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MAIZE IN THE MANAWATU

A FIELD STUDY OF THE EFFECTS OF SPACING AND VARIETY UPON THE GROWTH OF $\underline{\text{ZEA}}$ MAYS L.

A thesis

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TABLE OF CONTENTS

1

				Page
2	LIST	OF TABLES		v
	LIST	OF FIGURE	S	vii
	SUMM	ARY		viii
	INTR	ODUCTION		1
	DEFI	NITIONS		2
	CHAP	TER ONE	REVIEW OF LITERATURE	3
	1.1	Introduct	ion	4
	1.2	Aspects of	f Growth and Development	4
		1.2.1	The Terms Defined	4
		1.2.2	Quantitative Description and Analysis of Growth and Development	4
	<u>e</u>	1.2.3	Growth Analysis and its Parameters	5
	1.3	Some Facto Photo:	ors Influencing the Magnitude and Pattern of synthate Distribution in the Maize Plant	10
		1.3.1	The Development and Maintenance of Leaf Area in Maize	10
		1.3.2	Some Factors Determining Crop Growth Pate in Maize	16
		1.3.3	Patterns of Assimilate Distribution in Maize	29
		1.3.4	The Growth and Development of Yield in Maize	36
	2	1.3.5	Distribution of Dry Matter in the Mature Maize Plant	42
	1.4	The Field	Maturation of Grain Maize	43
	1.5	The Respon	nse of the Maize Plant to Intraspecific Competition	46
		1.5.1	Yield Density Relationships in Maize	47
		1.5.2	Changes in Individual Plant Characters Associated With Interplant Competition for Light	50
		1.5.3	Intraspecific Competition in Maize and Plant Barrenness	53
		1.5.4	The Quantitative Relationship Between Plant Fopulation and Crop Yield	56
	CHAP	TER TWO	METHODS AND MATERIALS	59
	2.1	Introducti	ion	60
		2.1.1	The Experimental Site	60
1		2.1.2	Experimental Layout	60
		2.1.3	Cultural Aspects	61
	2.2	Experiment	tal Methods	62
		2.2.1	Field Observations	62
		2.2.2	Measurements on Harvested Plants	63

ii

		Page
2.3	Statistical Methods	66
8	2.3.1 Preliminary Analysis of Data	66
	2.3.2 The Analysis of Variance	67
	2.3.3 Curve Fitting	68
	2.3.4 Growth Analysis	70
	2.3.5 Dry Matter Contents .	72
	2.3.6 Population Effects	72
	2.3.7 Correlations Between Yield and Yield Components	72
CHAP	PER TUREE RUSULTS	73
3.1	Introduction	74
3.2	Days to Flowering	74
3.3	Growth in the Size of the Stem	75
3.4	The Growth and Longevity of Leaf Area	76
	3.4.1 Leof Number, Area and Longevity, on a per Plant Basis	76
	3.4.2 Leaf Area Index and Leaf Area Duration	78
3.5	Growth in Shoot Dry Weight and its Components	78
	3.5.1 Growth in Weight on a Per Plant Basis	70
2.	3.5.2 Growth in Total Shoot Dry Meight per Unit Area	11
3.6	Growth in Yield	. 63
	3.5.1 Grain Dry Meight per Plant	52
 2	3.6.2 Changes in Dry Weight of Plant Parts During	
	Grain Filling	24
3.7	Yield and Yield Components	86
3.8	Node Number of Nodes Bearing Wars, and Dar Height	20
3.9	Tiller Numbers and Tiller Grain Production	03
3.10	Dry Natter Contents of Plant Constituents	O.A
3.11	Yield Density Relationships	с ·
CITVIJA	WR FOUR DISCUSSION	26
4.1	Methods	97
	4.1.1 Experimental Methods	97
	4.1.2 Statistical Methods	08
4.2	Experimental Results	101
	4.2.1 Growth, Composition and Longevity of Photosynthetic	
	Area	101
	4.2.2 Changes in Total Shoot Dry Weight and its Components	105
÷.	4.2.3 Growth Analysis	107
	4.2.4 The Growth of Grain Yield	113
	4.2.5 Yield and Yield Structure	115
	4.2.6 Plant Density Effects	118
	4.2.7 Field Maturation	120

iii

		iv
		Page
4.3	Conclusions	121
ACKN	OWLEDGEMENTS	123
BTBL	IOGRAFHY	
APPE	NDICES	A1
1	(a) Weather Data Recorded During the Experimental Period	A2
	(b) Accumulated Effective Degree Days	
2	Schedule of Events	A3
3	Regressions of Whole Huskless Ear Cob to Grain Ratio (Y) on Cob to Grain Ratio of Centre 4cm Section of Huskless Ear (X)	A4
.4	Regression of Mid Stem Diameter (Y) on Diameter of Stem Base (X) A5
5	Analysis of Variance of Stem Length and Expanded Leaf Number on the Main Stem	Аб
6	Coefficients of Polynomials Fitted to Data on Stem Length and expanded Leaf Number on the Main Stem	A7
7	Coefficients of Polynomials Fitted to Total Photosynthetic Area Data	A8
8	Analysis of Variance of Total Photosynthetic Area per Plant and Total Dry Weight per Plant	A10
9	Analysis of Variance of Fractions of Total Photosynthetic Area per Plant	. A11
10	Analysis of Variance of Total Leaf Area Index and Total Dry Weight per Unit Area	A1 3
11	Analysis of Variance of Dry Weight Fractions per Plant	A14
12	Coefficients of Polynomials Fitted to Dry Weight Data of Plant Parts	A18
13	Sample Analyses of Variance of Polynomials Fitted to Individual Plant Data for Population 3	A22
14	Analysis of Variance of Yield per Plant and Yield Components	A25
15	Analysis of Variance of Dry Matter Contents	A26
16	Coefficients of Polynomials Fitted to Dry Matter Content Data	A29
17	(a) Polynomials in Density Fitted to Grain Yield Data	A30
	(b) Analysis of Variance of the Logarithm of Grain per Plant on Plants per Square Metre	

•

LIST OF TABLES

	Table		Page
	1.1	Labelled Assimilate Distribution in Two Similar Naise Varietics	32
	1.2	Percentage of Total Shoot Dry Natter in Different Flant Parts at Haturity	13
	1.3	Labelled Assimilate Distribution in a Single Maine . Variety Grown at Two Spacings	56
	2.1	Summary of Plant Spacings	.61
	2.2	Variables Mensured on Scapled Plants	64
	2.3	Analysis of Vuriance For Fitted Polynomial of Degree k in Tire, Fitted to Data From n Harvests and b Replications	69
	3.1	(a) Days to 50% Tasseling, Anthesis and Silking	74
		(b) Analysis of Variance of Days to 50% Tasseling, Anthonic and Silking	- 75
	3.2	Stem Basal Diameter	75
	3.3	Days From Planting to 50% Senescence of Maximum Photosynthetic Area Attained	78
	3.4	Leaf Area Duration From 50% Silking Till 50% of the Maximum Photosynthetic Area was Seleccent	70
	3.5	Ratios of Plant Part Dry Weights at Maturity	00
	3.6	Values of Unit Leaf Rate Predicted by Linear Regression: of E upon LAI at 50% Silking	£1
	3.7	Date From Planting and From 50% Silking Till 95% Maximum Grain Dry Veight was Obtained	03
	3.8	Grain Leaf Ratio	C./
	3.9	Summary of Changes in Dry Weight of Hon-Grain Plant Components During the Period from their Peak Dry Weights After Flowering till 95% Total Grain Dry Weight was Obtained	85
	3.10	Summary of Changes in Dry Noight of Stem and Loaf Fractions from 50% Silking until 95% Total Grain Dry Weight was Obtained	95
	3.11	Yield and Yield Components	$\bigcirc 7$
	3.12	Percentage Composition of Total Ear Number per Plant	00
	3.13	Analysis of Variance of Total Ear Mumber per ha, Humber of Second Ears per ha, and Total Grain Yield	83
	3.14	Correlations of Total Grain Dry Weight per Plant with Various Characters	90
	3.15	Ear Dimensions	91
	3.16	Numbers of the Nodes at which the Three Heaviest Ears were Borne	91
	3.17	Height of Apical, Second and Third Ears	92
e'	3.18	Tiller Number per Plant	93
	3.19	The Percentage Distribution of Dry Weight per Plant Between the Main Stem and Tillers of the Two Varieties	94

•

v

		Vl
Table		Page
4.1	Coefficients of Variation (%) for Total Shoot Dry Weight Per Plot at Maturity, and Total Leaf Area per Plot at Day 103	97
4.2	Comparison of Standard Errors Calculated from Fitted Nultiple Regressions and from a One Way Analysis of Variance	99
4.3	Average Nonthly Temperatures and Accumulated Degree Days at the End of Each Month at Three Sites	1.04
4.4	The Distribution of Total Shoot Crop Growth Rate (COR) Between the Far and the Remainder of the Shoot For Each Variety for Population 3	107
4.5	Unit Leaf Rate and Leaf Area Ratio When LAI = 2.00	110
4.6	Summary of Relative Values of Yield and Yield Component.	116

LIST OF FIGURES

Figure	X	Following page
1	Experimental Layout	60
2	(a) Growth in Stem Length(b) Stem Length Growth Nate	75 .
3	 (a) Humber of Fully Expanded Leaves on the Main State (b) Rate of Appearance of Expanded Leaves on Main State (c) Relative Rate of Appearance of Expanded Leaves on Main Stem 	; 76 ;em
4	(a) Leaf Area Per Plant(b) Rate of Polative Leaf Growth	76
5	Specific Leaf Area	77
6	Percentage Distribution of Total Plant Photosyntheti	e 77
	Area	
7	Leaf Area Index	78
8	(a) Growth in Total Shoot Dry Veight Per Plant(b) Relative Growth Rate	78
<u>0</u>	Percentage Distribution of Total Shoot Dry Weight	79
10	(a) Unit Leaf Rate (b) Leaf Area Ratio	80,
11	(a) Total Shoot Dry Meight Per Unit Area(b) Crop Growth Rate	£1
12	 (a) Growth in Total Car Dry Weight Per Plant (b) Growth in Grain Dry Weight Per Plant (c) Grain Unit Leaf Rate 	.62
.13	Changes in Plant Component Dry Weights During Grouth	24
	<pre>(a) Stem (b) Leaf (c) Husk (d) Cob</pre>	
14	Dry Matter Content (Fresh Weight Basis) of Plant Components (a) Grain, Cob and Husk (b) Stem and Leaf (c) Rate of Increase in Grain Dry Matter Content	0.1
15	 (a) Quadratic Polynomial in Plant Density Giving Bes Fit to Grain Yield (b) Linear Regression of the Logarithm of Grain Veig Per Plant on Plant Density 	t 05 ht

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SUMMARY

An experiment is described in which two commercial dent maize varieties, M575, a late maturing hybrid, and KC3, an early maturing hybrid were grown at equidistant spacings in five populations of from 39,000 to 79,000 plants.ha⁻¹. Plants were sampled on ten occasions from 44 days after planting to field maturity, and leaf area, dry weights of shoot components, and dry matter contents determined. Analyses of variance were performed in the data, polynomials fitted to plot means of the variables, and growt an lysis carried out.

On average the late variety (W575) outyielded NC3 in grain production by 12%. Although ears in both varieties were similar in weight, they were more numerous in W575, particularly at wide plant space ys. Consequently yields in the two varieties were similar at high plant densities but superior in W575 at low plant densities. Tillers provided 10% of total shoot weight at 50% silking but bore only 2% of the final grain yield. Plants of the early variety possessed only 50% of the leaf area of the intervariety. The difference arose from a lower leaf number, smaller leaf size, and a smaller tiller component, which were slightly offset by longer internodes giving a greater proportion of stem area.

At maturity, KC3 was characterized by a lower proportion of atom, loof and cob, and a greater proportion of grain and tassel than the late variety. The proportion of husk was similar in both varieties.

The total shoot dry weight production of 1575 exceeded that of 103 because of a higher average crop growth rate and a longer period of growth. The late maturing variety was the more efficient in converting incident radiation into total shoot dry weight, but this efficiency are similar in both varieties for grain production.

Growth analysis revealed that the higher crop growth rate of the prior to silking was due primarily to an 11% higher unit loaf rate. The significantly lower leaf area ratio of this variety indicated a superiority of gross photosynthesis in this variety. The electronic of crop growth rate in W575 after flowering was principally due to its 67% higher leaf area index, and to the more rapid ageing of KC3. The grain leaf ratio, 0, of the early variety significantly exceeded that of W575, though it was comparatively uniform within any single variety.

Considerable losses of dry weight from non-grain shoot components occurred during the late grain filling period of both variaties. Nobilization of previously established reserves may have accounted for 0.45 and 4.2% of final grain yield in KC3 and W575 respectively. This proportion increased with plant density in KC3, but not in W575.

The time from silking to senescence was greater than that observed in many other countries. Leaf area was reduced to 50% of its maximum value approximately 10 weeks after silking, and 68 and 79 days elapsed between silking and 95% completion of grain filling in the early and late varieties respectively. Varietal differences in grain yield were due to differences in the length of the grain filling period rather than in the rate of grain filling. Reasons for delayed plant senescence and its implications on maize productivity are discussed.

The optimum plant population for grain production in KC3 did not occur within the range of densities tested, though that for N575 appeared to be close to the upper end of the range of plant densities grown. Optimum plant populations calculated from regressions of the logarithm of grain weight per plant on density were 92000 plants.ha⁻¹ (W575) and 157000 plants. ha⁻¹ (KC3), and appeared to reflect differences in plant size.

The rate of increase in grain dry matter content was significantly greater in W575 than in KC3.

Implications of these findings on plant growth and crop yield are discussed in the light of current knowledge and hypotheses on the physiology of growth and productivity in maize.

INTRODUCTION

The last five years have witnessed a dramatic increase in interest in maize growing in New Zealand. As a result several new variaties which were developed under conditions of high plant population density in North America (Downey, 1971 c) have been released for commercial grain production in New Zealand. In addition it has been established that a number of districts previously regarded as marginal for the groduction of this crop are in fact quite suited to growing maize for grain.

Because the optimum plant population for grain production is determined by the variety of maize planted and the environment in which it is grown (Dungan <u>et al</u>, 1958), it has become necessary to quantitatively evaluate the yield density relationship of commercial hybrids in the previously untested environments in which maize is now being grown.

Although maize has been grown in New Zealand for many years, a number of fundamental agronomic questions have remained unanswered. Desite a considerable recent expansion in area grown for grain, the average yield of maize in New Zealand is more than one third greater than that in the United States (Statistical Abstract of the United States, 1970). There is a total absence of any agronomic information in New Zealand to be used for this yield superiority of comparable genetic material when grown in this country.

The present study was carried out in an effort to remady some of these areas of deficiency. The stock commercial hybrid grown in For Zer hand over the last decade, M575, was chosen as a full season variety, there providing a baseline against which the relatively unknown short season variety, F03, could be compared. This experiment was designed to provide basic agronomic information on the growth and yield of two varieties of contrasting maturities when grown over a range of commercial field spacings theoget to be suitable for the Manawatu.

DEFINITIONS

For clarity throughout the thesis, the following terms are defined:

- (i) <u>Stem</u>: the main axis of the plant, including leaf she ths.
 The length of the stem is measured from ground level to the base of the tassel peduncle.
- (ii) <u>Leaf</u>: laminae, but not including leaf sheaths, except when used in connection with leaf area.
- (iii) Ear: the whole female inflorescence, including the chard.
- (iv) <u>Husk</u>: that part of the car remaining after the grain and cob have been removed, and includes the shank. The err without the husk is referred to as a huskless car.
 - (v) <u>Grain</u>: caryopses in which development has begun. Partially developed grains are included as well as chaffy material which receives attached to the grain when it is removed from the ach.
- (vi) <u>Cob</u>: the rachis, or main axis of the female inflorescence and which florets are borne. Such florets may be fertilized develop into caryopses. The cob therefore includes contributed florets borne on the distal region of the mature each.

(vii) <u>Tassel</u>: the male inflorescence, including the tassel podune ...

(viii) Stover: the total plant shoot less the mature grain.

CHAPTER ONE

REVIEW OF LITERATURE

This review provides a background against which the findings of the present experiment may be discussed. Aspects of the growth and development of maize are emphasised, and some of the factors affecting the efficiency with which the crop utilizes the ultimately limited supply of light are described. The review is largely restricted to maize, partly because it is the subject of a wealth of published literature (though related to a limited range of environments), and partly because it differs significantly in many respects from other cereals.

Following the introduction, qualitative and quantitative aspects of growth are discussed. The third section considers in detail the production, distribution and accumulation of assimilate in the maize plant. Section four briefly reviews maize grain maturation in the field, and section five deals with changes in the maize plant induced by competitive stress.

1.1 INTRODUCTION

Biological systems may be regarded as being comprised of a number of levels of organization, each level being characterized by its own relaxation time (time taken to recover from a small disturbance), which differs from that of an adjoining level by a factor of 10 - 100 (de Wit, 1969; Loomis <u>et al</u>, 1971). Thus 6-7 levels of organization can be identified with relaxation times ranging from minutes (intracellular molecular action) to centuries (a climax forest community). It is at present impossible to link more than two or three such levels in a single integrated study, and the experimentalist (and reviewer) must of necessity limit his activities to two, or at most three, adjoining levels of organization. This review will restrict its scope to the level of the experiment performed, and one level of organization below this (hour by hour plant and canopy responses).

1.2 ASPECTS OF GROWTH AND DEVELOPMENT

1.2.1 The Terms Defined

Within the orderly but complex progression undergone by a plant from the embryo to maturity at least two processes may be recognized (Bloch, 1961).

(i) Growth, which may embrace changes in magnitude of any measurable characteristic with time, but is normally regarded as the change in dry weight of the plant or plant part with time.

(ii) Development, or changes in form arising from differential growth along the axes of the plant, or between plant parts.

Although the processes are correlated (Bloch, 1961) both occur at rates which vary within and between the processes according to genotype and environment.

1.2.2 Quantitative Description and Analysis of Growth and Development

There have been many attempts to formulate specific laws of growth in higher organisms, but developmental variability has rendered these largely sterile (Whaley, 1961). Rather than using mathematical formulae to predict growth, use can be made of formulae to describe growth empirically as a continuous function of time.

In general, growth in higher organisms in total and in part follows an assymetrical sigmoid curve with time (Milthorpe, 1963). An early phase of exponential growth is followed by a phase of linear increase in which growth is restrained by differentiation or a shortage of some growth factor. As maturity and senescence approach, growth rate declines, and total weight tends towards an asymptote with time, or may even decrease as a result of respiration and shattering losses from the organism (Whaley, 1961).

Mathematical functions describing part or all of the growth curve have

been reviewed in detail elsewhere (e.g. Richards, 1959; 1969; Whaley, 1961; Gandar, 1970).

Briefly they fall into two groups (Richards, 1969).

(i) Those in which growth forms no asymptote as time increases indefinitely (e.g. polynomial in time, time power, exponential).

(ii) Those in which growth tends to an asymptote as time increases indefinitely (e.g. monomolecular, logistic and Gompertz).

Increasing the number of constants within any single family of curves improves the flexibility or the 'descriptive power' of the curve. Thus it is possible for an ordinary polynomial function with N constants to pass through every observation where N observations of growth are spaced in time. This implies that each constant is a summation of many complex physiological variables (Richards, 1969).

When a function with less than N coefficients is fitted to the data, some smoothing of data normally occurs, a characteristic that is at once useful and dangerous. Small variations in data may be spurious to the study being performed and therefore usefully eliminated, while the finer physiologically significant variations may be overlooked (Vernon and Allison, 1963; Buttery, 1969).

While ordinary polynomials are widely used descriptively, they exhibit atypical biological responses in that they are not bound to any final size (no asymptote formed), and the quadratic form is symmetrical about its stationary point. Nelder (1966) points out that inverse polynomials meet these two objections without losing the descriptive power of ordinary polynomials.

The fitting of mathematical expressions by least squares regression techniques to plant weight and area data as a method of simply obtaining 'growth analysis' parameters is becoming more popular. This method allows improved precision in estimating parameters at any one point in growth, as compared with the historical methods based on means and variances of each observation point (Buttery, 1969). Rate parameters may be obtained by differentiation of the derived continuous function.

Ordinary polynomials are frequently used (Vernon and Allison, 1963; Milthorpe, 1963; Hughes and Freeman, 1967; Koller <u>et al</u>, 1970; Koller, 1971), but other types of expression may describe the data more accurately (Hammond and Kirkham, 1949; Williams, 1964).

1.2.3 Growth Analysis and its Parameters

'Growth Analysis' is the term given to the technique of investigating growth through the use of growth parameters described below. Based on the assumption that dry weight changes are an adequate measure of net photosynthesis (Briggs <u>et al</u>, 1920) it aims to elucidate factors affecting dry matter yield. Analysis is frequently confined to the above-ground portion of the crop.

The following symbols will be used in discussion :-

- W = total dry weight (or total above-ground dry weight);
- LW = dry weight of leaves per plant;
- A = total leaf area per plant;
- RHO = the number of plants per unit area.

Growth analysis parameters can be divided into those which describe plant shape (morphological) and those which describe rates of change instantaneously and over a period (growth processes) (Evans and Hughes, 1961). We will now consider in summary some of these parameters and their interrelationships. The subject has been reviewed in detail elsewhere (Watson, 1952; 1968; Evans and Hughes, 1961; 1962; Blackman, 1961; Richards, 1969).

Morphological Parameters

(i) Specific Leaf Area (SLA) is the ratio of leaf area to leaf weight.

$$SLA = \frac{A}{Lw}$$

Specific leaf area shows a steady ontogenetic decrease in most plants (Eddowes, 1969 b; Koller <u>et al</u>, 1970), but at any point in ontogeny it appears to reflect the level of available photosynthate (de Wit <u>et al</u>, 1969). SLA decreases as light intensity incident on the leaf increases and leaf temperature decreases (Blackman and Wilson, 1951; Blackman, 1956; Blackman, 1961; Hughes and Evans, 1962), the effect being greater upon leaf thickness than leaf area (Friend, 1966).

(ii) <u>Leaf Weight Ratio</u> (LWR) is the ratio of leaf dry weight to total dry weight.

$$LWR = \frac{Lw}{W}$$

LWR reaches a peak 3 - 4 weeks after sowing in soyabeans, maize and wheat (Koller <u>et al</u>, 1970; van Eijnatten, 1963; Friend, 1966) and then steadily declines as growth of non-leaf structures occurs. LWR generally seems little affected by environmental stimuli except photoperiod (Evans and Hughes, 1961), though this is species dependent (Blackman, 1961).

(iii) <u>Leaf Area Ratio</u> (LAR) is the ratio of total leaf area to total dry weight.

$$LAR = \frac{A}{W}$$

A further relationship may be recognized:-

 $LAR = SLA \cdot LWR$

LAR reaches a peak 3 - 4 weeks after sowing and declines at a similar but greater rate than LWR as the plant matures (Watson and Baptiste, 1938; van Eijnatten, 1963; Friend, 1966; Hughes and Freeman, 1967; Koller <u>et al</u>, 1970). A reduction in LAR in increasing light reflects reductions in both SLW and LWR components (Blackman, Black and Kemp, 1955; Blackman, 1961; Warren Wilson, 1967).

(iv) Leaf Area Index (LAI) is the ratio of leaf area (with or without leaf sheaths and green supporting tissue) to ground area covered (Matson, 1947 a).

LAI =
$$A$$
 . RHO/Area

This gives a measure of size of the photosynthetic system (Gregory, 1926). Orientation, and vertical and horizontal distributions of leaf area index within the canopy determine the degree of internal canopy shading (Loomis and Williams, 1969). LAI is greatly affected by mineral nutrient supply (Watson, 1963 a; 1963 b). Watson (1952; 1968) regards variation in the development of LAI, and the time course of leaf area display over the summer in temperate climates as two important causes of yield variation in field crop...

(v) <u>Harvest Index</u> (HI) is the ratio of economic yield to biological yield (Donald, 1962).

HI = dry weight of grain / W.

This ratio is highly variable between and within a species (Eryant and Blaser, 1968; Brown <u>et al</u>, 1970; Singh and Stoskopf, 1971). It can be altered genetically without affecting biological yield, and is affected by thermoperiod, photoperiod (van Dobben, 1962), and cultural practices (Donald, 1962).

Growth Process Parameters

(i) <u>Unit Leaf Rate</u> (E) is the rate of dry matter increase per unit leaf area

 $E = \frac{dW}{dt} \cdot \frac{1}{A}$

This term (Briggs <u>et al</u>, 1920) is preferred to the equivalent alternative net assimilation rate (Gregory, 1917; 1926) as E is a net term covering energy losses in water and nutrient absorption and transport, as well as 'net assimilation' (gross photosynthesis - (dark + photorespiration)) (Evans and Hughes, 1961; Loomis <u>et al</u>, 1971).

E may be regarded as some measure of the efficiency of the photo synthetic system (Gregory, 1926; Watson, 1968). Leaf area is used here as the basis

for computing E, though leaf weight and other less accessible bases have been suggested (Williams, 1946; Brougham, 1960).

When E is computed by means other than from the continuous curves of weight and area with time, assumptions concerning the relationship between A and W between two sample points may reduce the accuracy of the optimate of E (Williams, 1946; Whitehead and Myerscough, 1962; Williams et al, 1965 b; Radford, 1967).

There is an extensive literature on factors affecting E. It is not solely determined by extrinsic plant factors as was formerly thought (Gregory, 1926; Heath and Gregory, 1938) and has been found to vary more between than within a species (Matson, 1947 a). Elexhibits an ontogenetic decrease (Thorne, 1960) which may be attributable to an increasing proportion of respiring tissue, and to decreasing photosynthetic capacity (Matsor <u>start</u>, 1966).

Physiological interpretation of the effects of external factors of E is difficult because of the complex nature of E (Richards, 10(9). I has been found to increase with increasing light intensity (Blackman and Fileon, 1951; Moss, 1965), with increasing temperature to some optimum termentare (Watson, 1952; 1963 b), and with increasing carbon dioxide concentrations (Wittwer, 1966; Hughes and Freeman, 1967), but is affected by plane autrient status only slightly except in acute deficiency states (Matson, 1947 b; 1963 c), 1963 b). There is some evidence that E may be controlled by metabolic sink demand (see Neales and Incoll, 1968). As a means of understanding production processes, measurement of E is regarded hopefully by some (Jatcon, 1952; 1968; Richards, 1969) and disparagingly by others (Loomis <u>et al</u>, 1971).

Unit leaf rate of a summer annual crop may be expected to peak at the time of greatest insolation (Warren Wilson, 1967), decline as mutual shading within the canopy intensifies, and it may reach a secondary peak corresponding with sink demand in some crops (e.g. potato, wheat, soyabeans) (Milthorpe, 1963; Stoy, 1965; Koller <u>et al</u>, 1970; Gandar, 1970), though apparently not in others (e.g. maize) (van Eijnatten, 1963; Vernon and Allison, 1963; Allison and Watson, 1966).

(ii) <u>Relative Growth Rate</u> (RGR) is the rate of dry weight change relative to total dry weight.

$$RGR = \frac{1}{W} \cdot \frac{dW}{dt}$$

Components of RGR may be recognized (Blackman, 1919; West et al, 1920)

 $RGR = E \cdot LAR$

Constant RGR with time implies exponential growth in which all material formed acts as 'growing capital'. Because differentiation occurs, this situation does not apply beyond the seedling stage when LAR is constant (Whaley, 1961). A better measure of 'growing capital' is leaf area, as in E, which is one of the components of RGR. However RGR does give an indication of the time taken for an organism to double its size (Williams, 1964), and is a useful concept in this respect.

Since LAR is more variable than E throughout the life of the plant, RGR might be expected to decline at a slightly steeper rate than LAR, as the slow ontogenetic decrease in E is felt (Richards, 1969). This has been confirmed experimentally (Briggs <u>et al</u>, 1920; Kidd <u>et al</u>, 1920; Williams, 1946; 1964; van Eijnatten, 1963; Koller <u>et al</u>, 1970).

The relative leaf area growth rate (RLGR) may be derived similarly. This parameter declines more rapidly with time than RGR, as leaf area growth normally ceases before dry matter accumulation is complete (Buttery, 1969).

(iii) <u>Crop Growth Rate</u> (CGR) is the rate of dry weight change per unit land area

$$CGR = \frac{dM}{dt}$$
 . RHO

Components of CGR may be recognized (Watson, 1958)

$$CGR = E \cdot LAI$$

The interrelationship of CGR, E, and LAI has been widely studied (Watson, 1952; 1956; Saeki, 1960; de Wit, 1965; Loomis <u>et al</u>, 1971). E is always small when CGR is large (Loomis and Williams, 1969).

Two kinds of relationships have been observed (Brown and Blaser, 1968). In one CGR forms a well defined maximum at an optimum LAI value, and E declines linearly as LAI is increased (Watson, 1958; Rees, 1963). In the second, CGR tends to an asymptote and E declines at a decreasing rate as LAI is increased (Brougham, 1956; Williams <u>et al</u>, 1965 b; 1968; McCree and Troughton, 1966 b; Buttery, 1970). The interrelationship of CGR, E and LAI is considered by many to be the most important of any among growth analysis parameters with respect to productivity (Watson, 1952; 1968; Loomis <u>et al</u>, 1971).

(iv) <u>Leaf Area Duration</u> (LAD) is the integral of LAI between two time limits, t₁ and t₂. It takes account of the magnitude and longevity of leaf area, and has the dimension of time (Watson, 1947 a).

$$LAD = \int_{t}^{t} LAI \cdot dt$$

Watson (1956), Thorne (1966) and Welbank <u>et al</u> (1966) claim a good relationship between LAD after flowering and final grain yield in cereals. The integral of percent cover may be a more definitive index (Loomis and Williams, 1969).

The grain leaf ratio, G, or the ratio of grain yield to LAD, which is a measure of the contribution to grain weight by unit leaf area index, appears to be fairly constant for any one variety in any one season (Watson et al, 1963; Thorne, 1966; Kirby, 1967; Gandar, 1970).

1.3 <u>SOME FACTORS INFLUENCING THE MAGNITUDE AND PATTERN OF PHOTOSYNTHATE</u> DISTRIBUTION IN THE MAIZE PLANT

The maize plant differs in many ways from small grain cereals. Lyte's description (<u>New Herbal</u>, 1619) quoted by Bonnett (1954) illustrates some of these differences.

"This corne is a marvelous strange plante....nothing resembling any other kind of grayne; for it bringeth forth his seede cleane contrarie from the place whereas the flowers grow, which is agaynst the nature and kindes of all other plants, which bring forth there fruit there, whereas they have borne their flower at the highest of the stalks grow idel and barren eares, which bring forth nothing but flowers or blossome The fruitful eares do grow, upon the sides of the stems amongst the leaves, which eares be great and thick, and covered with many leaves so that one cannot see the eares.... The grayne or seed which groweth in the eares is.... orderly about the eares, in nine or ten ranges or rows."

Growth and grain production of the maize plant, when well supplied with water and inorganic nutrients, depends primarily on

- (i) Production of photosynthate in the leaves, leaf sheaths and husks.
- (ii) The transport of synthesized organic compounds from the leaves and their distribution to metabolic sinks according to a pattern that varies with plant age. Photosynthate may be temporarily stored and remobilized at some later period.
- (iii) The irreversible accumulation of photosynthate as nonosmotically active starch in the grain (Beevers, 1969).

Factors affecting the source (leaves), distribution, and temporary and permanent storage of photosynthate in maize as an individual plant and as a community will now be considered in detail.

1.3.1 The Development and Maintenance of Leaf Area in Maize

Leaves in the adult maize plant are arranged alternately in two ranks (distichous array) with one leaf to each node (Bonnett, 1960). Total photosynthetic area is made up of the components leaf and sheath number and size, on the main stem, and on tillers when present. Husks present after emergence of the prophyll contribute little to total photosynthetic area when fully grown (c 2%) (Allison and Watson, 1966; Pendleton and Hammond, 1969).

(i) Initiation of Leaves and Leaf Number

Four to six leaf initials are formed in the maize embryo prior to seed dormancy, irrespective of variety (Kiesselbach, 1949; Brawn, 1968). Upon germination, growth of already formed leaves continues and more leaf initials are formed at the stem apex. Rate of formation of initials has been found to increase exponentially with time from onset of germination in one variety (Abbe and Phinney, 1951) but linearly in others (Stein, 1955). Plastochron length (time between initiation of successive leaves) at 20C averages 1.6 - 2.3 days (Abbe and Phinney, 1951; Grobbelaar, 1962). The length of the plastochron in cereals decreases as temperature rises in the 10 - 20C range, and with increasing light intensity (Friend <u>et al</u> 1962; Friend, 1966).

The vegetative phase, and leaf initiation, are terminated when the stem apex begins to elongate prior to forming tassel branch initials (Kiesselbach, 1949). This phase has been found to be the most variable in duration of the three main developmental phases of the maize plant (vegetative, reproductive and seed phases) (Bonnett, 1960), and is usually 20 - 30 days in length in adapted commercial varieties. (Siemer <u>et al</u>, 1969). Its length is affected by:-

(a) Genotype: Most of the variation between varieties in time to maturity under standard conditions is attributable to differences in the length of the vegetative period (Leng, 1951). Late maturing varieties will therefore have more leaves, more internodes, and are bigger plants than earlier maturing varieties (Kiesselbach, 1950; Eik and Hanway, 1965; Brawn, 1968). Leaf number has been used to characterize maturity classes in maize, and varies from 8 (Brawn, 1968) to 26 (Chase and Nanda, 1967) but is normally about 16 (Hanway, 1963).

(b) Photoperiod and Temperature: Maize is classified as a short day plant (i.e. short day lengths hasten flowering), though considerable variation in photoperiod sensitivity exists (Francis <u>et al</u>, 1969). Plants exposed to long photoperiods have a longer vegetative period, produce more leaves, are larger, and have delayed flowering in comparison to plants exposed to short photoperiods (under 10 hours) (Sirohi <u>et al</u>, 1966; Moss and Heslop-Harrison, 1968). This effect can be reproduced by growing the same genotype at high and low latitudes, the longer days of high latitudes

increasing leaf numbers and delaying maturity (Kiesselbach, 1950). Delaying planting date in a temperate locality, where day kongth is . increasing and temperatures rising reduces the length of the vegetative period significantly but increases leaf number slightly (Leng, 1951; Eik and Hanway, 1965; Bunting, 1968): Increased temperature accelerates growth and development, and the longer photoperiod increases leaf number. Seasonal variation in temperature profoundly affects the length of the time to flowering (Snaw and Thom, 1951 a), influencing leaf number to a lesser degree.

Low temperatures will reduce the number of leaves initiated (Duncan and Hesketh, 1968). Hesketh <u>et al</u> (1969) found that temperature and photoperiod changes affected late maturing varieties more than early maturing varieties.

(c) Cultural practices: Leaf number is reduced slightly as plant population increases, is increased by applications of starter fertilizer (Eik and Hanvay, 1965), and is reduced by severe water stress (Slavik, 1966; Slatyer, 1969).

(ii) The Growth of Maize Leaves and Leaf Sheatha

Although the plastochron length has been observed to decree to with time in maize, the phyllochron, or rate of leaf appearance is relatively constant, with new leaves appearing every 2 - 5 days (Grobbelaar, 1962; Bunting and Drennan, 1966). The growth of the maize leaf is described by Sharman (1942) and Kiesselbach (1949). The blade tip is the first part formed. The leaf meristem remains at the base of the leaf, and after the leaf blade and ligule have been formed, the meristem gives rise to the leaf sheath, which, as it grows, lifts the leaf blade out of the enclosing leaf wher1. Accompanying this is the extension of internodes by intercalary growth from meristems initiated early in leaf primordia development (Stein and Steffensen, 1959; Siemer <u>et al</u>, 1969). Internode lengths can be used to describe the stage of development of the plant (Hanway, 1970). Growth in the size of cells completes the growth in leaf width.

Successive leaves in maize are longer and broader than their prodecessors up to some point in time (Eik and Hanway, 1965) which may correspond with the beginning of floral initiation (Jewiss, 1966), following which length and breadth decline. Width differences in leaves are thought to mirror stem apex size at leaf initiation (Abbe <u>et al</u>, 1941). Leaves of late maturing varieties grow longer and wider than leaves from early maturing varieties (Eik and Hanway, 1965). The rate of growth of maize leaves is considered an important determinant of crop growth rate (Milthorpe, 1956), and is affected by genotype and environment:

(a) Genotype: Significant differences between varieties of maize in relative leaf growth rate (RLCR) have been measured under standard conditions (Duncan and Hesketh, 1968. Compare Muramoto <u>et al</u>, 1965 with cotton).

(b) Environment: Under conditions of adequate moisture an nutrients, temperature exerts an important influence on the rate of leaf gr th (Ragland <u>et al</u>, 1965). Duncan and Hesketh (1968) compared races of maize adapted to high and low altitude environments. Under controlled conditions, they found that mean RLGR increased from 0.09 at 150 to a peak of 0.27 at 330. Analysis revealed a significant race x temperature interaction. The RLGR of high altitude races was significantly hour at lower temperatures than that of low altitude races, and vice very for higher temperatures.

Changes in light intensity have less effect on leaf area than on leaf weight (Pendleton <u>et al</u>, 1966; 1967) (specific leaf area is affected as in Section 1.2.3). Increasing levels of shading over the vegetative period at first increase leaf area, then decrease it to the leaf area present under daylight illumination (at 40% daylight intensity). Further shading drastically reduces leaf area (Earley <u>et al</u>, 1967). Some of these effects may be mediated soon after leaf initiation (Milthorpe, 1957).

Generally, total leaf area continues to expand at a ranid rate until shortly before flowering, the area increasing thereafter at a very clow rate and reaching a poorly defined peak 1 - 2 weeks later. (Adelars and Milbourn, 1972 b). At this point, leaf sheaths comprise about 20% of the total photosynthetic area (van Eijnatten, 1963; Allison and Catson, 1966) but this figure is considerably less at early stages of development (Williams <u>et al.</u> 1965 b).

(iii) Tiller Production in Maize

Axillary buds in maize are initiated several plastochrons later than adjacent leaves (Sharman, 1942; Ledin, 1954). Those at lower nodes may give rise to tillers during the vegetative phase of growth. There is little published work on size, longevity, or leaf area of maize tillers, and inferences must be drawn from studies in cereals in which tillers contribute far more to total leaf area than they do in maize (Jewiss, 1966; Friend, 1966).

Factors favouring tillering in maize are:-

(a) A good supply of nutrients (particularly nitrogen and phosphorus) (Dungan <u>et al</u>, 1958; Langer, 1966), and water (Downey, 1971 a; b; 1972).

(b) A variety that tillers prolifically. There is considerable varietal variability in tillering capacity (e.g. Brawn, 1968; Adelana and Milbourn, 1972 a), some varieties not normally tillering at all (Duncan

and Hesketh, 1968).

(c) Thin spacing of plants (Downey, 1972). Tillers in maize may comprise 50% total dry weight where competition is not occurring (Rosenquist, 1941), and stand as tall as the main stem (Earley et al, 1971). Equidistant spacing favours tillering (Dungan, 1946; Kohnke and Miles, 1951) as does light enrichment (Pendleton et al, 1967). In other cereals (for example wheat) increasing light intensity promotes a greater degree of tillering and increasing temperature decreases tillering (Friend, 1965).

Tillers initiate leaves, tassels and ears in the same manner as the main stem (Kiesselbach, 1949) though there is a marked tendency for sex reversal in tillers of some varieties. Vascular connections between tiller and parent plant are maintained (Dungan, 1931) but tiller mortality is high during the period of ear formation, particularly where tillers are small in relation to the parent plant (Montgomery, 1909, quoted by Dungan <u>et al</u>, 1958; Adelana and Milbourn, 1972 a).

(iv) Leaf Area Duration in Maize

Leaf area duration can be considered from the viewpoint of leaf area index and leaf longevity (Section 1.2.3).

Experimental plantings at high densities have resulted in LAL values as great as 20 (Williams <u>et al</u>, 1965 a) but little is known of the longevity of such canopies. Plantings sown at commercial rates for grain normally have leaf area indices of 4 - 7 during grain filling (Allison, 1969; Pendleton <u>et al</u>, 1968; Adelana and Milbourn, 1972 b).

The vertical profile of LAI varies with density of planting (Eik and Hanway, 1965). At LAI of 5, leaf area distribution with height was found to be uniform over the middle metre of a maize canopy almost three metres in depth, falling away to zero on either side of this central zone (Lemon, 1967; Lemon and Wright, 1969). Crowding plants together alters this profile drastically. The bulk of the leaf area becomes noticeably concentrated in a layer near the top of the canopy at LAI values of greater than 10 (Williams <u>et al</u>, 1965 a).

The time course of leaf area index differs markedly from that of other cereals (Bunting and Drennan, 1966). At commercial spacings the rise in LAI is more gradual with time and a relatively high leaf area index is maintained for a longer time (Allison, 1964). At these rates of planting (40-80 K plants per ha) a LAI of greater than 4 is frequently maintained for 10 weeks, 8 of which may be after flowering (Williams <u>et al</u>, 1968; Allison, 1969). Since the bulk of dry matter in maize grain is accumulated after flowering (Bair, 1942; Miller, 1943; Sayre, 1948; Hanway, 1962; 1963; van Eijnatten, 1963), it appears that leaf longevity may play an important part in yield determination. The proportion of total leaf area made up by leaf sheaths, particularly just before maturity, is not as high as it is in the small grain cereals (Thorne, 1959; Allison, 1964). However the contribution to yield by sheaths on a unit photosynthetic area basis relative to that of the laminae may be greater in maise (Sharman, 1942; Allison and Watson, 1966; Pendleton <u>et al</u>, 1968) then in the small grained cereals (Thorne, 1959). Mitchell (1970) states that maise leaf sheaths contribute 6-10% of total photosynthate in mature plant.

There is little literature on factors affecting leaf longevity in maize. Where water and nutrients are not limiting, maize leaf longevity is affected by genotype (Eik and Hanway, 1965), and is reduced by high temperatures (Andrew <u>et al</u>, 1956).

Reduced light levels shorten the life of leaves in other species (Broughan, 1958 b), and long photoperiods can considerably delay leaf senescence in short-day plants (Clmsted, 1951; Krizek <u>et al</u>, 1966). In maize low light intensities induced by interplant competition reduce leaf longevity, though there may be an interaction with nutrient and water stresses involved. Thus as planting density increases there is a progressively increasing decline in leaf area from its peak value in the course of the season, caused by the senescence of lower leaves (Villians <u>et al</u> 1956; Allison, 1965). Extremely high levels of photosynthate in the lower caused by induced barrenness in maize appear to hasten leaf senescence (Allison and Veinmann, 1970) while levels intermediate between very ligh and those found in a normal fertile plant may delay senescence (Nosh, 1965).

Under good growing conditions leaf area declines to rewiretely 50% of its peak value 7 weeks after flowering (Iowa, U.S.). Comparable figures in Rhodesia are 8, 9, and 8 weeks, in Southern England 8-9 wools, and probably some weeks longer than this under the cooler humid conditions of the Netherlands, where Sibma lists the time of increasing crop growth rate from estimated complete crop cover as 12.5 weeks (Eik and Manway, 1965; Vernon and Allison, 1963; Allison, 1969; Allison and Weinmann, 1970; Adelana and Milbourn, 1972 b; Andrew et al, 1956; Sibma, 1968 respectively).

Grain yield has been found to be linearly related to LAI at silking up to LAI of 3.3, and to LAD after silking up to 155 days (Eik and Hanway, 1966). The time taken for final grain weight to be obtained at the linear rate of increase in grain dry weight observed early in kernel growth appears to bear a good relationship to final grain yield (Daynard <u>et al</u>, 1971). This time is probably closely correlated to leaf area duration. The grain-leaf ratio, G, has been found to vary considerably between maize varieties (Adelana and Milbourn, 1972 b).

1.3.2 Some Factors Determining Crop Growth Rate in Maize

As previously stated (Section 1.2.3), the general relationship between crop growth rate (CGR), leaf area index (LAI) and unit leaf rate (E) within a canopy is

$CGR = LAI \cdot E$

This relationship may be investigated directly by measuring the change in dry weight and leaf area with time between two (or more) successive harvests, usually a week apart (e.g. Buttery, 1970). Whether CGR is calculated from means and variances from these harvests or from regressions of dry weight and leaf area on time, averaging of CGR with time will occur, which obliterates short term effects of environment on CGR.

To improve the sensitivity of the correlation between environmental parameters and CGR, some instantaneous measure of crop growth rate is required. The development of gas analysis techniques, particularly infra red gas analysis (IRGA), has allowed growth to be measured almost instantaneously from changes in CO₂ concentration in a stream of air passed over the plant part, the whole plant, or the plant canopy (Moss, 1965).

Further elucidation of the plant response with age and to its environment has been made possible through measuring the photosynthetic response of leaves from different positions in the plant canopy, over a range of light intensity, water stress or nutrient status (e.g. Hesketh and Moss 1963; Duncan and Hesketh, 1968). Concomitant measuresents of the distribution of radiation available for photosynthesis within a crop stand (e.g. Yao and Shaw, 1964) allow estimation of crop response under given conditions (e.g. Moss, 1965), and provide basic information for generalized simulation studies of light and energy distribution, and crop production (e.g. Ideo and Baker, 1967; Duncan et al 1967; de Wit, 1965; de Wit et al, 1969). Predictions from simulated studies may be verified from observations in the field using assimilation chambers (e.g. Musgrave and Moss, 1961) or by measuring CO, flux in the field by analysis of turbulent transfer within and above the crop (e.g. Lemon and Wright, 1969). The latter method has the advantage of not interfering with the crop environment while measurements are being taken. Over longer periods of time simulated studies may be checked against growth analysis results (e.g. de Wit, 1969). Estimates of overall efficiency in converting absorbed radiation to products of growth indicate how far production falls below that potentially possible (Nichiporovich, 1956).

The results of studies using some of the approaches outlined above will now be considered.

(i) Net Photosynthetic Rates of Maize Leaves

Investigations of the biochemical pathways involved in carbon fixation have revealed two distinct pathways among common agricultural plants (Hatch

and Slack, 1970). Some characteristics of plants exhibiting each pathway have been reviewed by Hesketh and Baker (1967), Laetsch (1968), Downton and Tregunna (1968), Downton <u>et al</u> (1969), Stoy (1969), Zelitch (1969) and Loomis <u>et al</u> (1971), and will be briefly summarized here.

In one group ('Calvin Cycle' or C_3 plants) a 3-carbon molecule is formed as the first stable product of CO_2 assimilation. C_3 plants are frequently plants of temperate origin such as wheat, barley, and oats, and are characterized by relatively low rates of net photosynthesis on a unit leaf area basis (Pnet) in bright sunlight (up to 35 mg CO_2 . dm^{-2} . hr^{-1}), and a temperature optimum for photosynthesis of 20-25C. An inability to photosynthesize at CO_2 concentrations of less than 50 ppm CO_2 , and high rates of decarboxylation in the light (photorespiration) are also typical of C_3 plants.

The second pathway, recently discovered, is the C₄ dicarboxylic acid pathway, in which a 4-carbon molecule is the first compound formed in carbon assimilation. Plants exhibiting this type of pathway have in most cases originated from tropical areas (e.g. maize, sugar cane, sorghum, millet) and show high rates of Pnet in bright sunlight (50-60 mg CO₂.dm⁻².hr⁻¹), and a temperature optimum for photosynthesis of 30-35C. Leaf anatomy differs from that of C₃ plants and appears to favour rapid transport of photosynthate out of the leaf. Photorespiration occurs at a very low rate in most \dot{C}_4 species, and photosynthesis will continue until the CO₂ concentration in the air surrounding the leaf reaches 5 ppm.

The net effect is that the efficiency of fixation of incoming solar energy in the stable chemical bonds of the photosynthate falls much less rapidly with increasing light intensity in C_4 than C_5 plants at ambient air temperatures of 25-310 (Hesketh and Moss, 1963).

Illuminating maize leaves from either above or below with similar light intensities produces the same photosynthetic response. This is a consequence of a uniform distribution of chloroplasts between upper and lower leaf surfaces, a characteristic of monocotyledons not shared by dicotyledons.

The photosynthetic response of individual maize leaves to increasing light intensity conforms in shape to a rectangular hyperbola (Hesketh and Musgrave, 1962; Hesketh and Moss, 1963) of the form

 $Pnet = \frac{Pmax I}{I + K} - R \qquad (Duncan et al, 1967)$

where Pmax is the asymptotic rate of photosynthesis and is not normally reached at full daylight intensity; I is the light intensity; R is the dark respiration; K is a constant equal to I at Pmax. (All quantities are expressed on a unit leaf area basis). The net photosynthetic rate of maize leaves under conditions of adequate nutrition falls only slowly with age. A significant negative correlation between Pnet at the rapid grain filling stage and time to flowering was noted by Heichel and Musgrave (1969), a result which they attributed to ageing and weathering of leaves. Pmax and K therefore probably do not vary much with increasing depth within the maize canopy (Hesketh and Moss, 1963). Dark respiration rate has been observed to fall in shaded leaves when compared with recently illuminated leaves, as in other species (e.g. McCree and Troughton, 1966 a). The Duncan canopy photosynthesis model incorporates one light response curve for sunlit canopy leaves, and another for diffusely illuminated (shaded) leaves (Duncan et al, 1967). This is consistent with the observation that maize has no well defined peak in crop growth rate as leaf area index increases (Williams et al, 1965 ъ).

Respiration losses from a plant appear to have two components: a component coupled with growth, and proportional to photosynthesis, P, and a component proportional to total plant weight, W, related to the maintenance of non-growing plant material (McCree, 1969).

$$\mathbf{R} = \mathbf{K}_{1}\mathbf{P} + \mathbf{K}_{2}\mathbf{W}$$

Simulation studies with maize indicate that values of K_1 and K_2 are about 0.33 and 0.08 respectively (de Wit et al, 1969). As the plant grows, the ratio of R/W falls steadily. This picture of respiration in plants is more realistic than considering it as 0.2 - 0.4 of photosynthesis, as has been done in the past (e.g. Loomis and Williams, 1963; Duncan et al, 1967; Loomis et al, 1971). Because P is temperature dependent, K_1 probably will not alter substantially with temperature changes. K_2 is definitely temperature dependent, and will increase rapidly with temperature, reducing assimilate available for growth (e.g. Peters et al, 1971). Differences in whole plant respiration losses and the R/W ratio among varieties at comparable growth stages have been observed (Wu, 1971). Such an important loss of gross photosýnthate deserves a far more detailed examination than it has received to date.

Variation in Pnet rate in individual maize leaves well supplied with nutrients and water, and at a steady light intensity has been observed. A number of workers have reported variations in Pnet rate of 50% among lines of maize (Sheridan and McKee, 1967; Moss, 1969). Differences as great as 200% (25-90 mg CO₂' dm⁻². hr⁻¹) were noted by Heichel and Musgrave (1969), but this range could not be obtained in subsequent retesting (Moss, 1969), and may have been due to variations in stomatal resistance under field conditions (Loomis <u>et al</u>, 1971). When 12 lines of maize adapted to different altitudes were grown at 7 different temperatures (15-36C) under controlled conditions the range of Pnet rate averaged 27% over all temperatures (Duncan and Hesketh, 1968). Differences between the lines were highest (50, 30%) at the lowest and highest growth room temperatures respectively. Mean Pnet rate showed a growth room temperature optimum of 34C (probably 38C leaf temperature, a figure which agrees with that obtained by Winter and Pendleton (1970), in the field, and somewhat higher than the optimum air or leaf temperature for Pnet of 30 C given by Idso <u>et al</u> (1966)). Duncan and Hesketh also reported a significant race x temperature interaction, the high altitude races having the highest Pnet rate at low temperatures and the low altitude races the highest at high temperatures.

Increased carbon dioxide concentrations cause the light response curve to become more linear. Increases of 50% and 100% in Pnet rate were obtained when the CO_2 concentration was raised from 223 ppm to 325 ppm and 435 ppm respectively (Hesketh and Moss, 1963).

The hypothesis that the level of assimilate concentration in the leaf controls leaf photosynthetic rate is an attractive one, and widely held, though no direct evidence of a causal relationship has yet been produced. The state of the hypothesis has been reviewed in detail (Neales and Incoll, 1968). The position with regard to maize is by no means clear. Then 50% of the leaf laminae from maize were removed the dry matter increase per unit leaf area increased by 56%, suggesting that under normal circumstances maize leaves operate at well below their potential photosynthetic rate (Kiesselbach, 1948). In a comparable trial, Allison and Watson (1966) were able to demonstrate a non-significant increase in unit leaf rate (E) for two weeks following 50% defoliation but not after this period. Pnet may well have increased but the decrease in leaf area ratio may have masked this in the computation of E.

Removal of developing ears, or prevention of fertilization and hence grain formation are effective in reducing metabolic sink size in the maize plant. Kiesselbach (1948) reported that removal of ears at silking decreased total plant weight by 17%, but increased the yield of stover and roots by 59% and 18% respectively compared with untreated plants. Allison and Watson (1966) failed to obtain significantly different E values for normal and unfertilized plants over a four week period after silking. The removal of second ears was effective in reducing the mobilization of stem reserves during grain filling (Adelana and Milbourn, 1972 b). Direct measurements of Pnet give a more direct assessment of the effect of sink removal. Verduin and Loomis (1943) noted a build up in leaf sugar levels but no decrease in Pnet rate in barren plants compared with intact plants. Their method of gas analysis was highly inaccurate however. Moss (1962) using IRGA techniques and a sealed plastic field assimilation chamber (see Musgrave and Moss, 1961) containing 10 plants found that midday Pnet rates of barren maize plants fell steadily to 55% of that of normal plants one month after silking. Considerable accumulation of sugar in the stems of barren plants was noted. There appeared to be varietal variation in the response of assimilation to barrenness.

A recent hypothesis reviewed by Stoy (1969) suggests that photosynthesis is controlled by hormones produced by the sink. Maize plants grown at densities which are just below those that will naturally induce barrenness normally have a sink capacity that greatly exceeds source capacity, and it is unlikely that feed back inhibition of photosynthesis significantly reduces productivity of maize stands (Loomis <u>et al</u>, 1971).

(ii) Field Measurements of Canopy Net Photosynthetic Rates

Portable, sealed, air conditioned field chambers equipped with IRGA instruments, of the type developed by Musgrave and Moss (1961) have been used to measure canopy photosynthesis over a small enclosed area (4 m²). Moss et al, (1961) and Baker and Musgrave (1964 a) were able up show the striking effect of changing light intensity upon the rate of assimilation of a stand of maize enclosed in such a chamber. 90% of the variation in assimilation rate could be accounted for by variation in insolation. (Moss et al, 1961) Assimilation at noon on a clear day in a mature crop planted at 72000/ha was 18 mg CO2.dm⁻².hr⁻¹. During four days of heavy overcast weather, the net assimilation of carbon became negative. Using a similar chamber Baker and Musgrave (1964 b) were able to demonstrate a 40-50% drop in assimilation rate, from 19 mg CO_2 .dm. $^{-2}hr^{-1}$ on a clear day at noon as a result of low-level moisture stress, even though signs of wilting were barely visible. Moss et al (1961) observed a 20% decline in assimilation rate under similar circumstances, but with a smaller stress. Increasing CO2 concentration from 270 ppm to 510 ppm within the chamber increased the rate of assimilation by 20% from 25 mg CO2. dm. -2 hr -1 in 60% full sunlight. This parallells the 20% increase in unit leaf rate (which includes negative assimilation at night) observed by Ford and Thorne (1967) when the CO2 concentration in growth chambers in which maize was grown was raised from 300 ppm to 1000 .ppm.

The aerodynamic methods outlined by Lemon (1960) and Lemon and Wright . (1969) have the advantage of not interfering with the crop environment in

any way, but include an unknown CO2 contribution from the soil, which is probably not large compared with rates of CO2 assimilation under good conditions. The methods depend upon a well developed wind profile above the crop, a moderate, steady windspeed, and a homogeneous level crop upwind. Measurements using these methods have revealed a possible coupling between the wind speed within and above the canopy and CO2 assimilation, inder conditions of high intensity light and low wind speed (Wright and Lemon, 1966). It appears that under otherwise ideal growing conditions, a dense muize crop in a calm atmosphere may only assimilate at half the rate it attains under windy conditions (Lemon, 1963). Uchijima (1969) reports that under calm sunny conditions CO $_{2}$ concentration in a dense maize stand may only be 70%of normal, and under windy conditions 90% of normal. Short term 30, fluctuations (0.25-4 cycles / minute) originating from sources and sinks of CO, within the live maize crop have been detected by the aerodynamic method (Lemon et al, 1969). Photosynthetic rates for canopies measured by this method agree well with those obtained by the field chamber method, and a rate of 43.2 mg CO2.dm. -2hr -1 has been obtained on a clear afternoon is a stand with a LAI of 2.5 (Lemon, 1960). This method has proved useful in detecting sources and sinks of CO, within the canopy (Wright and Lemon, 1966). Data obtained emphasizes the importance of the upper leaves of the $\mathtt{cano}_{\mathrm{ev}}$ in CO, assimilation, particularly at low sun elevation angles; in a stand planted in 76 cm rows at 64000/ha, CO2 concentration in the air within the canopy fell from 358 ppm at 2000 hrs to 265 ppm at noon under conditions of high CO2 assimilation.

Measurements such as those above indicate the short term responses of the crop to the environment, and should bear a much better relationship to crop growth rates than the Pnet rate of isolated maize leaves.

(iii) Light Interception by the Maize Canopy and Crop Production

Observations on the vertical distribution of LAI and on the intensity of light at different depths within the canopy have confirmed that light attenuation in the maize canopy, like that in many other plant canopies (Brown and Blaser, 1969) conforms reasonably to the Bouguer-Lambert Law (Allen <u>et al</u>, 1964; Duncan <u>et al</u>, 1967; Loomis <u>et al</u>, 1968):

where I and Io are light fluxes to horizontal receivers at points within and above the canopy; e is the base of natural logarithms; L is the leaf area index above the point within the canopy; K is the extinction coefficient. K is small (0.3 - 0.5) in canopies where most of the leaves are vertical (Loomis et al, 1971).

 $\Gamma_1 \mathcal{J}$,

I = Io e^{-KL}

The Bouguer-Lambert Law implies that the maize canopy behaves as a homogeneous medium in which light is attenuated with depth. The relationship, as set out in /1/ is a simplification of the real situation, though it has proved useful in focussing interest on the relationship between light interception I /Io), and leaf area index. It has been variously modified to give a more realistic picture of the canopy (e.g. Saeki, 1960; Duncan <u>et al</u>, 1967).

Experimental investigations into the relationships among CGR, percentage interception of light, and LAI have indicated that $^{\rm I}/_{\rm C}$ is durvilinearly related to LAI, but linearly related to crop growth rate, particularly during the vegetative growth stage of crops including maize (e.g. soyabeans (Shibles and Weber, 1965); wheat (Puckridge and Donald, 1967); maize (Williams et al, 1965 b; Williams et al, 1968; Allison, 1969). The slope of the line relating $^{\rm I}/_{\rm IO}$ to CGR is dependent upon the relationship between the unit leaf rate and LAI which is itself dependent on the manner in which light is intercepted.

Variables which affect the amount of light intercepted and the manner in which it is intercepted, may be divided into those dependent on climatic factors, and those dependent on plant canopy characteristics.

(a) <u>Climatic Factors</u>: The intensity and nature of light reasoned by a horizontal surface is determined by :-

(1) The solar elevation angle B, which depends on latitude, season, and the time of day. At 40° S, B = 73° at noon in midsummer, and 27° at noon in midwinter.

(2) The solar intensity, Rs, which is affected by the pathlearth of the sun's rays as they pass through the atmosphere, and by the optical density of the atmosphere. On cloudy days Rs is only 20% of that on clear days (de Wit, 1965).

(3) The quantity of diffuse radiation, D. The ratio of D to total radiation varies with cloud cover (reaches 100% under heavy overcast conditions) and with time of day(highest when B is less than 30°), but is normally about 10% of total incident light (de Wit, 1965; Monteith, 1969).

Net radiation, or the radiation available at the earth-atmosphere interface, is the sum of all incoming and outgoing fluxes of shortwave radiation (300 - 3000 nm) and longwave radiation (3000 - 15000 nm). On sunny summer days net radiation intensity is about 1 cal.cm.⁻²min⁻¹. The shortwave component of net radiation contains photosynthetically active radiation (PAR), or radiation to which plants respond photosynthetically, in the 400 - 700 nm bandwidth. On average PAR comprises 60 - 80% of diffuse radiation, 45% of direct solar radiation, and 50% of total radiation (Monteith, 1969). If PAR or net radiation are to be measured accurately, the measuring sensor must respond only in the relevant band widths. This is particularly important when measuring PAR, as the crop acts as a highly selective filter the spectral balance of light altering as it passes through the conopy, which casts a green far-red shadow on the ground (Scott <u>et al</u>, 1968).

(b) <u>Plant Factors</u>: Leaf area index is closely related to the interception of PAR over a range of LAI values. Interception by maize at high plant densities reaches 95% at LAI values of 4.7 to 9 (Williams <u>et al</u>, 965 a; 1968; Monteith, 1969 from <u>Allen et al</u>, 1964 figures). Tooming (1559) reports that 1-2% incident PAR was transmitted to the ground by a maize stand with an LAI value of 6-7. Interception at high densities (215000 -700,000/ha) occurs largely in the top foot of the canopy (Williams <u>et al</u>, 1965 a), and Tooming (1967) states that 49-67% of incident PAR is intercepted by the first LAI unit it encounters, the range indicating a dependence on sun elevation, leaf angle, and planting rectangularity (ratio of interrow to intrarow spacing).

For a more precise description of the manner in which light is absorbed within the maize canopy, further analysis of the canopy is required. Models which simulate light conditions within a canopy have helpe, investigators pinpoint factors which influence light distribution in the complex array of leaves and supporting structure that comprise a canopy. The recent Duncan model for simulating photosynthesis in plant communities (Duncan <u>et al</u>, 1967) is regarded by Locmis <u>et al</u> (1971) as being the most theoretically rigorous. Briefly this model is based upon considerations of direct and diffuse light, transmission, reflection and absorption, foliage angle, and leaf area of randomly arranged leaves in a number of horizontal layers within the canopy. The light intensity, I, at any one stratum in the canopy is:

I = Io exp (-L $/F'/F_$ a, B / sin B) /2/

where Io and L are as in equation $\boxed{17}$; F'/F is the ratio between the area of a leaf and the shadow it casts for a particular leaf angle a, and sun elevation, B. Direct and diffuse light are separately treated. This model has given good agreement when tested in the field with a maize canopy (Loomis <u>et al</u>, 1968). Some of its limitations will be mentioned as they are encountered below. By simply linking the computed light intensity and leaf area in each stratm with the appropriate hyperbolic response curve of photosynthesis to light, canopy productivity can be simulated with some degree of success (Duncan <u>et al</u>, 1967).

Some canopy factors affecting light absorption can now be enumerated:

(1) Spatial distribution of leaves; - the planting pattern of maize dominates the distribution of light and net radiation within the canopy for much of the life of the crop. Parallells may be drawn between the distribution of net radiation and PAR in crops, provided it is remembered that absorption, transmission and reflection characteristics of maize leaves for net radiation and PAR differ considerably (Yocum et al. 1964).

When maize was sown in 98 cm rows, at high (77000/ha) and low (39000/ha) populations, planting rate had little effect on the quantity of net radiation reaching the ground (Aubertin and Peters, 1962). 90% of the 0.9 cal. cm. $^{-2}$ min⁻¹ net radiation incident above the crop was absorbed by the soil. In 52 cm rows the soil absorbed 44-68% incident net radiation, going from high to low planting rates. Results similar to this have also been obtained by Tanner et al (1960), Denmead et al (1962), and Yao and Shaw (1964). On cloudy days when incident light is mainly diffuse, a greater proportion of incident net radiation reached the ground (Dennead et al, 1962). Placing a white plastic reflector on the ground between rows of a stand of 40,000 plants/ha increased yield 13%, and beneath 60,000 plants/ha increased yield 6% (Fendleton et al, 1966). Rows oriented N-S intercept more net radiation (and PAR) than rows oriented E-W (Yao and Shaw, 1964; Idso and Baker, 1967), and experimental evidence suggests that rows oriented N-S yield slightly higher than those oriented E-W (Loomis et al, 1971). The magnitude of the advantage of N-S rows would be proportional to row width.

Warren Wilson (1960), using inclined point quadrats, has examined the ratio of the variance of foliage contacts to their mean. A regular horizontal distribution of leaves produces a ratio of less than 1, a clumped distribution such as that found in row crops at least during early growth, a ratio of greater than 1, and a canopy composed of randomly distributed leaves a ratio of 1. The Duncan model assumes random distribution of leaves, an assumption which permits the use of the Poisson distribution to estimate the probability of penetration of rays of direct light, as in equation $\int 2 \int (\text{Loomis et al}, 1971)$. This limits the use of the model when maize is grown in rows with a rectangularity of greater than 1.

Vertical separation of leaves profoundly affects the pattern of PAR-rich skylight within the canopy. During the reproductive phase most plants including maize, seem to have evolved with a vertical distance between leaves equal to more than twice the leaf width (Loomis and Williams, 1969). Dwarf maize plants such as those used by Pendleton and Seif (1961) may have their productivity restricted by an abrupt extinction of diffuse light within the canopy. Normal maize plants have a foliage density of around $0.02 \text{ cm}^2/\text{cm}^3$ (Lemon, 1967) or about 10% that of a dense pasture.

(2) Leaf optical properties:- Reflection and transmission of PAR by maize leaves have been described by Lenon (1963), Allen <u>et al</u> (1964), Yocum <u>et al</u> (1964), Tooming (1967) and Scott <u>et al</u> (1968). PAR is absorbed most strongly (90%) in the blue and red regions of the spectrum, and less strongly in the green (70%). The figure used by the Duncan model for mean leaf reflectivity is 17%, similar to that obtained by Yocum <u>et al</u> (1964). The maize canopy as a whole reflects 6-10% incident PAR. Transmission of PAR by a maize leaf is 7% of the incident value. Transmission rises to 50% in the near infrared bandwidth (Yocum <u>et al</u>, 1964). The Duncan model uses a mean leaf transmission of 5% of incident PAR (Duncan <u>et al</u>, 1967).

(3) Light absorption by non-photosynthetis structures: All structures on the maize plant exposed to the light environment except silks and tassels are capable of photosynthesis. Following tassel emergence tassels at the top of the maize canopy shade the foliage below to a significant degree. Duncan, Williams and Loomis (1967) calculated that at a planting density of 17000 plants/ha canopy photosynthesis is reduced 4% through shading by tassels. At 99,000 plants/ha the reduction was 18.1%. Early detasseling experiments detected only small advantages in grain yield, probably because of low planting rates (c 25000/ha), but later trials have confirmed that at high planting densities shading from tassels significantly reduces yield (funter et al, 1970 a).

 (4) Azimuthal Orientation of the canopy:- Most maize varieties alow no preferred leaf orientation with respect to the sun, but some have been reported in which leaves are distributed with a greater frequency in the E-W direction than in a N-S direction (Ross and Nilson, 1967; Local and Williams, 1969).

(5) Sunflecking and leaf movements:- Immediately wind disturbs the canopy, the light profile is altered, and leaves appear to oscillate in the wind at some natural frequency which is related to their size and the wind speed. Under a variety of wind conditions, maize leaves were found to oscillate at 0.05 - 7.0 cycles per second (Norman and Tanner, 1969). This means that lower leaves in the canopy are photosynthesizing in a transient light environment. Over the frequencies observed in maize, it seems unlikely that photosynthetic efficiency would be affected by rapid leaf movement <u>per se</u> (McCree and Loomis, 1969).

and the

(6) Foliage Angle:- de Wit (1965) distinguishes four canopy types according to the frequency distribution of angle classes within the mature canopy. Plagiophile canopies contain predominantly oblique leaves (declining from vertical or horizontal) while extremophile canopies have fet oblique leaves with most being in horizontal and vertical classes. Vertical leaves occur most frequently in an erectophile canopy, while a planophile canopy has a high frequency of horizontal leaves. De Wit further points out that the direct light intensity received by a leaf plane is completely determined by the intensity of the direct solar beam arriving at the earth's surface, the sun elevation angle a, the sun azimuth angle, and the elevation angle, B, of the leaf plane.

The curvilinear response of photosynthesis to light implies that a canopy will photosynthesize with high efficiency when all incident light is absorbed by a large area of dimly lit leaves. It has been suggested that this would be achieved by a vertical to horizontal orientation from the top to the bottom of the canopy (Verhagen <u>et al</u>, 1963; Donald, 1968). Simulated studies of the effect of leaf angle on productivity indicate that this type of canopy structure has a considerable productive advantage over a canopy in which horizontal leaf layers overlay vertical leaf leafers, particularly at LAI values in excess of 3.4 (Duncan, 1971). At LAI values of less than 3, leaf angle probably has little effect on productivity i.e. the quantity of light absorbed is more important than the manner of absorption. Advantages accruing to steeply angled leaves increase rapidly beyond LAI value of 3 (Duncan <u>et al</u>, 1967), and are largely independent of leaf type and geographical latitude up to about 60° (Duncan, 1971; Loomis et al, 1971).

Experimental evidence confirms some of the hypotheses concerning leaf angle and canopy productivity. Artificially induced leaf angle variation in barley seedlings over a range of LAI (2-12) indicated that high canopy Pnet rates were associated with a large area of steeply angled leaves (Pearce <u>et al</u>, 1967). Gardener, quoted by Mitchell (1970), obtained yield increases of 16% from barley lines with erect leaves compared with lax-leaved lines at comparable plant leaf areas. Increasing leaf angle by mechanical means raised grain yield in maize by 15% (Pendleton <u>et al</u>, 1968). Maize lines with upright leaves, when compared with isolines differing only in leaf angle, consistently produced more grain and total dry matter per unit LAI, particularly at higher populations (Hopper and Anderson, 1970). It is thought however that some of the productive advantage for maize may be due to improved lighting of leaves close to the developing ear (Pendleton <u>et al</u>, 1968), and Sinclair <u>et al</u>,(1971) were unable to detect any differences in
productivity between normal-leaf and erect-leaf isogene lines of the same maize hybrid when using aerodynamic, or leaf and plant charler methods.

Leaf angle distribution with depth has been measured in maine, using stratified analysis techniques. Loomis <u>ot al</u> (1968), investigating a variety exhibiting a planophile canopy, found that leaves near the top of the canopy changed abruptly from an erect to a horizontal solition as the tassel energed, carrying leaves upward and outward from the leaf whorl. The leaf angle distribution with depth changed from a semewhat expectsphile distribution near the top of the canopy to a more planophile distribution at the base. Increasing density of planting was found to increase the leaf angle. Ross and Milson (1967) describe the leaf angle distribution is in leaf angle. Ross and Milson (1967) describe the leaf angle distribution is write plagiophile leaf angle distributions have been reported (do Mit, 1945; Daynard, 1971). Changes in leaf angle can be genetically induced comparatively easily (Pendleton <u>et al.</u> 1968).

(iv) Efficiency of Conversion of Photosynthetically Active Rediction by the Vaige Gron Efficiency of conversion of PAR may be defined as:-

Efficiency = <u>chemical energy of plant natorial formed</u> FAR absorbed

The heat of combustion of plant material formed has be a set of atally determined as 4 kcal/g (Villiams et al, 1965 a; Loomis et al, 197. Efficiencies at specific times during the day under good growing or willions have been estimated. Lenon (1967), assuming 84% interception of . . calculated efficiency to be as high as 14% in a stand of 63000 plana/hs (LAI 4.3) when incident solar radiation was 0.8 cal.cm⁻².min⁻¹. The <u>ot al</u> (1961) observed that the efficiency curve over the day troughed at fiddry, possibly because of light saturation of the canopy (74000 plants/ha), or because some other factor essential to photosynthesis such as water was limiting, but probably because of the curvilinear photosynthetic response curve to light intensity. Efficiency of conversion of incident PAT, not corrected for absorption, peaked at 7% in this experiment. Uchijima (1969) ro arts energy conversion efficiencies of incident PAR (not corrected for absorption) ranging from 6-14% with a mean value of 10.2% which is rather similar to the 10% obtained by Lemon (1960) from a stand of LAI 3. Differences in efficiency may reflect differences in light intensity. The hyperbolic photosynthetic

response curve to light implies that efficiency and light intensity are negatively related.

When respiration rate overnight is included, efficiency falls. Over a 12 day period prior to tasselling a crop growth rate of 520 kg.ha. $^{-1}$ day⁻¹ (including recoverable roots) was obtained from a stand with a mean LAI of 11.5, and an extremely high density of 700,000 plants/ha. This represented a 6.4% conversion of absorbed PAR for the whole period, and was about a half of potential conversion efficiencies based on the quantum requirement of photosynthesis (Loomis and Williams, 1963) or the photosynthetic response curve to light of the Duncan model (Loomis <u>et al</u>, 1971) (cf. Buttery, 1970). Over a two month period corresponding with the rapid grain filling stage of the crop a net efficiency of conversion of absorbed PAR of 7.3% was obtained (Lemon, 1967). Efficiency of conversion of absorbed PAR of 7.3% was obtained (Lemon, 1967). Efficiency of conversion of absorbed, PAR over a two month grain filling period of 12.2 -12.9% based on 75-80% absorption of incident PAR in a Russian maize crop of LAI 6.0 has been claimed, giving an estimated growth rate of 600-720 kg.ha. $^{-1}$ day⁻¹ (Ustenko and Yagnova, 1967).

Loomis <u>et al</u> (1971) list crop growth rates and conversion efficiencies of absorbed PAR. A New Zealand crop is reported to have a COR of 290 kg.ha⁻¹ day⁻¹ and an efficiency of 6.1%. On an annual basis, a production of 17,000-25,000 kg.ha⁻¹ in New Zealand would have an efficiency of 2.2 - 3.0% or similar to that of a ryegrass sward. This does not include root growth. Sibma (1968) points out that by the time maize commences growth in the Netherlands, grass and winter wheat have already produced 10,000 kg.ha⁻¹ dry matter. In a cool climate such as this grass and maize have similar CGR values and similar efficiencies.

(v) Summary: Leaf Area Index and Crop Growth Rate

The dependence of CGR on the quantity of leaf surface has been well established (Watson, 1952; 1956; 1958; Williams <u>et al</u>,1965 b; Shibles <u>et al</u>, 1965; Thorne, 1966; Puckridge and Donald, 1967; Buttery, 1970). The relevance of leaf area has been shown to be due to its influence on the absorption of PAR. It has been shown that both percent absorption of solar radiation and CGR increase with LAI and approach a maximum at similar LAI (4-8) in the vegetative stage of growth of the maize canopy (Williams <u>et al</u>, 1965 b; 1968; Allison, 1969). During this stage CGR is linearly related to % incident PAR absorption. In the grain forming period factors influencing the source of photosynthate, and the initiation, maintenance and density of reproductive sinks affect CGR, and it may form a peak at some optimum LAI value (e.g. Allison, 1969; Buttery, 1970), or tend to an asymptote as LAI increases (e.g. Williams <u>et al</u>, 1968). CGR is often lower in this period than in the late preflowering phase, though this is frequently confounded with declining solar radiation intensity. Capacity of simulation models to predict reproductive growth is severely limited (Eastin, 1969).

The exact form of the relationship between CGR and LAI depends upon leaf area, leaf angle, leaf position, leaf movement, reflectivity and transmissivity by leaves, light absorption by non photosynthetic surfaces, the photosynthetic response to leaf illumination at different depths in the canopy, the brightness of the sun and its position and canopy turbulence. Feedback inhibition of photosynthesis (if it exists) may reduce the CGR, and nutrient and water deficiencies will drastically reduce productivity.

All of these factors, and others about which less is known, particularly in the reproductive stage of crop growth, make the relationship between the easily measured crop growth parameters CGR and LAI difficult to interpret, physically or physiologically.

1.3.3 Patterns of Assimilate Distribution in Maize

The distribution of assimilate from various leaf positions to metabolic sink sites and zones of temporary and permanent storage does not occur in a random fashion (Stoy, 1969; Biddulph, 1969). From data on leaf position, leaf area, vascular connections within the plant, sites of growth, and rates of growth, the likely distribution of assimilates can be predicted (Wardlaw, 1968).

The development of pulse-chase techniques using radioactive ⁴C as a marker or label for assimilation has greatly improved the state of knowledge of translocation patterns in plants. Studies with sugar cane and maize, which are similar in many aspects of translocation (Hofstra and Nelson, 1969 a; 1969 b), have revealed much about patterns of assimilate distribution in maize.

Photosynthesis in maize appears to occur mainly in the mesophyll and parenchyma chloroplasts, and the fixed CO₂ is transported rapidly in a bound form to the bundle sheath cells (Pristupa, 1964; Moss and Rasmussen, 1968; Hatch and Slack, 1970). Transfer as sucrose to vascular bundles in the leaf is rapid, and movement toward the leaf sheath occurs with little lateral movement (Hofstra and Nelson, 1969 a). At the leaf sheath the assimilate appears to diffuse throughout the sheath, then move down the stalk to the node below that adjacent to the point of attachment of the sheath to the stem (Sharman, 1942). Vascular strands from the stem and leaf anastomose at this point, and the assimilate may either lodge in the 'stem, go to the roots, move towards the developing ear or move to the stem apex and on into expanding leaves (Hartt <u>et al</u>, 1963; \cdot Biddulph, 1969). Movement from the fully expanded leaf and sheath is very complete. Fully expanded maize leaves, like those of other C₄ plants tested, export 70-80% of assimilated label in the first 4 hours after labelling, compared with the 40-50% for C₃ plants. The figures for both groups fall as temperature falls (Hofstra and Nelson, 1969 a; 1969 b; Eastin, 1970). Rate of movement of assimilate within the maize leaf and stem was found to be 150 cm/hr and 138 cm/hr in two separate studies (Hofstra and Nelson, 1969 a; Eastin, 1970) compared with 80-100 cm/hr for many other species (Hartt <u>et</u> al, 1963; Wardlaw, 1965; Biddulph, 1969).

The rate of translocation falls in response to low levels of temperature and light, and to nutrient and water stress. The general effect of these factors when their supply is reduced is to direct a greater proportion of assimilate to the shoot apices and less to the roots (Wardlaw, 1958; Eastin, 1969).

The distribution pattern of assimilate within plants changes markedly at flowering (Stoy, 1969) and the pattern in the maize plant is affected to a lesser degree by temporary storage and remobilization, and by contributions from tillers. Aspects of this distribution pattern will now be considered.

(i) <u>Assimilate Distribution Pattern in the Presilking and Silking</u> Maize Plant

Tracer studies in maize plants aged 3-6 weeks (Hofstra and Nelson, 1969 a) indicate that the plant root is the largest sink at this stage of development, followed by the apical meristem. While leaves of all ages retain some capacity to import assimilates, by the time the leaf blade has reached $\frac{1}{2} - \frac{1}{2}$ of its mature size only very small amounts of assimilate are imported from other leaves, the growth at the leaf base being almost entirely supported by assimilate from the already expanded part of the blade. The lower the position of the leaf, the higher the proportion (up to 50%) of its assimilates diverted to the root. Upper leaves export mainly to the stem apex and expanding leaves.

Following floral initiation, there is an increasing movement of assimilate to the growing ear and tassel, and translocation at silking has been investigated by Eastin (1969) in a series of experiments in which labelled CO₂ was fed to every second leaf on two varieties of maize. Relative total counts (%), which reflect the percentage of assimilated label, were determined on various plant parts four days after labelling, when the

pattern was stable (Eastin, 1970). Some of his results for one variety tested (W-415) are presented in Table 1.1. Figures relevant to the distribution of assimilate at silking are listed as <u>a</u> under Time. At this growth stage, the ear was the largest sink, though upper such growth and root growth were still continuing. A second maize hybrid similarly tested showed a significantly different assimilate distribution pattern at silking despite possessing extensive morphological similarities to W-415. The second hybrid accumulated more labelled assimilate in the stan near the ear and in the fed leaf than W-415.

(ii) Assimilate Distribution Pattern in the Postcilking Maise Plant

A rapid polarization of translocation towards the ear has been observed shortly after pollination, and accumulation of dry matter in the stem near the ear and in the ear shank occurs (Loomis, 1936; 1945; Petho, 1967). A simple sink-source relationship develops between the ear, and the leaves above and immidiately below the ear. Translocation from these leaves is rapid and more complete than at anthesis (Palmer and Musgrave, 1969). The ear is able to compete more successfully than vegetative structures for available assimilate when the assimilate stream is reduced by shading (Palmer, 1969). The data of Eastin (1969) presented in Table 1.1 further illustrate the large influence of the developing ear on the pattern of assimilate flow, particularly from leaves at and above the ear. Relevant figures are listed as <u>b</u> under Time. Varietal differences were r duced by comparison with those measured at silking but were still apparent, and Eastin (1969) suggests there is a genotype x developmental suge interaction, as well as a straight stage of development effect.

TABLE 1.1 (After Eastin, 1969).

C-14 Distribution after 4 days when various leaves are fed 1400₂ at two growth stages. Plants have 13 leaves and ear is in L-7 leaf axil. Stem 1 lies above the ear node and stem 2 below. Numbering is from top of plant down. Hybrid is 'V-415' at 45,000 plants/ha.

> Time: a At silking. b 20 days after silking

Fed Leaf		L-1	L-3	L-5	EL	Im 9	L-11
Plant Part	Time					_ ,	
Stem 1	8	31	27	8	-	-	
o com 1	'n	5	3	1	_	_	1
	5))	,	270	-	j.
Stem 2	a	7	13	8	11	41	56
	Ъ	2	1	3	2	24	35
	~	-		2			22
Root	a	1	• 2	2	3	40	27
	ď	-	1	1	1	1	4
Ear	a	42	42	76	72	4	3
	ď	88	91	91	93	61	35
Fed Leaf	а	13	11	7	15	15	13
and Sheath	b	4	4	4.	4	13	21
Tassel	a	3	3	-	1	-	-
	Ъ	-	-	-	-	-	_

C-14 Distribution as Relative Total Counts (%)

The pattern of assimilate distribution in a 'prolific' variety (sweet corn) has also been investigated (Eastin, 1969). Leaves below the apical ear were responsible for providing the bulk of assimilate to the second ear.

Planting density (Section 1.5.3, Table 1.3) also influences the pattern of assimilate distribution.

Tracer work has confirmed hypotheses concerning the contribution of various leaves to grain yield in maize, based on defoliation of parts of the canopy (e.g. Hoyt and Bradfield, 1962; Allison and Watson, 1966; Tanner and Daynard, 1967; Pendleton and Hammond, 1969; Eddowes, 1969 b). The relatively inflexible pattern of assimilate distribution in a given maize variety obviously interacts with the light regime of the canopy to determine the amount of assimilate reaching the ear. Maximum grain production would appear to be achieved by near-complete interception of incident light in as uniform a manner as possible by the leaves contributing most to the ear (cf Pendleton <u>et al</u>, 1967; 1968). If however lodging is limiting productivity, it would be important for light to penetrate to the lower leaves which feed the lower stem and roots. Data such as those reviewed above provide important information for model builders if the reproductive phase of maize growth is to be successfully simulated (Eastin, 1969).

(iii) The Relationship Between Tillers and the Parent Malae Plant

The existence of vacular connections between the tiller and the main stem of the maize plant at grainfilling has been demonstrated (Dungan, 1931). Some conditions under which assimilate is translocated from the tiller to the main stem during grain filling are:

(a) When the tiller is barren and the main stem bears a developing ear. A reverse flow of assimilate may occur if the main stem is barren and the tiller is supporting an ear (Bungan, 1931; Rosenquist, 1941).

(b) Where the main stem has been defoliated, and the leaves on the tiller left intact. Under these conditions the tiller may support grain filling in the main stem (Loomis, 1945).

(c) In prolific varieties supporting two or more ears on the main stem and no ear on the tillers (Earley <u>et al</u>, 1971).

Very little assimilate transfer will occur if both main stem and tillers bear developing ears. Tillers big enough to offer a significant degree of support seldom occur at populations greater than 40,000 plants/ha, except perhaps in situation (c). Present day single-eared varietian seldom produce fertile tillers at commercial planting densities (c 50,000/hd) and the transfer of assimilates from tiller to main stem or vice verse is insignificant (Kiesselbach, 1950; Earley et al, 1971). It is doubtful whether the highly competitive relationship which exists between tillers and the main plant in small grains (Bunting and Drennan, 1966) ever exists in maize, although vascular connections in small grains appear similar (Quinlan and Sagar, 1962).

(iv) Temporary Storage and Remobilization of Assimilates in Maize

While it is universally accepted that most of the grain dry matter in cereals is produced by photosynthesis after flowering, there is no agreement on the actual figure, nor of the role of temporary storage and mobilization during grain filling.

The subject has been extensively studied in small grain cereals and it appears that losses in weight by plant parts, notably the stem during grain filling may account for as much as 10% of the final grain yield, but often a lot less (e.g. Archbold, 1945; Stoy, 1965; Thorne, 1966; Rawson and Evans, 1971).

The stalk, shank, husk and possibly the cob of the maize plant appear to be able to store labile organic reserves which may be mobilized if the level of intraplant competition becomes high enough (Duncan <u>et al.</u>, 1965; Daynard <u>et al</u>, 1969). It has been demonstrated that the level of soluble solids in maize particularly carbohydrates rises above normal when the plant is barren (Sayre <u>et al</u>, 1931; van Reen and Singleton, 1952; Moss, 1962). Shading the plant (Mnipmeyer <u>et al</u>, 1962; Gille and Woodruffe, 1971) and reducing the leaf area (Sayre <u>et al</u>, 1931; Dungan, 1934; Duncan <u>et al</u>, 1965) are effective in reducing stalk sugar concentrations below those normal in the maize plant. The loss of sucrose from the stalk of defoliated plants accounted for 85-92% of dry weight lost by the stalk indicating that the loss of dry weight from the stalk occured largely as sucrose (Duncan <u>et al</u>, 1965).

The movement of dry matter from the stalk to the grain when the shoot was cut three weeks after fertilization and kept in the dark was demonstrated by Allison and Watson (1966). Grain dry weight was observed to increase 20% in maize shoots of a similar maturity after they had been cut and stacked for eight days (Aldrich, 1943). Similar movements of dry matter from the stem to the grain have been induced by partial defoliation of live plants (Hoyt and Bradfield, 1962).

Significant losses in stem dry weight during grain filling have been reported by other workers (Kiesselbach, 1950; Hay <u>et al</u>, 1953; Hoyt and Bradfield, 1962; Duncan <u>et al</u>, 1965; Daynard <u>et al</u>, 1969; Genter <u>et al</u>, 1970; Adelana and Milbourn, 1972 b). van Eijnatten (1963) reported loss in stem weight in the final week of his experiment, which was concluded before grain filling was complete. However a number of growth studies of normal maize crops have failed to reveal any changes in stalk dry weight after it has reached a maximum 1-4 weeks after silking (Miller, 1943; Sayre, 1948; Hanway, 1962; Allison and Watson, 1966). Allison (1969) reported no loss in stem weight from plants grown at 23,000/ha, but as density increased beyond this a greater proportion of the maximum stem dry weight was lost during the latter stage of the grain filling period.

Where dry weight is lost from the stalk of the maize plant, the loss begins 2-5 weeks after fertilization, and is steepest during the phase of rapid grain filling (Kiesselbach, 1950; Allison, 1969; Daynard <u>et al</u>, 1969; Adelana and Milbourn, 1972 b).

Losses in dry weight in other plant parts have also been recorded. Proportionally husks (shank included) lose more dry weight than stalks, and appear to do so at a lower level of intraplant competition than do stalks. The timing of the loss of dry weight again coincides with the period of rapid grain filling (Miller, 1943; Sayre, 1948; Hay <u>et al</u>, 1953; Allison and Watson, 1966; Allison, 1969; Hanway and Russell, 1969; Daynard <u>et al</u>, 1969).

There has only been one detailed report of loss in cob dry light during grain filling. Manson (1967) reported a 15% decline in cob dry weight between the 5th and the 8th week after pollination. Similar losses are not apparent in other literature (Sayre, 1948; Hanway, 1962; Hanway and Russell, 1969). Losses in dry weight from roots during grain filling have not occurred in some studies (Foth, 1962; Zuber, 1968; Taylor and Lund, 1970), though van Eijnatten (1963) reports a 5% decline in root weight in the last week (4th week after flowering) of his experi- at.

What is the absolute contribution of stored carbohydrate to grain yield? Kiesselbach (1950) found that the loss in weight in static accounted for 20% of the grain yield in 1921, and 12% in 1922. The amount of mobile sugars in the stem was calculated to be sufficient to produce 20% of the yield in a crop yielding 10,000 kg grain/ha (Duncan <u>et al</u>, 1965). Daynard <u>et al</u>,(1969) reported an average loss of 500 kg dry matter/ha from stem translocation, and 400 kg dry matter/ha from cobs, husks and shanks. A conversion ratio of stem success to grain dry matter of 0.5 - 0.64 was calculated by Duncan <u>et al</u>,(1965).

Adelana and Milbourn (1972 b) reported a 48% decline in dry weights of the combined stem and shank during grain filling in three variables when grown at 108,000 plants/ha. Changes in root dry weight were not a sured in the above experiments.

The concept of a pool of labile organic reserves in the stem and masks of the growing plant is an attractive one. It could act as a buffer between photosynthesis (principally light controlled) and growth requirements (principally temperature controlled), as well as controlling the level of intraplant competition (Duncan <u>et al</u>, 1965). The initial build up of assimilate may come about because ear sink capacity is limiting for 2-5 weeks after pollination (Daynard <u>et al</u>, 1969). The situation is not however as simple as this. Considerable differences between genotypes within years, and within genotypes between years have been observed (van Reen and Singleton, 1952; Daynard, 1969). Varying population pressure produces incompatient results. Kiesselbach (1950) obtained large reductions in stem weight at 19,000 plants/ha while Sayre (1948) and others obtained no reductions at 28,000 plants/ha. Daynard et al (1969) indicate only a 5% increase

in translocation from stem and husks as planting density increased from 44,700/ha to 124,300/ha, and Hanway and Russell (1969) report no differences at 38,700 and 58,100 plants/ha. Because the level of assimilates in stem and husks is a function of both supply and demand of assimilate it is likely to respond in a complex fashion to a range of environmental conditions.

1.3.4 The Growth and Development of Yield in Maize

The grain yield of a maize stand is made up of the following components (Leng, 1954):

(a) The number of plants per unit area (see section 1.5).

(b) The number of ears per plant.

(c) The weight of grain per ear.

(i) Number of rows per ear

(ii) Number of grains per row

(iii) Kernel weight

Aspects of ear number per plant, grain number per ear, and kernel weight will be considered.

(i) Ear number per plant

Ear initiation begins about eight days after tassel initiation, and proceeds basipetally with intervals of 1-2 days between successive initiations (Siemer et al, 1969). The last axillary bud which has reached some critical stage of development at tassel initiation forms the uppermost ear (Bonnett, 1954). In single eared maize varieties, the uppermost ear develops while the lower ears abort in acropetal succession (Bauman, 1960), some reaching considerable size before ceasing growth and disintegration In multiple eared types dominance is shared among two or three upper of the Prolificacy of ears per plant is a varietal characteristic, but a long and photoperiodic experience has been observed to increase the number of developed ears per plant (Moss and Heslop-Harrison, 1968) and ear prolificacy is strongly associated with lateness of maturity (Josephson, 1961). Ear number is reduced by increasing levels of intraplant competition for assimilate (e.g. crowding, or conditions of reduced light), as the assimilate sink capacity outstrips the supply (Bauman, 1960; Josephson, 1961; Collins et al, 1965). When plants are grown at high populations, a critical period during which second ears of semiprolific maize varieties abort has been shown to be 3-4 days prior to silking through till 8 days after silking. Approximately 80% of abortions occurred in this period (Prine, 1971).

(ii) The Determination of Kernel number per Ear

A detailed description of the anatomical and sequential development of floral parts is presented by Bonnett (1940; 1953; 1954) and Kiesselbach (1949). Only a summary is presented here. Kernel row number is determined about one week after ear initiation when spikelet-forming branch primordia form in pairs around the circumference of the base of the ear shoot primordium (Siemer et al, 1969). Kernel row number averages 16-18 but ranges from 4-30. It is not constant within a variety, or a plant, the upper ear normally having a greater row number than a lower ear (Kiesselbach, 1949; Alexander, 1952). As the ear shoot grows in length, spikelet primordia are laid down in acropetal succession behind the ear apex. The final potential kernel number per row is attained about three weeks after ear initiation and one week before silking.

There is good evidence to suggest that conditions prior to floral initiation control the potential kernel number in the maize ear (Heslop-Harrison, 1969). Photoperiodically long days increase the number of florets per row (Ragland <u>et al</u>, 1966). Long photosynthetic days, rather that the photoperiodically equivalent short photosynthetic day with a night break were more effective in this regard, indicating an interaction with nutrition (Moss and Heslop-Harrison, 1968). Langer (1966) suggests that the influence of mineral nutrition <u>per se</u> upon primordia formation is inhely to be small. Alexander (1952) reported that the number of florets initiated increased as soil fertility level increased. Hanway (1962) stated that silking was delayed in conditions of low fertility. Moderate drought stress will suspend the initiation of florets but unless the stress is covers or prolonged it will not reduce the final floret number significantly (Slatyer, 1969; Downey, 1971 a; Moss and Downey, 1971).

Silks arising from the basal florets emerge from the husk enclosing the ear before those from apical florets. Silks continue to grow us fertilization occurs (Kiesselbach, 1949). For fertilization to occur, silk emergence must synchronize with the pollen shedding period which is normally about 10 days long. If silk growth is retarded by water stress (Slatyer, 1969; Moss and Downey, 1971) or by the shading of leaves supplying assimilate to the ear (Section 1.5.3) apical florets are are frequently barren. The growth of brace roots also corresponds with this period and also constitutes a demand on available assimilate (Mitchell, 1970). Maize planted late in the season develops fewer kernels than early planted maize (Hatfield <u>et al</u>, 1965), in spite of the greater number of florets initiated in the longer days. The declining light conditions in

late summer possibly cause silking failure, or kernel abortion in the first 2-3 weeks of kernel growth (Daynard, 1969). Silking occurs later in second ears than in apical ears and yield of second ears may be severely reduced by barrenness (Josephson, 1961). Pollen insufficiency is unlikely to be a cause of infertility (Bonnett, 1954; Anderson, 1967), but pollen sterility may occur when maize is grown in short photoperiods (Moss and Heslop-Harrison, 1968). Hot drying winds, or moisture stress within the plant can cause dehydration of receptive surfaces on the silk and prevent pollen from adhering and germinating. Yield reductions under these conditions can be considerable (Shaw and Loomis, 1950; Robins and Domingo, 1953; Denmead and Shaw, 1960; Moss and Downey, 1971).

Except for the abortion of a small quantity of apical kernele (Daynard, 1969), all the primary yield components except weight per kernel have been determined by the time fertilization is complete.

(iii) Kernel Growth from Pertilization to Physiological Mat with

The early exponential increase in kernel dry weight with time gives way to a period of linear dry weight increase with time 1-3 weeks after fortilization. The beginning of the decline in kernel relative growth rate corresponds approximately with the attainment of maximum cob and huck dry 1962; Duncan and Hatfield, 1964; Allison, 1969). The phase of linear increase in dry weight with time lasts about three to five weeks (Show and Loomis, 1950; Daynard, 1969; Duncan and Hatfield, 1964; Kanson, 1967) before growth rate falls off and kernel dry weight reaches a maximum (Rench and Shaw, 1971), before declining slowly as respiration proceeds. No secondary maximum in kernel dry weight, such as occurs in wheat (Schoulith and Jenkins, 1970) has been reported in maize (Manson, 1967). Physiological maturity has been defined as that time when the kernel first attains its maximum dry weight (Shaw and Thom, 1951 b). Because of sampling worldbility associated with sequential harvesting, drying and weighing of ears, the point at which physiological maturity is reached is difficult to determine. Periodically removing, drying and weighing kernels from the same ear (Duncan and Hatfield, 1964) reduces sample variability without significantly influencing the growth of the remaining kernels. In practice, maize is considered physiologically mature when 95% of the maximum kernel dry weight is attained (Shaw and Thom, 1951 b). The time from 95% to 100% physiological turity was estimated by Hillson and Penny (1965) to be 12-13 days in one strain. Visual observation of the time of formation of the dark brown or black

abscission layer in the placental region of the grain (Kiesselbach and Walker, 1952) indicates that this is an accurate indication of physiological maturity (Rench and Shaw, 1971). The development of the 'black layer' can be observed with the naked eye over a three day period, and occurs first in apical kernels, and last in basal kernels. The black layer is entirely absent in parthenocarpic grains, and its occurrence is a reliable indication of fertilization having occurred (Daynard, 1969; Daynard and Duncan, 1969).

Considerable variation in the grain filling period from mid-silking to physiological maturity has been found. Some workers report it as fairly constant in any one environment at about 50 days (Kiesselbach, 1949; Shaw and Loomis, 1950; Shaw and Thom, 1951b), or 60 days (Hallauer and Russell, 1962). Cumberland et al (1971) suggested that the period of grain Filling in New Zealand is 53-55 days irrespective of variety. Other working have found this period to vary in length from 43 days to over 70 days, though maturity rankings of varieties did not alter between seasons (Dessureaux et al, 1948; Gunn and Christensen, 1965; Hillson and Penny, 1965; Hanway and Russell, 1969; Daynard and Duncan, 1969). Manson (1967) points out that sampling was discontinued when grain dry weight changes because small and variable in the majority of reports, and in fact grain day way to increase may have ceased later than reported. In trials over four . acons in Rhodesia, Manson reports linear increases in grain dry weight from 35-70 days after silking, and a maximum grain dry weight obtained 100 days after silking in a single Rhodesian hybrid. He suggests that the length of the period from silking to physiological maturity is frequently iled by the onset of cool dry autumn weather in more extreme climates. Since the termination of this period coincides with plant senescence it is reasonable to expect that a short photoperiod could shorten the grainfilling period (Krizek et al, 1966; Carr and Pate, 1967), though there is obviously an interaction with temperature (e.g. Andrew et al, 1956). Adelana and Milbourn (1972 b) reported a 90 day filling period in three maize varieties grown in Southern England, reflecting the important influence of lower summer temperatures in delaying plant senescence.

Genotype also has some influence. Early maturing varieties appear to have shorter grain filling period durations than late maturing varieties (Gunn and Christensen, 1965) but this finding may reflect mean temperature differences during ear filling for the two classes. The length of this period has been shown to be positively correlated with yield in wheat (Stoy, 1965) and in maize within years and planting rates, but not between years or planting rates (Hanway and Russell, 1969).

Since about 75% of the total kernel dry weight is accumulated during the linear phase of kernel dry weight increase (Shaw and Loomis. 1950; Daynard, 1969; Daynard et al, 1971), it is obvious that the length and rate of accumulation of this phase are important characteristics dater dainggrain yield. Dividing total grain weight by the linear rate of dry weight increase gives, what is termed by Daynard et al (1971), the effective filling period duration (EFPD). Variation in EFPD was highly correlated with yield within each of two years but explained little of the yield variation between years. Variation in the linear rate of grain dry matter increase among six varieties accounted for only 16% of the variation in grain yield. Little information is available on the relationship between MAPD and the length of the actual grain filling period. Reasons for variation in the length of the actual grain filling period in any one environment contre around genetic differences in the capacity of the kernel to accept Assimilate (Daynard, 1969). Cell division in the kernel is completed 2-3 weeks after fertilization, and growth thereafter is in cell size (Shaw and Loomis, 1950). Daynard (1969) postulates that conditions in these 2-3 works may profoundly influence final yield if the potential for kernel group is restricted by an inadequate cell number. Yield can be restricted of the size of the ear (Bauman, 1960) though the restriction is unlikely to be severe (Adelana and Milbourn, 1972 b). There are indications in early sold. Atiac crops that kernel number restricts yield (Hatfield ot al, 1965). The grain filling period of early crops coincides with higher light and ten sectore levels than late grown crops (Bonnett, 1960; Benoit et al, 1965), and yield is highly correlated with kernel number, suggesting that supply of photosynthate exceeds sink capacity. Yield of late plantings of maize is highly correlated with kernel weight rather than with kernel number. Cool conditions might be expected to extend the length of the filling period (Daynard, 1969) because rates of grain filling and leaf senescence are reduced (e.g. Andrew et al, 1956).

Variations in the growth rate of grain are influenced by the whole complex of factors which determine crop growth rate. Injury to leaf are will reduce grain growth rate (Dungan, 1934; Hoyt and Bradfield, 1962). Stress factors, or short day photoperiodic conditions (Krizek <u>et al</u>, 1966) leading to incipient senescence, reduce the length and ultimately the rate of grain filling. Water stress, through its influence on photosynthesis (Baker and Musgrave, 1964) will reduce grain growth rate and final yield (Slatyer, 1969; Downey, 1971 a; 1971 b).

It is doubtful if the rate of translocation of assimilate limits the growth rate of grain in cereals (Milthorpe and Moorby, 1969).

The rate of grain filling, like the length, is directly influenced

by the temperature (Bair, 1942; Ragland <u>et al</u>, 1965). This, plus the effect of high temperature in increasing rates of development prior to silking (Leng, 1951; Bonnett, 1960) is recognized in the present heat unit system for rating maturity of varieties. A base temperature, normally 100, is taken as minimum for growth, and "degree-days" are accumulated. Correction for very high or very low temperatures may be made (Gilmore and Robert, 1958) ("effective degree-days") and the accumulated heat units use to successfully rate maturity of varieties are repeatable over a range of environments (Gunn and Christensen, 1965; Neal, 1968; Iwata and Chube, 1969; Cuany, 1970; Nanda and Keltgen, 1970). Rate of grain filling reserves a peak under a 300/250 day-night temperature regime (Friend, 1966). Langer (1966) states that the supply of nutrients influences grain yield principally through its effect on leaf area, rather than through leaf efficiency.

Genotype also influences the rate of grain dry matter accumulation. Significant differences in the linear rate of dry matter accumulation that could not be attributed to LAI differences at the time of measurement have been recorded (Daynard et al, 1971).

It appears that the grain yield of a maize crop adequately supplied with growth factors, and with a LAI of 4-6, would be increased by choos interacting factors:

(1) Increased number of potential kernels per plant (Donald, 1997),
 either by increasing ear number per plant (Bauman, 1960; Josephson (1987),
 or by increasing ear dimensions, particularly ear length.

(2) Increased capacity for kernel growth, possible by increasing kernel depth on the ear (Rinke, 1960).

(3) Increased length of the growing period, since yield seems more closely related to this than to ear growth rate (Army and Greer, 1967; Duncan, 1969; Daynard et al, 1971).

Efforts to incorporate the above factors into the maize plant must be accompanied by research into factors affecting floret and kernel abortion, silk growth, and leaf and root longevity.

(iv) Yield Component Relationships in Maize

Under conditions of varying environmental stress yield components are frequently negatively correlated (e.g. in wheat: Stoy, 1965; Knott and Talukdar, 1971). The correlations may possibly be a result of genetic linkage (Rasmusson and Cannell, 1970), but are probably due to the secuential nature of component development imposed upon a changing level of limit of environmental resources (Adams, 1967; Adams and Grafius, 1971).

The degree of compensation is limited by the capacity of some components. Bauman (1950) reported that the gain in grain yield by the primary ear represented only 9% of the loss of the secondary ear, when filling on the second ear of a prolific hybrid was prevented. Higher gains (16-55%) by the first ear have been observed by Earley <u>et al</u> (1966) when second ear growth was eliminated by shading the growing plants.

Yield components within the ear show relationships among each other. and with yield, that change considerably as the environment changes (Eatfield et al, 1965; Singh, 1969). Hatfield et al (1965) report correlations among yield and yield components. Kernels per ear, and kornel row number in early-soun irrigated maize were negatively correlated with weight per kernel ($r = -.66^{**}$ and $-.67^{**}$ resp.) but positively correlated with yield ($r = +.75^{**}$ and $+.45^{**}$ resp.), indicating that variations in kernel number per ear accounted for more than 50% of yield differences. Kernels per row and weight per kernel bore little relationship to yield but were positively correlated with each other $(r = +.262^{\circ})$. A drought stress however drastically changed the pattern of correlation among yield components: kernels per row, and weight per ear became positively correlated with yield (r = +.47**, + .45** resp.), and were positively correlated with each other $(r = +.41^{**})$. Number of kernels per our and weight per kernel were consistently negatively correlated, suggesting a degree of compensation for these characters.

Hotorosis has been observed to increase weight per kernel, and hernels per row by large margins, but had little effect on car row number, and a negative effect on car number per plant (Leng, 1954).

1.3.5 Distribution of Dry Natter in the Mature Maize Plant

Attempts to assess the dry weight of maize roots under field conditions have met with varying success, but it appears that roots comprise 7-14.0 of mature total weight in modern high yielding varieties, and up to 22.0 of mature total weight in older lower yielding varieties (Weihing, 1935; Kiesselbach, 1948; Foth, 1962; van Eijnatten, 1963; Wu, 1971). The proportion may reach 33% in young vegetative plants (Foth, 1962), and roots are still a significant sink of assimilate during grainfilling (see Table 1.1). Roots formed a greater percentage of total weight in late maturing varieties than early maturing varieties in one report (Weihing, 1935).

The relative proportions of the total top dry matter made up by the constituent parts show considerable variability in the literature. Table 1.2 summarizes the data presented in the literature based on maize plants in which fertilization and grain growth has been successful. (Miller, 1943; Sayre, 1948; Kiesselbach, 1948; 1950; Hay <u>et al</u>, 1953; Hanway 1962; 1963; van Eijnatten, 1963; Allison and Watson, 1966; Bryant and Blaser, 1968; Allison 1969; Hanway and Russell, 1969; Brown <u>et al</u>,

1970; Hunter et al, 1970 b; Adelana and Milbourn, 1972 b).

The distribution of dry matter in the shoot is affected by genotype. Late maturing varieties have a greater proportion of leaves, stems and husks and a lower proportion of cob and grain in the mature shoot than do early varieties (Bryant and Blaser, 1968).

The data listed in Table 1.2 indicate a harvest index (roots excluded) of 0.38 - 0.58 which is somewhat greater than that of small grain coreals (0.27 - 0.51) (Bunting and Drennan, 1966; Singh and Stoskopf, 1971) and is attributed in part to the length of the grainfilling period in maize-(Allison, 1964). Tillers are usually less efficient in grain production than themain stem, even in small grain coreals where profuse sillering occurs (Donald, 1968). This is particularly true in maize, where at commercial planting rates tillers are normally small (Dungan <u>et al</u>, 1958; Downey, 1972). Kiesselbach (1950) reports the harvest index (roots excluded) of main stems to be 0.45 and of tillers to be 0.19 under conditions that favoured the production of large tillers.

TABLE 1.2 Percentage of total shoot dry matter in different plant parts at maturity.

Plant Part		· <u>Percentare</u>	Range	
		(Medium maturity - after Hanway, (1963).	(Over maturities from literature).	
Stalk (+ leaf sheaths)		24	18-29	
Leaves		13	8-13	
Husk + Shank	٢	7	5-9	
Cob		9	8-11	
Grain		48.	38-53	
		100		

1.4 THE FIELD MATURATION OF GRAIN MAIZE

Grain filling is accompanied by a substantial lowering of grain moisture content. The reduction begins about 10 days after fertilization (Schmidt and Hallauer, 1966), and continues at a rapid rate (1-1.3% per day) until by 30-50 days after kernel growth commences, dry matter (DM) content of the grain is 50% total fresh weight (Kiesselbach, 1950; Manson, 1967; Mitchell, 1970). Rate of loss of moisture is approximately linear with time for the next 40 days (Gunn and Christensen, 1965; Hillson and Penny, 1965) and is accompanied by shrinkage of the ear (Shaw and Loomis, 1950). The rate of loss of moisture is less than in the previous period and DM

content of the grain rises to about 75% before the rate of loss decreases again (Schmidt and Hallauer, 1966). Loss of moisture from the cob occurs more slowly than from the grain (Kiesselbach, 1950; Miles and Reamonga, 1953).

(i) Grain Dry Matter Content at Physiological Maturity

Grain dry matter content has previously been used as an index of the occurrence of physiological maturity. Aldrich (1943) stated that grain was physiologically mature when grain DN content reached 65%, even though his own data contained important exceptions to this general statement. A number of reports indicate that grain LN content at physiclogical maturity ranges from 60-70% (Shaw and Loomis, 1950; Kiesselbach, 1950; Hilloon and Penny, 1965). Other workers report that grain DN content may range from 50-60% at physiological maturity in some varieties, particulary those maturing late (Dessureaux et al, 1948; Shaw and Thom, 1951 b; Gunn and Christensen, 1965). Miles (1958) considered that dry matter can be translocated to the grain until grain DM content reaches 74%. Dute presented by Manson (1967) supports this contention. Miles postulated that relues less than 74% indicated the operation of some factor other than adaptation in terminating grain filling. He suggested that consistent low temperatures might be this factor. Such conditions would be conducive to the formation of the black closing layer in the kernel (Daynard and Duncan, 1969).

The variation in grain DN content at cessation of grain filling indicates that this is an unreliable index of the occurrence of physiclogical maturity.

(ii) Factors Affecting the Rate of Field Drying of Maize

The rate of loss of water from grain on the plant is controlled by environmental factors and plant factors.

Environmental factors influence the supply of energy to the grain for evaporation, and the steepness of the vapour pressure gradient from the grain to the air. Many of the parameters used to assess the microclimate of the maize canopy measure both energy supply and the vapour pressure gradient, as the two are interrelated. Hallauer and Russell (1961) attempted to relate the rate of loss of grain moisture from silking to physiological maturity to six weather factors (open pan evaporation, wind movement, relative humidity, duration of sunshine, precipitation, and the accumulated mean air temperature above 10C, or degree days). Rates of moisture loss varied among years within varieties, indicating a variable environmental effect. Degree days was the only parameter to be consistently and positively related to rate of drying. Schmidt and Hallauer (1966) reported that grain moisture loss was significantly related to air temperature when grain DM content was less than 70%, and significantly related to relative humidity when grain DM content exceeded 70%. Low temperature and high relative humidity slow the rate of moisture loss from grain considerably (e.g. Andrew et al, 1956).

Plant factors affecting rates of grain drying are not well affined. Significant differences in rates of grain moisture loss among variaties have been reported (Hallauer and Russell, 1961; Hillson and Penny, 1965). Hallauer and Russell (1962) found regressions indicating that the rate of grain moisture loss is a horitable character. 'Fast drying' and 'alow drying' lines could be recognised. Later silking was associated with a more rapid rate of drying from husked cars (Purdy and Crane, 1967 a). Gunn and Christensen (1965) could find no differences in rate of drying from 30-100 days after silking among 49 hybrids of varying maturity, theorem at any one time after silking late maturing hybrids had a higher grain moisture content than early maturing hybrids. Results obtained by Cumberland and Farrell (1971) over a small range of grain dry matter contents in a number of varieties grown in New Zedand confirmed the latter of Gunn and Christensen's findings but revealed considerable varietal differences in the rate drying.

High plant populations are associated with a higher kernel moisture content at any one time (Colville, 1962).

The rest of the plant even when defoliated continues to supply the ear with moisture (Crane, 1958; Troyer and Ambrose, 1971), though it is suspected that after black layer formation most of this moisture is retained in the cob.

Small ears were associated with a more rapid loss of moisture from the huskless ear (Purdy and Crane, 1967 a).

Faster rates of grain drying were associated with a thinner, more permeable grain pericarp (Crane <u>et al</u>, 1959). Removing the pericarp from kernels of 'fast' and 'slow' drying maize hybrids resulted in almost identical rates of moisture loss or uptake. The permeability of the pericarp was not affected when the grain was killed (Purdy and Crane, 1967 b).

Results indicate that osmotic pressure within the kernel has inconsistent effects on moisture loss. Crane <u>et al</u> (1959) stated that low osmotic pressure was associated with rapid drying, but Purdy and Crane (1967 b) report the converse. The results of Nass and Crane (1970 a) indicated that osmotic pressure hore no relationship to fact or slow grain drying rates.

Endosperm type however does appear to affect rate of under movement to and from the kernel. Alberts (1927) noted that maize with a floury endosperm absorbed more water from the air over a 3 day period from maize with a starchy endosperm. Significantly different rates of grain drying among nine endosperm mutants have been found by Mass and Crane (1970 a; 1970 b). They postulated that the amount of hydrophilic compounds, such as reducing sugars and water soluble polysaccharides play a role in regulating water loss from grain. This has yet to be verified conclusively.

1.5 THE RESPONSE OF THE MAIRE PLANT TO INTRASPECTFIC COMPETITIC

Crop yield is basically a population characteristic and is the less related to the characteristics of the plant than to its performe sunder population stress (Wu, 1971). Plants are highly plastic in their properse to stress, and it is widely recognized that maximum productivity is obtained from a community of suppressed indviduals competing for limited resources within that community.

Donald (1963) states that:

"Competition occurs when each of two or more organisms seeks the measure it wants of any particular factor or thing and when the immediate only of the factor or thing is below the combined demand of the organizer.

The factors for which competition among plants occurs are water, light, nutrients, oxygen and carbon dioxide. Light differs from all other factors. It is ultimately limited in supply by factors outside of human control. It cannot be stored, and light must be intercepted instantaneously, or it is lost as an energy source for photosynthesis. Competitive advantage accrues to the plant whose leaf (or leaves) first interceptothe light stream (Donald, 1963).

While it is intended to consider specifically competition for light, it is recognized that the response of the plant to light supply may impair its ability to compete for other growth factors whose ultimate supply can be modified more easily. The multiplicative effects of competition for more than one growth factor are illustrated by Donald (1958) who showed

the importance of the outcome of competition for light even when the competing plants were under severe nutrient stress.

Holliday (1960 a; 1960 b) has proposed two general relationships between plant yield and plant density. He suggests that the solid dry weight of products of vegetative growth tend to an asymptote as plant density increases indefinitely. Willey and Heath (1969) assert that this asymptotic relationship holds for total plant weight also. The total weight of the products of reproductive growth (principally grain yield in cereals) however follows a parabolic response as plant density increases indefinitely, with some planting density being optimal for grain production. The apparent ubiquity of these two relationships among widely divergent species has led to the formulation of general mathematical expressions relating total crop yield and grain yield to planting density.

The effects of intraspecific competition on the yield-density rolationship, and on the morphology and the physiology of the maize plant have been reviewed exhaustively elsewhere (see Dungan <u>et al</u>, 1958; Stringfield, 1962; Rossman and Cook, 1966; Downey, 1971c).

A summary of findings from papers relevant to the points outlined above, and to the present study will be given here.

1.5.1 Yield Density Relationships in Maize

By comparison with other cereals, the decline in maize grain field at plant populations in excess of that optimal for grain production is a given environment is sharp (Donald, 1963; Willey and Heath, 1969). Because the sink capacity of vegetative plant structures appears to be limited foring grain filling in maize, Moss (1962) suspected that total plant yield would conform to a similar parabolic response as plant density increased. The may occur at extremely high plant densities (King <u>et al</u>, 1970), but for practical purposes total plant weight tends to an asymptote as plant density increases (Rutger and Crowder, 1967; Williams <u>et al</u>, 1968; Bryant and Blaser, 1968; Eddowes, 1969 a; Adelana and Milbourn, 1972 a).

Increasing the supply of the factor for which competition is most intense appears to increase the optimum planting density for grain production, until the supply of that factor or of some other factor falls below the requirements of the crop. Thus where nutrients and water are limiting, increasing the level of nutrients (Lang et al, 1956; Dungan et al, 1958) and reducing the level of water stress (Stickler, 1964; Dale and Shaw, 1965; Giesbrecht, 1969; Andrew and Peek, 1971) increase the optimum plant population for grain yield. It is probable that increasing CO₂ concentration when it is limiting photosynthesis (Moss <u>et al</u>, 1961) would have similar effects.

Interplant competition for light begins when the leaf of one maize plant begins to shade the leaf of another. Eddowes (1969b) suggests that this begins to occur at LAI values greater than 0.5, which corresponds to a plant population of about 5000 plants/ha at maturity (Stringfield, 1962). As light intensity increases, more leaf area is required to observe the light (Brougham, 1958b). The linear relationship between crop growth rate in the vegetative phase and percent light interception considered previously, implies that a planting density producing a LAI sufficient to intercept 95-100% of incident light would be optimal for preflowering growth. The complex relationship between LAI and crop growth rate during the prosth reproductive structures suggests that some factor other than light interception merce may be operative.

Increased leaf area may be provided by either increased leaf area per plant, or increased plant density, or by a concurrent increase in both. In areas of bright sunlight, little cloud, and high temperatures foring the growing season (e.g. Southern Africa, U.S.A.) plants are larg , and where water and nutrients are not limiting, population optime for grain production range from 40,000-20,000 plants/ha (e.g. Rutger and Crowier, 1967; Allison and Eddowes, 1958; Milliams et al, 1968; Allison, 969; Giesbrecht, 1969; Brown et al, 1970; King et al, 1970; Luss et al, 1971; Rutger, 1971; Andrew and Peek, 1971). Trial work in New Zealand Las indicated that the population optima for grain production in this country range from 60,000-80,000 plants/ha. (Cumberland, Farrell and Honore, 1971). In areas where temperatures are lower during the growing season (.... Canada) growth in leaf area is reduced (Hunter et al, 1970 b) and plants growth considerably smaller in the cool humid cloudy conditions of Central Coastal Europe. Extensive vegetative growth is not however a prere disite for high grain yield per plant (Earley et al, 1967). Allison and Eddowes (1968) noted that the optimum planting density for grain production in England was almost twice that in Rhodesia. At flowering the leaf area indices at comparable planting rates were more than twice as large in Rhodesia than in England. The optimum plant density for grain production in Europe is 70,000-120,000/14 (Bunting and Blackman, 1951; Andrew et al, 1956; Berger, 1962; Bunting, 1966; Cunard, 1967; Eddowes, 1969a; Adelana and Milbourn 1972a).

It is likely that the plant populations at which 95% of the asymptotic value of total plant dry weight is attained bears some relatively constant relationship to the optimum plant density for grain production (Adelana and Milbourn (1972a). Eddowes (1969c) found that the two plant densities coincided with each other in Britain. American work suggests that the optimum population for grain production is the lower of the two (Rutger and Crowder, 1967; Williams <u>et al</u>, 1968; Bryant and Blaser, 1968; King <u>et al</u>, 1970). Coincidence or otherwise of these two planting rates depends on

whether the light (and temperature) environment favours reproductive growth more than vegetative growth or vice versa. The optimum stand density obviously depends very much on the type of growing season encountered.

There are considerable genotypic differences in population optima for grain yield. In any one environment small varieties (dwarfs, or early maturing) might be expected to have a higher optimum plant density for grain yield than large varieties (late matering). Results generally confirm this supposition (e.g. Duncan, 1954; Sowell <u>et al</u>, 1961; Colville <u>et al</u>, 1964; Brown <u>et al</u>, 1970).

Varieties with upright leaves intercept less light per unit leaf area than do those with horizontal leaves (Pendleton <u>et al</u>, 1968) and would be expected to exhibit a higher optimum density for grain yield (Dur. ..., 1969). A plant ideotype with upright leaves such as these is postulated of one which interacts weakly with its neighbour and uses its share of environmental resources efficiently (Donald, 1968). It is doubtful if neighbouring plants of such a 'pacifist' type would be able to compensate for a minsing or shall plant as adequately (Hozumi <u>et al</u>, 1955; Dungan <u>et al</u>, 1958; Giesbrecht, 1961) as the agressively competitive varieties at present in use. The use of such an ideotype should reduce the incidence of suppressed plants, · but would not alter the occurrence of misses in the stand.

General trends in planting optima related to plant size are comptimes reversed by a genetically based population 'tolerance' or 'intolerance'. Varieties tolerant and intolerant of crowding can be recognized within any maturity class of maize, and little is known of the reasons for the differences. The incidence of barrenness is much higher among intelerant varieties than tolerant varieties at high levels of population stream. Hybrids are more tolerant of high population pressure than open pollimeted lines (Stringfield and Thatcher, 1947). The inbreds Hy2 and UP9 are examples of lines tolerant and intolerant of high plant populations respectively. They confer these same characteristics on hybrids derived from them (Lang <u>et al</u>, 1956; Earley <u>et al</u>, 1966).

Many investigations into yield-density relationships in maize have confounded row width effects with those of planting density. Certainly, where planting rate is varied within a constant row width, this is the case. The need for a horse freeway between rows has disappeared, but in some cases 100 cm row widths have not. Such a row width gives a 13 cm spacing within the rows, at a planting rate of 75,000 plants/ha. A high rectangularity such as this undoubtedly causes unnecessary plant distortion above and below ground (Haynes and Sayre, 1956), and allows the waste of incident light on the ground between the rows. The trend towards more equidistant spacing of single plants is accompanied by an increase in optimum plant density for

grain yield (Hoff and Mederski, 1960; Pendleton and Seif, 1961; Brown et al, 1970; Stivers et al, 1971). Yield increases of up to 10% have accompanied the move towards equidistant spacing. The greatest increases are at the higher plant densities, when all other growth factors are adequately supplied (Dungan, 1946; Kohnke and Miles, 1951; Mederski et al, 1965; Colville, 1966; Lutz et al, 1971). Some hybrids seem better adapted to narrow rows than others (Brown et al, 1970; Stivers et al, 1971). There appears to be a greater yield response to row width reduction in short hybrids than in tall hybrids (Pendleton, 1965; Colville, 1966). Statistical significance of a hybrid x row width interaction is however seldom obtained (Thompson, 1967; Duvick and Noble, 1969).

1.5.2 Changes in Individual Plant Characters Associated with Internlant Competition for Light

Changes in plant characters in response to increasing competitive stress result from either cooperative intraspecific interaction, or compatitive intraspecific interaction (Black, 1966; Duncan, 1969), terms fill, used by Hozumi <u>et al</u>, (1955).

(i) Changes Associated with Cooperative Interaction

(a) Plant height: Hosumi <u>et al</u> (1955) noted that short mained and elongated at a more rapid rate than taller ones that were chading them. This was termed 'cooperative' interaction, because the shorter plants tended to catch up with taller ones, even though this was initially induced by competition for light. There appears to be a certain level of mutual shading at which a plant attains its maximum height (Dungan <u>et al</u>, 1958; Milliams <u>et al</u>, 1965a; Duncan, 1969). Increases in height as planting rate increases are normally 5% (Colville and McGill, 1962) or less (St. 1967).

(b) Ear height: Mutual shading appears to increase the length of internodes near the ear, but often shortens internode length above the ear. This results in the leaves (Williams <u>et al</u>, 1965a) and the ears being borne higher up the plant at higher populations. Increases in opical ear height of 15% have been recorded (Stringfield and Thatcher, 1947; Colville and McGill, 1962; Rutger and Crowder, 1967).

(c) Leaf Angle: Leaves are more erect at higher plant densities. This improves the lighting of leaves feeding the ear (Williams <u>et al</u>, 1965a; Loomis <u>et al</u>, 1968).

(ii) Changes Associated with Competitive Interaction

Although shorter plants grow in height more rapidly than tabler ones, the reverse tendency is observed in plant weight increase (heauni et al, 1955; Koyama and Kira, 1956). Duncan (1969) estimated that a 10 cm difference in maize plant height could reduce dry matter production by 20% at low populations and by 50% at high populations. Data from interplanted dwarf and normal varieties confirm the importance of plant height in plant competition (Pendleton and Seif, 1962). Beyond the level of mutual shading that produces maximum stalk elongation, plants become increasingly variable in height and weight (Koyama and Kira, 1956; Duncan, 1969). It is obvious that the level of competitive stress varies considerably from plant to plant within any one stand. This will affect a number of plant characters:

(a) Yield: Total weight per plant and total grain weight per plant Corease as planting rates are increased beyond the level where interplant competition begins. The harvest index increases alightly with provable density (Bryant and Blaser, 1968), up to that density which induces plant barrenness, beyond which hervest index falls rapidly (King <u>et al</u>, 1970). The rate of decline in per plant grain and total weights with increasing density will depend upon the environment and the variety grown.

Differential changes in components of yield occur as population stress increases. Among the components of yield, ear number is the most highly correlated with yield per plant (Colville, 1962). Increases in them, density reduce the number of ears per plant (Stickler, 1964; Colling et al. 1965; Rutger and Crowder, 1967; Hanway and Russell, 1969; Edde.... 19500). Population tolerance appears to be positively associated with ear prolificacy (Lang et al, 1956; Downey, 1971c; Adelana and Nilbourn, 1972a). Becauce ears abort acropetally and not all at the same relative rate, the crolific variety may continue to yield with the upper of its two or three cond, when the single-eared variety is completely barren, under comparable love of stress (Bauman, 1960; Zuber et al, 1960; Josephson, 1961; Collins et al, 1965). In general ear weight declines with increasing density, though Haynes and Sayre (1956) at increasing but relatively low populations record an increase in ear weight accompanying a reduction in ear number. The highest yields of grain have been produced by stands with an average ear weight in the range 130-240 gm (Haynes and Sayre, 1956; Dungan et al, 1958; Colville, 1962; Stickler, 1964; Rutger and Crowder, 1967). Kernel row number is little affected by increases in planting density (Stringfield and Thatcher, 1947), but the number of kernels per row is substantially reduced (Singh, 1969). This latter effect may be due to delayed cilking (Lang et al, 1956), or kernel abortion (Daynard et al, 1969) which progressively reduce the number of kernels per row as plant density increases.

Figures drawn from data presented by Colville (1962) further illustrate the interrelationship of yield components, yield, and planting density. When planting density of irrigated, well fertilized maize was doubled from 30,000 plants/ha to 60,000/ha grain yield per plant declined by 36%. Ear number and weight per ear both declined by 20%. This was accupanied, by a decline in car longth and diameter of 16% and 5% respectively. Over the same range of density increase, kernel weight and kernel number declined by 7% and 15% respectively. Linear regressions of kernel weight, and per plant and ear weight on plant density gave a highly significant fit to the data. In single cared variables it appears that kernel number/point is reduced less (comparatively) and kernel weight more by compatition than in multiple cared varieties, where car number is more variable (Markey ot al, 1966; Adelana and Milbourn, 1972a). Other studies indicate that the yield of grain per plant declines at an increasing rate as plant movelation increases (Duncan, 1958; 1969; Brown et al, 1970). There is little ' indication that maximum maize grain yield per unit area occurs which intraplant competition is minimal, as postulated by Donald (1963).

Components of total yield, excluding the ear fraction, also were with population stress. Wu (1971) noted that roots constituted 13% of a plant dry weight at 62,000 plant/ha, and 11% at 124,000 plants/ha (a 15% reduction). The ratio of stem to leaf at a given growth stage stays relatively constant over the range of commercial planting densities from and Blaser, 1968) but decreases significantly at densities up to 700,000 plants/ha (Williams et al, 1965a).

(b) Time to Flowering: Pollen shedding appears to be delayed about 0.6 day per 10,000 plants/ha increase in planting rate (Dungan <u>et al</u>, 1958; Colville 1962). The delay in silking is greater, being about 1 day per 10,000 plant/ha population increase (Stringfield and Thatcher, 1947; Kohnke and Miles, 1951; Lang <u>et al</u>, 1956; Dungan <u>et al</u>, 1958). The interval between pollen shedding and silking increases by 0.4 day per 10,000 plants/ha population increase. du Plessis and Dijkhuis (1967) demonstrated a negative correlation between the length of the period between 50% pollen shed and 50% silking, and grain yield. Moss and Stinson (1961) indicate that grain yield is very dependent upon the occurrence of normal silking.

(c) Leaf Area: Leaf area index continues to increase up to 700,000 plants/ha (Williams et al, 1965a). Stickler (1964) found that the combined

leaf area of the three leaves nearest the ear declined by 7% when plant density was increased by 50% from 40,000/ha to 60,000/ha. Data of Allison (1969) indicates that a 300% increase in planting density from 23,000/ha to 74,000/ha was accompanied by a 32% reduction in leaf area per plant and a 55% reduction in per plant shoot weight. A 400% increase in plant density from 24,500/ha to 98,000/ha was associated with a 70% decrease in individual shoot weight and a 56% decrease in leaf area per plant. Since the ratio of leaf weight to shoot weight is little affected over these population ranges (Bryant and Blaser, 1968), this in 10% an increase in specific leaf area, which has been reported as the shoet (Eddowes, 1969b).

(d) Stem Diameter: Steas become noticeably thinner at high plant populations (Colville and EcGill, 1962; Rutger and Crowder, 1967).

(e) Increased Lodging: At high plant densities maize plan ... have poorly developed roots and weak stems supporting an ear high up of the plant. It is therefore not surprising that lodging increases demonstrally as plant population increases (Milliams <u>et al</u>, 1955a; Rooman and Soda, 1966; Duncan, 1969; Downey, 1971c).

1.5.3 Intraspecific Competition in Maize and Plant Barranness

The decline in grain yield as plant population increased beyond the optimum occurs independently of barrenness, but barrenness causes the yield maximum to occur at a lower population density, and accelerates the decline beyond that point (Duncan, 1969). Four major methods have been used to investigate the factors controlling barrenness. They are: artificial shading, biochemical correlation, radio-tracer studies of assimilate distribution in the field, and induced male sterility.

(i) Studies in Artificial Shading: There is a striking parallell
 between the performance of maize hybrids in artificial shade, and their
 performance in dense stands (Stinson and Moss, 1960; Moss and Stinson,
 1961; Earley et al, 1966; 1967). Shade tolerance and population tolerance

appear to be closely linked. No differences between shade (and population) tolerant and intolerant varieties in ability to photosynthesize or to export sugar to the stem could be detected (Stinson and Moss, 1960; Moss and Stinson, 1961). Population tolerant and intolerant varieties both initiate ears normally at high rates of planting, but rates of ...k growth are remarkably different under intense shade stress (Sass and L. Fel, 1959; Moss and Stinson, 1961). This indicates that the period of late ear growth and fertilization is particularly critical in yield determination at high populations (Earley <u>et al</u>, 1967). This is further suph almost by the fact that at high populations (or under deep shade) tolerant critics outyield intolerant varieties in filled ear number per plant but not in weight per ear (Stinson and Moss, 1960).

Moss and Stinson (1961) point out that tolerant and intolerant varieties may differ in metabolic reactions occurring after photosynthesis, resulting in differences in the amount of assimilate channelled to the ear. Under stress conditions, total assimilate available is reduced and silk growth in intolerant varieties is retarded.

(ii) Biochemical Correlation: Attempts have been made to encrede to certain plant constituents with population or shade tolerance. Unipacyer et al (1962) found that shading reduced the carbohydrate conter and increased the mitrate content of maize, but data obtained fid that support the conclusion that nitrate assimilation was limited by the carbohydrate metabolism. In general shading affected nitrogen metabolicm to a greater degree than carbohydrate metabolism. The concentration of nitrate reductace in plant material has been found to be light dependent (Hageman et cl., 1961). Nitrate reductase is the enzyme responsible for the initial reduction of nitrate, so that eventually the nitrogen atom can combine with the carbohydrate moiety to form amino acids (Hageman et al, 1967). Increasing shade (and population) tolerance is accompanied by increasing levels of nitrate reductase (Zieserl et al, 1963). Nitrate content was found to increase and nitrate reductase to decrease in rough proportion to the level of shade obtained from dense planting or shade structures (Hageman et al, 1961). The level of nitrate reductase in plant tissue is heritable (Hageman et al, 1967). This suggests that grain production of tolerant hybrids at low light levels is more closely related to its ability to , reduce nitrate than to the effects of reduced carbohydrate supply.

(iii) Radiotracer Studies of Assimilate Distribution in the Field:
The only known study in this category was reported by Eastin (1969).
(See Section 1.3.3 for details). Data showing the percentage distribution
of photosynthate from fed leaves of plants growing at 52,000 plana/ind

and 104,000 plants/ha is presented in Table 1.3. Eastin suggests that vegetative growth still occurring in the plant grown at the high population was competing successfully with the ear for assimilate. An analysis of the leaf area distribution revealed that at the high population the upper five leaves had a total LAI of 2. Data of Williams et al (1965a, 1968) suggest that 50-60% of the incident light would be intercepted by these leaves and considerably less than half of the photosynthate generated, would make its way to the ear. The population-induced differences in assimilate distribution are very similar to differences between ecopact and normal maize types (Sowell et al, 1961). Such a situation of continued vegetative growth beyond silking obviously promotes barrenness at high populations, and coupled with increasing variability in the degree of suppression as population increases, leads to a rise in the propertion of barren plants. Obviously uneven planting will accentuate this problem.

(iv) Induced Male Sterility: It has been commonly observed that male-sterile plants are less likely to be barren. This has been related to the lower auxin activity in the tassel of male sterile plants which renders the tassel a weaker competitor for available photos...the sprior to silking than that of a normal male fertile plant (Mitchell, 1970). This in turn allows greater ear (and silk) growth. Combinations of 75% male sterile plants and 5% fertile plants to ensure fertilization have resulted in steads with a higher population tolerance (Anderson, 1967; Nitchell, 1970).

TABLE 1.3 (After Eastin, 1969)

C-14 Distribution after 4 days when various leaves are fed ...CO₂. Flant has 13 leaves and is in L-7 leaf axil. Stem 1 lies above the ear node and stem 2 below. Hybrid is DeKalb XL15A. Numbering is from the top down.

Growth stage is silking.

bensity: a 52,000 plants/ha b 104,000 plants/ha

Fed heat		L-1	L-3	L-5	EL	1-9	1244 1
Flant Part	Densi tv						
Stom 1	a	55	24	12	2	2	2
	ъ	34	28	15	1		1
Stem 2	a	14	11	21	35		
	b · · ·	11	21	30	$\cdot \not \land_{t} \not \land_{t}$	RT POL	
Root	• a		5	6	9		-10
	ď	2	6	8	7	36	10
Ear	a	23	49	54	39	×	, sy
	ъ	25	28	37	23		2
Fed Leaf	a	8	4	4	10	6	
and Sheath	Ъ	9	6	3	13	ê în	
lassel	a	8	1	4	1	ð.	*
	20	8	5	_			

C-14 Distribution as Relative Total Counts ()

1.5.4 The Quantitative Relationship Between Plant Population and

Yield.

Quantitative expressions of the relationship between crop yield and plant density are useful for two main reasons (Willey and Heath, 1969): Firstly, so that agronomic comparisons may be made between comparable levels of plant stress; and secondly, so that the yield density relationship can be predicted from a limited amount of data.

Willey and Heath (1969) have recently presented a comprehensive review of mathematical relationships put forward to explain the general relationship between plant density, and individual plant weight or erop yield.

Only one general model has been proposed to describe the response of maize grain yield to changes in plant density. Duncan (1958) found that the logarithm of grain weight per plant (w) was linearly related to density (p) up to 62,000 plants/ha:

$$w = k10^{bp}$$

01.

$$\log w = \log k + bp$$

where b is the coefficient of linear regression of log w with p, and k is a constant. Duncan was able to show that the population at which maximum grain yield occurred (^pmax) was inversely proportional to b:

$$P_{max} = - \frac{1}{2.303.5}$$

This enables the entire grain yield density relationship to be cormined from yield data obtained at two populations. Data from densitie the range 15,000 plants/ha to 62,000 plants/ha give a good fit to the relationship (Willey and Neath, 1969; Brown <u>et al</u>, 1970). Luncan (1950) pointed out that data obtained from plant densities outside this range tended to deviate from this relationship. The relationship could not satisfactorily explain the yield density data of Maynes and Sayre (1950), and cannot usefully describe the asymptotic relationship between could weight and plant density (Willey and Heath, 1969).

Reciprocal equations, based on some mathematical relation based on some mathematical relation based on the reciprocal of mean yield per plant and density are regarded to alley and Heath (1969) as offering the best possibilities for accurate and meaningful description of the yield density relationship.

Shinozaki and Kira (1956) were the first to propose a reciprocal equation:

$$w^{-1} = Ap + B$$
 \sum

where A and B are constants. This is identical to the equation provide a general mathematical expression which described parabolic and asymptotic yield density curves, Bleasdale and Nelder (1960.) proposed the modified reciprocal equation:

$$w = \Theta = Ap = B$$

where Θ and \emptyset are parameters having constant values for any particulation is set of data, and A and B are constants. The theoretical properties of such inverse power response curves have been discussed recently by Head (1970). Bleasdale (1967) has indicated that \emptyset might be taken as unity for practical purposes. The equation then becomes:

When G is less than 1 the curve described a parabolic yield density response. When G is greater than or equal to 1, an asymptotic yield density relationship is described. Thus this single expression is able to handle both of the generalized yield density response function.. Furthermore, the constants are claimed to have some biological meaning (Milley and Heath, 1969).

Kira et al (1956) noted that the logarithm of the weight of a plant part (log w_p) was linearly related to the logarithm of total weight.

$$\log w = \log k + a_p \log w_p \qquad \qquad \boxed{4}$$

where a_p and k are constants. This implies that an allowetric relationship exists between total weight and the weight of the plant part, brought about in this case by changing population constants. The author found that this equation adequately described allow arised at from a number of crops. If $a_p = 1$, the ratio w_p/w is constant. If a is less than 1, the ratio w_p/w is decreasing as density increased.

Bleasdale (1967), by substituting equation $\int 4\int$ into equation $\int 3\int$ has shown that the relationship among Θ_{part} , Θ_{total} and Φ_{p} can be expressed as:

i.e. where Θ total = 1, where total yield tends to an asymptote as density increases, a_p , the linear regression coefficient of the regression of log w on log w_p , is equal to Θ part. It follows that if both total weight per plant and the weight of a significant plant part are known for two plant densities, then the whole of the relationship between the yield of the plant part of interest and plant density can be estimated (Bleasdale, 1967). Where total weight is of interest, Θ is total by some routine which minimises the residual sums of squares (MINI) and Heath, 1969; Mead, 1970).

The modified reciprocal yield density equation has been successfully fitted to maize data, including that of Haynes and Sayre (1956) (Fery and Janick, 1971). In this case grain was taken as the plant part, and total shoot weight as total weight. The fit obtained was significantly better than that obtained using Duncan's (1958) equation. The validity of using the allometric relationship to determine Θ part when the plant part is not present throughout the whole life of the plant is questioned by Willey and Heath (1969).

CHAPTER TWO

METHODS AND MATERIALS

The first section of this chapter is devoked to describing the layout of the trial which was an investigation of effects of plant density on the growth and yield of two varieties of maize under field conditions. Fractices employed in growing the crop are listed.

Section 2 outlines the methods used in measuring growth of plant parts and plant development in the field and on harvested plants. This chapter concludes with a section describing the methods of statistical analysis employed during the examination of the data.

2.1 INTRODUCTION

2.1.1 The Experimental Site

The experiment was laid out on a block of flat land 0.22 ha in area, located in the microclimate plots of Plant Physiology Division, D.S.I.R., Palmerston North. The latitude of the site is 40° 23'S, and the altitude 30m above sea level.

The soil in the area is classified as Manawatu fine sandy loom, which at this site is non-uniform in character (J.D. Cowie, pers. comm). The soil profile comprises a very variable depth of fine sandy loam (up to 100 cm) overlying medium sand. Gravel is encountered 90-185 cm below the soil surface.

Temperature and rainfall data recorded at Grasslands Division, D.S.I.R., 1 km to the east of the site, and solar radiation data recorded at Plant Physiology Division 1 km to the NE of the site, are presented in Appendix 1 (a).

2.1.2 Experimental Layout

The experimental design consisted of a 5 x 5 latin square, allowing each of five treatments (spacings) to appear once in every row and once in every column of the design (i.e. 5 replications). A latin square was randomly selected from a number presented in Fisher and Yates (1963), and treatments randomly assigned to the five letters of the design. Each of the 25 main plots was split longitudinally for variety, and the two varieties were allocated randomly to one or other half of the split plot. The layout is illustrated in Fig 1. Plants were sown at five equidistant spacings using a string grid to ensure correct placement. The subplot width was a constant 2.28m, allowing a variable number of rows (4-6) to be sown. Since equal numbers of plants from the two centre rows of the subplot were sampled at each spacing main plots were uneven in length. The symmetry of the design however meant that all columns were of the same length. Details of plant spacings and plant densities are given in Table 2.1.

Allowance was made for four adequately guarded plants at each of ten previously designated sample points, while leaving two guard plants between sampling points along the row.

No special provision for access was made parallell to the rows of plants. A narrow access path was allowed at the end of each plot, and the ends of the plots and the whole perimeter of the area were protected by a further two rows of guard plants.

FIG. 1 Experimental Layout

Two varieties: K = KC3; W = W575Subplot numbers are 1, 2,.....49,50 Five spacings are 1, 2, 3, 4, 5

(see Table 2.1)

(a) Subplot Layout

Scale 1cm = 3m



(b) The 5x5 Latin Square

4	1	3	5	2
1	5	2	4	3
3	4	1	2	5
5	2	4	3	1
2	3	5	1	4

Numbers 1....5

Represent

Spacings 1....5

TABLE 2.1 Summary of Plant Spacings

Notation	<u>Equidista</u> <u>spaci</u>	nt plant	Plant Density				
	inches	Cm	Plants.ac-1	Plants.ha	a <mark>-1</mark>		
1	20.0	50.8	15682	38750	(39K)		
2	18.0	45.7	19360	47840	(48E)		
3	16.5	41.9	23040	56933	(571)		
4	15.0	38.1	27875	68889	(69K)		
5	14.0	35.6	32003	79082	(7917)		

2.1.3 Cultural Aspects

Details of cultural operations are presented in the schedule of operations in Appendix 2. The plot area had a previous history of cropping, and a crop of oats was cut from it in the spring of 1969 prior to the area being ploughed. A soil test carried out at ploughing indicated a sufficiency of calcium and phosphorus, and a marginal potassium deficiency. Following a normal cultivation, a total of 167, 161 and 182 kg/ha of elemental nitrogen, phosphorus and potassium respectively were applied in an effort to forestall iny nutrient deficiency. Chemical insecticide was incorporated into the soil prior to powing.

Seed of an early and a late maturing variety (KC3, and Wisconsin 575 (1575) respectively) was provided by Thomas Corson and Son Ltd., Globorne. TC3 is a modified single cross hybrid (G.J. Graham, pers. comm.), classified as an 80 day relative maturity variety. (The relative maturity rating is based on the number of days from emergence to physiological maturity when grown under test in the U.S.). U575 is classified as a 115 day variety and is a three way hybrid. Germination tests conducted prior to sowing showed final counts of 95% and 98% for KC3 and W575 respectively. Two seeds have sown at 5 cm depth at each planting station, using a hand planter. Because of the estimated time taken to sow and subsequently harvest and dissect plants, one column of the latin square was sown on each of five days, and all subsequent operations were carried out at the same time from sowing in all replications.

The first replication, or column of the design, was sown on 12.11.69. The rows of emerged plants were recognizable in all replicates 7 days after sowing. Pre-emergent and post-emergence herbicides (Appendix 2) were opplied as recommended (L.J. Matthews, pers. comm.), and complete weed control was maintained by the chemicals throughout the experiment. No post-sowing cultivation was carried out.
Transplanting commenced 9 days after emergence. Where plants were missing from projected sampling areas, plants sown concurrently with those in the plots, but in peat pots and sterilized potting mixture, were transplanted. Such plants were noted and avoided in subsequent sampling. Where guard plants were missing, transplants were made from positions where two plants had emerged. Conditions for transplanting were excellent, and no failures were observed, even though 3% of the total stand was transplanted. From a week after transplanting, plants were not visually identifiable from the others in the stand.

Transplanting and thinning occurred concurrently. By 12.12.69 thinning and transplanting were complete and healthy plants were growing at every planting station. No deaths of experimental plants were recorded during the remainder of the experiment.

The plants were individually side dressed by hand 39 days after sowing with 113 and 60 kg/ha of elemental N and K respectively. A visible magnesium deficiency was rectified by foliar application of gnesium sulphate.

Pests were a minor problem. Slug killer eliminated slugs invading the plot from its surrounds soon after establishment. Aerial application of insecticide in early March controlled minor infestations of corn ear worm (<u>Helicoverpa armigera conferta</u>) and army caterpillar (<u>Pseudoletia</u> <u>separata</u>). No infectious disease was observed in the crop throughout its life.

The season could be described as dry and warm (Appendix 1). Irrigation was applied to the whole plot prior to sowing and twice during each of the months of January and February. A total of 250 mm of water was applied on these occasions (see Appendix 2). In spite of this, the plants were visibly water stressed at some stages in their growth.

2.2 EXPERIMENTAL METHODS

Field observations were accompanied by sequential destructive sampling of plant shoots. The first harvest occurred 44 days after sowing, and the next three were spaced at about 10 day intervals. Harvests 5 and 6 were at fortnightly intervals, and harvests 7-10 were spaced three weeks apart (Appendix 2).

2.2.1 Field Observations

The plants were observed daily for tassel emergence, pollen shedding and silking. The number of days from sowing till 50% of the remaining plants eligible for sampling had emerged tassels, shed pollen, and had silked were recorded. The tassel was judged to be emerged when it was

visible in the whorl without manipulating surrounding leaves. Pollen shedding was considered to have occurred when anthers were exserted from the tassel spikelets. The first appearance of silks emerging from the tip of the prophyll indicated the occurrence of silking.

2.2.2 Measurements on Harvested Plants

At each harvest three plants were randomly selected from the three or four available at the sampling point chosen for that harvest. Sampling points were harvested in a fairly rigid sequence from one end of the plot to the other to facilitate the locating and counting of plants. The plants were cut off at ground level, labelled, and tillers, if present, were tied to the main stem. The 30 plants from the replicate harvested ' that day were transported to the laboratory for weighing and dissection. When small, the plants awaiting analysis were stored in a refrigerator at 1C. Later when plants became larger this proved impossible. Where irrigation requirements of the crop clashed with harvesting, plants were stored in a refrigerated room at 1C with cut ends immersed in buckets of water.

All harvests involved the total shoot except harvest 9, when the plant appeared dead, and only the ears were removed. The variables measured at each harvest are listed in Table 2.2.

(i) Photosynthetic Area: Fully expanded leaves were removed at the point of attachment to the leaf sheath, and area was estimated as follows:

Area = maximum length x maximum width x 0.73 (McKee, 1964) (the conversion figure of 0.73 is more accurately determined by McKee than the 0.75 of Hontgomery (1911), and Saxena and Singh (1965).

Leaves not fully emerged were divided into that portion exposed to hight, and that portion not yet exposed. The exposed portion was laid beneath a perspex sheet marked with a grid showing square centimetres. With the help of cardboard leaf shapes of known area, the exposed area of the leaf was measured directly. The remainder, attached to the stem formed a cylinder at harvest 1. The area of this cylinder was calculated from length and stem diameter measurements. In subsequent harvests the stem was regarded as a truncated cone. The stem base mean diameter was measured across the cut base and the mid stem diameter estimated from a regression of mid stem diameter on stem base diameter (Appendix 4). The photosynthetic area of the husks was neglected in these measurements. Tillers were treated similarly, but data were recorded separately.

In later harvests leaf margins, leaf tips and leaf sheaths became senescent. The area of photosynthetic tissue was measured directly, as before, neglecting senescent areas. TABLE 2.2 Variables Measured on Sampled Plants

FW = fresh weight

DW = oven dry weight

DNC = dry matter content on a fresh weight basis

Variable .	Harvest Number
Tiller Number	1-8, 10
Laminae Area	1-8
Stem base diameter	1-8
Length of leaf sheath covering stalk and base of tassel peduncle	1-8
Stem length to tassel peduncle base	1-8
Height of upper three ears on each plant	3-8
Node number of nodes bearing upper three ears o each plant	2-8
If tillers present, FW of tillers and mainstem	1-8, 10
FW, DW and DMC of stem	1-8, 10
FW, DW and DMC of leaves	1-8
FM, DW and DMC of tassel	2-8, 10
FW, DW and DMC of husk	3-10
FM, DW and DMC of dead leaves .	7,8,10
FM, DM and DMC of huskless ear	3 (KC3), 3,4 (W575)
DEC of grain	4-10 (KC3), 5-10(W575)
dos lo DMC	4-10 (KC3), 5-10(W575)
Cob to grain ratio (regression method)	5,6(KC3), 6(3575)
Cob to grain ratio (direct)	7-10
DW cob	7-10
DW grain	7-10
DW of 100 kernels	8-10

Measurements on grain-bearing huskless ears:

Ear number	8-10
Huskless ear length	· 8-10
Effective huskless ear length	8-10
Huskless ear base diameter	8-10
Number of rows of grain	8-10

(ii) Lengths and Counts: The stem lengths on the main stem and tillers were measured from the stem base to the point of attachment of the tassel peduncle. Ear heights were measured from the base of the stem to the ear-bearing node. The numbers of the nodes bearing the three heaviest ears on each plant counting from the base, were recorded. In later harvests, the length of the huskless ear was measured from the base of the cob to the apex. The effective huskless ear length was that length of the cob actually supporting grain. The huskless ear base diameter was also measured, as was the number of rows of grain on the ear.

(iii) Weights: Where tillers were present, the fresh weights of tillers and main stem were recorded and used as a basis for apportioning total plant dry weight between tillers and the main stem. With the exception of ears, plant components from tillers and the main stem were bulked within each plot for dry weight determination.

The shoot was dissected into the following components:

Leaves, including all unexpanded leaves and leaf sheaths above the stem apex, or above the point of attachment of the tassel peduncle prior to tassel emergence.

Stem, including leaf sheaths below the point of attachment of the tassel peduncle.

Dead leaves (non-green leaves).

Tascol, with tassel peduncle.

The ear, removed from its point of attachment flush with the stem.

The ear was separated into the husk and the huskless ear. The husk was easily removed by breaking the shank at its junction with the cob. The husk in this instance included the shank. Separation of cob and grain was not practicable until harvest 7. At harvest 5,a 4 cm section from the centre of the huskless ear of KC3 was removed. The grain and cob were dissected and dry weights determined (see below). Cob to grain ratios were determined for this variety from a regression of the 4cm cob to grain ratio on the total cob to grain ratio of the same ear when fully dissected (See Appendix 3). The proportion of cob and grain in the huskless ear was estimated using this regression.

At harvest 6 a similar practice was adopted for both varieties, the regression this time being the 4cm cob to grain ratio on total cob to grain ratio of different ears. The relationship between the two was generally poor, and analysis (not presented) showed differences in the slopes of the regressions for the two varieties to be significant at the 6% probability level. Separate regressions were used to estimate the proportion of cob and grain in the huskless ears of the two varieties (Appendix 3). From harvest 7, huskless ears were dried <u>in toto</u> in a forced draught oven at 850 for 72 hours and shelled by hand while still warm. The size of the maize plants prohibited oven drying while intact. Leaves, stems, husks and tassels from each subplot were proceed through a green feed chopper. Aliquots of the resulting chaff were dried in a forced draught oven for 48 hours at 850, along with samples of train and cob dissected from 4 cm sections of the centres of all care. Dry matter contents obtained on a fresh weight basis for each plot were used to estimate oven dry weights of whole plant components.

Kernel weights were determined on previously dried kernels. Four lots of 100 kernels from each plot were brought to a constant in fature content after 16 hours exposure to a temperature of 850, cooled in a desiccator, and weighed.

2.3 STATISTICAL METHODS

Following the calculation of individual plant dry weight components, data from the three plants per subplot were bulked, and punched into cards. All analysis described below was carried out with the all of the Massey University IEM 1620 computer. Some standard programmes were used in the analysis: others were written where necessary, and are available on request.

2.3.1 Preliminary Analysis of Data

Data from one of the subplots of KC3 spacing 5 were missine that variables measured throughout the experiment. Preliminary analyses of the data involved estimating the values for all variables for the missing plot, and examining the data to see if they satisfied the assumptions of the analysis of variance. For both operations the split plot aspect of the design was neglected and the layout was considered a normal latin square. The value of any observation (Y_{ijk}) may be written for this statistical model as:

$$\begin{split} \mathbf{Y}_{\mathbf{ijk}} &= \overline{\mathbf{Y}} + \mathbf{R}_{\mathbf{i}} + \mathbf{C}_{\mathbf{j}} + \mathbf{P}_{\mathbf{k}} + \mathbf{e}_{\mathbf{ijk}} \\ \overline{\mathbf{Y}} &= \langle \text{the overall mean} \\ \mathbf{R}_{\mathbf{i}} &= \text{the effect of the ith row (i = 1...5)} \\ \mathbf{C}_{\mathbf{j}} &= \text{the column effect (j = 1...5)} \\ \mathbf{P}_{\mathbf{k}} &= \text{the effect of the kth population (k = 1...5)} \\ \mathbf{e}_{\mathbf{ijk}} &= \mathbf{a} \text{ random error term.} \end{split}$$

Values for missing plots were calculated according to the usual formula (Snedecor and Cochran, 1967) from the latin square made up only of KC3 data for the particular harvest under consideration. Error degrees of freedom were reduced by 1 in all subsequent analyses of variance. In

the case where polynomials were fitted to KC3 data at the highest population, the degrees of freedom for error were reduced by the number of harvests involved.

In the analysis of variance it is assumed that row, column and treatment effects are additive, and that the random error values, e_{ijk}, are normally distributed with a mean of 0 and a variance of 6².

Residuals were calculated from main plot totals (i.e. varietal effects neglected) for all variables at several harvests, and were plotted on normal probability graph paper. Results indicated that weight, area, length and time to flowering data did not require transformation within harvests. Moisture content and tiller number data were transformed using arcsine transformation and the square root transformation respectively.

Arcsine transformation: $X' = \arcsin \sqrt{X}$ Square root transformation = $X = \sqrt{X}$.

The data were now ready for more definitive statistical analysis.

2.3.2 The Analysis of Variance

Data was analysed within harvests using an analysis of variance for a latin square with split plots. It was based upon the following fixed effects regression model:

 $Y_{ijkl} = \overline{Y} + R_i + C_j + P_k + e_{ijk} + V_l + (PV)_{kl} + e_{ijkl}$ where Y_{ijkl} , \overline{Y} , R_i , C_j and P_k are as before $e_{ijk} = a \text{ random mainplot error term}$ $V_l = \text{the variety effect of the lth variety (l = 1,2)}$ $(PV)_{kl} = \text{the interaction term between the kth population and the}$ lth variety.

eijkl = a random subplot error term.

All interactions among columns, rows and populations were dropped into the main plot error term, and all interactions involving varieties except the population x variety interaction were incorporated in the subplot error term.

The analysis of variance, and tests of significance were constructed and carried out as outlined by Snedecor and Cochran (1967). Standard errors for treatment comparisons between various means were calculated according to formulae presented by Cochran and Cox (1957). Differences .among means were tested for statistical significance at the 5% and 1% level of probability using Student's t-test. (Snedecor and Cochran, 1967).

2.3.3 Curve Fitting

Polynomials in time were fitted to the subplot means of variables from each of the two varieties. Where analyses of variance revealed no statistically significant population effect (i.e. data on stalk length, expanded leaf number and dry matter content), values were pooled for population within varieties. Otherwise polynomials were fitted to data from each variety at each population level.

Polynomials and accompanying analyses of variance were fitted to data using a least squares multiple linear regression computer programme described by Burr (1969). In addition to polynomial coefficients and analyses of variance, this programme also printed the inverse matrix, the covariance matrix and the multiple correlation coefficient for each succeeding degree of fitted polynomial.

The method used has been outlined in principle by Gandar (1970), and initially involved performing a two way analysis of variance on the data, based on a regression model of the form:

$$Y_{ij} = \overline{Y} + R_i + H_j + e_{ij}$$

where Y_{ij} , \overline{Y} , and e_{ij} are as before

 R_i = the effect of the ith replication (i = 1...5)

 II_{j} = the effect of the jth harvest (j = 1...10).

Polynomials of successive degree (from 0 to k) were fitted to the data from individual harvests. The general form of the regression was:

$$Y_{ij} = \overline{Y} + b_1 (t - \overline{t}) + b_2 (t - \overline{t})^2 \cdots + b_k (t - \overline{t})^k + e_{ij}$$

where $b_1 \dots b_k$ = partial multiple regression coefficients

t = the time from sowing in daysand Y_{ij} , \overline{Y} and e_{ij} are as before.

It can be shown (Snedecor and Cochran, 1967) that the sums of squares of the deviations of the $Y_{ij's}$ from the harvest mean ($\sum y^2$) can be partitioned into

(1) Sums of squares of deviations of values fitted by regression from their means ('sums of squares due to regression', $\sum \hat{y}^2$)

(2) The sums of squares of deviations from the fitted values. $(\sum d^2)$. i.e. $\sum y^2 = \sum \hat{y}^2 + \sum d^2$.

The 'goodness of fit' of the regression, and the significance of the

deviations from the regression of some variable on time can be tested against the within group mean square, as outlined in Table 2.3.

Polynomials of degree 0....k in time were tested in this manner. The value of k corresponded with the lowest degree of the polynomial at which the deviations from the regression were statistically nonsignificant. This provided a test of the null hypothesis that powers of $(t - \overline{t})$ creater than k explained none of the sums of squares due to deviations from the regression.

Examination of the data revealed that variability in dry weight components and total dry weight increased with time. The regression equations on which the analysis of variance and the polynomial fitting procedures were based were divided through by Jt. This was effective . in stabilizing the variance, but had the advantage over other more drastic transformations of not affecting the magnitude of the regression coefficients. In both cases polynomials of the form

 $\widehat{\mathbf{Y}} = \mathbf{B}_{0} + \mathbf{B}_{1}\mathbf{t} + \mathbf{B}_{2}\mathbf{t}^{2} \dots + \mathbf{B}_{k}\mathbf{t}^{k}$

where $\widehat{\Upsilon}$ = the estimated value $B_0 \dots B_k = polynomial coefficients$

were fitted to the data and used directly in later computations. Formally the same degree of polynomial was fitted to data for a particular variable in the interest of later computation. This meant that occasionally a non-significant term was included in the polynomial, or a significant term was excluded.

2.32 Analysis of variance for fitted polynomial of degree h in time, filted to data from n harvests and b replications.

source	df	SS	MS	F
Acan	1	SCA	MSM=SSM	MAS/s ²
Replications	b-1	SSC	CMS=STC/b-1	CHS/s ²
Harvests	n-1	SSH	ú.	
Regression	k	SSR	MSR=SSR/k	MSR/s ²
Deviations from	1			
regression	n-k-1	SSD=SSH-SSR	MSD=SSD/n-k-l	MSD/s ²
Within group	b(n-1)-n+1	SSE	$s^2 = SSE/b(n-1)-n+1$	

Fiducial limits of individual estimates from the polynomial were obtained according to the method outlined by Snedecor and Cochran (1967),

and Rao (1965).

$$\operatorname{Var}\left(\widehat{\mathbf{y}}\right) = s^{2} \left[\frac{1}{n} + \sum_{i=1}^{k} \sum_{j=1}^{k} (\mathbf{x}_{i} \cdot \mathbf{x}_{j}) \mathbf{c}_{ij} \right]$$

where

Var (\hat{y}) = variance of an individual y x_i, x_j = the ith and jth independent variables in the polynomial (t, t², t³...t^k) s² = the error mean square from the analysis of variance of the polynomial n = the number of y observations to which the regression was , fitted C_{ij} = the value of the ith row and jth column of the inverse

The standard error of the estimate of y is

$$SE(\widehat{y}) = \sqrt{Var(\widehat{y})}$$

matrix.

The approximate fiducial limits of \hat{y} were determined by multiplying SE (\hat{y}) by the two sided value of Student's t-distribution at the 5% significance level, with n - (k + 1) degrees of freedom (where n = number of harvests).

.3.4 Growth Analysis

Growth analysis parameters were derived by integration and differentintion of quartic polynomial curves fitted to leaf area data and cubic polynomial curves fitted to total, ear and grain weight data. The parent polynomials and the calculated growth analysis parameters were plotted using the graph output on the computer. Where $B_0 \dots B_3$ and $C_0 \dots C_4$ are polynomial coefficients of weight (W) and leaf area (A) curves respectively, the following relationships may be recognised at any instant of time.

1. The leaf area ratio is:

$$LAR = \underline{A}_{W} = \frac{C_{0} + C_{1}t + C_{2}t^{2} + C_{3}t^{3} + C_{4}t^{4}}{B_{0} + B_{1}t + B_{2}t^{2} + B_{3}t^{3}}$$

2. The leaf area index is:

LAI = L. RHO = $(C_0 + C_1 t + C_2 t^2 + C_3 t^3 + C_4 t^4)$. RHO where RHO is the number of plants per unit area

3. The unit leaf rate is:

$$E = \frac{dW}{dt} \cdot \frac{1}{A} = \frac{B_1 + 2B_2 t + 3B_3 t^2}{C_0 + C_1 t + C_2 t^2 + C_3 t^3 + C_4 t^4}$$

4. The relative growth rate is:

$$RGR = \frac{dV}{dt} \cdot \frac{1}{W} = \frac{B_1 + 2B_2t + 3B_3t^2}{B_0 + B_1t + B_2t^2 + B_3t^3}$$

5. The crop growth rate is:

 $CGR = \frac{dW}{dt} \quad RHO = (B_1 t + 2B_2 t + 3B_3 t^2) \quad Auto.$ The relative leaf growth rate (RLCR) was obtained by an analogous method. 6. The leaf area duration is:

LAD =
$$\int_{t_1}^{t_2} LAI \cdot dt$$

= $\begin{bmatrix} c_0 t + c_1 t^2 & c_2 t^3 + c_3 t^4 & c_4 t^5 \\ \hline 2 & 3 & 4 & c_5 \end{bmatrix}_{t_1}^{t_2}$

Fiducial limits for LAR, E, RGR, RLGR and CGR were calculated. An outline of the method used follows:

(a) The variances of A and W were calculated as in Section 2.3.3. (b) The variance of the growth rate $\frac{dW}{dt} = B_1 + 2B_2t + 3B_3t^2$

was obtained as in Section 2.3.3, using an application of the standard formula:

 $Var(ax + by) = a^2 Var(x) + b^2 Var(y) + 2 ab Cov(x,y).$ The value of $Var(\frac{dL}{dt})$ was similarly obtained.

(c) the variances of ratios such as $\frac{dW}{dt} \cdot \frac{1}{W}$, $\frac{dL}{dt} \cdot \frac{1}{L}$, $\frac{dW}{dt} \cdot \frac{1}{A}$ and $\frac{A}{W}$ were calculated using the standard formula for the variance of a ratio (Kendall and Stuart, 1958):-

$$\operatorname{Var}\left(\frac{\widetilde{X}}{\widetilde{Y}}\right) = \frac{\operatorname{Var}(X)}{\Upsilon^2} + \frac{\chi^2 \operatorname{Var}(Y)}{\Upsilon^4} - \frac{2 \operatorname{Lov}(2) \cdot \chi}{\Upsilon}$$

where X and Y are two variables.

The covariance term in the case of RGR and RLGR could be evaluated. The coefficient multipliers for the variance and covariance terms obtained as before from the inverse matrix, were calculated by multiplying the differential equation by its parent polynomial; so that, for example Cov ($\frac{dW}{dt}$, W) = Var (B₁)t + 2 Var (B₂) t³ + 3 Var (B₃) t⁵ + Cov (B₀, B₁) + 2 Cov (B₀, B₂) t + 3 Cov (B₀, B₃) t² + 3 Cov (B₁, B₂) t² + 4 Cov (B₁, B₃) t³ + 5 Cov (B₂, B₃) t⁴

As before $t_{(n-k-1)}$ (0.05) values were calculated and the approximate 95% confidence level of the ratio obtained.

In the case of the unit leaf rate and leaf area ratio, A and d were considered to be independent and the covariance term assumed therefore to be negligible. Degrees of freedom for the t(0.05) value were obtained from a mean value of k for the weight and area curves.

The relationship between E and LAI at flowering was investigated by fitting polynomials in LAI to unit leaf rate data obtained by growth analysis.

2.3.5 Dry Natter Contents

Polynomials in time were fitted to raw dry matter content data (see section 3.10) for both varieties using the method outlined above. Rates of increase in dry matter content were calculated and computer plots of the polynomials and rates were made. Approximate 95% confidence limits of the estimates were calculated as before.

2.3.6 Population Effects

Yield density relationships were empirically examined by fitting polynomials in density to yield data by the method outlined in the previous section which is similar to the empirical method outlined by Warren (1963). The regressions of the logarithm of grain weight per plant on plant density for each variety were calculated, and the optimum population density for grain yield was calculated as outlined by Duncan (1958).

2.3.7 Correlations Between Yield and Yield Components

Correlations between yield and individual yield components were calculated from the data from harvests 8-10.

CHAPTER THREE

RESULTS

In this chapter results from the experiment are presented in an order which is only approximately chronological. The early sections outline the growth and development of the total shoot while later sections contain data on grain yield, its relationship to plant density, and the field maturation of the crop.

Reference is made throughout the chapter to Appendices containing supporting information and selected analyses, and these can be found at the back of the thesis. Extensive use is made of fitted polynomials. Their coefficients, with samples of analyses of variance showing goodness of fit are also located in the Appendices.

3.1. INTRODUCTION

No plant deaths were observed in the period from the completion of transplanting to maturity. Lodging did not occur even at the highest plant densities. No data are therefore presented relating to establishment or to variations in plant number with time.

3.2. DAYS TO FLOWERING

Days from planting to 50% tasselling, anthesis and silking are given in Table 3.1 (a). Highly significant varietal differences for all these parameters were revealed in analyses of variance (Table 3.1 (b)). On average, tasselling, anthesis and silking occurred 12.8, 11.2 and 9.4 days earlier in KC3 than in W575. An increase in plant population was accompanied by a small but significant delay in tasselling and silking, the effect being greater in W575. By comparison the different population trends on time to anthesis in the two varieties proved non significant.

Variable	Variety		Pop	ulation			
		39K	48K	57K	59K	79K	S.E
Days to 50%	KC3	55.0	55.8	56.0	56.2	56.4	0.00
tasselling	₩575	67.2	67.8	68.8	69.8	70.0	0.00
Days to 50% anthesis	KC3	64.8	64.4	64.6	63.8	63.4	1 10
	W575	74.2	74.4	74.8	75.8	77.6	1.19
Days to 50%	KC3	64.0	65.0	64.8	65.0	66.0	0.54
silking	W575	73.2	73.0	74•4	75.4	76.0	0.74
Days from 50%	KC3	-0.8	+0.6	+0.2	+1.2	+2.6	
anthesis to 50% silking	₩575	-1.0	-1.4	-0.4	-0.4	-1.6	1.09

TABLE 3.1 (a) Days to 50% tasselling, anthesis and silking.

¹S.E. for comparison of means between or within varieties between populations.

·(b)	Analysis	of	variance	of	days	to	50%	tasselling,	anthesis	and
					silki	ıg		3		

Source	df	Mean Squares							
		Tasselling	Anthesis	Silking	Anthesis to silking				
Rows	4	11.000 **	8.420 ns	7.720 *	1.400 ns				
Columns ·	4	10.100 **	21.820 **	16.070 **	1.300 ns				
Populations	4	7.500 *	1.870 ns	9.120 **	3.350 ns				
Error 1	12	1.800	2.970	1.687	2.650				
Varieties	1	2061.00 **1	557.00 **	1113.92 **	36.980 **				
Var. x Pop.	4	1.420 ns	9.570 ns	2.120 ns	6.130 ns				
Error 2	19	1.895	4.074	1.084	3.316				
Total	48	* .05>P>.	01 ** P<.	01 ng	not significan	t			

The length of the interval between anthesis and silking differed significantly in the two varieties, silking preceding anthesis by 1.0 day in W575 but occurring 0.8 day after anthesis in KC3. The effect of plant population on this interval, though nonsignificant, suggested that the two varieties were responding differently in this respect.

3.3 GROWTH IN THE SIZE OF THE STEM

Analysis of variance of stem length (Appendix 5) revealed no significant population effect. Polynomial curves fitted to stem length data for each variety are shown in Fig 2(a) (coefficients are listed in Appendix 6). Stem length of KC3 significantly exceeded that of W575, atil KC3 had silked, following which the relationship reversed its rank. Stem growth rate followed similar trends.

A significant degree of stem growth occurred after 50% silking (Fig 2(a)), with the stem length of KC3 increasing by 17% and that of W575 by 19%.

Stem base diameter (Table 3.2) showed significant varietal and population trends. The decrease in stem base diameter with time can probably be attributed to a steady disintegration of basal leaf sheaths and mobilization of lower stem reserves.



DAYS

TABLE 3.2 Stem basal diameter. (cm)

Time	Variety	1 39K	opulatio 57K	n 79K	S.E. ¹	Variety+ Effect	Population+ Effect	
Day 55	KC3	3.11	2.86	2.67			**	
	W575	3.39	2.85	2.89	0.107	**		
Day 103	KC3	2.61	2.60	2.44			**	
	₩575	3.01	2.70	2.48	0.112	**		

¹S.E. for comparison of means between or within varieties between populations. ⁺From analyses of variance **P < .01

3.4 THE GROWTH AND LONGEVITY OF LEAF AREA

In this section, leaf area is defined as the area of the upper surface of green laminae plus the area of green stems and leaf sheaths.

3.4.1. Leaf Number, Area and Longevity, on a per Plant Basis.

Fitted curves describing the change in the number of fully expanded leaves on the main stem of the two varieties are plotted i. Fig 3(a) (see Appendix 6 for coefficients). Analyses of variance (Appendix 5) revealed no significant population effect after day 44. Highly significant differences between the varieties were apparent after the flowering of KC3. When all leaves had fully expanded, W575 on average bore 3.2 more expanded leaves on the main stem than did KC3.

The rate of appearance of expanded leaves on the main stem -103significantly exceeded that of W575 at day 45, but fell consistently from that time until at day 53 the rates coincided at 0.36 leaf.day⁻¹ (1 leaf every 2.8 days). The rate of expanded leaf production fell to zero at a point soon after silking in both varieties, the exact time being obscured by the inability of the fitted curve to reproduce the sharp ending of expanded leaf production. Similar varietal differences, though not as great, were apparent in the relative rate of leaf production (Fig 3(c), the displacement of the W575 curve in time by comparison with that of KC3 being similar to the difference between varieties in time to silking.

The fitted curves of leaf area per plant are presented in Fig 4(a) (See Appendix 7 for coefficients). Analyses of variance (Appendix 2) indicated that photosynthetic area per plant pooled for both varieties was nonsignificantly affected by population density. However, fiducial limits





(b) Rate of Relative Leaf Growth



of the fitted curves reveal that an increase in plant population from its lowest to its highest level significantly (.05>P>.01) reduced per plant leaf area in W575 but not in KC3. Highly significant varietal differences were apparent from day 65 onwards, and when growth in leaf area had virtually ceased 10 days after 50% silking, the average KC3 clant possessed 58% of the total leaf area of the average W575 plant at the same crowth stage. A small but steady decline in KC3 leaf area after this date, particularly apparent at the highest population, was not observed in W575.

The relative leaf area growth rate (RLGR) is presented in Fig 4(b). Significant varietal differences existed in the pretasselling state, and during senescence, though RLGR was little affected by plant spacing.

Although plant spacing generally had a small influence on loaf area, the ratio of leaf area to leaf weight, or the specific leaf area (SLA), increased significantly with plant population (Fig 5). In both varieties, SLA peaked at tassel emergence, and fell steadily from that point onwards. With one exception, at any one time during the grain filling period EC3 was characterized by thicker leaves (lower SLA) than W575. The period at which SLA responded with greatest sensitivity to plant population were and emergence, and the late grain filling period.

The percentage composition of total leaf area per plant for the varieties at three growth stages is illustrated in Fig. 6. The reduction in tiller leaf area components at high plant populations across by varieties was shown to be significant (Appendix 9) while main stor load area components were reduced only slightly (non significantly); the reduction of tiller leaf area from 30% and 20% of total leaf area at low populations in W575 and KC3 respectively to much lower levels was due to a fall in tiller numbers (Section 3.9) rather than a reduction in leaf area or se, and it was this variation that was principally responsible for the rietal and spacing differences in total leaf area composition. Analysis of arcsine transformed percentage composition data (not presented) revealed significant varietal differences in the proportions of stem and laminae areas. Stem area comprised a relatively constant 18.9% and 15.5% of total leaf area after flowering in the lowest population of KC3 and W575 respectively. At the highest population the stem area proportion was non significantly reduced to 17.2% and 14.0% respectively, due to a reduction in stem thickness (Table 3.2).

The time from planting till 50% of the maximum leaf area had genesced is given in Table 3.3. Spacing appeared to have little consistent effect on leaf senescence, but the photosynthetic area of W575 was maintained for significantly longer (8.4 days) than that of KC3.

FIG. 5 Specific Leaf Area

are standard errors for comparison between or within varieties between populations indicates time of 50% silking



FIG. 6 Percentage Distribution of Total Plant Photosynthetic Area

1,3,5 are populations of 39K,57K,79K plants.ha⁻¹ MS,ML are stem and leaf areas on the main stem TS,TL are stem and leaf areas on tillers

(a) 20 Days Prior to Silking



(b) At Silking



 1
 3
 5

 TS
 Image: second second

(c) 30 Days After Silking



KC3

W575

Variety		Popu	lation			Mean
and some that had a set	39K	48K	57K	69K	7 9K	
KC3	138.0	137.8	135.8	138.4	136.3	137.26
W575	142.8	144.7	148.3	145.4	147.1	145.66

TABLE 3.3 Days from planting to 50% senescence of maximum.photosynthetic area attained. (estimated from fitted polynomials)

3.4.2 Leaf Area Index and Leaf Area Duration.

The time course of leaf area index (LAI) is plotted in Fig.7, and analyses of variance of LAI are presented in Appendix 10. As would be expected, highly significant differences among plant populations and varieties were revealed. During the period of early grain filling, the KC3 canopy displayed on average 58% of the LAI displayed by W575.

Leaf area duration (LAD) from 50% silking till 50% of the maximum photosynthetic area was senescent is presented in Table 3.4. LAD increased consistently with plant population, and showed significant varietal differences.

TABLE 3.4	Leaf area duration from 50%	% silking till 50% of the max. Tur
đ	photosynthetic area was ser	nescent (days).
	(calculated from fitted po	lynomials)

Variety	Population							
*	39K	48K	57K	69K	7 9K	rican		
KC3	157.3	185.2	194.6	257.8	276.4	214.5		
W575	272.4	295.9	323.2	371.1	429.0	338.3		

Varietal comparison:

t = 3.45 * * (8 df)

3.5 GROWTH IN SHOOT DRY WEIGHT AND ITS COMPONENTS.

Included in this section are evaluations of relationships between weight and leaf area.

3.5.1. Growth in Weight on a per Plant Basis

The fitted curves of total shoot dry weight are shown in Fig 8(a) (Appendix 7 for polynomial coefficients). By silking, each variety had accumulated 38% of its final shoot dry weight. Analyses of variance (Appendix 8) revealed a reduction in shoot dry weight per plant at high

FIG. 7 Leaf Area Index

indicates time of 50% silking

L.S.D. (.05) of population 3

1,3,5 are populations of 39K,57K,79K plants.ha⁻¹



I I

5 3

150

DAYS

110

7

04 30

LAI

W575





populations, this effect attaining significance after day 35. At maturity an average KC3 shoot growing at 79K plants.ha⁻¹ weighed 70% of that of a KC3 plant growing at 39K plants.ha⁻¹. The comparable figure for W575 was 58%. Varietal differences in total shoot weight were apparent at 50% silking but became significant during early grain filling and were highly significant at maturity, when an average KC3 shoot weighed 78% of that of an average W575 shoot.

Relative growth rates (RGR) are shown in Fig 8(b). Calculated fiducial limits of the derived curves indicate that the slight decrease in RGR which accompanied increases in plant density within the range tested was not significant. During the grain filling period (day 75 to day 150) the RGR of the average W575 shoot significantly exceeded that of KC3.

Components of total shoot dry weight were influenced by variety and plant spacing. Analyses of variance of each component (Appendix 11) showed that the reductions in stem and leaf dry weights per plant accompanying an increase in population from 39K to 79K plants.ha⁻¹ were significant from day 55 onwards. Total ear, and ear components as they were differentiated, showed similar consistent significant decreases in dry weight as plant population increased. At maturity the weights of all individual KC3 shoot components, with the exception of tassel dry weight, were less than those of W575, although this ranking for stem and ear fractions was reversed during periods of their active growth. At anthesis the tassel dry weight of KC3 plants non significantly exceeded that of W575. Tassel weight rose sharply to a peak at anthesis and declined rapidly as pollen was shed. Because of shattering and weathering losses the weights of tassel and dead leaf fractions at the later harvests were not accurate, and these losses are probably the chief reasons for the decline in total shoot weight at the last harvest.

The changes in dry weight of stem, leaf, and the ear components will be considered in more detail in Section 3.6.

The percentage composition of total shoot dry weight at two growth stages is illustrated in Fig 9. Analyses of variance of arcsine transformed percentage composition data (not presented) indicated that at silking, significant differences between varieties in the proportions of tassel and leaf existed. KC3 was characterized by 9% tassel and 26% leaf, compared with 6% tassel and 30% leaf in W575.

At maturity (taken as day 145 for KC3, day 187 for W575), grain and total ear over the range of spacings comprised 51-54%, and 68-70% of total

1,3,5 are populations of 39K,57K,79K plants.ha⁻¹ S,L,D,T,H,C,G are stem,leaf,dead,tassel,husk,cob,grain,dry weight fractions respectively.





KC3 shoot weight respectively. Comparable figures for W575 were 44-51%, and 62-67% respectively, varietal differences being highly significant. Relative to W575, KC3 at maturity was characterized by a significantly lower percentage of stem, leaf and cob, and a significantly higher percentage of grain and tassel. Varietal differences in the proportion of husk and dead leaf at maturity were non significant. Increased rates of planting were accompanied by slight but consistent increases in the proportion of leaf, grain and dead leaf, slight decreases in the proportion of stem and husk, and no change in the proportion of tassel or cob. None of these responses to population density attained statistical significance.

Ratios of various dry weight fractions are presented in Table 3.5, and illustrate some of the above points. Cob to grain ratio differed significantly between the varieties, and showed a non significant decrease at high population densities. (For definitions of plant fractions, see p. 2.)

Variable	Variety	Po; 39K	pulation 57K	79K	S.E. ¹	Variety ⁺ Effects	Population ⁺ Effects
Total ear to remainder	KC3	2.40 .	2.21	2.21	0.34	**	ns
	W575	1.85	2.02	2.11			*********
Grain to stover	KC3	1.09	1.07	1.19	0.13	**	ns
	W575	0.83	0.98	1.07			
Cob to	KC3	0.186	0.166	0.172	0.024	**	ns
0	₩575	0.264	0.219	0.203	0.021		

TABLE 3.5 Ratios of plant part dry weights at maturity.

¹S.E. for comparison of means between or within varieties between populations ⁺From analyses of variance. ** P<.01. ns not significant None of the population x variety interactions was significant.

Growth analysis confirmed many of the above observations. Unit leaf rate (E), and leaf area ratio (LAR) with their fiducial limits are presented graphically in Fig 10. E was significantly (.05 > P > .01) reduced during rapid grain filling in both varieties when plant population was increased from 39K to 79K plants.ha⁻¹. E (KC3) significantly exceeded E (W575) over the same period. A halt in the decline of E with time was apparent during early grain filling in both varieties at low rates of planting. This

FIG. 10 (a) Unit Leaf Rate

indicates time of 50% silking

L.S.D. (.05) of population 3

1,3,5 are populations of 39K,57K,79K plants.ha⁻¹



period coincided with a time of declining irradiance (Appendix 1 (a)), when it would be expected that E would fall with time. LAR showed responses similar in degree but reversed in rank (i.e. LAR was significantly increased by plant density, and was significantly lower in KC3).

Analyses of variance (not presented) of polynomials in LAI fitted to values of E at silking for each spacing within each variety revealed that the quadratic term was not significant, and that a significant linear relationship existed between E and LAI. The regression equations of best fit were:

 \widehat{E} (KC3) = 10.603 - 0.956 LAI (r = 0.95*, 3 df)

 \widehat{E} (W575) = 8.419 - 0.600 LAI (r = 0.89*, 3 df)

A summary of the values of E predicted by these regressions, with appropriate fiducial limits, is presented in Table 3.6. Differences in unit leaf rate between the two varieties over an LAI range of 2-4 barely attain significance at the 5% level.

TABLE 3.6	Values	of	unit	leaf	rate	predicted	by	linear	regressions	of	E
			upon	LAI	at 5	0% silking.	. ((g.cm ⁻²	.day ⁻¹) x 10	⁴).	

Variety	Leaf Area Index					
	2	• 3	4	5	6	
KC3	8.69	7.74	6.78	5.82	4.86	
1575	7.22	6.62	6.02	5.42	4.82	
L.S.D. (.05) (mean over both regressions)	1.30	0.83	0.63	0.72	1.14	

3.5.2. Growth in Total Shoot Dry Weight per Unit Area.

Curves of total weight per unit area are presented in Fig 11(a). Analyses of variance (Appendix 10) showed that high density plantings significantly outyielded low density plantings from day 55 onwards. At maturity, yield of KC3 and W575 plants growing at 39K plants.ha⁻¹ was '70% and 85% respectively that of plants growing at 79K plants.ha⁻¹. Highest total yields were always obtained from the highest plant densities, and the total yield of KC3 per unit area at maturity was 78% of the peak yield of 25,500 kg.ha⁻¹ produced by W575 at the narrowest plant spacing.

Crop growth rates (CGR) are illustrated in Fig 11(b). CGR peaked near silking in W575, but a short time before silking in KC3. The derived curve in the preflowering phase, as indicated by the computed fiducial limits

- indicates time of 50% silking
- L.S.D. (.05) of population 3

1,3,5 are populations of 39K,57K,79K plants.ha⁻¹



(b) Crop Growth Rate



is not very reliable, and this possibly accounts for the continuous decline in growth rates among the high and medium population KC3 stands. The highest crop growth rates were always associated with the highest planting rates except in the late grain filling period. During early grain filling CGR was significantly lower at the lower plant densities, while over the whole grain filling period (day 70-150) the CGR of W575 at any one time significantly exceeded that of KC3 at comparable spacings. At their respective flowering dates the varieties showed no differences in their maximum crop growth rates, both being 290 kg. ha.⁻¹ day⁻¹.

3.6 GROWTH IN YIELD

The growth in total ear dry weight per plant is shown in Fig. 12(a). At 50% silking, both varieties had accumulated 6% of their final ear weight, this being made up of husk (and shank), cob, florets and silks. Analyses of variance (Appendix 11) revealed that KC3 ear dry weight significantly exceeded that of W575 at any point in time until day 125, when the total ear weight of W575 surpassed that of KC3. Increases in population density significantly depressed total ear weight. An increase in plant population from 39K to 79K plants.ha⁻¹ was accompanied by a reduction in total mature ear weight.per plant of 41% in W575, and 31% in KC3.

3.6.1 Grain Dry Weight per Plant

Growth in grain dry weight per plant is illustrated in Fig 12(b). The effects of population and variety (Appendix 11) paralleled these found for total ear dry weight. The reductions in mature grain weight per plant in W575 and KC3 when the plant population was increased from 39K to 79K plants. ha⁻¹ were 38% and 27% respectively. Grain weight of W575 exceeded that of KC3 for the first time at day 135.

Because of the difficulty in ascertaining the time at which grain growth rate fell to zero, the time at which 95% of final grain yield had been attained was chosen as a more precisely determined growth stage to which plant processes could be related. The times from planting and silking till 95% completion of grain filling are given in Table 3.7. These are obtained from curves fitted to grain weight data. Significant varietal differences were apparent in both periods, the grain filling period being 11.2 days longer in W575 than in KC3. The elapsed periods from emergence to 95% final grain yield for KC3 and W575 were 127 and 147 days, corresponding with accumulated effective degree day totals of 1043 and 1173 respectively (Appendix 1(b)).



indicates time of 50% silking

L.S.D. (.05) of population 3

1,3,5 are populations of 39K,57K,79K plants.ha⁻¹



The grain unit leaf rate, E (G), or the ratio of the fate of grain growth to leaf area, is plotted in Fig 12(c). Fiducial limits of this ratio indicate that no significant differences due to plant spacing existed, although the ratio generally fell with increasing plant density. Differences between varieties are apparent up to day 110. β (G) was significantly greater for KC3 during early grain filling, but in the later grain filling period was similar for both varieties. Comparison with Fig. 10(a) reveals that during the latter phase of rapid grain filling (day 90-110 for KC3, day 125-150 for W575), E (G) exceeded unit leaf rate by a non significant amount, indicating that grain growth rate in this period exceeded the growth rate of the entire shoot.

The grain leaf ratio, presented in Table 3.8, shows highly significant varietal differences, with less difference among spacings.

TABLE 3.7	Days from planting and from 50% silking till 95% maximum g	rain
	dry weight was obtained.	
	(from fitted polynomials)	

Variable 🔗	Variety	Population					
4		- 39K	48K	57K	69K	79K	
Days from	KC3	125	129	140	133	139	133.2
planting	₩575	151	157	149	155	156	153.6
Days from 50%	KC3	61	64	75	. 68	73	68.2
silking	₩575	78	84	75	80	80	79.4
95% of max.	KC3	6880	7990	8110	9580	10740	
grain yield (kg.ha ⁻¹)	W575	8690	10560	10340	10880	11210	

Comparison of varietal means:

Days from planting to 95% max. grain dry weight : t = 7.91 ** (8 df)Days from silking to 95% max. grain dry weight : t = 3.70 ** (8 df) TABLE 3.8 Grain leaf ratio (kg.ha⁻¹.day⁻¹) (calculated from fitted polynomials)

Variety			Population	n		
	39K	48K	57K	69K	79K	Mean
KC3	43.04	45.60	43.95	38.62	39.95	42.23
W575	30.23	34.76	31.09	29.19	25.59	30.17

Varietal comparison: t = 6.15 ** (8 df)

3.6.2 Changes in Dry Weight of Plant Parts During Grain Filling.

Fitted curves of dry weight per unit area for stem, leaf, husk and cob are shown in Fig. 13 (source polynomials listed in Appendix 12). Husk and stem showed consistent and considerable losses in dry weight during the latter period of grain filling in both varieties, while leaf dry weight, with the exception of the highest KC3 population, increased during the early part of the same period. Cob weight generally remained constant over this time except in the case of W575 at the widest spacing, where cob weight appeared to fall significantly.

A summary of changes in dry weight of the cob, husk, leaf and stem over the latter period of grain filling is given in Table 3.9. The net overall loss in dry weight from these parts in KC3 increased with plant density, while the loss in W575 seemed independent of population pressure. Table 3.10 summarizes net changes in stem and leaf fractions from silking till 95% completion of grain filling. In only one case, that of the high population KC3 treatment, did the weight of these fractions fall below their value at silking, and the loss of 366 kg.ha⁻¹ represented 3.4% of the final grain yield. In all other cases, the loss of dry weight in non-ear structures did not exceed their gain in weight immediately after silking.



<u>TABLE 3.9</u> Summary of changes in dry weight of non-grain plant components (kg.ha⁻¹) during the period from their peak dry weights after flowering till 95% total grain dry weight was obtained. (from fitted polynomials)

Variable	Variety		Nean '		
		39K	57K	79K	/
Stem	KC3	-192	-733	-1480	-801.7
	₩575	-317	-428	-854	-503.0
Leaf	KC3 *	+23	-28	-605	-203.3
	W575 *	+57	+85	+340	+160.7
Husk	KC3	-143	-339	-851	-44.3
	W575	-203	-97	-185	-161.7
Cob	KC3	0	0	0	0
	W575	-950	0	. 0 .	316.7
Net change	. KC3	-312	-1100	-2936	-1449.3 .
	₩575	-1413	-440	-699	-850.7
Net change as	KC3	• 4.53	13.56	27.33	16.89
% of 95% max.	₩575	16.26	4.25	6.23	8.43
grain weight					

* Till day 124 only.

(from fitted polynomials)

Variable	Variety	39K	Population 57K	n 79K	Mean
Stem	кс3	+1173	+730	– 18	+628.3
	W575	+1850	+1090	+ 1246	+1395.3
Leaf	KC3 *	+96	+120	-348	-44.0
	W575 *	+ 2 32	+149	+375	+252.0
Net changes in stem and leaf during 95% grain fill	KC3 W575	+1269 +2082	+850 +1239	-366 +1621	+584.3 +1647.3

* Till day 124 only.

<u>TABLE 3.10</u> Summary of changes in dry weight of stem and leaf fractions (kg.ha⁻¹) from 50% silking until 95% total grain dry weight was obtained.
3.7 YIELD AND YIELD COMPONENTS.

Yield of grain per unit area, and components of yield are presented in Table 3.11. Analyses of variance of components on a per that basis are given in Appendix 14. Reduction in yield per plant as population pressure increased was brought about by decreases in differing yield components in the two varieties. In W575, in contrast with KC3, it occurred principally because of a significant reduction in ears per plant : analysis revealed that this was due to a decrease in the number of second ears per plant (Table 3.12) which were more plentiful in W575 than in KC3. Contratently, the variety x population interaction for this component was highly significant (Table 3.13). The fall in yield per KC3 plant occurred, however, because of non significant reductions in grains per ear and weight per grain, as well as in ears per plant.

No significant effects of spacing or variety on weight per grain, or on grains per ear were found, though the average EC3 car cossessed 6% less grains per ear than did an average W575 ear. Within the ear itself, no significant differences were revealed in rows of grain, but a significantly greater number of grains per row were present in W575 ears. Grains per row were reduced non significantly by increased plant density over the range tested.

TABLE 3.11 Yield and yield components

(data pooled for the last three harvests)

Variable	Variety		Pop	ulation			s.e. ¹
8 		39K	48K	57K	69K	79K	*
Grain yield kg.ha ⁻¹	KC3	6772 (114.8)	8445 (143.2)	8554 (145.0)	9954 (168.8)	11041 (187.2)	
(bushels.ac at 15.5% MC)	₩575	8235 (139.6)	10287 (174.4)	10049 (170.4)	10829 (183.6)	10978 (186.1)	(14.47)
Grain.plant ⁻¹ (g)	KC3	174.7	176.5	150.2	144.4	139.1	21.48
	W575	212.5	215.0	176.5	157.1	138.	
Ears.ha ⁻¹	KC3	42120	49960	60720	70420	80840	3557
	W575	54250	61650	63250	70420	77320	
Ears.plant ⁻¹ $(x 10^2)$	KC3	108.9	104.4	106.7	102.2	102.2	7.03
	W575	140.0	128.9	111.1	102.2	97.	11.02
Grain weight.ear-1	KC3	160.4	169.1	140.8	141.3	136.6	20.57
(g)	W575	151.8	166.8	158.9	153.7	141.9	
Grains.ear ⁻¹	KC3	584	581	504	538	531	38.5
	₩575	572	606	590	591	554	
Rows of _1	KC3	17.693	17.342	17.155	17.288	17.9	0.430
grain.ear	₩575	17.389	16.898	16.862	17.190	17.050	
Grains.row ⁻¹	KC3	32.97	33.54	29.42	31.15	29.51	1.948
	W575	32.87	35.81	34.99	34.44	32.45	
Weight.grain ⁻¹ (x10 ²)	KC3	27.731	29.808	28.011	26.671	26.141	1.049
(g)	W575	26.238	28.037	27.558	26.635	26.291	

¹S.E. for comparison of means within or between varieties between populations

TABLE 3.12. Percentage composition of total ear number per plant. (data pooled for the last three harvests).

Variable	Variety			Populatio	on	
		39K	48K	57K	69M	7 9K
Apical ears	KC3	92.0	95.8	93.8	97.8	97.8
	W575	71.4	77.6	90.0	97.8	100.0
Second ears	KC3	4.0	2.1	-	-	2.2
*	W575	23.8	13.8	2.0	2.2	-
Tiller ears	KC3	4.0	2.1	6.2	2.2	-
	₩575	4.8	8.6	8.0	-	-

TABLE 3.13. Analysis of variance of total ear number per ha, number of second ears per ha, and total grain yield. (data bulked over last three harvests)

Source	df	Mean Squ	are	i.
		Total ears.ha-1	Second ears. ha ⁻¹ +	Grain kg.ha ⁻¹
Rows	4	1.970 x 10 ⁷ ns	4.523 x 10 ⁷ ** ·	2.145 x 10 ⁶ ns
Columns	4	5.970 x 10 ⁶ ns	$2.307 \times 10^7 *$	4.522 x 10 ⁵ ns
Populations	4	1.462 x 10 ⁹ **	$7.805 \times 10^7 **$	1.77° x 10 ⁷ **
Error 1	12	4.586×10^7	4.596 x 10 ⁶	2.580 x 10 ⁶
Varieties	1	2.590 x 10 ⁸ **	2.752 x 10 ⁸ **	$1.575 \times 10^7 **$
Var. x Pop	4	1.232 x 10 ⁸ **	6.346 x 10 ⁷ **	1.399 x 10 ⁶ ns
Error 2	19	1.740×10^7	1.220×10^7	1.060×10^6
Total	48			

* .05>P>.01 ** P<.01

+ Data square root transformed prior to analysis

ns not significant.

Correlations between yield per plant and various characters are presented in Table 3.14. Correlations between yield in KC3, and grain weight per ear, grains per ear and grains per row increased with planting density. On the other hand correlations between the yield of W575 and ears per plant, grains per ear and rows of grain per ear increased with plant density. The varieties as a whole showed other differences also. Yield in KC3 was closely related to grain weight per ear, grains per ear and grains per row, whereas yield in W575 varied closely with ears per plant and rows of grain per ear, as well as grain weight and number per ear. Variation in yield in both varieties showed only a small positive relationship to variation in weight per grain. There was a highly significant negative correlation between grains per row and row number in KC3 and W575 ($r = -.423^{**}$, $-.624^{**}$ respectively) indicating a degree of compensation for these characters.

Ear dimensions, and a summary of associated analyses of variance, are presented in Table 3.15. Cob length, and huskless car base diameter were significantly reduced as population increased. Effective cob length however was not significantly reduced by increasing plant density, nor did it differ significantly between varieties. As would be expected, the proportion of cob length occupied by grain differed significantly between the varieties, the effective cob length of KC3 and W575 being 97.6% and 87.8% respectively of total cob length. These proportions seemed little affected by plant density.

Correlations between ear dimensions and yield per plant appear also in Table 3.14. At low populations, cob length was more closely related to yield than was effective cob length. At higher populations the situation was reversed. Over all spacings there was little change in the correlations between yield and either of these characters.

3.8. NODE NUMBER OF NODES BEARING EARS, AND EAR HEIGHT

The numbers of the nodes (counting from the stem base) at which each of the three heaviest ears were borne are presented in Table 3.16. Plant spacing had no effect on the node at which any of the ears were borne, but W575 bore its ears an average of 2.33 nodes higher up the stem than did KC3. The data also illustrate the establishment of apical dominance among the upper ear primordia. At day 55, all three W575 ear primordia were approximately the same weight. By day 66, the upper two had become heavier than the third ear, and by day 89 the pattern observed at maturity was established in which the apical ear exceeded the second ear in weight, which in turn was heavier than the third ear. A similar pattern commencing about 10 days earlier was observed in KC3.

TABLE 3.14 Correlations of total grain dry weight per plant with various characters. (data from last three harvests).

L = Populations 39K and 48K bulked (28 df)

H = Populations 69K and 79K bulked (28 df) (25 df for KC3)

T = Bulked over all populations (73 df) (70 df for KC3)

Variable		Weight	t of grain p	lant ⁻¹		
-1	L	KC3 H	Т	L	м575 Н	Т
Ears.plant ⁻¹	•397 *	054	.260 *	•401 *	•567 **	.616 **
Grain weight. ear ⁻¹	•787 **	•956 **	•924 **	.668 **	.80.* **	.706 **
Grains.ear ⁻¹	•798 **	•924 **	.860 **	.660 **	• 5 82 **	.633 **
Grains.row ⁻¹	.362 *	•788 **	•674 **	.305	.065	.126
Rows of grain. ear ⁻¹	.423 *	.134	•254 *	.403 *	.647 **	.621 **
Weight.grain ⁻¹	.064	.171	•374 **	.286	.199	•344 **
Cob length	·659 **	.786 **	.783 **	•545 **	.518 **	.559 **
Effective cob length	•548 **	. 844 **	•777 **	•592 **	.640 **	•559 **
Huskless ear base diameter	• 347	.637 **	•599 **	•198		.162

* . 05>P>.01 ** P<.01

TABLE 3.15. Ear dimensions

(data	bulked	over	last	three	harvests)	
---	------	--------	------	------	-------	-----------	--

Variable	Variety	39K	Population 57K	79K	s.E. ¹	Variety Effect	² Popul- ation ² Effect
Cob length	KC3	18.93	18.26	17.36	0.749	**	*
(cm)	₩575	20.96	21.16	19.65			
Effective	KC3	18.56	17.67	17.02			
cob length	(%)	(98.0)	(96.8)	(98.0)	0.991	ns	ns
(cm)					(+)		
(S of cob	W575	18.12	18.97	17.14			
length)	(%)	(86.5)	(89.5)	(87.2)		(-)	
Huskless ear	KC3	5.29	5.18	5.05			
base diam-					0.100	104	*
eter (cm)	W575	4.93	5.10	5.05			

¹S.E. for comparison of means within or between varieties between populations. ²From analyses of variance. *.05>P>.01 ** P<.01 ns not significant None of the variety x population interactions was significant.

*Comparison of the varietal means of Effective cob longth x 100% cob length

following arcsine transformation: t = 9.78 ** (8df)

TABLE 3.16.	Numbers	of	the	nodes	at	which	the	three heaviest	ears	'C	borne.
	(number:	ing	is	acrope	tal)					

Day	Variéty	Heaviest	Ear Second	Third	Variety ⁺ Effect	Population ⁺ Effect
	KC3	4.67	4.59	3.67		
55	- Xe				**	ns
	W575	5.20	5.28	5.33		£
	KC3	5.49	4.49	3.49		
65					**	
	W575	7.39	7.33	6.33		
	KC3	5.68	4.68	3.68		-
89			1		**	ns
	W575	8.03	7.01	6.01		

⁺From analyses of variance. ** P < .01 ns not significant. There were no significant variety x population interactions. The heights of the ears above the ground are given in Table 3.17. Highly significant varietal and population effects were apparent in the heights of all three heaviest ears at maturity. When the plant population of KC3 was increased from 39K to 79K plants.ha⁻¹ it was accompanied by an increase of 25%, 34%, and 55% in the height at which the apical, second and third ears were borne. Comparable figures for W575 were 14%, 14% and 18% respectively. These figures indicate that most of the differences in ear. height were brought about by elongation of the stem below the third ear.

Variable	Variety	39K	Population 57K	79K	S.E. ¹	Variety ⁺ Effect	Pop- + ulation Effect
Apical ear height	KC3	63.5	67.5	79.3	6.13	**	**
	₩575	89.8	93.5	102.0			
Second ear height	KC3	45.3	49.1	60.7	5.18	**	**
	₩575	75.1	79.1	85.8			
Third ear height	KC3 W575	26.7 58.0	30.8 63.5	41.5 69.2	5.48	**	**

TABLE 3.17. Height of apical, second and third ears. (cm)

¹S.E. for comparison of means between or within varieties between populations ⁺From analyses of variance ** P<.01 There were no significant variety x population interactions.

3.9. TILLER NUMBERS AND TILLER GRAIN PRODUCTION

Tiller numbers per plant over three periods corresponding rough with presilking, early grain filling, and late grain filling are presented in Table 3.18. A steady decline in tiller numbers from day 44 throughout the life of the plant was observed at low and medium populations. At the highest population, tiller number increased into the early grain filling period but declined dramatically during the late grain filling phase. Both population and varietal effects were significant throughout the life of the plant, low populations and W575 being characterized by a higher tiller number per plant.

TABLE 3.18. Tiller number per plant.

Data for the three periods are bulked over harvests 1-3, 4-6, 7-10 respectively.

Period	Variety	39K	Population 57K	7 9K	Population Effect ⁺	Varietal Effe ct⁺
H 1 - 3	KC3	0.44	0.22	0.13	. **	*
	₩575	1.36	0.60	0.18		
	KC3	0.36	0.18	0.18		
H 4 - 6	1/575	1.07	0.38	0.22	*	*
	KC3	0.27	0.07	0.04		
Н 7-10	₩575	0.82	0.13	0.13	*	*

Results from analysis of variance of square root transformed data. There were no significant variety x population interactions.

* 0.05>P>0.01 ** P < 0.01.

The ratios of grain dry weight borne on tillers and the main stem to their respective dry weights at 50% silking are presented in Table 3.19. The ratio was much lower for tillers than for the main stem in both varieties. Although the ratio for the main stem of KC3 was higher than that of M575, the reverse was the case among tillers. When tillers sampled from harvests 2-7 were examined, it was found that 66% of KC3 tillers possessed staminate inflorescences instead of normal tassels, and were barren. Only 25% of W575 tillers exhibited this condition, which was not significantly affected by population in either variety.

TABLE 3.19. The percentage distribution of dry weight per plant between

the main stem and tillers of the two varieties.

- (a) Total dry weight at flowering.
- (b) Mature grain dry weight, bulked over the last three harvests.

Category	Variety	Main Stem	Tillors
(a) (%)	KC3	89.54	10.46
	W575	89.17	10.83
(b) (%)	KC3	98.67	1.33
и	W575	97.50	2.50
(c) $(g \cdot g^{-1})$	KC3	1.545	0.178
	1/575	1.261	0.266

(c) The ratio of mature grain dry weight to total dry weight at flowering (i.e. at 50% silking).

3.10. DRY MATTER CONTENTS OF PLANT CONSTITUENTS.

Analyses of variance of dry matter contents (DNC) of stem, 1000, prain, cob and husk were performed on raw data, and on arcsine transformed data (Appendix 15). As only slight differences existed in the variance ratios of the two sets of analyses, and no significant effects due to plant spacing were revealed, polynomials in time were fitted to the variant means of the raw data. These are plotted in Fig. 14, and the polynomials are listed in Appendix 16. Significant varietal differences existed between the dry matter contents of all fractions except the husk over most of the lives of the plants, with the KC3 fraction being drier at any one time from planting than the corresponding W575 fraction. Cob dry matter content establed that of the grain at a DMC of 39% and 36% in KC3 and W575 respectively. 95% completion of grain filling coincided with a KC3 grain DMC of 64, the comparable figure for W575 being a DMC of 68%.

A significant difference in the rate of increase in grain DMC was found (Fig. 14(c)). The grain of W575 increased in dry matter content at a significantly faster rate than that of KC3, despite the longer grain filling period of W575 (Table 3.7).

3.11 YIELD DENSITY RELATIONSHIPS.

The quadratic polynomial in plant density giving the best fit to grain yield from each variety pooled over the last three harvests is plotted in





Fig. 15 (coefficients Appendix 17). The curves suggest that the optimum plant density for grain yield was lower for W575 than KC3, and that the range of densities grown in this trial certainly did not encompass this optimum for KC3, though it may have for W575.

Linear regressions of the logarithm of grain weight per plast on plant density are presented in Fig 15(b), and the accompanying analysis in Appendix 17. The population optima for grain production calculated from these regressions (Duncan, 1958) are:

KC3 = 157683 plants. ha⁻¹ (63839 plants. ac⁻¹)

W575= 92125 plants. ha⁻¹ (37298 plants. ac⁻¹)





(b) Linear Regression of the Logarithm of Grain Weight Per Plant on Plant Density



L.S.D. (.05)

CHAPTER FOUR

DISCUSSION

A critical evaluation of some of the methods employed in the experiment and in analysis of the data precedes the general discussion of experimental results, and the conclusion.

4.1. METHODS.

These may be conveniently divided into experimental and statistical methods.

4:1.1. Experimental Methods

The results exhibited a high degree of variability, as even lified by data in Table 4.1.

.1. Coefficients of variation (3) for total shoot dry weight per plot at maturity, and total leaf area per plot at dry 103.

Variable	Variety	Population					
		39K	4 EK	57K	69K	7 9K	Nean
Total shoot	KC3	21.2	10.1	14.5	9.1	5.9	12.2
weight. plot-1	₩575	22.2	8.9	11.2	3.1	11.4	11.4
Total leaf	KC3	29.2	10.5	12.3	15.1	13.6	18.1
area. plot ⁻¹	W575	12.8	12.8	13.8	14.9	24.6	17.8

To the genetic variability of the plant material was added variation from at least three other sources:

(a) Environmental variation experienced by the replicates brought about by the sowing and sampling of a single replication each day for five days.

(b) An unknown degree of water stress experienced by the crop at and shortly after silking. The stress was unevenly applied within the crop because of the highly variable soil type. Results published by Baker and Musgrave (1964b) indicate that noon photosynthetic rates were probably reduced by 40% while the crop was water stressed and that fertilization and grain filling were affected to a variable degree (Robins and Domingo, 1953; Denmead and Shaw, 1960).

The relatively low correlations between the logarithm of grain ry weights per plant, and plant density (Fig. 5(b)) (cf Duncan, 1958; Brown et al, 1970) were probably mainly due to inherent variation from the two sources noted above. It is also probable that heterogeneity masked some real effects in the analysis of variance (e.g. spacing and varietal effects for some yield components).

(c) The indirect assessment of dry weights of plant components using a subsample of plant material to establish the dry matter content conindividual plant components introduced a source of error which can be eliminated in studies of smaller plants.

A serious omission in growth studies of this nature is any assessment of root growth. Furthermore, few inferences can be drawn from the literature concerning the role of roots in plant growth, as little comprehensive and accurate work has been done in this field. Root weight probably comprised up to $\frac{1}{2}$ of total plant weight prior to flowering, and 7-14% of total weight at maturity (Section 1.3.5). It is possible that roots may have formed a smaller proportion of total weight at maturity in the early variety, KC3 (Weihing, 1935). Omission of root dry weight data resulted in an underestimate of the growth analysis parameters, crop growth rate, unit leaf rate, and leaf weight ratio, and an overestimate of leaf area ratio, particularly in the preflowering growth phase. The precise role of roots in interplant and intraplant competition, though probably important, remains unknown.

A recent emphasis in growth analysis has been toward frequent small harvests of plant material in an effort to assess short term plant response (Hughes and Freeman, 1967), particularly where regression techniques of growth analysis have been employed. Harvest intervals employed in this experiment of 10-21 days imply that a degree of interpolation between sampling times must be exercised in interproting the results, and the results must be viewed with this in mind.

4.1.2. Statistical Methods.

The collection and analysis of data from two varieties planted on the same day but differing in rate of development poses a dilemma. A choice must be made between sampling and analysing data at one point in time when both varieties have experienced a common environmental influence, or sampling and analysis of data from comparable growth stages. Since the relative maturities of the two varieties in this environment were not known prior to the experiment, and because comparable growth stages are often not easily identified, the former alternative was chosen. Analysis of variance single harvest during active growth therefore generally showed high significant varietal differences.

Comparisons of plant data at similar growth stages was made possible through the use of curves fitted to data by multiple regression techniques, and the use of the calculated fiducial limits of these curves.

The regression technique has other advantages. As noted by Buttery (1969), the effects of sampling error are reduced by comparison with those apparent in the one way analysis of variance carried out on data from a single harvest. This is usually reflected in smaller, more consistent standard errors (Table 4.2).

TABLE 4.2 Comparison of standard errors calculated from fitted multiple regressions and from a one way analysis of variance. Example: KC3, 57K plants. ha⁻¹

Variable	Technique	Time (deys)						
		50	75	100	125	150	175	
Total shoot	Regression	5.40	5.78	6.04	8.37	16.92	11.99	
weight.plant ⁻¹	Anover	5.14	5.11	13.31	12.71	27.46	4.19	
Total leaf	Regression	176	155	191	299			
area.plant ⁻¹ (cm ²)	Anovar	334	135	310	153			

Smaller treatment effects can be distinguished. This is a particularly useful attribute when considering rates of change, or ratics of rates of change in time (Buttery, 1969).

While the regression technique in no way improves the original data, the smoothing of short term variations inherent in the curve fitting method proved to be advantageous in this instance. Variation spurious to the objectives of the experiment and induced by a varying degree of water stress was reduced, and the effects due to intended long term treatments were clarified. One possible disadvantage of the technique could have been the loss of relevant detail. However, since most of the variation was apparently due to short term environmental fluctuations whose effects are hard to identify, little information of explanatory value was masked by the fitting of curves.

The technique does have other limitations. The general shape of the fitted curve largely reflects the type of mathematical expression upon which it is based. (e.g. Williams, 1964). Polynomials as a group are characterised by a high degree of symmetry which is atypical of many biological responses. For example, in Fig. 3(a) it appears that fully expanded leaves continued to appear after flowering. As previously noted, the fitted polynomial of low degree is unable to duplicate the abrupt ending of expanded leaf appearance shortly after flowering. It is possible that the choice of inverse polynomials (Nelder, 1966) or of expressions which tend to an asymptote as time increases indefinitely (Richards, 1950) is the mathematical bases for fitted curves may have resulted in a more satisfactory biological fit to the data, though subsequent analysis would have been more complex. More frequent sampling of data would have also curtailed the freedom of the selected mathematical expression in dictating the shape of the fitted curve.

LIBRARY MASSEY UNIVERSITY Curve fitting occasionally involves a compromise between statistical goodness of fit and biological reality. Polynomials of high degree may fit data well, but the shape, and particularly the slope (rate of change) may be biologically meaningless, and consequently a poorer statistical fit may be preferred. An example of this occurred in this experiment, where cubic polynomials gave a more realistic fit to grain weight data, although fourth order polynomials resulted in a significantly better statistical fit. On the other hand, low order polynomials can oversimplify a biological situation. An example of this may have occurred with cob day weight (Fig 15(d)), although the real situation is not known. In this case deviations from the mean in all cases except that of the lowest population 3575 treatment were non significant, and the fitted means masked slight but consistent declines in cob weight with time, which may have been the result of a more complete separation of cob and grain material at later harvests.

It has been noted (Gandar, 1970) that where polynomials are initial to transformed data and growth parameters calculated from detratafor of quantities, the values of the growth parameters are influenced by the transformation employed, because different sums of squares are minimized in the curve fitting routine.

For example, the polynomial in time (t) fitted to total shoct dry weight data (\mathbf{Y}) on a per plot basis from M575 population 4 was:

 $\hat{\mathbf{Y}} = -5.446 \times 10^2 + 1.109 \times 10t + 5.502 \times 10^{-2} t^2 - 3.767 \times 10^{-4} t^3$

When the regression equation was divided through by \sqrt{t} , the polynomial of best fit became

$$\widehat{Y} = -7.456 \times 10^2 + 1.769 \times 10t - 8.746 \times 10^{-3} t^2 - 1.921 \times 10^{-4} t^3$$

In the first case the sum of squares minimized in fitting the regression to data from n harvests and m replications was

$$\sum_{i=1}^{n} \sum_{j=1}^{m} \left[\mathbb{W}_{ij} - \widehat{\mathbb{W}}_{i} \right]^{2}$$

In the second case the sum of squares minimized was

$$\sum_{i=1}^{n} \sum_{j=1}^{m} \left[\frac{W_{i,j}}{\sqrt{t_{i}}} - \left(\frac{W_{i}}{\sqrt{t_{i}}} \right) \right]^{2}$$

As apparent above, the two curves differ, and give rise to different growth rates, which may lead to different interpretations being placed on the data. The mild transformation applied to the weight data in this experiment did not result in meaningless growth rates. This was not, however, the case when the more extreme logarithmic transformation was applied to data prior to regression analysis.

In this experiment the advantages of curve fitting as an aid to data analysis considerably outweighed the disadvantages, and the technique was instrumental in clarifying treatment and varietal responses. When associated with the computer plotting of the continuous function with time, curve fitting becomes a powerful graphic aid which explains the dynamic changes of parameters far more clearly than do the methods of classical analysis.

4.2. EXPERIMENTAL RESULTS

A superficial examination of the growing crop indicated that U575 was a large, leafy, late maturing variety with a tendency towards tillering and a semiprolific habit, while NC3 was a small, less-leafy, early maturing variety generally exhibiting a single-eared uniculm habit.

The results of the experiment revealed other important varietal differences, and these will now be discussed in detail.

4.2.1. Growth, Composition and Longevity of Photosynthetic Area

There was a striking varietal difference in the total loaf area (i.e. total photosynthetic area) per plant (Fig 4). An average mature M575 plant possessed 72% greater leaf area than a comparable MC3 plant, the advantage being due to a 31% advantage in leaf number on the main stem, a 16% advantage in mean leaf size, and a greater total contribution of stem area and tiller leaf area. Husk area, neglected in this experiment, was unlikely to have been more than 2-4% of total leaf area (van Eijnatten, 1963; Allison and Watson, 1966) and was larger in total for W575 than MC3. Because the husk is borne in the deep shade of the canopy the effect of neglecting this component was considered small.

The larger number of leaves borne on the main stem of M575 reflected both a more rapid average rate of expanded leaf appearance (1 every 5.4 days, vs. 1 every 5.9 days for KC3), and a longer period from emergence to flowering (Table 1) (Bonnet, 1960). The greater number of tillers produced by M575 (Table 3.18) was probably responsible for the slower rate of expanded leaf production (Fig 3(b)) in this variety 5-7 weeks after sowing. The rate of leaf production in KC3, though high initially, fell off at an earlier

date relative to silking than that of N575. Whether this was related to the disproportionately large growth of the tassel and car fractions of NC3 by silking (Fig 9) is not known, but it may have been a cause or a result of this. The data suggest the possibility that either compatition between vegetative and reproductive growth was more intense in the later variety, or that sites of reproductive growth in the early variety pousecoed a clear cut advantage over sites of vegetative growth in attracting (vallable assimilate. Specific leaf area (SLA) data (Fig 5) suggest that the growth in KC3 laminae area continued during this period at the example of laminae dry weight. Accepting that SLA (a measure of leaf thickness) reflects in part the state of intraplant competition (de Vit et al, 1969), data presented in Fig 5 indicate that the former of these two hypotheses is the mest plausible at or shortly after silking, and that the latter hypothesis may well represent the mechanism by which reproductive growth of IC3 was so favoured. The temperature regime and the supply of other factors such as nutrients and water would also have contributed in an undetermined measure to the pattern of leaf growth.

Relative leaf growth rates (Fig 4(b)) showed similar treads in both varieties. Because RLCR includes tiller leaf area, the absence of an early advantage accruing to KC3 is further evidence of intraplant stread induced by the greater demands of tiller formation in W575. The values for RLCR recorded for both varieties prior to flowering compare favourably :10° those reported by Duncan and Hesketh (1968) in a controlled environment of the strength of the streng

The principal response of leaves to varying plant population pressure was not one of reduced area (Fig 4) or number, but of thickness (March As plant population was increased from low to intermediate levels, there was a significant reduction in tiller number, particularly in V575 (Table 3.18), and a correspondingly significant reduction in leaf area per plant in the larger variety (Fig 6). Leaf area is far less responsive to changes in light intensity than is leaf weight (Blackman, 1961; Pendleton <u>et al</u>, 1966; 1967; Friend, 1966; Earley <u>et al</u>, 1967).

The lack of any significant spacing effect upon leaf number is indicative of a situation in which interplant competition was low prior to tassel initiation. This finding does not contradict that of Eik and Hanway (1965), which indicated that leaf number fell slightly as planting consity increased. Unfortunately, no statistical analysis accompanied their lata.

The composition of total leaf area per plant differed significantly between the varieties (Fig 6), the chief differences being due to the higher tiller contribution in W575, particularly at wide plant spacings.

The smaller proportion of stem area in this variety was due to its larger leaves and shorter internodes, the average length of an internode supporting a leaf being 12.7cm in this variety and 14.0cm in KC3.

Changes in the distribution of total leaf area between the laminae and the stem as plant population increased reflect changes in stem diemeter (Table 3.2) resulting in stem area declining more rapidly than laminae area.

The course of leaf area index with time (Fig 7) emphasizes the long period in which a high stable LAI value is maintained during great filling in the maize crop. The small non significant increase in L.1 of word in W575 during grain filling but prior to senescence appeared to be the result of continued growth in tiller leaf area. Conversely, the decline in leaf area observed in KC3, which attained significance at the narrowest plant spacing, was seen to be caused by the death of lower leaves on the main stem. This pattern of senescence at high plant densities is similar to that observed by Allison (1969), and may have been due to the reduced water uptake and induced premature senescence. Alternatively, it may have been due to a high level of intraplant competition, which was sufficient to mobilize lower leaf components (Kess and Peaslee, 1965) and to thus promote senescence.

Leaf area duration after silking (Table 3.4) reflected differences in LAI of the different stands (Fig 7), for little consistent variation in leaf longevity could be attributed to treatment effects (Table 3.4). Leaf area durations reported here are similar to those obtained electrone for maize (e.g. Adelana and Milbourn, 1972 b) but considerably exceed those reported for small grain cereals (e.g. Gandar, 1970).

Allison (1964) contended that maize is a high yielding crop in part because of the long functional life of its leaves. It appears that this may also be one of the major reasons for the high average maize yields in New Zealand (Berger, 1962) (See Introduction). Both varieties in this trial displayed near maximum leaf area for an average of 10 weeks after silking (Table 3.3). This was 1-2 weeks longer than that reported in Rhodesia (Allison, 1969; Allison and Weinmann, 1970), 3 weeks longer than that reported by Eik and Hanway (1965) in Iowa, U.C.A., and is similar to that reported from Southern England (Adelana and Milbourn, 1972 b). It also seems probable that leaf longevity in the cool environment of the Tetherlands was greater than in the present experiment (Andrew <u>et al</u>, 1956), though no confirmatory data are available.

These data do not suggest that the rapidly shortening autumn day length of the higher latitudes dominates plant senescence, though this obviously will have some effect (Krizek et al, 1966). An explanation supt be sought through some other environmental parameter. Andrew et al (1956) attributed the long plant longevity apparent in the Netherlands to lower surver temperatures and higher humidities. A comparison of mean monthly temperatures and accumulated degree days at Vageningen, Visconsin (Andrew other, 1956) and Massey University in the years appropriate to the respective experiments is given in Table 4.3.

TABLE 4.3. Average monthly temperatures and accumulated degree d is it the end of each month at three sites. Sources: Andrew et al, (1956); Appendix 1b.

		Average	Nonthly Te	mperature (с).		
			Nonth				1
Site	November	December	January	February	Marel.	April	Mon
Visconsin	10.9	19.2	20.3	20.9	14.7	12.4	16.4
Magoningen	13.7	16.6	18.1	16.9	14.5	12.3	15.0
Massey	14.3	18.1-	19.2	17.8	18.0	14.7	17.0
	Acc	umulated De	egree Days	from 1st Nor	vember (C)	l
			Month				
Site	November	December	January	February	Harch	Arril	
Wisconsin	64	339	657	992	1144	12	
Wageningen	130	329	580	801	936	1000	
Massey	159	410	701	916	1172	1332	

The climate at Massey University was characterized by cooler average temperatures in the late summer, with only a gradual fall in mean temperature in the autumn. Additionally, the average temperature during the season reported from Wisconsin exceeded 26.7C (80F) on three occasions, while the maximum average daily temperature at Massey was 23.6C. Leaf longevity appears to be inversely related to environmental temperature (e.g. Frougham, 1958 Ъ).

It seems probable that the rapid fall in temperature during the autumn in continental climates, in combination with a rapid shortening of the

photoperiod, constitute a thermoperiodic and photoperiodic stimulus that hastens senescence. The more temperate conditions prevailing in maritime countries not only lengthen leaf life, but, in the case of New Zealand, provide good conditions for grain filling for an extended period into the autumn. The comparatively disease free conditions in this country also contribute to long leaf life.

4.2.2 Changes in Total Shoot Dry Maight and Its Corponents.

The 28% superiority of 3575 in total shoot weight stored from a longer period of growth at a greater rate than NC3. Assuming the 95% maximum shoot dry weight was attained at the same time as 95% menimed grein dry weight (Table 3.7), the 20 days additional growth by 3575 were evenly split between the presilking and post silking periods. The men. crop growth rates of NC3 and 3575 from planting until 95% of the maximum dry weight had been obtained were 128 kg.ha.⁻¹ day⁻¹ and 148 kg.ha.⁻¹ day⁻¹

The shoot weight advantage of M575, although apparent from day 60, did not attain statistical significance until early in the grain "Alling period, and from that point on, the total shoot weights of the to verifies diverged at an increasing rate. Reductions in total shoot dry weight in response to increased density of planting did not attain statistical significance until day 55. This was considerably later than the time when interplant competition is thought to begin (Eddowes, 1969 b), and though some interaction between individuals may occur very early in the life of the crop, it does not appear to significantly suppress total shoot growth until LAI values of 1-2 have been obtained. Under conditions of lower light intensity and reduced nutrient supply interaction between plants may well reduce dry weight per plant at lower LAI values. The influence of plant density in the range tested upon total shoot weight of the larger variety was considerably greater than that experienced by KC3, a finding which is consistent with differences in plant size (Section 4.2.6). The major initial reduction in plant weight as spacings narrowed was in the tiller component. This was followed by reductions in all main stor components.

Individual components of the total shoot weight of the two varieties (Fig 13) differed significantly at maturity. When mature, all shoot components of KC3, with the exception of tassel dry weight, weighed less than their W575 counterparts. The composition of total shoot weight (Fig 9) reveals that the early variety (KC3) was characterized by a lower proportion of vegetative structures and a higher proportion of reproductive structures when compared with the late variety. Significantly different total ear to remainder ratios (Table 3.5) for the two varieties reinforce this observation, which applies generally to varieties of contracting maturity (Bryant and Blaser, 1968; Adelana and Milbourn, 1972 b). Then crowded, both varieties appeared to respond by diverting assimilate from emporting structures (stens, husks) to structures more directly related to reproductive growth (leaves and grain). Thus the support struct res appeared to buffer the plant against competitive stress which threatened the production of grain.

Crop growth rates (Fig 11) peaked prior to silbing in 203, 1 - shortly after silking in the late variety. The precise point of maxium 212 in KC3 is obscured because it occurred near the end of the range of the independent variable, time. Literature on comparable trials is a rade. From data supplied by Allison (1969), CCR appeared to peak at differ, but data of Williams <u>et al</u> (1968) indicated that CCR peaked 10-20 days prior to silking. Adelana and Milbourn (1972 b) found little change in CC: from 20 days prior to silking until 35 days after silking, though at no 100 did CCR exceed 240 kg.ha⁻¹ day⁻¹ in this cool English environment.

The timing of the peak crop growth rate will obviously be influenced by trends in radiation and temperature, and these could expl in variations present in the literature. In the present trial however the two varieties appeared to be reacting differently in this respect. The previously noted reduction in the vegetative growth of KC3 prior to silking (Section 4.2.1) coincided with rapid early growth of the ear fraction (see Fig. 12a), the net effect being a steady decline in CC2. Conversely, the high CGR of W575 near silking appeared to be at the expense of early ear growth, and was due to vegetative growth which continued at a considerable rate over this period. In this respect W575 and KC3 resemble <u>normal</u> and <u>connact</u> maize types. The vegetative growth of <u>compact</u> mains has been reported as ceasing abruptly in favour of ear growth at flow ring, while the continuing vegetative growth of <u>normal</u> maize beyond this time appeared to penalize early ear growth at high plant densities (Scall and Ohlrogge, 1961).

Table 4.4 summarises appropriate growth rates across all spacings for each variety, and illustrates the observations made above.

TABLE 4.4

The distribution of total shoot crop growth rate (CGR) between the ear and the remainder of the shoot for each variety for population 3 (kg.ha⁻¹.day⁻¹). (from fittel curves).

A: 10 days prior to 50% silking Time B: 50% silking C: 10 days after 50% silking

Fraction	Variety		Time	
		Α	- B	C
Total shoot	KC3	262.8	245.9	226.6
	W575	253.4	261.0	250.2
Total shoot	KC3	90.3	70.8	52.9
minus ear	1/575	173.1	130.2	02.0
Far	KC3	172.5	175.1	1.24.7
	· W575	80.3	130.8	168.2
LSD (0.05)		2		
Ear *		73.35	46.36	29.21
Frection				

* For population 3, pooled for both varieties.

Crop growth rates of the two varieties at the highest plant density were equal at silking, at 290 kg.ha⁻¹.day.⁻¹. According to Loomis <u>et al</u>, (1971) this represents an efficiency of conversion of absorbed photosynthetically active radiation of 6.1% in this environment. The maximum total shoot production of 25,500 kg.ha⁻¹ corresponds approximately with an annual efficiency of conversion of absorbed PAR of 3.0% (Loomis <u>et al</u>, 1971). In terms of total dry weight the late variety with its higher mean crop growth rate clearly utilized incoming radiation more efficiently than KC3 during the course of the growing season (cf. Ustenko and Yagnova, 1967), though this ranking may well have been reversed if KC3 had been planted at a population producing a mean LAI equal to that displayed by W575 (Section 4.2.3). In terms of grain production, both varieties utilized incoming radiation with a similar efficiency, KC3 having the advantage at high plant densities.

4.2.3. Growth Analysis.

Growth analysis attempts to relate the increase in dry weight on a per plant or per unit area basis to the efficiency of the photosynthetic system (the unit leaf rate), and to some measure of the size of that system.

Using the notation of Section 1.2.3. two general relationships are recognized, viz:

CGR = E. LAI (whole crop approach) and RGR = E. LAR

(single plant approach)

• where $LAR = SLA \cdot LMR$.

This type of analysis places considerable dependence upon the adequacy of the surface area of photosynthetic surfaces as a measure of the size of the photosynthetic system. Recent symposia (See Refs A and C have emphasized that spatial orientation of photosynthetic elements is of considerable importance, and becomes at least as important to photosynthetic area at LAI values encountered at the higher plant densities of this experiment. Literature surveyed in Section 1.3.2 underscores this point. Other workers indicate that the size of mesophyll cells simplificantly influences photosynthetic rate (Vilson and Cooper, 1967).

A further assumption inherent in growth analysis is that all photosynthetic areas have equal productive capacity. It is well known that old leaves are less efficient photosynthetically than young leaves, though the influence of age on leaf efficiency appears to be less marke. In maine than in many other species (Moss & Peaslee, 1965). Leaf sheaths a maine are probably less efficient per unit area than laminae. Contain, this is the case with barley (Thorne, 1959). Maine leaf sheaths comprise 14-20% of total photosynthetic area, yet Mitchell (1970) states that they are responsible for 6-10% of total photosynthate, the inference being that they are less efficient than laminae. Orientation of photosynthetic surfaces obviously plays some part in this case, and Mitchell's statement is not accompanied by supporting data.

Thus leaf area index, while a useful quantitative measure of canopy size lacks qualitative definition when used as the sole description of the size of the plant photosynthetic system. Reference has already been made to the effects of neglecting root weight data in growth analysis. It must therefore be with these limitations in mind that growth analysis is used as an analytical tool.

The ways in which crop growth rate changed with time have been referred to previously. Early trends were dominated by a rapid rise in leaf area index (Fig 7), while in the phase of declining crop growth rate LAI was generally static, and E declined as the leaves aged and the levels of radiation and temperature fell (Appendix 1a). The higher average CGR of W575 throughout the period of active growth was entirely attributable to the considerable advantage in mean IAI enjoyed by this variety throughout the season.

Significant varietal differences in crop growth rate prior to silking when LAI values were similar, imply that fundamental differences in unit leaf rate were present. A problem exists in that unit leaf rate is a dependent variable, and its value is itself influenced by LAI. This is demonstrated by the differences in unit leaf rate induced by interplant competition (Fig 10) which are principally the result of different levels of mutual shading among stands of differing LAL. The relationship between E and LAI in maize has been shown to be curvilinear (Williams et al, 1968; Buttery, 1970), but when, in the present study, polynomials in LAI were fitted to E at silking, the curvilinear term failed to account for a significant amount of the variation in E. Because mean LAI values of the two variaties differed considerably at silking it is reasonable to expect linear regressions of E on LAI to differ in slope. Nevertheless differences in the predicted values of E at the LAI values within the range of both varieties (LAI = 3-4) differed significantly at the 55 level (Table 3.6). Further verification of a varietal difference in E was sought by comparing F for the two varieties at a comparable level of mutual shading (LAI = 2.00)corly in the lives of the plants. The results, presented in Table 4.5, i licate that the unit leaf rate of 1575 was approximately 90% that of KC3.

TABLE 4.5

Unit leaf rate and leaf area ratio when LAI = 2.00. (E obtained from fitted curves. LAR obtained from actual values by linear interpolation between day 44 and day 55).

X03							
	1	2	3	4	5	Mean	3 a 1
Ξ	10.42	12.97	13.55	12.51	17.80+	13.45	
T.A.R	83.53	111.58	117.25	124.73	132.67÷	113.05	
Day	52.9	48.0	47.8	44.0	42.94	47.2	
575			Spacing				,
	1	. 2	3	4	5	Nean	
т <u>.</u>	11.05	10.26	10.54	15.80	11.64	11.86	
7.AR	120.93	131.93	126.44	140.07	136.09	131.00	
Day	47.2	46.8	46.4	46.2	44.8	46.3	

+ Extrapolated.

Comparison of Varietal Means (8df)

E t = 1.010 hs LAR t = 1.893 hs Days t = 0.509 hs

Deleting NC3 pop. 5, %575 pop 4 because of atypical E values: Varietal Comparison (6df) E t = 1.997 significant at 10% level LAR t = 2.043 significant at 10% level Days t = 0.841 ns

Canopy efficiencies may be compared by examining the decline in 7 as LAI increases (Buttery, 1970). Taking the mean value of E at LAI = 2.00 as 100%, E at LAI = 4.0 (from Table 3.6) was 50.4% and 50.7% for KC3 and 1575 respectively, indicating that no gross differences in canopy structure existed between the varieties at that growth stage, and over that range of LAI. Simulation studies sugrest (Duncan <u>et al</u>, 1967; Duncan, 1971) that the influence of leaf angle on productivity is slight at these LAI values.

At comparable growth stages, leaf area ratio was consistently less for KC3 than for W575 (Fig 10 and Table 4.5). Since, as McCree (1969) moints out, whole plant respiration is made up of a component proportional to current photosynthesis (which is equated with total leaf area in growth analysis) and a component proportional to the total weight of the plant, as IAR falls so the ratio of whole plant (respiration/photosynthesis) increases. This suggests that either the unit respiration rate or the root to shoot ratio of KC3 was considerably lower than that of W575, or that the gross photosynthetic rate in KC3 exceeded that of W575 by an even greater margin than did the unit leaf rate. All three alternatives are possible. (Wu, 1971; Weihing, 1935; Heichel and Musgrave, 1969 respectively), but the latter seems the most probable explanation. The positive relationship between leaf thickness and net photosynthetic rate which has been reported in Lolium (Wilson and Cooper, 1967) offers a possible explanation of these differences, for, with the exception of the period at tasselling. MC3 was characterized by thicker leaves than W575 at comparable growth stages (Fig 5). Relative values of leaf thickness may however merely reflect the levels of mutual shading in the two varieties.

Because unit leaf rate represents the quotient of two fitted polynomials, variation in the value of E may possibly reflect variations in the curves which are properties of the mathematical expressions rather than having any physiological basis. The reliability of the estimate of E depends very much upon the accuracy with which the two curves of weight and leaf area describe the raw data (Gandar, 1970). It seems probable, however, that the delay in the seasonal decline of E with time observed among KC3 plants at the widest spacing reflects the influence of increased sink capacity upon unit leaf rate. As noted previously, the level of intraplant competition appeared low among this group of plants at silking. The increasing demands of the developing ear during early grain filling appeared to raise the level of intraplant competition (as shown by the halt in the decline in specific leaf area in Fig. 5) which possibly resulted in an increase in unit leaf rate. The phenomenon of apparent assimilate control of net photosynthetic rates has been observed in maize and other species previously (Neales and Incoll, 1968). In view of the rapid fall in LAR during this time, this may reflect a considerable increase in gross photosynthesis and/or, root to shoot ratio. The absence of any comparable effect among KC3 plants at higher densities is consistent with the higher basal level of intraplant competition present at higher plant densities.

W575 showed a similar effect, but less marked and less affected by plant spacing. Such a response seems indicative of some stimulus upon unit leaf rate provided by the growing ear against a background of already considerable intraplant competition caused by a higher level of mutual shading and more rapid vegetative growth in this variety. Alternatively this apparent varietal difference could reflect some difference in sink gradient towards the ear consistent with the observation that of the two varieties, individual plants of the early variety sustained a more consistent level of reproductive growth over the range of spacings tested.

Trends in relative growth rate can be analysed similarly. The small but significant RGR superiority of W575 during grain filling was due to the large differences in LAR between the varieties which more than offset the lower unit leaf rate of W575 during most of the grain filling period. The large varietal differences in LAR themselves arose from substantial differences in the proportion of total shoot weight made up by the leaf fraction (Fig 6), and a small advantage to W575 in specific leaf area (Fig 5). This is not the complete picture however, as SLA and leaf weight ratio refer only to laminae, and LAR is based upon total photosynthetic area. The general effect of plant population density on these growth analysis parameters could be predicted from earlier observations that LAR and LAI increased with plant density, and that E accordingly fell. The increase in LAE was almost matched by a fall in E, the net result being a nonsignificant reduction in RGR at high plant populations. Nonsignificant increases ' in the leaf weight ratio, and significant increases in specific leaf area were the basic causes of the rise in LAR with plant density.

The relationship between the changes in grain dry weight and plant leaf area is open to similar investigation. The value of the grain unit leaf rate, E (C), illustrates important differences between the two varieties during grain filling (Fig. 12c). Although this parameter is entirely analagous to X, it refers only to changes in the grain dry weight fraction. In conjunction with E, this parameter yields information on assimilate distribution from the leaves and other plant sources to the developing grain. Although comparison of the absolute growth rates of total plant shoot and gr in fractions yields similar information, relating the absolute growth rate to the basis of leaf area per plant provides additional information on the efficiency of leaf area in grain production. It is this parameter, integrated over the time from flowering to maturity, that is the basis of the grain leaf ratio, G, proposed by Watson <u>et al</u> (1963).

In this experiment the mean value of G for KC3 was 40,5 higher than that of W575. This difference could be related directly to the higher average value of E (G) for VC3 which significantly exceeded that of U575 from at least 25 days to 50 days after silking. This difference between the varieties arose from the LAD of KC3 being 63%, but the grain yield being 89% of comparable W575 values. The shallow peak in G (Table 3.8) observed in both varieties across the range of spacings was probably due to the low harvest index of the tillers (Table 3.19) which were plentiful at wide spacings (Table 3.18). The progressive fall in G as plant density increased beyond 46% plants.ha⁻¹ is analagous to the observed fall in E and E (G) as leaf area index increased, leading to a rise in the lovel of rutual shading.

The absolute values of E (G) and G have little value in comparisons between species or between environments. Their variability is indicative

of the tenuous relationship which exists between leaf area index and crop growth rate during grain growth, particularly in maize in which barreness can be induced more readily by mutual shading than in those cereals which bear their grain in terminal inflorescences above the leaf canopy and whose grain has a significant photosynthetic capability. Both C and E (C) however have indicated that some difference exists in the distribution pattern of assimilates within the plant. Whether this difference is merely due to differing levels of mutual sheding, or whether it reflects more fundamental differences in distribution patterns arising from differing levels of intraplant competition or differing levels of sink "emptiness" connot be determined from these data. Considerable varietal differences in assimilate distribution patterns have been shown to exist (Eastin, 1769).

In spite of its limitations, growth analysis has proved useful in identifying fundamental varietal differences in unit leaf rate, and in the efficiency of leaf area in producing grain. More refined investigations are necessary to clarify the relationships between crop growth rate and leaf area index, and to verify differences in photsynthetic efficiency and initiate distribution in these varieties.

7.2.4. The Growth of Grain Vield ..

Comparison of mean E (G) values (Fig 12), and mean E values (Fig 10) reveal that B (G) exceeded E from at least 25 days to 50 days after silking in HC3, and from 50 days to 70 days after silking in M575. Consistent offects of plant population density in the time when E (G) returned to equality with E wore observed in HC3, E (G) exceeding E for a longer oriod at narrower plant spacings. No corresponding response to plant. Jonaity was exhibited by M575.

The later stages of grain filling in both varieties were accompanied by a considerable loss in dry weight from the remainder of the plant, specially the stem and husk, but in rare cases from the leaf and cobfractions (Fig 13). This loss began 30-40 days after silking, and continued for a considerable period after 95% maximum grain weight was attained (Table 3.7). A balance sheet of losses in dry weight from non-grain components during grain filling reveals that the loss expressed as a proportion of final grain yield was higher for KC3 than W575, and that this proportion increased consistently with plant population density until at the highest density the combined weight of stem and leaf fractions fell below their weight at 50% silking. No correspondingly consistent response to crowding wer observed in W575.

It is an interesting and pragmatic hypothesis to link these observations in a cause and effect sequence, and propose that the husk and stem act as sources of labile reserves which are mobilized under conditions of internal stress imposed by grain filling. It must be noted however that exchanges of assimilates with roots over this period are unknown, though some root growth has been reported during grain filling (Foth, 1962).

Accepting a figure for the conversion of reserves to grain of 0.5 (Duncan et al, 1965), a maximum figure of 13.7% of final grain yield of KC3 at 79K plants.ha⁻¹ may have been derived from reserves mobilized from the remainder of the plant shoot. The corresponding mean values for EC3 and W575 are 8.4% and 4.2% respectively, and are similar to those found elsewhere (Kiesselbach, 1950; Daynard et al, 1969), though somewhat less than those reported by Adelana and Milbourn (1972 b). The estimates of the contribution of mobilized assimilate to grain yield in the present trial are conservative. The last 5% of total grain yield thus far unaccounted for was almost certainly not derived from current photosynthesis, in view of the continuing decline of stem and husk weight beyond the time then 95% final grain yield was attained (Fig 13), and the rapid senescence of leaf area close to this time (Table 3.7).

Varietal differences in the pattern of dry weight loss from non-grain shoot structures may reflect differences in the mobility of reserves, or differences in the outcome of competition for vegetative and reproductive growth in the two varieties. Alternatively, they may indicate function of the differences in the ability of the developing ear to attract assimily on the differing costs to the remaining plant structures, so that ear group was maintained in high density EC3 plants at the expense of the lower leaf reserves, and consequently leaf area (Fig. 4).

The anomalous loss of cob dry weight from W575 at the wide spacing (Fig 13) is in part an artefact of curve fitting (Section 4.1.2). A tentative explanation is that this significant loss of weight reflected a high level of competition between developing ears in plants which at this spacing were semiprolific in habit, and which led to an increased mobilization of cob reserves. The loss is greater than that reported by Manson (1967), who worked with a variety of unspecified prolificacy.

The length of the period from silking to 95% maximum grain yield differed by 11.2 days between the varieties (Table 3.7), and is consistent with the suggestion that late varieties have a longer grain filling period (Gunn & Christensen, 1965). The average length of the period of grain filling considerably exceeded the average length of time required for grain filling in the United States, (Kiesselbach, 1949; Shaw & Loomis, 1950; Hillson & Penny, 1965) and is more comparable to that found in Rhodesia (Manson, 1967). This is consistent with the greater longevity of the leaves (Section 4.2.1). In the present trials the fitted polynomials of grain weight on time indicated that the mean periods from planting to 100% grain filling were 155.0 days and 169.7 days for KC3 and W575 respectively. These were 21.8 days and 16.1 days respectively after 95% completion c rain filling, i.e. considerably longer than the 12-13 days reported by Hillson and Penny (1965) in the U.S.A.

Varietal differences in final mean grain yield per unit arc. are almost entirely due to differences in the length of the grain filling period, as the mean grain growth rate over the grain filling period was 127 kg.ha⁻¹.day⁻¹ and 130 kg.ha⁻¹.day⁻¹ for KC3 and W575 respectively. This confirms that variations in maize grain yield in any single environment can be principally related to the length of the grain filling period rather than the rate of filling (Hanway & Russell, 1969).

4.2.5. Yield and Yield Structure.

The average grain yields of both varieties (8953 kg.ha⁻¹ dry weight or 151.8 bu.ac⁻¹ at 15.5% MC for KC3; 10076 kg.ha⁻¹ or 170.8 bu.ac⁻¹ respectively/for M575) are higher than average for the district, though no allowance for losses of grain during harvest is made in this experiment. It is, however, obvious that maize can be grown successfully for grain in the Manawatu.

The relative values of the yield components (Table 3.11) are surmarized in Table 4.6, and indicate the source of yield differences. Ear number per plant was the primary component principally responsible for the yield superiority of W575, and it was in the incidence of second ears on the main stem that the varieties differed most. Nonsignificant differences in the remaining primary yield components accounted for the rest of the yield differences. The small advantage of W575 in weight of grain per ear sense from a larger number of grains per ear which more than offset the all with lower weight per grain. Within the ear, the number of rows of grain were similar, and the greater number of grains per ear found in W575 arose from a significantly greater number of grains per row.

Variable	Varietal Means	Comparison Population	Neans	
	KC3/W575	KC3. 39K/79K	W575. 30K/79K	
Grain. area ⁻¹	0.889	0.613	0.750	
Primary Component	3			
Plants. area-1	1.000	0.490	0.490	
Ears. plant ⁻¹	0.904	1.065	1.431	
Grains. ear ⁻¹	0.940	1.100	1.032	
t. grain ⁻¹ 1.027		1.061	0.998	
Secondary Compone	ents			
Grain. plant ⁻¹	0.873	1.251	1.531	
Ears. area ⁻¹	0.930	0.521	0.702	
Wt. grain. ear ⁻¹	0.968	1.174	1.070	
Rows grain. ear ⁻¹	1.024	0.985	1.020	
Grains. row ⁻¹	0.918	1.117	1.013	

TABLE 4.6 Summary of relative values of yield and yield components.

Tillers of both varieties proved to be highly inefficient grain bearing structures in their own right (Tables 3.12; 3.19). The high incidence of sex reversal apparent among the tillers of KC3, and to a lesser degree in the other variety, was a contributory factor. Allowing for this however, the 10% of shoot dry matter diverted into tiller production at flowering could well have been deployed in main stem structures. Situations where tillers may prove useful, such as when the main stem is under severe stress (Loomis, 1945), are unlikely to occur under the conditions of low population that promote tillering. The most efficient plant habit for grain production in maize, as in wheat (Donald, 1968), is the uniculm one, and a high incidence of tillers indicates that a higher plant population powld have been supported (Dungan et al., 1958).

Perhaps the most remarkable varietal difference in yield structure was the manner in which grain yield per unit area responded to increased .plant population (Fig 15). An increase in the planting density of W575 was accompanied by a diminishing increase in yield per unit area, whereas the response of KC3 was much closer to a linear increase in yield per unit area over the range of densities tested. Analysis revealed that the chief varietal difference lay in the change in ear number per plant. Hoving from low to high plant densities, W575 changed from a semiprolific habit (Table 3.12) to a strictly single-eared habit. KC3 maintained its singleeared habit at all plant densities, the changes in yield per plant in this variety arising principally from a reduced yield per ear. The fall in ear weight in KC3 was due to a reduction in weight per grain accompanied by a larger reduction in grains per row. The fall in ear weight in '575 was less than that of KC3, and was brought about by a reduced number of grains per ear, in which both rows of grain per ear and grains per row were reduced.

Intraplant competition during grain filling appeared to vary with plant spacing. Using weight per grain and grains per ear as an index of internal competition for assimilates, intraplant competition from floret initiation through grain filling appeared to be minimal at 50,000 plants. ha⁻¹ in both varieties. At lower populations competition between ears on the same plant was sufficiently high to impose an internal stress on the plant comparable to that experienced by plants bearing single cars at much higher . plant densities. This has been noted before in maize (Haynes and Sayre, .1956) and wheat (Puckridge and Donald, 1967). Donald (1963) suggests that intraplant competition is high when interplant competition is low and this experiment supports this suggestion. However, contrary to Donald's postulate, yield per unit area was not maximal when intraplant correctition was at its lowest level. It seems that there may be a variety x stage of development interaction, for by comparison with KC3, intraplant competition appeared to be higher at silking in W575, and lower during the latter phases of grain filling, as weight per grain at the highest population of NC3 was 87.7% that obtained under minimum intraplant competition, compared with 93.7% for M575. This pattern appears to be characteristic of semiprolific and single-eared varieties when under population stress (Earley et al, 1966).

Correlations of yield per plant with components of yield have previously employed in an attempt to identify factors limiting grantfield (Hatfield <u>et al</u>, 1965). It must be emphasized that such correlations do not imply causal relationships, but merely indicate the degree of variation shared by both variables. High within-sample variability will reduce the value of the correlation without in any way affecting existing biological relationships.

Yield per plant in both varieties was only weakly correlated with weight per grain, suggesting that factors limiting the completeness of filling of individual grains probably did not restrict yield per plant. Conversely, the high correlations existing between number of grains per ear and yield per plant in both varieties suggest that yield may have been limited by grain number. Correlations of characters within the ear indicate that row number in W575, and grains per row in KC3, were important determinants of yield. The poor statistical relationship between yield per plant and ear number evident in KC3 seems indicative of the small contribution of second ears to yield in this variety. The reverse is true for W575.

As plant density increased, a pattern consistent with an increasingly restrictive number of sites for grain filling emerged, sugrecting that the reduction of ear number and grains per ear in response to plant population in the presilking and early grain filling periods (Prine, 1971; Daynard, 1969) was excessive, particularly at high plant densities, in view of the good grain filling conditions that were to later prevail.

Examination of cob length data (Table 3.15) revealed that 12% of the cob of W575, representing the distal section, did not bear grain. The comparable figure for KC3 was 3%, suggesting that resolving the corres of lack of fertilization of tip kernel abortion (Daynard, 1969) are thely to benefit W575 more than KC3 in similar circumstances to those at present under discussion.

4.2.6. Plant Density Effects.

The influence of crowding upon some plant characteristics has been discussed concurrently with other data, and the general effects of plant density upon plant components and performance of the two varieties examined appeared to be consistent with their differences in size at maturity. Consequently, at any single spacing in the range tested, #575 would be expected to interact more strongly with its neighbours than would MC3.

Cooperative responses to plant interaction showed varietal differences. While plant spacing had no significant effect on stem length, it had a considerable influence upon ear height (Table 3.17). The increase in ear height was greatest (absolutely as well as proportionally) in KCV, reaching 55% for the third ear in that variety. Almost all the elongation took place in the stem below the third ear node, and indicated that of the two varieties the prolonged (or renewed) intercalary growth of KC3 was the more sensitive to the light regime under which the plant was growing. The absence of a significant increase in stem length at high plant densities indicates that considerable telescoping of internodes above the ear must have occurred, because the number of the node at which the ear was attached was not affected by plant spacing. In this respect KC3was proportionally the more competitively aggressive of the two varieties during this phase of reproductive growth. It responded to crowding with a considerable elongation of the lower stem, which moved the ear (and leaves near the ear) closer to the top of the canopy and to the light source, and thus probably improved the nutrition of the ear (Eastin, 1969).
Times to tasselling, silking and anthesis (Table 3.2) were generally delayed by high plant populations, the delay being greater for M575 than Expressed as days per 10,000 plants. ha⁻¹ over the range of densities KC3. tested, average delays in tassel emergence, anthesis and silking were: for KC3: 0.35 day, -0.25 day, 0.5 day; for W575; 0.7 day, 0.85 day, 0.7 day respectively. These are somewhat less than those reported by Dungan et al (1958). The conventional increase (du Plessis & Dijkhuis, 1967; Downey, 1971 c) in the period between anthesis and silking was apparent in 103 though W575 exhibited the reverse trend. It appears that tassel growth in KC3 from emergence to anthesis was more rapid when mutual shading was intense, and may be another manifestation in this variety of the inordinate sensitivity of intercalary meristem activity to prevailing light levels. It is however common knowledge that time to anthesis is dependent on weather conditions at anthesis. The varietal interaction in the length of the period from anthesis to silking, while probably genetic in origin, may also reflect the differences in intraplant competition between the varieties at this time.

Grain yield data show that W575 was the more consistent of the two varieties in grain yield per unit area over the density range tested (Fig 15). The range of densities did not include the optimum plant population for grain yield in KC3, though it may have for W575. In the light of Vis, there seemed little point in fitting yield data to the generalized addfied reciprocal yield density equation (Bleasdale and Nelder, 1960). Instand, yield data were fitted to the more restrictive (Willey and Heath. 1000) yield density equation proposed by Duncan (1958). Extensive extra tion was employed in calculating population optima for grain yield, and the reliability of these estimates is therefore not high. In addition the regressions of logarithm of grain yield per plant on density accounted for only 49% and 41% of the variance for W575 and KC3 respectively. However. in the absence of better estimates, the calculated population optima for grain production of 157683 plants. ha⁻¹ (KC3) and 92125 plants. ha⁻¹ (N575) appear to be reasonable. These are generally higher than those currently recommended in New Zealand (Cumberland, Farrell and Honore, 1971) and may in part reflect a high level of plant nutrition in this trial. The question of whether these estimates reflect fundamental varietal differences in population tolerance, or whether they merely reflect differences in plant size cannot be answered with certainty. If it can be assumed that water stress experienced during plant growth did not unduly affect the numbers of developing ears and kernels, or subsequent grain filling, it is likely that competition during grain filling would be principally for light.

Leaf area per plant is the only available index of the individual plant's capacity to compete for light. On this basis, both varieties exhibited similar tolerance of crowding, for leaf area of the mature KC3 plant was 58% that of M575, and the calculated optimum plant density for grain yield in M575 is 58% that of KC3. If the foregoing is correct, it is obvious that at any one plant spacing within and above the range tested, the two varieties were subjected to levels of interplant competition which differed considerably. This underscores the ability of KC3 to outyield '575 at any single level of interplant stress.

Research indicates that prolificacy is positively related to population tolerance. This suggests that the population optime for ration yield calculated by Duncan's method may well be optimistic in the mass of the single-eared smaller variety, and conservative for the semiprolific larger variety. The increase with plant population in the period from 50% anthesis to 50% silking observed in KC3 (Table 3.1 a) also indicates that barrenness could limit grain production in this variety at a lower level of interplant stress than in W575. There seems little doubt however that had both varieties been grown at 100000 - 120000 plants/ha in this trial, KC3 would have significantly outyielded the larger variety. Incorporation of the prolific habit into KC3 would appear to enhance its capacity to yield well at plant densities beyond the range encompassed by this experiment, provided that other productive characters were not sacrificed in the process.

4.2.7. Field Maturation

The consistent varietal differences in dry matter content at any one time (Fig 14) virtually disappear when varieties are compared at similar growth stages. Growth in the period prior to silking was accompanied by a steady increase in the dry matter contents of stem and leaf.

Grain dry matter content had reached 64% and 68% respectively when grain filling was 95% complete in KC3 and W575. This varietal variability suggests that grain filling ceased for physiological reasons associated with plant senescence, rather than because translocation in the grain was prevented by the level of grain moisture. Temperature data (Appendix 1a) show that average temperatures in late March and early April were till greater than the 10C postulated as being sufficiently cool to terminate grain filling (Miles, 1956).

At maturity, a gradient in DMC can be distinguished. Increasing levels of DMC occur from stem, to husk (including shank), on to the cob, and thence

to the grain, indicating that the remainder of the plant is supplying moisture down this gradient to the ear. The observed pattern of DMC of the cob and grain fractions where the DMC of the cob exceeded that of the grain until both were about 30-40%, after which the position reversed, is identical to that observed elsewhere (Kiesselbach, 1950; Miles and Remmenga, 1953).

The significant varietal difference in the rate of grain D10 increase was unexpected. The individual husks of W575 were observed to be shorter than the ear, but more numerous than those of KC3. The hushs of WC3 were longer than the ear and adhered to it tightly. Grain of WC3 been to gain rapidly in DMC about ten days earlier than W575, and therefore how the benefit of slightly warmer weather.

A positive relationship between lateness of silking and faster rates of field grain drying has been recorded previously (Purdy and Crane, 1967a), though it was not apparent in the extensive tests performed by Gunn and Christensen (1965). In the present instance, the reasons for the varietal difference may be due to the looseness of the husks in W575 (Trover and Ambrose, 1971). Varietal differences in hydrophilic compounds in the grain (Mass and Crane, 1970 b) or differences in grain pericarp thickness (Crane <u>et al</u>, 1959) may also be involved. The underlying causes for the varietal difference appear to be worthy of further study.

Differences in the rate of grain DNC increase are of considerable agronomic and economic importance; the place of maize in a cropping programe in the Manawatu is in part determined by the success with which succeeding crop can be established before winter sets in. In this trial the plaw rate of field drying by KC3 annulled the advantage of its earlier physiological maturity. Since the cost of drying grain has an important bearing on the economics of maize growing (Cumberland and Farrell, 1971), if a singurate of field drying proves to be a characteristic of short season maize crops this may jeopardize the place of maize in the existing cropping pattern of the Manawatu.

4.3 CONCLUSIONS

The optimum plant density for grain production for the Manawatu in this season appeared to be higher than those currently recommended for New Zealand (Cumberland, Farrell and Honore, 1971), and was considerably higher for the small variety (KC3) than the large variety.

A number of other varietal differences in plant structure, function, and pattern of growth having an important influence upon the relative agronomic value of the two varieties are also apparent.

The early variety, KC3, while unable to exploit the environment efficiently at low plant densities, demonstrated a number of valuable

agronomic traits : this small single-eared plant exhibited a high unit leaf rate, and a high ratio of reproductive/vegetative growth. The early establishment of leaf area, the decline in vegetative growth at flowering, and a small lift in photosynthetic rate after flowering, ensured rapid early growth of ears. The developing grain of KC3 displayed a considerable capacity to mobilize and attract assimilate which had previously been deposited in the stem and the husk, and in situations of considerable interplant stress, from the leaf fraction also. Conversely, 3575, a large leafy, full season semi-prolific hybrid, was able to exploit the environment efficiently at low levels of interplant stress, principally by producing more ears. This variety was characterized by a lower harvest index arising from a longer period of vegetative growth than that of NC3. 1575 appeared to have limited ability to mobilize stem and husk reserves in order that grain growth might continue when the plant was under competitive stress, and early growth of the ears was penalized in favour of continuing vegetative growth.

Both varieties deployed resources wastefully in tiller production, this being very apparent in N575 at low plant densities. Yield an probably restricted by the capacity of the growing grain of both varieties to accept available assimilate rather than by the length of the grain filling period. The limited number of sites at which grain filling could occur and the capacity of the sites to accept assimilate, appeared to prevent both varieties from taking full advantage of the long period of good grain filling conditions encountered in the autumn.

The yield structure and agronomic characteristics of EC3 indicate that when this variety is grown at its population optimum for grain yield in a predictable environment, it should prove to be highly productive. How ver, where the established plant population is variable, and where the elimite fluctuates between growing seasons, the more flexible yield structure of W575 may be preferred.

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APPENDICES

* .05> P>.01

** P<.01

ns not significant at the 5% level

 R^2 , the square of the multiple correlation coefficient, is presented with polynomial coefficients in Appendices 11, 13-16. It represents the fraction of the sums of squares of deviations of the dependent variable from its mean that is attributable to the regression. In each case it has been corrected for degrees of freedom such that

$$R^2 = 1 - \frac{df1}{dfk} (1 - Ru^2)$$

Appendix 1 (a) Weather Data Recorded During the Experimental Period

Solar radiation data measured with an Eppley pyranometer at Plant Physiology Division, D.S.I.R., Palmerston North. Maximum and minimum temperatures, and rainfall measured with standard meteorological instruments at Grasslands Division, D.S.I.R., Palmerston North.

All data except rainfall is presented as five day average.



Appendix 1 (b) Accumulated Effective Degree Days



Appendix 2	Schedule of Events	
Day From	Doto	·
POWINE	20.0.60	Elet playshed
	5 11 60	Piot piougned.
*	5.11.69	Portilizon annlied 240km 18 8 NDV
4	0.11.09	to the O 22 he
		to the 0.22 ha 67 kG
		piot area 45 kg trea
×	F 44 CO	Disced in alter application.
×	7.11.69	Applied Aldrin granular insecticide and
		propachlor weedicide at 36 kg/ha and 4.5kg/
		ha respectively. Followed with
		light harrowing.
*	10.11.69	Application of 5 cm irrigation water.
0	12-16.11.69	Sowed crop.
7	19-23.11.69	Emergence.
9–13	25.11.69	Application of slug killer 10 kg/ha.
11-15	27.11.69	2.5 kg a.i/ha Atrazine weedicide applied.
16	28.11-2.12.69	Bulk of transplanting and thinning.
22-26	12.12.69	Stand now complete.
39	21:12.69	Sidedressing applied = 66kg KCl
		to the 0.22 ha plot =146kg urea
	×	area - on an individual plant basis.
44	26-30.12.69	Harvest 1.
49-53	4.1.70	Application of 5 cm irrigation water.
51-55	.6.1.70	Sprayed crop with 27 wv mignetium sulphate
-		solution.
55	6-10.1.70	Harvest 2.
56	7-11.1.70	Mean date of mid tassel, KC3
65	16-20.1.70	Harvest 3.
69	20-24.1.70	Mean date of mid tassel, W575
73–77	28.1.70	Application of 5 cm irrigation water.
75	26-30.1.70	Harvest 4.
89	9-13.2.70	Harvest 5.
86-90	10.2.70	Applied 5 cm irrigation water.
97-101	21.2.70	Applied 5 cm irrigation water.
103	23-27.2.70	Harvest 6.
109-113	5.3.70	Aerial application of Phosdrin Electicide.
124	16-20.3.70	Harvest 7.
145	6-10.4.70	Harvest 8.
166	27-31.4.70	Harvest 9.
187	18-22.5.70	Harvest 10.

A3

Regressions of whole huskless ear cob to grain ratio (Y) Appendix 3 on cob to grain ratio of centre 4 cm section of huskless ear (X). (a) From the same ear. Variety = KC3. Harvest 5.

Y = 1.108X + 0.691 (r = 0.94**)

Source	df		N.S.	F
Constant	1 -		5.151	
Х	1		8.016×10^{-1}	101.50**
Error	13	÷	7.901×10^{-3}	

(b) From different ears.

(i) KC3 Harvest 6.

Y = -.228X + .417 (r = 0.05 ns)

Source	df	M.S.	F
Constant	1	2.836	
x	1	1.086×10^{-2}	0.52 ns
Error	22	2.078×10^{-2}	

(ii) W575 Harvest 6.

Y = 2.311X - .318 (r = 0.78**)

Source	df	M.S.	F
Constant	1	3.738 x 10	
Х	1	1.303 x 10	74.29**
Error	23	1.755×10^{-1}	

Appendix 4 Regression of mid stem diameter (Y) on diameter of stem base (X).

Source	df	M.S.	F
Constant	1	2.367×10^2	
х	1	7.859×10^{-1}	46.84**
Error	48	1.678×10^{-2}	

Y = .570X + .491 (r = 0.70**)

<u>Appendix 5</u> Analysis of Variance of Stem Length and Expanded Leaf Number on the Main Stem. (Pooled data for each plot)

(a) Stem length per plant. (cm)

Source	df		Mean Square	
· ·		Day 44	Day 75	Day 124
Rows	4	1.491 x 10 ³ **	5.046×10^3 ns	2.399×10^3 ns
Columns	4	7.718 x $10^2 **$	4.250×10^3 ns	8.321×10^3 ns
Populations	4	8.227 x 10 ns	8.140×10^2 ns	8.593×10^3 ns
Error 1	12	7.359 x 10	5.941 x 10^3	2.687×10^3
Varieties	1	3.411 x 10 ³ **	7.176×10^3 ns	4.849 x 10 ⁴ **
Var. x Pop.	4	1.364×10^2 ns	1.103×10^2 ns	2.063×10^3
Error 2	19	2.011×10^2	2.093×10^3	1.176×10^3
Total	48			

(b) Expanded leaf number on the main stem.

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Source	df			
		Day 44	Day 65	Day 103
Rows	4	8.720 **	4.443 x 10 **	1.930 ns
Columns	4	4.170 *	1.718 x 10 ns	3.030 ns
Populations	4	3.420 *	1.003 x 10 ns	6.030 ns
Error 1	12	9.367×10^{-1}	7.747	6.563
Varieties	1	1.800×10^{-1} ns	8.820 ns	8.653 x 10 ² **
Var. x Pop.	4	3.800×10^{-1} ns	3.757 x 10 ns	5.030
Error 2	19	9.895×10^{-1}	2.165 x 10	7.084
Total	48			

A6

Appendix 6

Coefficients of Polynomials Fitted to Data on Stem Length and Expanded Leaf Number on the Main Stem. Polynomials, fitted to plot means give values for three plants, and are of the form $Y = D_0 + D_1 t + D_2 t^2 + D_3 t^3 + D_4 t^4$

(cm)	
(number)	

Variable	Variety		х.		Coefficien	t		S.E. per plant
-		D _O	D ₁	D ₂	D ₃	D ₄	R ²	at day 100
Stem	ксз х	-2.229×10^3	+8.373 x 10	-8.577×10^{-1}	$+2.876 \times 10^{-3}$	10	0.965	3.14
Length	W575 X	-2.019×10^3	-1.397×10^2	+3.236	-2.852 x 10 ⁻²	+8.646 x 10 ⁻⁵	0.983	(cm) 3.45
Expanded Leaf	ксз х	-2.765 x 10 ²	+1.348 x 10	-2.175 x 10 ⁻¹	+1.539 x 10 ⁻³	-4.031 x 10 ⁻⁶	0.952	0.180 (number)
main stem	W575 X	$+1.474 \times 10^2$	-1.008 x 10	+2.431 x 10 ⁻¹	-2.231 x 10 ⁻³	+7.012 x 10 ⁻⁶	0.973	0.243

X Deviations from regression significant at 5% level

Appendix 6

Appendix 7

(a) Coefficients of Polynomials Fitted to Total Photosynthetic Area Data. Polynomials, fitted to plot means, give values for three plants, and are of the form

Total Area = $C_0 + C_1 t + C_2 t^2 + C_3 t^3 + C_4 t^4$ (cm²)

Variety	Populatio	n				S.E. per plant			
		co		°1	°2	°3	c ₄	R ²	(cm ²)
KC3	39K	-2.056	x 10 ⁵	+1.038 x 10 ⁴	-1.753×10^2	+1.279	-3.420×10^{-3}	0.772	339.6
	4 8K	-2.204	x 10 ⁵	$+1.107 \times 10^4$	-1.850×10^2	+1.326	-3.472×10^{-3}	0.813	
	57K X	-1.496	x 10 ⁵	$+7.618 \times 10^3$	-1.286×10^2	+9.449 x 10 ⁻¹	-2.563×10^{-3}	0.904	191.5
	69K	-1.149	x 10 ⁵	$+5.938 \times 10^3$	-1.000×10^2	$+7.414 \times 10^{-1}$	-2.041×10^{-3}	0.852	
	7 9K	-1.060	x 10 ⁵	$+5.283 \times 10^3$	-8.370 x 10	+5.841 x 10 ⁻¹	-1.536×10^{-3}	0.823	247.7
₩575	39K	-2.907	x 10 ⁵	$+1.409 \times 10^4$	-2.283 x 10 ²	+1.625	-4.285×10^{-3}	0.690	593.5
1000	48K	-1.718	x 10 ⁵	$+7.943 \times 10^3$	-1.177×10^2	$+7.780 \times 10^{-1}$	-1.952×10^{-3}	0.678	ž
1.18	57K .	-2.091	x 10 ⁵	$+1.001 \times 10^4$	-1.587×10^2	+1.102	-2.827×10^{-3}	0.591	479.6
	69K	-1.316	x 10 ⁵	$+5.798 \times 10^3$	-8.056 x 10	$+5.073 \times 10^{-1}$	-1.241×10^{-3}	0.813	
	7 9K	-1.792	x 10 ⁵	+8.522 x 10 ³	-1.341×10^2	+9.348 x 10 ⁻¹	-2.426×10^{-3}	0.737	369.5

X Deviations from regression significant at 5% level.

Appendix 7

Appendix 7 (continued)

Appendix 7 (continued)

(b) Coefficients of Polynomials Fitted to Total Dry Weight Data.

Polynomials, fitted to plot means, give values for three plants and are of the form

Variety	Population	Coefficient			÷2	S.E. per plant	
s - 1		Bo	^B 1	^B 2	^B 3	R ²	at Day 100 (g)
KC3 -	39K 48K 57K X 69K 79K	-5.672×10^{2} -7.789 x 10 ² -6.763 x 10 ² -3.662 x 10 ² -6.203 x 10 ²	+1.144 x 10 +2.116 x 10 +1.804 x 10 +7.716 +1.709 x 10	+9.039 x 10^{-2} -4.364 x 10^{-2} -3.160 x 10^{-2} -5.982 x 10^{-2} -3.875 x 10^{-2}	-5.842×10^{-4} -1.017 x 10 ⁻⁴ -1.168 x 10 ⁻⁴ -3.589 x 10 ⁻⁴ -7.679 x 10 ⁻⁵	0.967 0.980 0.979 0.974 0.971	9.70 6.04 6.39
W575	39K 48K 57K 69K X 79K	-3.292×10^{2} -1.926 x 10 ² -2.568 x 10 ² -5.446 x 10 ² -1.442 x 10 ²	-1.495×10^{-1} -2.902 +2.553 +1.109 x 10 -8.291 x 10 ⁻¹	+2.592 x 10^{-1} +2.382 x 10^{-1} +1.298 x 10^{-1} +5.502 x 10^{-2} +1.487 x 10^{-1}	-1.136×10^{-3} -9.720×10^{-4} -5.516×10^{-4} -3.767×10^{-4} -6.212×10^{-4}	0.967 0.984 0.980 0.983 0.973	12.34 6.83 6.54

Total weight = $B_0 + B_1 t + B_2 t^2 + B_3 t^3$ (g)

X Deviations from regression significant at 5% level.

A9
<u>Appendix 8</u> Analysis of Variance of Total Photosynthetic Area per Plant and Total Dry Weight per Plant. (Pooled data for each plot)

Source	df	Mean Square						
		Day 44	Day 65	Day 103				
Rows	4	3.671 x 10 ⁷ **	1.775 x 10 ⁷ ns	2.036×10^7 ns				
Columns	4	1.854×10^7 ns	1.742×10^7 ns	4.977×10^6 ns				
Populations	4	3.585 x 10 ⁶ ns	3.117×10^7 ns	2.852×10^7 ns				
Error 1	12	2.670×10^6	1.460×10^7	1.080×10^7				
Varieties	1	7.170×10^4 ns	9.086 x 10 ⁸ **	1.341 x 10 ⁹ **				
Var.x Pop.	4	7.375 x 10 ⁶ ns	1.878×10^7 ns	3.914×10^7 ns				
Error 2	19	4.539×10^{6}	1.038×10^7	1.457×10^7				
Total	48		11.2.5.9.0.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1					

(a) Total Photosynthetic area per plant. (cm²)

(b) Total dry weight per plant. (g)

Source	df .			Mean Squa	are		
		Day 44		Day 103		Day 187	
Rows	4	$3.471 \times 10^3 *$	**	3.558 x 10 ⁴	ns	2.898×10^4	ns
Columns	4	$1.278 \times 10^3 *$	**	9.392×10^3	ns	1.512×10^4	ns
Populations	4	3.136×10^2 r	ns	3.138 x 10 ⁵	**	1.973×10^5	**
Error 1	12	2.179×10^2		1.304×10^4		1.309×10^4	
Varieties	1	3.712×10^2 r	ns	3.158 x 10 ⁵	**	7.655 x 10 ⁵	**
Var.x Pop.	4	5.264×10^2 r	ns	6.191×10^4	*	2.588×10^4	ns
Error 2	19	3.275×10^2		1.979×10^4	1	1.404×10^4	
Total	48						

<u>Appendix 9</u> Analysis of Variance of Fractions of Total Photosynthetic Area per Plant.

(Pooled data for each plot)

Source	df	Mean Square							
		Day 44		Day 75		Day124			
Rows	4	1.136×10^7	**	7.343 x 10 ⁶	**	4.756×10^6	ns		
Columns	4	7.190×10^6	*	2.261 x 10 ⁶	ns	6.110 x 10 ⁶	ns		
Populations	4	5.007×10^5	ns	4.303 x 10 ⁵	ns	3.595×10^5	ns		
Error 1	12	1.321×10^{6}		1.243 x 10 ⁶		5.621×10^6			
Varieties	1	1.837×10^{6}	ns	5.346 x 10 ⁸	**	9.039 x 10 ⁸	**		
Var.x Pop.	4	1.900 x 10 ⁶	ns	6.016 x 10 ⁶	ns	1.802×10^6	ns		
Error 2	19	1.291×10^{6}		4.241×10^{6}		4.480×10^6			
Total	48								

(a) Main stem laminae area per plant. (a	om	-]
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(b) Main stem stem area per plant. (cm^2)

Source	df	Mean Square							
		Day 44		Day 75		Day 124			
Rows	4	3.749×10^5	**	4.357 x 10 ⁵	ns	4.960×10^4	ns		
Columns	4	1.492×10^5	*	2.544 x 10 ⁵	ns	4.091 x 10 ⁵	ns		
Populations	4	2.113×10^4	ns	2.704×10^5	ns	2.687 x 10 ⁵	ns		
Error 1	12	3.636×10^4		4.297×10^5		2.006 x 10 ⁵			
Varieties	1	2.608 x 10 ⁵	*	2.203 x 10 ⁶	**	5.865 x 10 ⁶	**		
Var.x Pop.	4	4.255×10^4	ns	3.455×10^3	ns	5.258 x 10 ⁴	ns		
Error 2	19	4.659×10^4		1.068 x 10 ⁵		8.200×10^4			
Total	48			1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 -		na a marina di anti a com			

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Appendix 9 (continued)

Source	df	Mean Square							
		Day 44		Day 75		Day 124			
Rows	4	3.052 x 10 ⁶	**	4.819 x 10 ⁶	ns	9.379 x 10 ⁶	ns		
Columns	4	1.183 x 10 ⁶	ns	1.391×10^7	ns	1.838×10^7	*		
Populations	· 4	1.035 x 10 ⁶	ns	3.514×10^7	*	2.879 x 10^7	**		
Error 1	12	$4.618 \ge 10^5$		6.643 x 10 ⁶		5.191 x 10^6			
Varieties	1	3.224×10^6	ns	1.983 x 10 ⁷	ns	8.237×10^7	**		
Var. x Pop.	4	1.155×10^6	ns	1.428×10^7	ns	1.349×10^7	ns		
Error 2	19	$1.117 \ge 10^6$		6.154 x 10 ⁶		6.164×10^6			
Total	48								

(c) Tiller laminae area per plant. (cm²)

(d) Tiller stem area per plant. (cm^2)

Source	df A		Me	an Square		÷	ě.
		Day 44		Day 75		Day 124	
Rows	4	1.564 x 10 ⁵	*	1.209 x 10 ⁵	ns	3.921 x 10 ⁵	ns
Columns	4	6.492×10^4	ns	2.848 x 10 ⁵	ns	9.050 x 10 ⁵	ns
Populations	4	9.192 x 10 ⁴	ns	1.040 x 10 ⁶	**	1.433×10^6	*
Error 1	12	3.984×10^4		1.481 x 10 ⁵		2.994×10^5	
Varieties	1	6.538 x 10 ⁴	ns	1.548 x 10 ⁵	ns	3.321 x 10 ⁶	**
Var. x Pop.	4	7.895×10^4	ns	1.358 x 10 ⁵	ns	5.757 x 10 ⁵	ns
Error 2	19	6.140×10^4		1.384 x 10 ⁵		2.681 x 10 ⁵	
Total	48						

Appendix 10 Analysis of Variance of Total Leaf Area Index and Total Dry weight per unit area.

Source	df	Mean Square						
	а. Г	Day 44		Day 65		Day 103		
Rows	4	1.254	**	6.438 x 10 ⁻¹	ns	8.416 x 10 ⁻¹	ns	
Columns '	4	5.760×10^{-1}	**	$5.401 \ge 10^{-1}$	ns	1.337×10^{-1}	ns	
Populations	4	1.136	**	6.761	**	8.522	**	
Error 1	12	8.069×10^{-2}		5.076×10^{-1}		4.792 x 10 ⁻¹		
Varieties	1	3.348×10^{-2}	ns	3.080 x 10	**	4.617 x 10	**	
Var. x Pop.	4	3.211×10^{-1}	ns	2.757×10^{-1}	ns	8.083 x 10 ⁻¹	ns	
Error 2	19	2.129×10^{-1}		4.436×10^{-1}		6.302×10^{-1}		
Total	48	 						

(a) Total leaf area index.

(b) Total dry weight per unit area. (kg.ha⁻¹)

Source	df		Mean Square	
		Day 44	Day 103	Day 187
Rows	4	1.178 x 10 ⁶ **	1.215 x 10 ⁷ ns	7.029 x 10 ⁶ ns
Columns	4	3.926 x 10 ⁵ **	2.155 x 10^6 ns	2.894 x 10 ⁶ ns
Populations	4	$6.070 \times 10^5 **$	$2.414 \times 10^7 *$	7.412 x $10^7 **$
Error 1	12	6.978×10^4	5.190 x 10^{6}	2.990×10^6
Varieties	1	3.142×10^5 ns	8.959 x 10 ⁷ **	2.424 x 10 ⁸ **
Var. x Pop.	4	2.695×10^5 ns	$1.180 \ge 10^7$ ns	2.201 \times 10 ⁶ ns
Error 2	19	1.574×10^5	7.468 x 10 ⁶	4.013×10^{6}
Total	48			

<u>Appendix 11</u> Analysis of Variance of Dry Weight Fractions per Plant. (data pooled for each plot)

Source	df	df. Mean Square						•	
	1		Day 103		Day 145		Day 187		
Rows	4		2.216×10^3	ns	1.455×10^4	ns	1.131 x 10	4 ns	
Columns	4		4.656×10^3	ns	6.438 x 10 ³	ns	7.473 x 10	3 ns	
Populations	4		2.114×10^4	**	8.180 x 10^4	6*	4.396 x 10	4 **	
Error 1	12		3.468×10^3		1.195 x 10 ⁴	•	6.783 x 10	3	
Varieties	1		2.360 x 10^5	**	3.114 x 10 ⁴	ns	5.093 x 10	4 *	
Var. x Pop.	4		2.221×10^3	ns	6.824×10^3	ns	3.123 x 10	³ ns	
Error 2.	19	8	2.855×10^3		1.353 x 10 ⁴		7.566 x 10	3	
Total	48								

(a) Grain dry weight per plant. (g)

(b) Stem dry weight per plant.

(g)

Source	df		1	Mean Square			
6		Day 44		Day 103		Day 145	
Rows	4	 4.519×10^2	**	$7.557 \ge 10^3$	*	9.148 x 10 ³	*
Columns	4	1.570×10^2	**	5.843 x 10^2	ns	5.445 x 10^3	ns
Populations	4	1.763 x 10	ns	2.362×10^4	**	2.422×10^4	**
Error 1	12	1.880 x 10		1.788×10^3		2.050 x 10 ³	
Varieties	1	 6.884×10^2	**	1.978 x 10 ⁵	**	1.300 x 10 ⁵	**
Var. x Pop.	4	3.956 x 10	ns	1.027×10^4	*	4.952×10^3	ns
Error 2	19	4.674 x 10		3.034×10^3		2.176×10^3	
Total	48	 		i i i i i i i i i i i i i i i i i i i			

Appendix 11 (continued)

Source	df	-	Mean Square					
			Day 44		Day 89		Day 124	
Rows	4		1.329×10^3	**	8.749×10^2	ns	9.958×10^2 ns	
Columns	4		5.310×10^2	*	6.241×10^2	ns	$6.284 \times 10^2 \text{ ns}$	
Populations	4		2.103×10^2	ns	1.862×10^3	**	$3.823 \times 10^3 **$	
Error 1	12		1.249×10^2		2.824×10^2		3.900×10^2	
Varieties	1		1.125×10^2	ns	4.348 x 10 ⁴	**	5.324 x 10 ⁴ **	
Var. x Pop.	4		2.775×10^2	ns	1.232×10^3	ns	7.835×10^2 ns	
Error 2	19		1.525×10^2		7.179×10^2		3.628×10^2	
Total	48							

(c) Leaf dry weight per plant. (g)

(d) Husk dry weight per plant. (g)

Source	df		Mean Square	
		Day 89	Day124	Day 187
Rows	4	8.326×10^2	ns 9.969×10^2	ns 1.468×10^2 ns
Columns	4	3.817 x 10	ns 3.450×10^2	ns 3.296×10^2 ns
Populations	4	5.335×10^3	** 1.280 x 10 ⁴	** 3.021 x 10 ³ **
Error 1	12	4.189×10^2	6.277×10^2	2.499×10^2
Varieties	1	1.226×10^3	ns 1.198 x 10 ⁴	** 1.309×10^3 *
Var. x Pop.	4	1.671×10^{3}	* 2.161×10^3	ns 1.937×10^2 ns
Error 2	19	4.728×10^2	$1.104 \ge 10^3$	2.683×10^2
Total	48			

Appendix 11 (continued)

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Source	df		Mean Square	
		Day 103	Day 145	Day 187
Rows	4	1.027×10^3	ns 3.872 x 10 ²	ns 3.638 x 10 ² ns
Columns	. 4	9.269×10^2	ns 1.884×10^2	ns 8.140×10^2 ns
Populations	4	1.008×10^4	** 4.146×10^3	** 2.968 x 10 ³ **
Error 1	12	6.187×10^2	2.441×10^2	3.793×10^2
Varieties	1	7.943×10^4	** 1.942 x 10 ⁴	** 1.553 x 10 ⁴ **
Var. x Pop.	4	2.737×10^3	** 6.460×10^2	ns 3.434×10^2 ns
Error 2	19	5.936×10^2	3.704×10^2	2.326×10^2
Total	48 0			

(e) Cob dry weight per plant. (g)

(f) Tassel dry weight per plant. (g)

Source	df	90	Mean Square	
		Day 55	Day 75	Day 103
Rows	4	4.757 x 10 *	5.783 x 10 ns	1.318 x 10 ns
Columns	4	3.835 x 10 *	4.222 ns	1.303 x 10 ns
Populations	4	2.949 x 10 ns	1.312×10^2 ns	$1.420 \ge 10^2 **$
Error 1	12	1.115 x 10	6.685 x 10	1.417 x 10
Varieties	1	1.013 x 10 ³ **	1.965×10^2 ns	3.354 x 10 ns
Var. x Pop.	4	7.749 ns	2.321 x 10 ns	7.641 x 10 ns
Error 2	19	1.791 x 10	5.389 x 10	2.900 x 10
Total	48			

Appendix 11 (continued)

Source	df			Mean Square		
		Day 124		Day 145		Day 187
Rows	4	4.919×10^2	*	3.049 x 10 ³	۲	8.040 x 10 ² ns
Columns	4	2.940×10^2	ns	1.213×10^3	ns	4.392×10^2 ns
Populations	4	1.539×10^2	ns	7.097×10^3	* *	1.029×10^3 ns
Error 1	12	9.345 x 10		9.265 x 10^2		5.736 $\pm 10^2$
Varieties	1	2.299×10^2	ns	1.525 x 10 ⁴	**	4.566 x 10 ⁴ **
Var. x Pop.	4	2.463 x 10	ns	1.051×10^3	ns	1.494×10^3 ns
Error 2	19	1.580×10^2		1.242×10^3		6.891 x 10 ²
Total	48					

(g) Dead leaf dry weight per plant. (g)

(h) Total ear dry weight per plant. (g)

Source	df		Mean Square	
		Day 55	Day 89	Day 145
Rows	4	1.315 x 10 ns	6.175 x 10 ³ ns	2.243 x 10 ⁴
Columns	4	1.152 x 10 ns	3.926×10^3 ns	6.693×10^3
Populations	4	· 2.240 x 10 *	2.835 x 10 ⁴ **	1.768 x 10 ⁵ **
Error 1	12	4.392	3.923×10^3	2.032 x 10^4
Varieties .	1	$3.606 \times 10^2 **$	1.508 x 10 ⁵ **	1.846 x 10 ⁵ **
Var. x Pop.	4	6.716 ns	5.551 x 10^3 ns	1.311×10^4 ·
Error 2 a	19	7.155	2.765×10^3	2.184 x 10 ⁴
Total	48			

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Appendix 12

12 Coefficients of Polynomials Fitted to Dry Weight Data of Plant Parts.

Polynomials, fitted to plot means give values for three plants, and are of the form

Plant part dry weight =
$$B_0 + B_1 t + B_2 t^2 + B_3 t^3$$

Fraction	Variety	Populatio	n	Co	efficient			S.E. per plant
2) 6			B _O	^B 1	^B 2	^B 3	R ²	at day 100 (g)
Stem	ксз з	3 9K	-6.907×10^2	+2.317 x 10	-1.755×10^{-1}	+4.152 x 10 ⁻⁴	0.944	3.90
		s 57k	-6.364×10^2	+2.150 x 10 '	-1.699×10^{-1}	$+4.200 \times 10^{-4}$	0.971	2.31
		7 9K	-6.411×10^2	+2.201 x 10	-1.805×10^{-1}	$+4.561 \times 10^{-4}$	0.954	2.52
	W575	39K	-8.570×10^2	+2.633 x 10	-1.680×10^{-1}	+3.337 x 10 ⁻⁴	0.957	5.10
		57K	-6.979×10^2	+2.217 x 10	-1.596×10^{-1}	$+3.672 \times 10^{-4}$	0.965	3.12
		7 9K	-5.457×10^2	+1.673 x 10	-1.073×10^{-1}	$+2.086 \times 10^{-4}$	0.958	3.13
Leaf	KC3	39K	-4.299×10^2	+1.871 x 10	-2.136×10^{-1}	$+7.870 \times 10^{-4}$	0.960	2.34
e 2		K 57K	-2.192×10^2	+9.829	-1.025×10^{-1}	$+3.487 \times 10^{-4}$	0.971	1.72
		7 9K	-1.226×10^2	+5.531	-4.343×10^{-2}	$+8.929 \times 10^{-5}$	0.960	1.91
	₩575	3 9K	-5.409×10^2	+2.194 x 10	-2.170×10^{-1}	+7.113 x 10 ⁻⁴	0.956	435
		57K	-4.662×10^2	+1.925 x 10	-2.026×10^{-1}	$+7.003 \times 10^{-4}$	0.969	2.62
		7 9K	-4.665×10^2	+1.937 x 10	-2.103×10^{-1}	$+7.518 \times 10^{-4}$	0.963	2.60

X Deviations from regression significant at 5% level.

Appendix 12

Appendix 12 (continued)

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Fraction	Variety	Population	B _O	^B 1	Coefficient B ₂	^B 3	R ²	S.E. per plant at day 150 (g)	ndix 12
Husk	KC3 X	39K 57K	-6.104×10^{2} -5.200 x 10 ²	+1.762 x 10 +1.480 x 10	-1.342×10^{-1} -1.128×10^{-1}	$+3.191 \times 10^{-4}$ +2.686 x 10^{-4}	0.939 0.930	2.71 2.24	(Continue
	₩575 X X	79K 39K 57K 79K	-5.020×10^{2} -5.083 x 10 ² -3.108 x 10 ² -1.742 x 10 ²	+1.240 x 10 +1.240 x 10 +7.953 +3.830	-6.895×10^{-2} -5.032 x 10 ⁻² 1.492 x 10 ⁻²	$+3.103 \times 10^{-4}$ +1.052 x 10 ⁻⁴ +9.964 x 10 ⁻⁵ +2.819 x 10 ⁻⁶	0.885 0.891 0.913 0.884	2.18 4.51 2.26 2.05	(þe
Соъ	KC3	39K 57K 79K	+1.025 x 10^2 +7.587 x 10 +7.129 x 10				0.082 0.004 0.005	1.56 1.02 0.96	
	₩575	39K 57K 79K	+6.569 x 10^{2} +1.203 x 10^{2} +9.723 x 10	-6.120	+1.806 x 10 ⁻²		0.471 0.279 0.160	3.11 1.28 1.32	

X Deviations from regression significant at 5% level.

Appendix 12 (continued)

Fraction	Variety	Population			Coefficient			S.E. per plant
			ВО	^B 1	^B 2	^B 3	\mathbb{R}^{2}	at day 150 (g)
rain	ксз	39к 🛸 .	-4.893×10^3	$+1.042 \times 10^2$	-6.541×10^{-1}	$+1.344 \times 10^{-3}$	0.954	11.41
	x	48K	-4.080×10^3	+8.704 x 10	-5.467×10^{-1}	$+1.141 \times 10^{-3}$	0.991	
¥.		57K	-2.825×10^3	+5.928 x 10	-3.621×10^{-1}	$+7.464 \times 10^{-4}$	0.959	8.52
	X	69K	-3.248×10^3	+6.723 x 10	-4.066×10^{-1}	$+8.149 \times 10^{-4}$	0.976	
		7 9K	-2.142×10^3	+4.255 x 10	-2.311×10^{-1}	+4.096 x 10 ⁻⁴	0.968	6.86
	W575	39K	$+8.580 \times 10^2$	-3. 964 x 10	+4.682 x 10 ⁻¹	-1.415×10^{-3}	0.915	16.16
	X	48K	$+9.958 \times 10^2$	-3.957 x 10	+4.336 x 10 ⁻¹	-1.242×10^{-3}	0.968	
	x	57K	-6.430×10^2	+8.293 x 10 ⁻¹	+1.118 x 10 ⁻¹	-4.395×10^{-4}	0.958	9.04
	X	69K	-1.264×10^3	+1.749 x 10	-2.608×10^{-2}	-9.326 x 10 ⁻⁵	0.971	
S	x	79K	-5.077×10^2	+4.203 x 10 ⁻¹	+9.198 x 10 ⁻²	-3.612 x 10 ⁻⁴	0.969	6.03

X Deviations from regression significant at 5% level.

Appendix 12 (continued)

Polynomial coefficients fitted to total ear dry weight data give values for three plants and

are of the form

Ear dry weight = $B_0 + B_1 t + B_2 t^2 + B_3 t^3 + B_4 t^4$ (g)

Variety	Population			Coeffic	eient	1		S.E. per plant
		BO	^B 1 [·]	^B 2	^B 3	^B 4	R ²	at day 150 (g)
ксз	39к	$+3.407 \times 10^3$	-1.554×10^2	+2.400	-1.423 x 10 ⁻²	+2.899 x 10 ⁻⁵	0.964	12.28
	57K	$+2.387 \times 10^3$	-1.104×10^2	+1.722 .	-1.032×10^{-2}	+2.136 x 10 ⁻⁵	0.976	8.47
	79K	-3.131×10^2	+2.247	$+7.419 \times 10^{-2}$	-3.361×10^{-4}		0.964	7.39
₩575	3 9K	$+7.418 \times 10^2$	-3.599 x 10	+4.874 x 10 ⁻¹	-1.572×10^{-3}		0.939	15.82
	57K	$+2.924 \times 10^3$	-1.208×10^2	+1.680	-9.026×10^{-3}	$+1.693 \times 10^{-5}$	0.975	8.27
	7 9K	$+2.755 \times 10^3$	-1.124×10^2	+1.545	-8.265×10^{-3}	$+1.541 \times 10^{-5}$	0.977	6.49

<u>Appendix 13</u>. Sample Analyses of Variance of Polynomials Fitted to Individual Plant Data for Population 3.

Source	df	K	03	W575	
		MS	F	MS	F
Mean .	1	6.098 x 10 ⁹	1	1.644×10^{10}	
Replications	.4	5.250 x 10 ⁶	2.64	6.103 x 10 ⁷	3.98
Regression	4	2.914×10^8	146.80 **	3.381 x 10 ⁸	21.97 **
Deviations	3-	1.128×10^7	5.68 *	3.599×10^7	2.34 ns
Within group	28	1.985 x 10 ⁶		1.538 x 10 ⁷	
Total	40		1.2.1		

(a) Leaf area per plant. (cm²)

(b) Total dry weight per plant. (g)

Source	df	KC	3	W57	'5
		MS	F	MS	F
Mean	1	1.001×10^5		1.212×10^5	
Replications	4	1.033×10^2	2.06	6.445 x 10	0.71
Regression	3	1.585×10^4	316.50 **	2.491×10^4	273.40 **
Deviations	5	1.647×10^2	3.29 *	9.321	0.10 ns
Within group	32	5.009 x 10		9.113 x 10	
Total	45		and the second secon	1	and the second

Appendix 13 (continued)

(c) Total ear dry weight per plant. (g)

Source	df	KC	3	W575			
		MS	F	MS ·	F		
Mean.	1	3.259 x 10 ⁴		2.962×10^4			
Replications	44	8.649 x 10	2.70	1.194 x 10	0.31		
Regression	4	6.463×10^3	201.90 **	9.583×10^3	251.90 **		
Deviations	4	1.324 x 10	0.41 ns	• 7.577 x 10	1.99 ns		
Within group	32	3.201 x 10		3.804 x 10			
Total	45				1		

(d) Stem dry weight per plant . (g)

Source	df	KC	3	W575	
		MS	F	MS	F
Mean	1	1.186 x 10 ⁴		1.646×10^4	
Replications	4	8.795 x 10	2.51	1.046 x 10	0.60
Regression	3	1.117×10^3 .	127.70 **	2.196×10^3	126.80 **
Deviations	5	9.494	1.09 ns	2.934 x 10	1.69 ns
Within group	32	8.746		1.732 x 10	
Total	45				

(e) Leaf dry weight per plant . (g)

Source	df	KC3	3	W575	
		MS	F	MS	F
Mean	1	2.673 x 10 ³		5.556×10^3	
Replications	4	4.256	2.66	1.794 x 10	5.15
Regression	3	4.947 x 10	30.86 **	1.981×10^3	56.93 **
Deviations	3	6.343	3.96 *	5.610	1.61 ns
Within group	24	1.603		3.480	
Total	35				

12

Appendix 13 (continued)

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(f) Husk dry weight. (g)

Source	df	KC3		₩575	
		MS	F	MS	F
Mean	1	1.535×10^3		1.086×10^3	
Replications	4	1.715×10^{-1}	0.06	1.955	0.88
Regression	3	1.935×10^2	697.60 **	2.031×10^2	91.23 **
Deviations	5	1.098 x 10	3.96 *	1.349 x 10	6.06 *
Within group	32	2.774		2.227	
Total	45				

(g) Grain dry weight. (g)

Source	df	KC3		₩575	а.
		MS	F	MS	F
Mean	1	2.400×10^4		2.053 x 10 ⁴	
Replications	4	1.067×10^2	4.00	4.293 x 10	1.51
Regression	3	1.507×10^3	56.52 **	3.656×10^3	128.60 **
Deviations	2	4.438 x 10 -	1.67 ns	2.287×10^2	8.04 **
Within group	20	2.665 x 10		2.843 x 10	
Total	30				

(h) Cob dry weight. (g)

Source	df	KC3		W575	
		MS	F	MS	F
Mean	1	1.439 x 10 ⁵	590.50 **	3.618 x 10 ⁵	887.9 **
Replications	4	3.410×10^2	1.40	2.287×10^2	0.56
Regression	-				
Deviations +	4	8.520 x 10	0.35 ns	4.032×10^2	0.99 ns
Within group	16	2.437×10^2		4.075×10^2	
Total	25				

+Deviations from the mean.

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<u>Appendix 14</u> Analysis of Variance of Yield per Plant and Yield Components. (Data pooled over last three harvests)

Source	df			Mean Squat	re		
		Grain. plant ⁻¹	Ears. plant ⁻¹	Grains. ear-1	Rows. ear ⁻¹	Grains. row ⁻¹	Weight. grain ⁻¹ (g)
Rows	4	6.394×10^3 ns	6.991 x 10 ⁻² ns	1.912×10^3 ns	2.402×10^{-1} ns	1.070 x 10 ns	6.200 ns
Columns	4	2.002×10^3 ns	2.546×10^{-2} ns	3.583 x 10 ³ ns	2.153×10^{-1} ns	8.061 ns	1.122 ns
Population	4	5.782 x 10 ⁴ **	$9.304 \times 10^{-1} **$	4.554×10^3 ns	5.510×10^{-1} ns	1.790 x 10 ns	1.140 x 10 ns
Error 1	12	1.007×10^4	1.698×10^{-1}	3.671×10^3	4.128×10^{-1}	1.109 x 10	3.939
Varieties	1	5.892 x 10 ⁴ **	1.388 **	1.522 x 10 ⁴ ns	2.111 ns	9.766 x 10 **	6.489 ns
Var. x Pop.	4	6.419×10^3 ns	$5.554 \times 10^{-1} **$	3.305 x 10 ³ ns	2.358×10^{-1} ns	1.035 x 10 ns	1.874 ns
Error 2	19	4.257×10^3	5.259×10^{-2}	3.720×10^3	5.099×10^{-1}	7.957	1.563
Total	48						the second s

<u>Appendix 15</u> Analysis of Variance of Dry Matter Contents. (Data have been arcsine transformed)

Source	df		Mean Square		
		Day 103	Day 145	Day 187	
Rowa ·	4	2.055 x 10 ns	2.650×10^{-1}	ns C.735	*
Columns	4	2.195 x 10 ns	5.655	ns 5.110	*
Populations	4	1.257 x 10 ns	4.500	ns 4.530	ĸ
Error 1	12	8.201	1.822	1.277	
Varieties	1	$1.520 \times 10^3 **$	6.629 x 10	** 7.517 x 10	* *
Var. x Pop.	4	6.977 ns	1.190	ns 1.025	ns
Error	19	1.151 x 10	1.810	2.862	
Total	48	******			

(a) Grain dry matter content (%).

(b) Cob dry matter content (%).

Source	df		Mean Square	
4 2		Day 103	Day 145	Day 107
Rows	4	1.341 x 10 **	1.844	ns 5.119 x 10 **
Columns	4	1.052 x 10 *	1.279	ins 1.188 x 10 no
Populations	.4	3.266 ns	9.093	ns 3.341 x 10 *
Error 1	12	2.785	1.122 x 10	7.508
Varieties	1	$4.980 \times 10^2 **$	9.005	ns 3.813 x 10 ² **
Var. x Pop.	4	1.698 x 10 ns	3.418×10^{-1}	ns 7.798 ns
Error 2	19	9.379 x 10	5.835	1.351 x 10
Total	48			

Appendix 15 (continued)

Source	df	Day 103		Mean Squares Day 145	3	Day 187	
Rows	4	2.786	ns	1.401 x 10	ns	5.307	ns
Columns	'4	3.978	ns	1.015 x 10	ns	3.845×10^2	××
Populations	4	2.963	ns	3.554 x 10	ns	1.119 . 10	ns
Error 1	12	3.393		$1.477 \ge 10$		1.172 x 10	
Varieties	1	2.147 x 10	**	2.878 x 10	ns	1.552×10^2	≠ ×
Var. x Pop.	4	4.582	ns	6.345	ns	1.289 x 10	ns
Error 2	19	2.958		7.673		1.400 x 10	
Total	48			an general de la canada de la can			

(c) Husk dry matter content (%).

(d) Stem dry matter content (%).

Source	df		Mean Squares	
		Day 44	Day 89	Daý 145
Rows	4	1.139	÷ 5.210 **	6.194 **
Columns	4	5.020×10^{-1}	$15 5.173 \times 10^{-1} \text{ ns}$	2.049 ns
Populations	4	4.360×10^{-1}	$1s 5.655 \times 10^{-1} ns$	2.717 ns
Error 1	12	3.484 x 10 ⁻¹	5.607×10^{-1}	8.882 x 10^{-1}
Varieties	1	1.254 r	as 4.730 x 10 **	1.227 x 10 *
Var. x Pop.	4	3.338×10^{-1}	$13 8.428 \times 10^{-1} \text{ ns}$	1.402 ns
Error 2	19	4.946×10^{-1}	5.302×10^{-1}	2.119
Total	48			

Appendix 15 (continued)

Source	df			Mean Squares			
		Day 44		Day 75		Day 124	
Rows	4	1.684	*	4.982	ns	3.762	ns
Columns	.4	1.177	*	8.817	ns	7.859	ns
Populations	4	7.518 x 10^{-1}	ns	2.457	ns	7.260	ns
Error 1	12	3.169 x 10 ⁻¹		3.376		2.731	
Varieties	1	3.283	**	2.378 x 10	**	7.3 99 x 10	**
Var. x Pop.	4	1.123×10^{-1}	ns	1.185×10^{-1}	ns	8.698 x 10	1 ns
Error 2	19	3.811×10^{-1}		1.298		2.984	
Total	48						

(e) Leaf dry matter content (%).

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Appendix 16. Coefficients of Polynomials Fitted to Dry Matter Content Data.

- Polynomials are of the form

DMC	=	E ₀ +	E.t +	$E_2 t^2 +$	$E_z t^3 +$	E,t4
(%)		0	1	2	2	4

Fraction		Variety	** ::		Coefficient			R ²	Approx. S.E. at	
			EO	^E 1	E2	E ₃	E4		(a) 100 days (b) 150 days	
Stem	x x	KC3 W575	-2.838 x 10 +2.966 x 10	+1.186 -1.322 x 10	$-1.022 \times 10^{-2} +$ +2.550 x 10 ⁻² -	-2.949×10^{-5} -1.784 x 10 ⁻⁴	+4.199 x 10 ⁻⁷	0.925 0.925	0.375 (a) _{0.362} %	
Leaf	x	KC3 W575	+7.936 x 10 -1.026	-4.574 +2.621 x 10 ⁻¹	$+1.060 \times 10^{-1}$ - $+1.541 \times 10^{-3}$ -	-9.605 x 10 ⁻⁴ -1.644 x 10 ⁻⁵	+3.034 x 10 ⁻⁶	0.936 0.946	0.493 (a) _{0.353} %	
Husk		KC3 W575	-2.769×10^2 -1.671×10^2	+1.061 x 10 +6.533	$-1.411 \ge 10^{-1} + -8.796 \ge 10^{-2} + 10^{-2}$	+8.098 x 10 ⁻⁴ +5.160 x 10 ⁻⁴	-1.651×10^{-6} -1.069×10^{-6}	0.912 0.881	(b) ^{1.327} % 1.449	
Соъ	X	KC3 W575	-1.558 x 10 ² -2.402 x 10	+4.081 +2.958 x 10 ⁻¹	$-2.812 \times 10^{-2} +$ +4.189 x 10 ⁻³ -	+6.763 x 10 ⁻⁵ -1.886 x 10 ⁻⁵	×	0.975 0.947	(ъ) ^{0.899} % 1.289	
Grain	x x	KC3 W575	-1.157×10^2 -1.733×10^2	+2.100 +2.705	-5.648×10^{-3} -7.353 x 10 ⁻³	2		0.986 0.982	(ъ) ^{0.732} % 0.934	

X Deviations from the regression are significant at the 5% level.

Appendix 16

Appendix 17 (a) Polynomials in Density Fitted to Grain Yield Data.

(1) Coefficients of polynomials of the type Yield = $A_0 + A_1 p + A_2 p^2$ (p = plants.me⁻²) (kg.ha⁻¹)

Variety		Coefficient	R ²	C.E. at	
	л _о	Δ1	^A 2		(k _i -, -, -,)
KC3	+2.516 x 10 ³	$+1.232 \times 10^3$	-2.068 x 10	0.670	213.2
W5 7 5	-2.837×10^2	$+3.090 \times 10^3$	-2.122×10^2	0.255	456.1

(2) Analysis of variance of fitted polynomial .

Source	df	KC3		W575		
		MS	F	ES	F	
Mean	1	2.004 x 10 ⁹		2.538 x 10 ⁹		
Replications	4	1.924×10^5	0.16	2.784 x 10 ⁵	C.11	
Linear term	1	5.064×10^7	42.28**	1.767×10^7	6.00*	
Quadratic term	1	2.983×10^4	0.02ns	3.143×10^6	1.24ns	
Deviations	2	1.012×10^6	0.85ns	1.631×10^6	0.65ns	
Within group	16 ¹	1.198 x 10 ⁶		2.528 x 10^6		
Total	251		1 ,	df loog for VOZ		

(b) Analysis of Variance of the Logarithm of Grain per Plant on Plants per Square Metre.

Source	df	KC3		W57		
		MS	F	MS	F.	×
Mean A	1	1.201×10^2		1.259×10^2	*	
Regression	1	3.934×10^{-2}	16.02**	1.153×10^{-1}	22.70**	
Within group	231	2.455×10^{-3}		5.077 x 10^{-3}		
Total	25 ¹					

1 df less for KC3