPLDY)	0,7667
Root fraction RF (FRT)	0,400
Leaf fraction LF (FRL)	0,723
Accumulated HU (HUST)	130

From the data listed in Table 4.2 the initial value for L is calculated using Eqn. 3.15.

The length of the vegetative growth period is measured on an accumulated HU scale, whereas that of the reproductive phase on a day scale. The reasons for this are discussed in Chapter 3.

When the crop's HU requirement for the vegetative phase (HUVEG) has been met, it moves from the vegetative into the reproductive growth phase. The HU requirements for SA 60 and SR 52 are 754 and 778 respectively (See Chapter 3). Although no accurate measurements were made, it is estimated that tasseling commences 120HU before 50% silking (i.e. (HUTAS) = (HUVEG) - 120).

The number of days from silking to maturity is read into the computer as (NDAM). For hybrids SA 60 and SR 52 this period was measured as 56 and 72 days respectively (See Chapter 3).

Climatic inputs

The climatic data required to drive the simulation model are mean hourly radiant flux density (I), daily maximum and minimum temperature (Tmax and Tmin) and air temperature at 8H00 and 20H00. In the computer programme these variables are read in as (IRAD), (MAXT), (MINT), (IT8) and (IT20) respectively.

The hourly I values are converted to I_v by multiplying by a factor of 0,445. In the case of the Cedara data I values are recorded with a Kipp solarimeter. Where for short periods readings are not available, mean I values (MRAD) are used. Radiant flux density readings are limited to relatively few meteorological stations. Sunshine data are far more common. Mathematical models that can be used to estimate radiant flux density from hourly sunshine data, have been developed locally (Schulze, 1975; Erasmus, 1975) and could be incorporated in the simulation model to provide the required I values where solar radiation readings are not available.

At Cedara most of the growth studies were conducted under a wire hail shelter which intercepted a proportion of the incoming solar energy. The fraction of solar energy transmitted through the hail shelter was measured for each hour of the day and the values are presented in Table 4.3. These values are read into the computer as the variable (HSTR) and are used when the growth of maize under the hail shelter is simulated. For simulations outside the hail-guard the transmission factor, (HSTR), is set at one.

Table 4.3: Hourly hail shelter transmission factor (HSTR).

Hour								
5	6	7	8	9	10	11	12	13
,718	,755	,803	,828	,875	,910	,922	,922	,912

Hour							
14	15	16	17	18	19	20	21
,901	,886	,880	,841	,823	,798	,770	,740

Tmax and Tmin are required to calculate the HU according to Eqn. 3.1. The air temperatures at 8H00 and 20H00 are used in the calculation of respiration as discussed in the section dealing with respiration losses.

Daily gross DM production

The hourly $\underline{P}$ values calculated according to Eqn. 2.1 are accumulated at the end of the day. The gross daily DM gain, $\underline{DMG}_g$ (CSDAG), is calculated as follows:

$$\underline{DMG}_g = \underline{P}_d \; 0{,}682 \quad \ldots\ldots\ldots\ldots \quad \text{Eqn. } 4.2$$

where $\underline{P}_d$ is the total CO_2 fixed during hours 5 to 21, and 0,682 the factor converting CO_2 to carbohydrates.

Respiration losses

Respiration losses are calculated according to the method described by McCree (1970). Here respiration is divided into two components, viz.

(1) a growth component, which is the respiration needed for the construction of new plant tissue; and

(2) a maintenance component, or respiration required to replace obsolete or degenerate material in the plant by 'fresh' organic material.

Construction respiration is a function of the amount of photosynthate produced during the day ($\underline{P}_d$) whereas the maintenance component is dependent on the total crop biomass ($\underline{W}$). For white clover, McCree (1970) calculated respiration as follows:

$$\underline{RES} = 0{,}25 \, \underline{P}_d + 0{,}015\underline{W} \quad \ldots\ldots\ldots\ldots \quad \text{Eqn. } 4.3$$

Later work by McCree (1974) on grain sorghum and white clover showed that the maintenance component is dependent on temperature and species, whereas construction respiration is independent of these two factors. From his results he arrived at the following equations for night respiration:

$$\underline{RES}_n = \underline{kP}_d + \underline{C_t W} \text{ .... Eqn. 4.4}$$

where $\underline{RES}_n$ = night respiration

The value of $\underline{k}$ for both crops was 0,14 whereas $\underline{C}_t$ at 30°C was 0,0143 and 0,0054 for clover and sorghum respectively and was highly dependent on temperature. McCree (1974) gave the temperature relationships for $\underline{C}_t$ as

$$\underline{C}_t = \underline{C_{30}} \quad (0{,}044 + 0{,}0019\ \underline{T}_n + 0{,}0010\ \underline{T}_n^2) \text{ .... Eqn. 4.5}$$

According to McCree and Van Bavel (1975) an 'average' plant should lose about 1% of its carbon during a 'normal' 24 hour day through maintenance respiration. However, citing Penning de Vries (1974 b) they concluded that theoretical calculations indicate a loss of 2%, whereas empirical measurements in excess of 3% have been reported.

In support of the findings of McCree (1974), Penning de Vries (1974 a & b) also demonstrated that maintenance respiration was temperature and species dependent. For maize he reported a 24 hour loss at 25°C of 1,5% of total biomass compared to about half this value at 18°C.

Palmer, Heichel and Musgrave (1973) quoted a maintenance respiration coefficient for maize of about 1% per 24 hour day.

In the simulation model $\underline{P}$ is calculated according to Eqn. 2.1 and gives the net photosynthetic rate of the crop. Hence, $\underline{P}_d$ is the net amount of CO_2 fixed during the day. Allowance therefore has only to be made for respiration losses during the night period. The results discussed above, suggest that for maize dark respiration factors $\underline{k}$ and $\underline{C}_{30}$ should be of the order of 0,14 and between 0,005 to 0,01 respectively.

Respiration has not been studied in the present research programme. By means of an iterative process different values of $\underline{k}$ and $\underline{C}_{30}$ were tested using the simulation model. For this purpose the growth data from 1969/70, which is presented in Fig. 3.6, was used. Good agreement (See Fig. 4.3.) between the estimated and measured yields and $\underline{L}$ values was achieved when the values for $\underline{k}$ and $\underline{C}_{30}$ were 0,5 and 0,012 respectively. The same values for $\underline{k}$ and $\underline{C}_{30}$ were then used to simulate the growth of hybrid SA 60 at different population densities, for different seasons and changing planting dates, as well as a single crop of hybrid SR 52. The results are presented in Figs. 4.2, 4.4, 4.5 and Table 4.6, and show good agreement between measured and estimated $\underline{DM}$ yields and $\underline{L}$. The estimated respiration factors given above can therefore be used with confidence.

The temperature correction of McCree (1974) (Eqn. 4.5) was applied to the maintenance respiration coefficient ($\underline{C}_{30}$). $\underline{T}_n$ was taken as the mean of the recorded air temperature at 20H00 and 8H00. At 18°C and 25°C $\underline{C}_t$ values therefore amounted to 0,005 and 0,009 respectively. These values are not very different from the 24 hour readings at the same temperature by Penning de Vries (1974 a & b). They are also similar to the factor of 0,006 used by De Jager (1974).

The construction respiration factor, $\underline{k}$, of 0,5 is considerably higher than those measured by McCree (1970,1974) which ranged from 0,14 to 0,25. It is also higher than the 0,20 used by De Jager (1974). However it is in close agreement with the theoretical values of 0,5 and 0,45 calculated by De Wit, Brouwer & Penning de Vries (1970). In their simulation model 'ELCROS' these workers also obtained reasonably good agreement between simulated and measured growth rates when using a $\underline{k}$ value of 0,5.

In the simulation model the net $\underline{DM}$ gain $\underline{DMG}_n$ for the day is calculated according to Eqn. 4.6.

$$\underline{DMG}_n = \underline{DMG}_g - (0{,}5 . \underline{DMG}_g + 0{,}012\ (0{,}044 + 0{,}0019\ \underline{T}_n + 0{,}0001\ \underline{T}_n^2)\underline{W})$$

...... Eqn. 4.6

where $\underline{DMG}_n$ is the net daily *DM* gain (g/m^2),
$\underline{DMG}_g$ is the gross daily *DM* gain (g/m^2),
$\underline{T}_n$ is the mean of the temperatures at 20H00 and 8H00 (^oC), and
$\underline{W}$ is the total dry biomass of the crop (g/m^2).

Partitioning of daily production

During the vegetative growth phase the net *DM* produced is partitioned at the end of the day to the roots and leaves according to Eqn. 3.6 and Eqn. 3.11 respectively. In the case of both equations, but particularly in the case of Eqn. 3.6, extrapolation to beyond the range of points used in the calculation of these equations is required early in the growing season.

DM is partitioned to the leaves according to the linear Eqn. 3.11 in preference to the quadratic Eqn. 3.12, although a slightly improved fit was obtained by fitting the latter to the original data. The reason for choosing the linear regression is that at emergence *DL* is virtually equal to *LF*. In the case of Eqn. 3.12 this condition is never met, with the result that insufficient *DM* is partitioned to the leaf and *LF* decreases at an excessively high rate, so that leaf growth ceases 30 to 40 days after emergence instead of near silking time. This problem was overcome by using Eqn. 3.11.

Partitioning to the roots and leaves stopped at silking, or, in the case of leaves, earlier, should *DL* decrease to less than zero before silking.

The partitioning of *DM* accumulated after silking is done at maturity as described below under 'Grain yield'.

Update crop status

Before the start of the new day, the status of the crop is updated i.e. the net DM produced is added to the previous crop yield to give new total, root and leaf DM yields. From the leaf DM a new L (ALAI) value is calculated using Eqn. 3.15. Although the best fitting linear regression of LA vs. LM was Eqn. 3.13 and an improved fit was obtained with quadratic Eqn. 3.14, these two equations are not used in the simulation model, as the intercept means that at zero LM the LA is not zero. In young crops considerable errors would therefore result from using these functions. Furthermore, in the case of the quadratic function (Eqn. 3.14) extrapolation beyond the range of readings on which the function is based, shows that a ceiling L of 4,93 exists. In practice L values considerably higher than this are possible.

The HU for the day are added to the previous accumulated total and when the required level is reached, the commencement of tasseling (HUTAS) and 50% silking (HUVEG) is signalled.

Leaf senescence and crop maturity are functions of the number of days from 50% silking. At the end of every day during the reproductive phase, the LG factor (FALAI) is calculated according to Eqn. 3.16 and a test for crop maturity is made. Once LG becomes less than one, the L value at silking is multiplied by the LG factor to give a new L value for the following day. When crop maturity is reached the end of the growth simulation is signalled and the final grain yield is calculated as described in the next section.

Grain Yield

When the crop has reached phsiological maturity the grain yield is calculated according to Eqn. 4.7 and the simulation is stopped.

$$\underline{GRY} = (\underline{DY}_m - \underline{DY}_s) \cdot \underline{GF} / 0{,}875 \text{ .... Eqn. 4.7}$$

where $\underline{GRY}$ is the grain yield at $12\frac{1}{2}\%$ moisture (g/m^2),

$\underline{DY}_m$ is the dry yield of topgrowth at maturity (g/m^2), and

$\underline{DY}_s$ is the dry yield of topgrowth at silking (g/m^2).

The $\underline{GF}$ (GRFR) values used are based on the results discussed under the heading 'Grain formation' in Chapter 3 and are listed in Table. 3.9.

SENSITIVITY TEST ON THE MODEL

From Cedara radiation and temperature data, the growth of hybrid SA 60 planted at a population density of 3,59 plants/m^2 and emerging on the 25/11/1969, was simulated using the constants and inputs listed in the previous section. The estimated $\underline{DM}$ yield and the $\underline{L}$ value at silking are presented in Table 4.6. By increasing or decreasing a single growth factor in the model by 5% or 10%, and keeping all other parameters constant, the sensitivity of the 'dynamic' growth model to changes in the particular factor was measured. These results are given in Table 4.5. The relative sensitivity is expressed as the ratio of the final results with a 10% (or 5%) change in a given parameter to the final result obtained with the original model.

Table 4.5: The relative sensitivity of the growth simulation model to changes in the various constants and initial inputs (1969/70).

Factor changed	Proportionate change relative to standard	Relative sensitivity			
		DM yield at Silking	DM yield at maturity	Grain yield	L
b (vegetative)	1,10 0,90	1,12 0,87	1,05 0,95	1,00 1,00	1,03 0,96
b (reproductive)	1,10 0,90	1,00 1,00	1,03 ,97	1,05 0,94	1,00 1,00
c (vegetative)	1,10 0,90	1,08 0,92	1,03 ,97	1,00 1,00	1,02 0,98
c (reproductive)	1,10 0,90	1,02 0,98	1,04 0,95	1,06 0,93	1,00 1,00
K_v	1,10 0,90	1,05 0,94	1,02 0,97	1,01 0,99	1,01 0,98
k (const. respiration.)	1,10 0,90	0,78 1,23	0,84 1,16	0,89 1,11	0,94 1,06
C_{30} (Maint. respiration.)	1,10 0,90	0,99 1,01	0,98 1,02	0,97 1,03	1,00 1,00
RF at 15 days	1,10 0,90	1,07 0,92	1,06 0,94	1,05 0,94	1,10 0,90
LF at 15 days	1,05 0,95	1,17 0,83	1,24 0,78	1,29 0,75	1,68 0,64
Total DM yield at 15 days	1,10 0,90	1,05 0,94	1,05 0,94	1,05 0,95	1,09 0,90
Regression coefficient Eqn.3.6	1,10 0,90	0,94 1,06	0,97 1,02	1,00 1,00	0,98 1,01
Regression coefficient Eqn3.11	1,10 0,90	2,86 0,05	2,27 0,04	0,76 0,02	242,04 0,02
Regression coefficient Eqn3.15	1,10 0,90	1,18 0,81	1,11 0,88	1,06 0,94	1,15 0,85

The 'dynamic' growth model appears to be comparatively insensitive to changes in the efficiency factors b and c of the photosynthetic function (Eqn. 2.1). A 10% change in the b and c values, during either the vegetative or reproductive growth phase, resulted in a maximum change in final *DM* or grain yield estimate of 7% and a maximum difference in L value of 4%. Most marked was the effect of a 10% change in the b value during the vegetative phase which produced between 12% and 13% variation in the *DM* yield at silking. Except for the b value during the reproductive phase, the recorded measurements of the efficiency factors b and c did not fluctuate by more than 10% from the mean for maize planted at a population density of 3,59 plants/m^2. Hence the b and c values employed in this model can be used with confidence.

Changes in the extinction coefficient (K_v) also had a surprisingly small effect on *DM* yield and L value. The most significant response was in *DM* yield at silking where a 10% decrease in K_v resulted in a 6% decrease in *DM* yield. The effect on *DM* yield at maturity, final grain yield and L value, did not exceed 3%. A mean K_v value can therefore be used with confidence for a given population density, plant spacing or cultivar type.

As regards respiration, the growth simulation model proved to be particularly sensitive to the construction respiration factor k, especially during the vegetative growth period. The difference in *DM* yield at silking exceeded 20% for a 10% change in k. Although still very marked, the difference was less for total *DM* yield at maturity and grain yield.

Changes in the maintenance respiration constant (C_{30}) had little effect on yield and L estimates. Since maintenance respiration is calculated from the *DM* yield present, its influence on *DM* accumulation becomes progressively greater as the crop grows.

The model is sensitive to the composition of the crop at the start of the simulation. This is particularly true for LM, the reason being that the partitioning of accumulated DM to the leaf is dependent on LF. This in turn effects the amount of solar energy that is intercepted by the crop. Similarly, the rate at which DM is partitioned to the leaves relative to LF (Eqn. 3.11) and the specific leaf area (i.e. regression coefficient of Eqn. 3.15) have a marked effect on the final yield and L values of the crop. Compared to the partitioning of DM to the leaves, RF at the start and the rate of DM partitioning to the roots (Eqn. 3.6) had a comparatively small effect on the final crop performance.

From the above it is apparent that the model is most sensitive to factors and relationships that effect the rate of leaf growth, since this has a marked influence on the amount of light energy intercepted by the crop and hence its photosynthetic rate. The accuracy of the growth simulation model, therefore, depends to a large extent on these relationships. Further work on the partitioning of DM to the leaves and on the specific leaf area is indicated.

VALIDATION OF THE SIMULATION MODEL

The growth of the hybrids SA 60 and SR 52 was simulated for the period fifteen days after emergence to maturity from Cedara solar radiant energy and temperature data, and their yields estimated.

The simulated results were compared with the actual field measurements of crops listed in Table 3.1 that were grown at 2,39, 3,59 and 4,78 plants/m^2. Some of these comparisons are illustrated in Figs. 4.2, 4.3 and 4.4 which represent the hybrid SA 60 grown at 2,39, 3,59 and 4,78 plants/m^2 respectively, and Fig. 4.5 which shows the comparison for SR 52 grown at 4,78 plants/m^2.

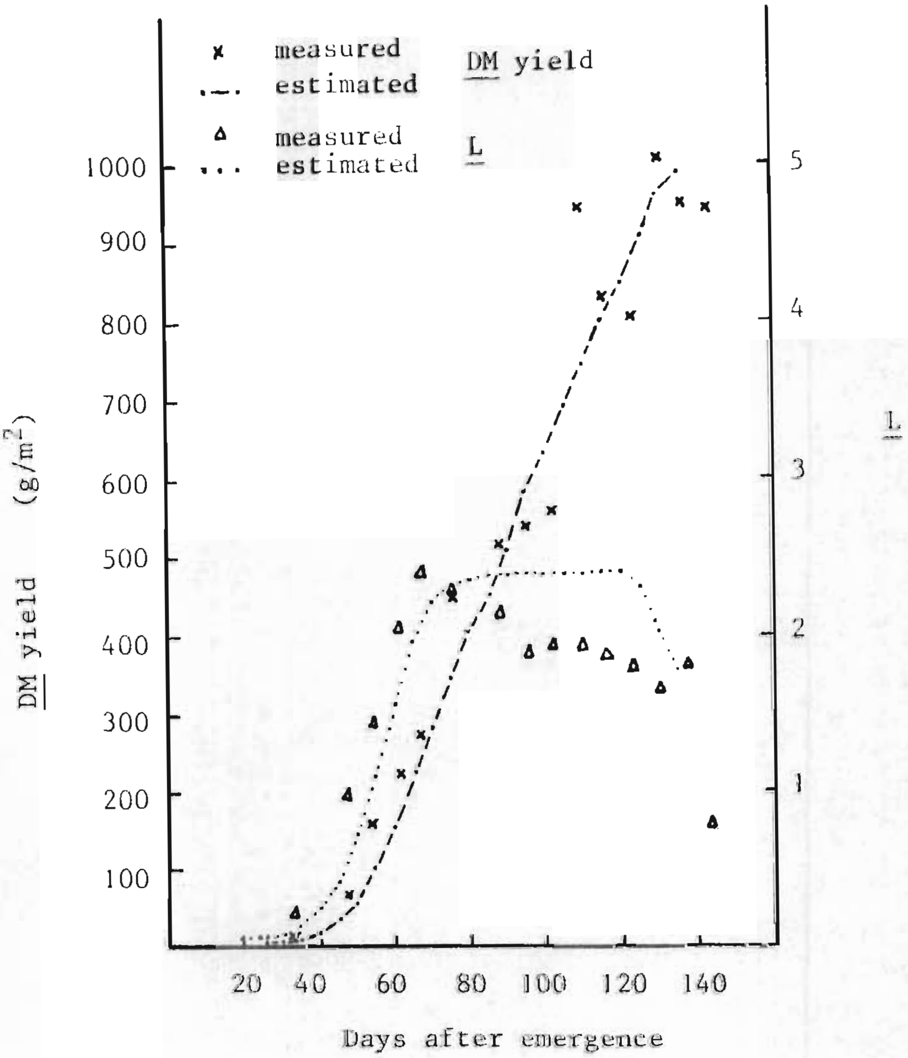

Fig. 4.2: Comparison between the estimated DM yield and L and the measured values at different growth stages for a crop of SA 60 growing at 2,39 plants/m^2 (1973/74 data).

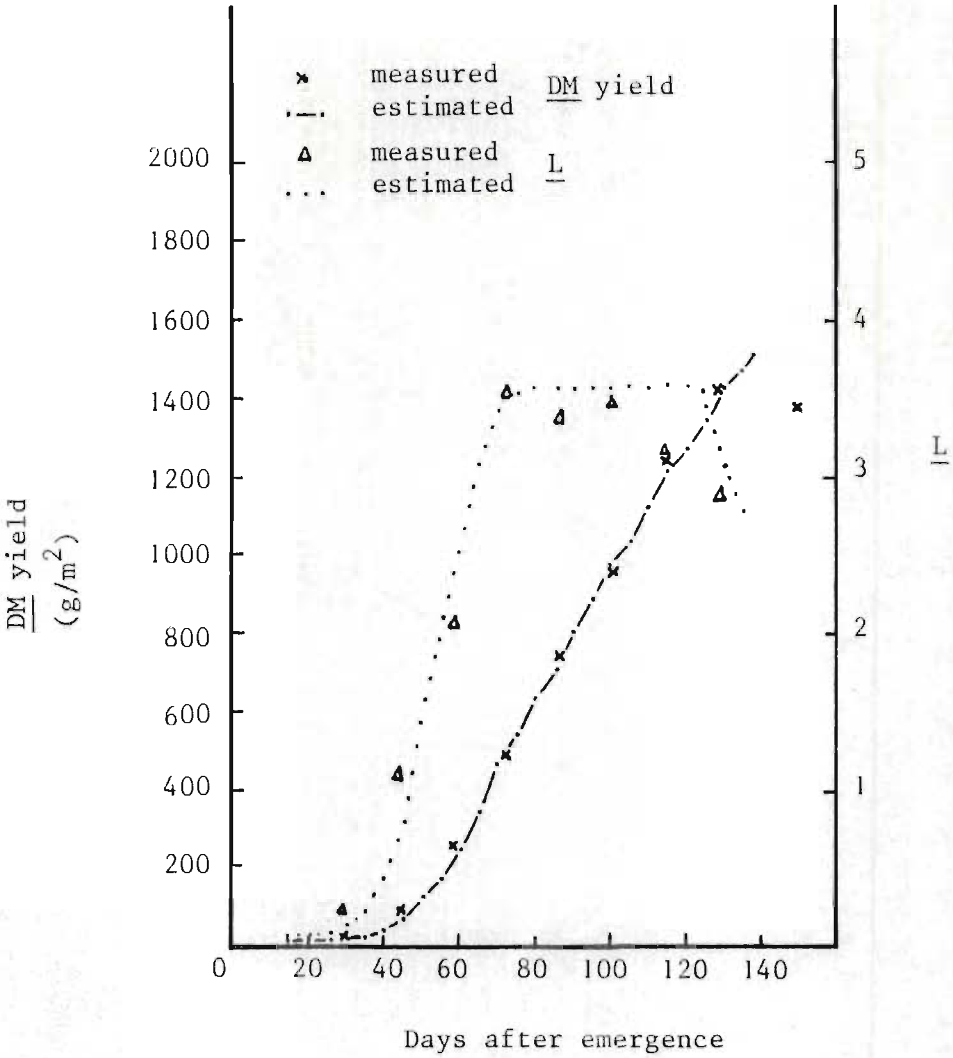

Fig. 4.3: Comparison between the estimated DM yield and L and the measured values at different growth stages for a crop of SA 60 growing at 3,59 plants/m^2 (1969/70 data).

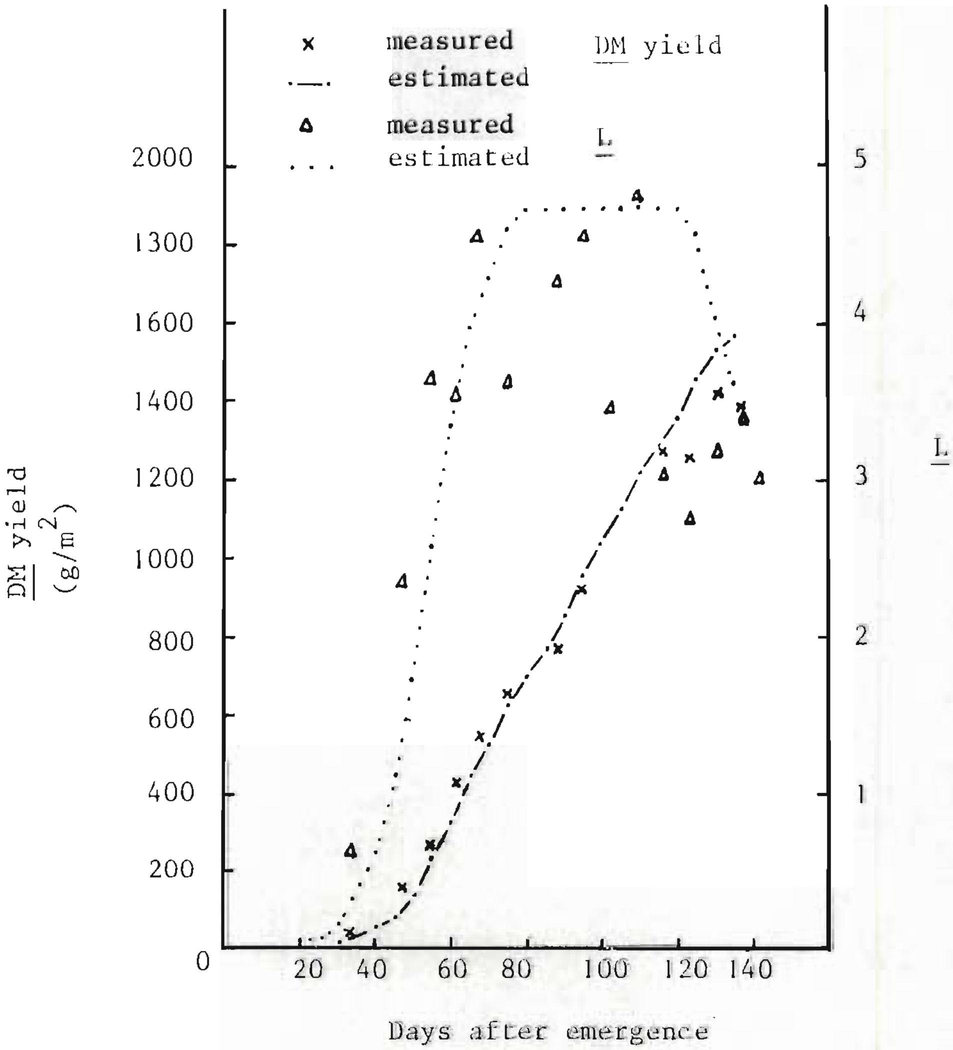

Fig. 4.4: Comparison between the estimated DM yield and L and the measured values at different growth stages for a crop of SA 60 growing at 4,78 plants/m^2 (1973/74 data).

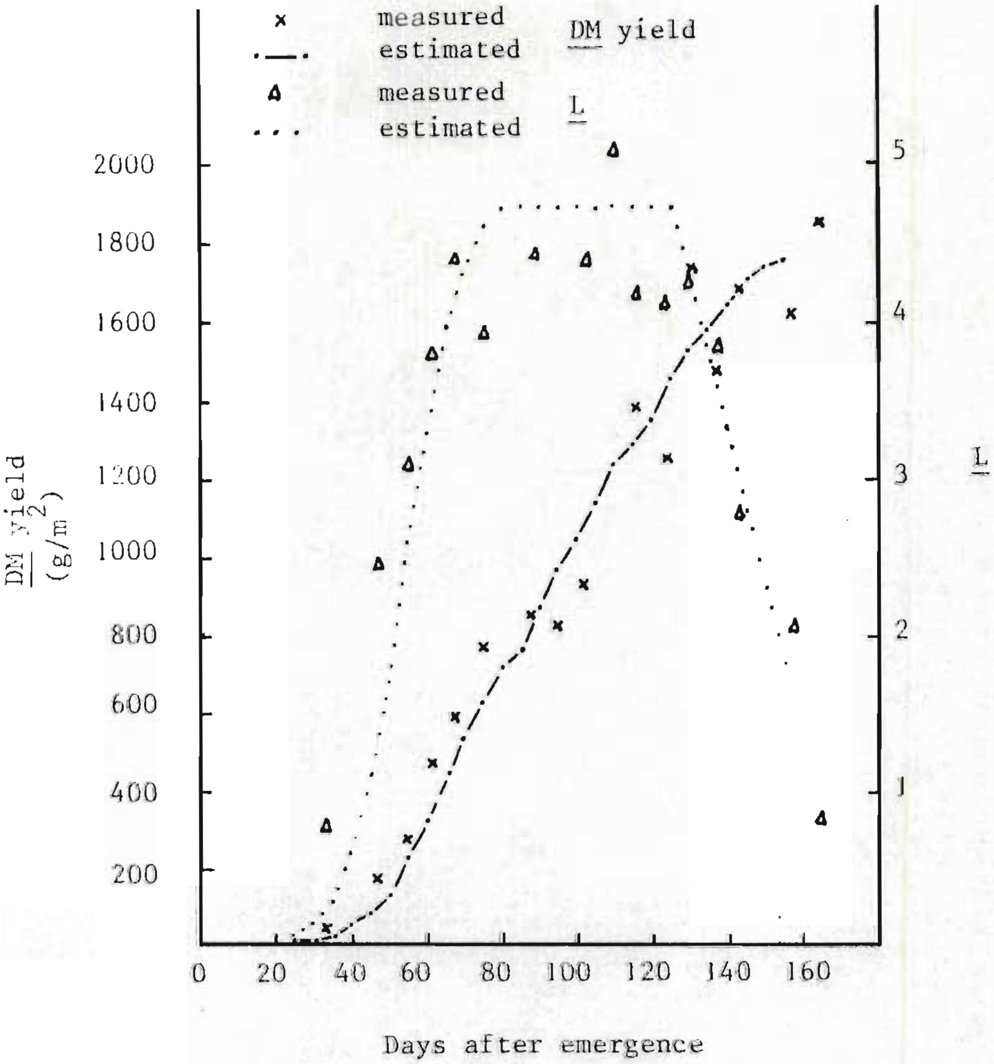

Fig. 4.5: Comparison between the estimated DM yield and L and the measured values at different growth stages for a crop of SR 52 growing at 4,78 plants/m^2 (1973/74 data).

In the four illustrated examples good agreement was obtained between the estimated and measured performance of the crops, particularly as regards DM accumulation. Estimates of L were slightly lower than the measured values during the early part of the growth period.

A summary of the estimated and recorded DM yields at different growth stages and of different plant components and of L at silking for twelve crops grown during the years 1969/70 to 1974/75 is given in Table 4.6. On the average the model overestimated grain DM yields by 5,2% and under-estimated vegetative production by 5,5%. With one exception grain yield estimates were accurate to within 10% of the measured yield. The SA 60 crop planted at 4,78 plants/m^2 on 17/11/71 yielded only 511g grain DM/m^2 compared to an estimate of 639g DM/m^2. The low measured yield in this case was caused by a high incidence of barren stalks and certainly did not represent the potential for the crop in that season.

As regards population densities, the over estimate in grain yields occured mainly in the higher population densities, which could indicate that the GF used in these crops was too high relative to that for the lower populations.

Table 4.6: Measured (M) and estimated (E) grain DM yield, DM yield at maturity and silking, and L at silking for twelve crops, and the estimated values as a percentage of those recorded.

Hybrid	Population	Emergence date	Grain DM			DM at Maturity			DM at silking			L		
			M	E	E/M	M	E	E/M	M	E	E/M	M	E	E/M
	Plants/m^2		g/m^2	g/m^2	%	g/m^2	g/m^2	%	g/m^2	g/m^2	%	g/m^2	g/m^2	%
SA 60	4,78	16.11.70	615	642	104,4	1673	1578	94,3	805	699	86,8	4,60	4,66	101,3
SA 60	4,78	17.11.71	511	639	125,0	1419	1568	110,5	719	693	96,4	4,42	4,62	104,5
SA 60	4,78	16.11.73	594	651	109,6	1435	1595	111,1	705	704	99,9	4,41	4,70	106,6
SA 60	4,78	13.12.73	488	532	109,0	1366	1466	107,3	650	549	84,9	4,18	4,31	103,1
SA 60	4,78	19.11.74	651	642	98,6	1663	1645	98,9	719	766	106,5	-	-	-
SA 60	3,59	25.11.69	527	567	107,6	1472	1506	102,3	674	646	95,8	3,48	3,55	102,0
SA 60	2,39	17.11.71	414	402	97,1	1097	991	90,3	460	400	87,0	2,28	2,31	101,3
SA 60	2,39	16.11.73	402	439	109,2	947	1004	106,0	415	402	96,9	2,19	2,34	106,8
SA 60	2,39	13.12.73	-	325	-	-	910	-	360	298	82,8	2,23	2,19	98,2
SA 60	2,39	19.11.74	435	431	99,1	1130	1039	91,9	422	448	106,2	-	-	-
SA 60	2,39*	19.11.74	507	457	90,1	1339	1159	86,6	566	533	94,2	-	-	-
SR 52	4,78	16.11.73	827	893	108,0	1727	1775	102,8	760	736	96,8	4,47	4,72	105,6
MEAN					105,2			100,2			94,5			103,3

* Maize planted in 0,91m rows as compared to 1,83m rows for all other 2,39 plants/m^2 populations listed

One reason for the over and under estimation of the model of grain and vegetative DM yield respectively, can possibly be sought in the respiration factors used. As discussed earlier these were not measured, but were estimated. A small reduction in $\underline{k}$ and an increase in $\underline{C}_{30}$ would favour vegetative growth and reduce production during the grain filling period.

The total above ground DM yield at maturity and the $\underline{L}$ value at silking were estimated with a high degree of accuracy. On the average the DM yield and $\underline{L}$ estimates were 0,2% and 3,3% respectively higher than the measured values.

From the comparisons presented above it can be concluded that the simulation model can be used with confidence to predict the growth and yield of a maize crop from meteorological solar radiation and temperature data.

APPLICATION OF THE MODEL

De Jager (1974) lists a number of uses of a maize growth simulation model. The ones that are probably of greatest agronomic significance, are:

- The assessment of the environmental potential of an area for the production of maize;

- The prediction of the consequence of applying certain management procedures e.g. growing the crop in 0,9m rows as opposed to 1,8m rows; and

- Predicting the consequence of a certain breeding policy.

An example of an assessment of the potential of an area for the production of grain and silage is given in Table 4.7. These yields were estimated from solar radiation and temperature readings taken at Cedara during different parts of the seasons 1969/70 to 1974/75. The estimated yields are higher than those listed in Table 4.6, the reason being that in calculating the values for Table 4.6, allowance was made for interception of solar energy by the hail shelter under which the crops were grown. In the case of Table 4.7 the yields were calculated for natural conditions. It should also be noted that the grain yields in Table 4.7 are presented at the standard 12½% moisture level and not in terms of DM as in the earlier parts of this dissertation.

Table 4.7: Theoretical estimates of grain (12½% moisture) and silage DM yields of the hybrid SA 60 grown at Cedara at a population density of 4,78 plants/m^2 and emerging on 15 October, 15 November and 15 December respectively, for the period 1969/70 to 1974/75.

Year	Emergence Date						MEAN	
	15th October		15th November		15th December			
	grain	silage DM	grain	silage DM	grain	silage DM	grain	silage DM
	g/m^2	g/m^2	g/m^2	g/m^2	g/m^2	g/m^2	g/m^2	g/m^2
1969/70	816	1900	871	1921	681	1885	691	1902
1970/71	776	1989	798	1754	557	1665	621	1803
1971/72	786	1890	791	1764	616	1737	640	1797
1972/73	697	1824	730	1652	610	1608	594	1695
1973/74	709	1954	806	1796	677	1677	639	1809
1974/75	638	1677	689	1622	647	1655	576	1651
MEAN	737	1872	781	1752	631	1704	627	1776
SD	61	102	58	98	43	89	37	82

The data in Table 4.7 show that as regards solar radiation and temperature, crops of SA 60 maize growing at Cedara and emerging on 15 October and 15 November should give similar grain yields, but a 20% reduction in yield can be expected where the crop emerges in mid-December. The measured yields from 1973/74 which are presented in Table 4.6, show a similar decline (viz. 18%) between the crops emerging in November and December. As regards total DM, October planted maize gave an estimated yield that was, on the average, 6% higher than for a November planted crop, whereas the December planted crop gave an expected yield that was only 3% lower than that for November planted maize. The latter difference compares favourably with the 5% measured in 1973/74 and presented in Table 4.6.

The results in Table 4.7 show that the maize hybrid SA 60 planted at Cedara during the period early October to early November should yield between 737 and 781g of grain (12½% moisture) per m^2 or 1752 to 1872g silage DM per m^2, provided it is grown at a population density of 4,78 plants/m^2 in 0,91m rows and is supplied with adequate moisture and fertilizer.

In South Africa moisture is the climatic factor that is most commonly limiting production. The value of this growth simulation model can therefore be greatly enhanced by including an analysis of the rainfall data. This can be achieved by combining this model with the moisture model of Mallett (1972).

A shortcoming in the use of the model for estimating the potential of an area for maize production, is the limited solar radiation data that is available in this country. However, solar radiation can be predicted with a high degree of accuracy from sunshine data (Erasmus, 1975, Schulze, 1975) which is more commonly available.

The use of the model as a management tool for decision making is illustrated in Table 4.6 using the climatic data from the 1973/74 and 1974/75 seasons and an emergence date of mid-November, the farmer having to choose between growing maize at 4,78 plants/m^2 in 0,91m rows or at 2,39 plants/m^2 in 1,83m rows, would have found that for the lower population the expected grain yield was only 67,2% of that for the higher population. The measured difference in yield for the two populations was identical to the estimated difference.

The use of a model in predicting the consequences of a breeding policy is also illustrated by the results listed in Table 4.6. A breeder might wish to know the effect of a longer grain filling period and higher GF value on final grain yield. The comparison of the 1973/74 results for SR 52 and SA 60 provides a good example of the answer he would receive. All the functions used in the simulation model were the same for these two hybrids, except that SR 52 had a slightly longer vegetative period, a 16 day longer grain filling period and a higher GF value. SR 52 gave an estimated grain yield that was 37,2% higher than SA 60. The measured difference between the two hybrids was 39,2%. Similar comparisons can be made to determine the effect of higher efficiency factors b and c or a difference in K_v value. Estimates of the effect of a 10% change in these factors are given in Table 4.5. The simulation model can therefore assist to formulate a breeding policy by pinpointing those characteristics where improvement should lead to the greatest progress.

DISCUSSION

A computer simulation model, similar to any research programme, should never remain static and be considered as final. It requires continual updating as new developments take place. Likewise this applies to the model described in Chapter 4. Good agreement has been achieved between the growth and yield estimates and the actual measurements taken in the field (See Table 4.6, Figs. 4.2, 4.3, 4.4 and 4.5). In its present form the model can therefore be used with reasonable confidence to estimate the potential of an area and to decide between different management or breeding strategies. However, its practical usefulness would be greatly improved by using it in combination with a moisture model of the type developed by Mallett (1972).

The reliability of a simulation model is largely dependent on (1) the validity and accuracy of the component instantaneous models, and (2) the accuracy of the climatic data. The sensitivity analysis (See Table 4.5) showed that the simulation model is not equally sensitive to all the instantaneous models. For example, changes in the constants of those equations concerned with the calculation of respiration and DM partitioning to the leaves have a considerably greater effect on growth and yield estimates than do changes of the same order in the photosynthetic or light interception functions.

From the foregoing it becomes obvious that accuracy in the calculation of respiration is most important. This research programme did not include respiration studies. The respiration constants used were determined by iteration of initial estimated values in the simulation model until accurate crop yield estimates resulted from 1969/70 weather data. The respiration constants were then validified by comparing model estimates with actual yields in subsequent years. It is also apparent from the literature that the respiratory processes of the plant are by no means clearly understood.

Research in this field should be fruitful and should lead to an improvement of the respiratory functions used at present in the simulation model.

The sensitivity of the model to changes of the constants concerned with DM partitioning to the leaves, particularly Eqn. 3.11, suggests that this is an area where the maize breeder has considerable scope for improving the efficiency of the crop. Small increases in DL can markedly change the composition and final performance of the crop.

At present, temperature plays a comparatively minor role in the simulation model. It is a factor in the calculation of maintenance respiration and the HU accumulation during the vegetative growth period and hence the timing of anthesis. However, it is known that temperature affects leaf expansion (Schwabe, 1963; Blackman, 1970; and Biscoe & Gallagher, 1975). Since, as shown above, the model is extremely sensitive to leaf development, the inclusion of a temperature factor in the leaf development model should improve the overall simulation model considerably. Although temperature had no apparent effect on the instantaneous photosynthetic model (See Figs. 2.5, 2.6 and 2.7), through its effect on leaf growth and hence L, it should affect the overall photosynthetic performance of a crop. It must be stressed, however, that the increased photosynthetic rate due to a more rapid leaf growth at higher temperature will, at least in part, be compensated by the earlier cessation of leaf growth and flowering of the maize crop.

The partitioning of DM to different plant organs as described in Chapter 3 is based on data from maize crops growing under conditions of high moisture and nutritional supply. Monsi & Murata (1970) showed that when soybean plants were under drought stress more DM is channelled to the roots, instead of to the leaves, than is the case for unstressed plants. It is possible that a similar situation will arise when plants are subjected to nutritional stress. For more general use therefore, modification of the leaf and root partitioning functions (Eqn. 3.6, 3.11) is required, suggesting studies on the interrelationship of DM partitioning and moisture, and possibly nutritional, stress. As regards the distribution of DM to the roots, the function (Eqn. 3.6) used is based on limited data. However, the sensitivity analysis (Table 4.5) indicated that the simulation model is insensitive to variations in the rate of DM distribution to the roots, particularly as regards the important grain and DM yield estimates at maturity. Hence, the present function can be used with confidence.

The photosynthetic efficiency factors b and c used in the simulation model are based on measurements done on hybrid SA 60. If, as suggested in Chapter 2, the photosynthetic efficiency at high light intensities (b), during the reproductive growth is governed by the sink demand of the crop, then differences between cultivars can be expected. For example, a multi-eared cultivar with a large number of kernels (or storage sites) could be expected to have a higher sink demand than one producing only a single ear with limited kernel numbers. Furthermore, since shading by the tassels appears to play an important role in crop photosynthesis at low light intensities, cultivar differences in the constant c, are possible.

In the validation exercise of Chapter 4 the same b and c values were used to simulate the growth of hybrids SA 60 and SR 52, two cultivars with considerably different yield potentials. It is interesting to note that the b and c values obtained with SA 60, gave good agreement when used to simulate the growth of SR 52 (See Fig. 4.5 and Table 4.6). The only difference in inputs used between the simulation presented in Figs. 4.4 and 4.5 were that in the case of SR 52 (Fig. 4.5) the periods emergence to silking and silking to physiological maturity were 24 HU and 16 days respectively more than for SA 60. Furthermore, when estimating the grain yields GF values of 0,86 and 0,73 were used for SR 52 and SA 60 respectively (See Table 3.9). The estimated grain yield for SR 52 was 37% higher than for SA 60 as compared to the 39% difference in the measured values. The yield difference between the hybrids can almost entirely be attributed to the longer grain filling period of SR 52 compared to SA 60. This shows that without changing the actual photosynthetic efficiency of a crop, considerable genetic improvement is possible by the manipulation of other physiologic factors, such as the length of grain filling period and the partitioning of DM to the different plant organs.

The simulation model proved to be insensitive to changes in the extinction coefficient ($\underline{K}_v$) of the crop. This suggests that comparatively little improvement can be expected by changing the leaf angle of the plants. However, the light profile measurements done on hybrid RO 1E, which has a more vertical leaf display than SA 60, indicated that variations of over 50% in $\underline{K}_v$ are possible through genetic manipulation (See Fig. 1.8). Differences of this magnitude must undoubtedly have a significant effect on the performance of a maize crop. The $\underline{K}_v$ value for RO 1E was calculated from limited data and is therefore of doubtful accuracy. Further work in this direction could be most valuable.

The main objective of the overall research programme, of which the work reported on in this dissertation is a part, is to develop a practical computer model that can be used to simulate the growth of a maize crop and estimate its final yield from hourly and daily weather data. The simulation model described in Chapter 4 and listed in Appendix 1, deals specifically with the relationships between crop growth and development and solar radiant energy and, to a lesser extent, temperature. It could be incorporated either as it stands or in a modified form into a more general simulation model embracing other growth factors such as moisture and plant nutrients.

An efficient computer simulation model can be a powerful tool for the agricultural planner, who has to establish the potential of an area, the adviser, who has to guide the farmer in his management decisions, and the researcher for pinpointing priority areas for research. Particularly in the first two cases, simplicity and a low usage of computer time, are important factors which will determine the practical use of a model. Complex micro-meteorological models, such as the one developed by Stewart & Lemon (1969), are unsuitable in this regard. The growth simulation model described in Chapter 4 and listed in Appendix 1, was executed in less than three minutes using a comparatively small and slow IBM 1130 computer.

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APPENDIX I

```
C     PROGRAM TO CALCULATE MAIZE PRODUCTION FROM SOLAR RADIATION,TEMPERA
C     -TURE AND CANOPY DATA
C     ******************************************************************
C     CLIMATIC DATA ON DISK 14
C     KEY TO SYMBOLS USED GIVEN AT END OF PROGRAM
      DEFINE FILE 10(2000,32,U,IJK),20(10000,2,U,JKI)
      DIMENSION IZ(12),IZZ(12),IRAD(32),MAXT(2),MINT(2),IT8(2),IT14(2),
     1IT20(2),HSTR(24),ALBE(24),MRAD(24)
[redacted]
      DATA IZ /0,31,59,90,120,151,181,212,243,273,304,334/
      DATA IZZ /0,31,60,91,121,152,182,213,244,274,305,335/
C     ******************************************************************
C     TITLE
      READ(2,1000)(HSTR(J),J=1,20)
      WRITE(3,1001)(HSTR(J),J=1,20)
C     ******************************************************************
C     HAILSHELTER TRANSMISSION FACTOR = HSTR
      READ(2,1002)(HSTR(J),J=5,21)
C     ALBEDO = ALBE
      READ(2,1002)(ALBE(J),J=5,21)
C     NO.OF SIMULATIONS (NSIM) AND NO.OF DAYS TO EACH PRINT OUT (IPRIN)
      READ(2,1003)NSIM,IPRIN
C     MEAN RADIATIN USED WHEN METEOROLOGICAL DATA INCOMPLETE
      READ (2,1004) (MRAD(J),J=5,21)
      DO  40 KK=1,NSIM
      WRITE(3,1005)(HSTR (J),J=5,21), (ALBE(J),J=5,21)
C     ******************************************************************
C     CONSTANTS USED IN CALCULATIONS
      READ(2,1006)BVEG,BREP,CVEG,CREP,RESCO,RESMA,EXTK,GRFR
C     ******************************************************************
C     INPUT DATA
      READ(2,1007) HUST,NDAM,HUVEG,TPLDY,FRTOP,FRL,POP
      WRITE(3,1008)BVEG,BREP,CVEG,CREP,RESCO,RESMA,EXTK,GRFR,HUST,NDAM,
     1HUVEG,TPLDY,FRTOP,FRL,POP
      TOTDY=TPLDY*POP
      DY=TOTDY*FRTOP
      DYL=DY*FRL
      ALAI=.0218*DYL
C     ******************************************************************
C     FIND EMERGENCE DATE ON FILE
      READ(2,1009)IEMDA,IEMMO,IEMYR
      WRITE(3,1010)IEMDA,IEMMO,IEMYR
      IF(IEMYR-((IEMYR/4)*4))  2,  1,  2
    1 XX=FLOAT(IZZ(IEMMO)+IEMDA)*100.+FLOAT(IEMYR)-16000.
      GO TO   3
    2 XX=FLOAT(IZ(IEMMO)+IEMDA)*100.+FLOAT(IEMYR)-16000.
    3 IEM=XX
      IK=1
      DO  38 I=1,2000
      READ(10'IK)IRAD
      IF(IRAD(32)-IEM) 37,  4, 37
C     ******************************************************************
    4 IJ=IK
      IJJ=IK*5-4
      NDAY=1
      IDAY=0
      HU=0.
C     CALCULATE HU TO TASSELING
      HUTAS=HUVEG-120.
      WRITE(3,1011)
```

```
C     ******************************************************************
      READ(20'IJJ)MAXT,MINT,IT8,IT14,IT20
      DO  36 II=1,200
      READ(10'IJ)IRAD
C     TEST DATA ON DISK
      IF(MAXT(2)-MINT(2))  7,  5,  7
    5 IF(IT8(2)-IT20(2))  7,  6,  7
    6 IF(IRAD(32)-MAXT(2))  7,  8,  7
    7 WRITE(3,1012)IRAD(32),MAXT(2),MINT(2),IT8(2),IT14(2),IT20(2)
    8 CONTINUE
C     ******************************************************************
C     INITIALIZE B + C
      IF(HU-HUTAS)  9,  9, 10
    9 C=CVEG
      GO TO  11
   10 C=CREP
   11 IF (HU-HUVEG) 12, 12, 13
   12 B=BVEG
C     ******************************************************************
C     RETAIN YIELD,LAI,NDAY FOR SILKING
      YVEG=DY
      ALVEG=ALAI
      NDAYV=NDAY
      FRLS=FRL
      FRROS=FRROT
      GO TO  16
   13 B=BREP
      IF(IDAY-NDAM) 14, 39, 39
   14 IDAY=IDAY+1
C     ******************************************************************
C     CALCULATE SENESCENCE
      FALAI=1.888-.0208*IDAY
      IF(FALAI-1.) 15, 16, 16
   15 ALAI=ALVEG*FALAI
   16 CONTINUE
C     ******************************************************************
C     CALCULATE ACCUMULATED HU
      TMAX=FLOAT(MAXT(1))*.1
      TMIN=FLOAT(MINT(1))*.1
      IF(TMAX-30.) 18, 18, 17
   17 TMAX=30.
   18 IF(TMIN- 10.) 19, 20, 20
   19 TMIN=10.
   20 DAHU=(TMAX + TMIN)/2.-10.
      IF(DAHU-25.) 22, 22, 21
   21 DAHU=10.
   22 HU=HU+DAHU
      T20=FLOAT(IT20(1))
      IJJ=IJJ+5
      READ(20'IJJ)MAXT,MINT,IT8,IT14,IT20
C     ******************************************************************
C     START OF SIMULATION
      IF(HU-HUST) 35, 23, 23
   23 FRROT=(TOTDY-DY)/TOTDY
      FRL=DYL/DY
      GSDAG=0.
      DARAD=0.
C     ******************************************************************
      DO  27 J=5,21
      IF (IRAD(J)) 25, 24, 24
```

```
   24 IF(IRAD(J) -2000) 26, 26, 25
   25 IRAD(J)=MRAD(J)
   26 RAD=(FLOAT(IRAD(J)))*HSTR(J)
      VRAD=RAD*.445
      DARAD=DARAD+(RAD*.0036)
C     ******************************************************************
C     CALCULATE FRACTION OF VISIBLE ENERGY INTERCEPTED
      FINTV=(1.-(EXP(-EXTK*ALAI)))
C     ******************************************************************
C     SUBTRACT REFLECTED ENERGY
      FAV=FINTV*(1.-ALBE(J))
      A=FAV
C     ******************************************************************
C     PHOTOSYNTHETIC MODEL
      P=(VRAD*(B*1.8*ALAI))/((B*1.8*ALAI)/(C*   .022*A)+VRAD)*3.6
C     ******************************************************************
C     CONVERSION TO DRY MATTER
      GSDAG=GSDAG+(P*.682)
   27 CONTINUE
C     ******************************************************************
C     RESPIRATION LOSS
      DLSCO=GSDAG*RESCO
      T=(FLOAT(IT8(1))+T20    )*.1 /2.
      IF(T-40.) 29, 29, 28
   28 T=20.
   29 DLSMA=TOTDY*RESMA*(.044+.0019*T+.0010*T*T)
      FRESM=DLSMA/TOTDY
C     (MCCREE,1974)
      TOTDG=GSDAG-DLSCO-DLSMA
      TOTDY=TOTDY+TOTDG
      IF(HU-HUVEG) 30, 32, 32
C     ******************************************************************
C     PARTITIONING OF PHOTOSYNTHATE
C     CALCULATE TOP FROM TOTAL GROWTH
   30 DG=(TOTDG*(1.-(.0826+.452*FRROT)))
      DR=(1.-DG/TOTDG)
C     ******************************************************************
C     CALCULATE LEAF FROM TOTAL TOP GROWTH
      DL=-.464+1.631*FRL
      IF(DL) 33, 33, 31
   31 DGL=DG*DL
      DYL=DYL+DGL
C     ******************************************************************
C     SPECIFIC LEAF AREA
      ALAI=.0218*DYL
      GO TO  33
C     ******************************************************************
C     PRINT CALCULATED VALUES ON DAYS DIVISIBLE BY 'IPRIN'
   32 DG=TOTDG
   33 DY=DY+DG
      Y=DY+.005
      TOTY=TOTDY+.005
      G=DG+.005
      IF(NDAY-((NDAY/IPRIN)*IPRIN)) 35, 34, 35
   34 WRITE(3,1013)NDAY,GSDAG,TOTDG,DLSCO,DLSMA,TOTY,Y,ALAI,DARAD,HU,
     1FRROT,DR,FRL,DL,FRESM,T,A
   35 NDAY=NDAY+1
      IJ=IJ+1
   36 CONTINUE
   37 IK=IK+1
```

```
   38 CONTINUE
C     ******************************************************************
C     CALCULATE GRAIN YIELD
   39 GRYD=(DY-YVEG)*GRFR
C     GRAIN YIELD AT 12.5 PER CENT MOISTURE
      GRY=GRYD/.875+.05
      WRITE(3,1014)YVEG,FRROS,DY,FRLS,GRYD,NDAYV,GRY,NDAY
C     ******************************************************************
   40 CONTINUE
C     KEY TO SYMBOLS USED -
C     A=ABSORBANCE           ALAI/AL=LAI         ALBE=ALBEDO
C     B + C=PHOTOS. EFF. FAC CO=CONSTRUCTION     D=DRY
C     DA/DAY=DAY             DL + DR=PARTITION TO LEAF + ROOT
C     EM=EMERGENCE           EXTK=EXTINCTION COEFI ICIENT
C     F=FACTOR               FR=FRACTION         G=GAIN
C     GR=GRAIN               GS=GROSS            HU=HEAT UNITS
C     HSTR=HAIL SHELTER TRANSMISSION             I=INTEGER
C     INT=INTERCEPTION
C     L=LEAF                 LS=LOSS             M=MEAN OR MATURITY
C     MA=MATURITY            MO=MONTH            MAX=MAXIMUM
C     MIN=MINIMUM            N=NUMBER            POP=POPULATION
C     P=PHOTOSYNTHESIS
C     RAD=RADIATION          REP=REPRODUCTIVE    RES=RESPIRATION
C     RO/ROT=ROOT            S=SILK              ST=START
C     T=TEMPERATURE OR TOTAL                     TOT=TOTAL
C     T8,T14,T20=TEMPERATURE AT HOURS 8,14,20    TOP=TOP GROWTH
C     TAS=TASSEL             VEG=VEGETATIVE      V=VISIBLE OR VEGETATIVE
C     Y=YIELD                YR=YEAR             Z/ZZ=DAY OF YEAR
      STOP
C
 1000 FORMAT(20A4)
 1001 FORMAT(1H1,'  MAIZE GROWTH SIMULATION'/1X,20A4)
 1002 FORMAT(12X,17F4.3)
 1003 FORMAT(2I5)
 1004 FORMAT (12X,17I4)
 1005 FORMAT('0 HAIL SHELTER TRANS. HOURS 5-21'/ 1X,17F6.3 / '0 ALBEDO
     1         HOURS 5-21' / 1X,17F6.3)
 1006 FORMAT(12X,8F6.0)
 1007 FORMAT(12X,F6.0,I6,5F6.0)
 1008 FORMAT('0        BVEG      BREP      CVEG      CREP  '  RESCO     RE
     1SMA      EXTK      GRFR'/8F10.3/'0       HUST      NDAM      HUVEG
     2   TPLDY     FRTOP      FRL        POP'/ F10.0,I10,5F10.4)
 1009 FORMAT(3I3)
 1010 FORMAT('0'EMERGENCE DATE      ',3I3)
 1011 FORMAT('0  DAY   DAILY GAIN     RESPIRATION        DRY YIELD
     1LAI   DAILY      HU   ROOT        LEAF   RESP MA   T       A'/'
     2   GROSS      NET  CONST.  MAINT.   TOTAL      TOP          RAD. ENER.
     3          FRAC PART FRAC PART FRAC'/'          GM-2    GM-2     GM-2
     4  GM-2    GM-2    GM-2              MJ/M-2'/)
 1012 FORMAT(1X,'ERROR',6I10)
 1013 FORMAT(1X,I4,9F 8.2,4F5.2,F6.3,F5.1,F6.3)
 1014 FORMAT('0  DRY YIELD AT SILKING - G/M**2',F24.1,10X,'ROOT FRACTION
     1 AT SILKING',F10.2/'0   DRY YIELD AT MATURITY - G/M**2',F23.1,10X,
     2'LEAF FRACTION AT SILKING',F10.2/'0   GRAIN DRY YIELD - G/M**2',F2
     39.1,10X,'DAYS TO SILKING',I22/'0   GRAIN YIELD 12.5 PER CENT MOIST
     4URE - G/M**2',F10.1,10X,'DAYS TO MATURITY',I21)
      END
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