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SOME ASPECTS OF THE GROWTH OF TWO WHEAT VARIETIES  
UNDER FIELD CONDITIONS

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## SUMMARY

Two spring wheats, Raven, a standard commercial variety, and Pitic 62, a Mexican semidwarf variety, were grown in the field at densities of 11.1, 44.4 and 177.7 plants  $\cdot m^{-2}$ . Plants were sampled from each plot at 5 to 9 day intervals from shortly after emergence until maturity and the dry weights of plant parts together with relevant morphological information were recorded. The appearance of leaves and tillers on marked plants was also recorded in parallel with these samplings.

Pitic 62 outyielded Raven at all densities because of higher grain numbers and despite lower grain weights. Tiller numbers, which were similar for both varieties, were responsible for most of the yield variation with density. Infection by barley yellow dwarf virus was a factor complicating the interpretation of these results since it appeared that Pitic 62 was more susceptible to this disease than Raven.

Total dry matter production per plant or per area was similar in each variety and growth analysis, in which the polynomial regression technique was employed, indicated that this was also true of growth rates. Varietal differences in unit photosynthetic rates (net assimilation rates) appeared from ear emergence onwards because leaf senescence was more rapid in Pitic 62 and because ear area made a larger contribution to total photosynthetic area in this variety. Approximately 55% of the ear area in Pitic 62 was due to awns. The grain to straw ratio of Pitic 62 was greater than that of Raven because of heavier ears and lighter stems. These differences were thought to arise from varietal differences in the activity of apical and intercalary meristems. It was concluded that further study of the physiological regulation of growth processes would be required before the differences in plant form and growth patterns observed in the experiment could be more closely correlated with grain yield.

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## INTRODUCTION

This study provides some basic information on the growth and development of two wheat varieties under field conditions. The varieties chosen, Raven, a standard commercial variety of Australian origin, and Pitic 62, a high-yielding Mexican semidwarf wheat, provided a contrast in grain to straw ratio which reflected the trend in wheat breeding towards varieties with an increased proportion of grain to total dry weight. In field trials in the Manawatu Pitic 62 had outyielded Raven and the difference had been attributed to increased tillering in the semidwarf variety (J. M. McEwan, pers. comm.). However critical information on the physiological processes underlying the superior yields of semidwarf wheats such as Pitic 62 under New Zealand conditions was lacking and there was little published work elsewhere. A preliminary attempt to rectify this deficiency by examining the growth of one semidwarf and one standard variety was made in this experiment.

## 1.1 THE ANALYSIS OF GROWTH

Growth may be defined in many ways (Bloch, 1961; Steward, 1968) but no definition can be satisfactory under all circumstances. A pragmatic approach to this problem is to express growth in terms of its most accessible attribute, that of mass measured as dry weight. In this thesis the term growth will, unless otherwise specified, refer to the increase in the mass of an organism in time. In following sections the study of growth will be discussed first in terms of the method of "growth analysis", an approach traditionally associated with the plant sciences, and second in terms of the quantitative analysis of growth, an approach which has arisen diffusely from a wider background.

### 1.1.1 Growth Analysis

In the method of growth analysis plant growth is seen primarily as a balance between carbon assimilation and respiration. By measuring the amount of plant material and the size of the supporting photosynthetic system it is therefore possible to derive quantities which indicate the amount, rate and efficiency of photosynthesis and thus of growth processes (Watson, 1968; Steward, 1969). The development of this concept has been reviewed by Williams (1946), Watson (1952, 1968), Blackman (1961) and Richards (1969).

The relationships used in growth analysis are conveniently divided into two groups, those typifying the morphogenetic condition of the plant and those describing its growth processes (Evans and Hughes, 1961). The following notation will be used in definitions of the more important of these quantities:

W = total plant dry weight or dry weight per unit area of ground;

$W_1$  = leaf dry weight;

A = total leaf area per plant;

L = leaf area per unit area of ground.

#### Morphogenetic relationships

- i) The leaf weight ratio (LWR) is the ratio of leaf dry weight to total dry weight.

$$\text{LWR} = \frac{W_1}{W}$$

ii) The leaf area ratio (LAR) is the ratio of leaf to total weight.

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

Other morphogenetic relationships are defined by Evans and Hughes (1961).

#### Growth process relationships

i) The growth rate (GR) of a plant at any instant of time is the increase in dry weight per unit time.

$$\text{GR} = \frac{dW}{dt}$$

A similar definition is used for the crop growth rate (C) introduced by Watson (1958).

ii) The relative growth rate (R) of a plant at any instant of time is the increase in dry weight per unit weight present per unit time.

$$R = \frac{1}{W} \cdot \frac{dW}{dt} = \frac{d(\log_e W)}{dt}$$

Similar quantities may be calculated for other plant parts, including the relative rate of leaf area increase.

iii) The unit leaf rate (E) of a plant at any instant of time is the increase in weight per unit leaf (or assimilatory) area per unit time.

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

This quantity is also called the net assimilation rate following Gregory (1926) but the older term, unit leaf rate (West, Briggs and Kidd, 1920), is preferable since confusion with "net assimilation" is avoided. Similar quantities have also been calculated on bases such as leaf weight, leaf protein nitrogen (Williams, 1946) or total chlorophyll (Hunt and Cooper, 1967).

There are interrelationships between and within the morphogenetic and growth process relationships. Some of these are given by Blackman, Black and Kemp (1955), Evans and Hughes (1961, 1962), Whitehead and Myerscough (1962) and Jackson (1963), while Emezc (1962) has proposed an alternative system of relationships. The two most important relations

$$R = E \cdot \text{LAR}$$

$$\text{GR} = E \cdot A$$

were first given by West et al. (1920) although the second generally appears in the form

$$C = E \cdot L$$

The separation of the biologically important but complex parameter, R, into components E and LAR has been long used as a means of partial discrimination between the internal and external groups of factors affecting growth. The early expectation that E would be substantially independent of internal factors and reflect changes in the external environment (Briggs, Kidd and West, 1920; Gregory, 1926; Heath and Gregory, 1938) was shown by Williams (1946) and Watson (1947) to be unfounded. Continued research on the variation in E has shown its dependence on the degree of self-shading in the plant or canopy (Watson, 1958; Williams, Loomis and Lepley, 1965; Buttery, 1970), on age (Thorne, 1960, 1961) and upon sink size (Milthorpe, 1963; Thorne and Evans, 1964; Moorby, 1970). Further analyses such as those of Watson and Hayashi (1965) and Watson et al. (1966) on the magnitude of the photosynthetic and respiratory components of E indicate that this is not a quantity lending itself to simple interpretation. Similarly the leaf area ratio, once thought to depend mainly on internal factors, has been shown to be affected in a complex manner by both internal and external factors (Evans and Hughes, 1961). The leaf area index, L, which appears in place of LAR in the alternative form of growth analysis based on crop growth rate is likewise a complicated parameter (Watson, 1956). In spite of such difficulties these relationships remain the key equations of growth analysis since they permit the study of growth in terms of components reflecting the capacity (LAR, L) and efficiency (E) of the process, a virtue first stressed by Gregory (1926) and since exploited by many others.

The formulae and relationships given above state the instantaneous values of the quantities in question. In practise it is impossible or difficult to record changes in W and A continuously so that mean values for the growth analysis parameters must be calculated from samples taken from the populations under study at intervals through the period of the experiment. To derive formulae giving these means, the instantaneous values must be integrated over the period between samplings, a process which in all cases requires assumptions about relationships between W, A and time. Radford (1967) gives derivations of and discusses the assumptions which underlie the traditional equations for the means of quantities used in growth analysis. Once appropriate formulae for means have been obtained the remaining problem of

traditional growth analysis is the calculation of the values from experimental data. Methods used to calculate means and variances are considered by Cornish (1936), Goodall (1945), McIntyre and Williams (1949) and Evans and Hughes (1961).

These classical methods of growth analysis contrast with a more recent approach in which use is made of regression techniques to obtain the growth analysis quantities. This approach has been used in related studies for a number of years (Hammond and Kirkham, 1949; Glenday, 1955; Kheiralla and Whittington, 1962; Rees and Chapas, 1963) but only more recently has it been used directly for growth analysis (Vernon and Allison, 1963; Milthorpe, 1963; Williams, 1964; Muramoto, Hesketh, El-Sharkawy, 1965; Buttery, 1969; Laing, 1969; Moorby, 1970; Goldsworthy, 1970). The method consists of fitting polynomials or other curves to dry weight and leaf area data and using derived curves for growth analysis. For example if

$$\begin{aligned} W &= f(t) \\ A &= p(t) \\ \text{then } GR &= \frac{dW}{dt} = f'(t), \\ E &= \frac{1}{A} \cdot \frac{dW}{dt} = \frac{f'(t)}{p(t)}, \\ \text{and } R &= \frac{1}{W} \cdot \frac{dW}{dt} = \frac{f'(t)}{f(t)} \end{aligned}$$

This technique is described by Vernon and Allison (1963), Hughes and Freeman (1967) and Radford (1967). The method is relatively free from the assumptions associated with the traditional approach (Radford, 1967) and is more accurate and less laborious. Disadvantages have not been stressed in the literature although the analysis of Williams (1964) demonstrates some of the difficulties.

### 1.1.2 The Quantitative Analysis of Growth

When an attribute of growth is plotted against time the growth curve formed is characteristically sigmoid. Such curves lend themselves to mathematical description, and, by their very ubiquity, are suggestive of some deeper significance. For this reason there have been attempts over the years to develop a quantitative analysis of growth with the hope that the mathematical description of the process will provide clues to its nature (e.g. Reed, 1920; Laird, Tyler and Barton, 1965). The fact that the complex processes of growth can be adequately described with a comparatively simple equation cannot,

however, constitute proof that the function in question represents a physiologically meaningful generalization about growth, for, as Gray (1929) and others (Kavanagh and Richards, 1934; Thompson, 1942; Bertalanffy, 1960) have pointed out, the fit of an equation to observed points is determined mainly by the number of constants and the flexibility of the function used.

An alternative approach to the quantitative analysis of growth which has been more widely followed is based on the derivation of a law of growth from axioms. The growth functions in Table 1 have all, at one time or another, been deduced, using physiological arguments, and advanced as more or less comprehensive laws of growth (Blackmar, 1919; Glaser, 1938; Robertson, 1923; Bertalanffy, 1960; Medawar, 1940, respectively); these and others are reviewed by Prodan (1968), Steward (1968) and Richards (1969). There have also been independent but conceptually similar attempts to derive models of growth from different starting points (Weiss and Kavanau, 1957; Collot, 1968; Monsi, 1968; Richards, 1969). The difficulties of the axiomatic-deductive approach to the quantitative analysis of growth are considered by Medawar (1945) and Steward (1968), while less pessimistic views are put forward by Bertalanffy (1960) and Richards (1969).

Table 1 Common Growth Functions.

Function	Synonyms or related (*) functions	Equation
Exponential	Compound interest law	$W = be^{kt}$
Time-power	Parabola	$W = bt^k$
Logistic	Autocatalytic, Verhulst-Pearl law, generalized logistic *, hyperbolic tangent *	$W = \frac{a}{1 + be^{-kt}}$
Negative exponential	Decaying exponential, monomolecular, diminishing returns, (Putter-) Bertalanffy *, Mitscherlich *	$W = a(1 - be^{-kt})$
Gompertz	Spillman *	$W = ae^{-he^{-kt}}$

A further approach to the analysis of growth is one in which an accurate empirical description of the growth of an organism is sought without the form of the function used for this purpose being regarded as of any particular physiological importance. For this purpose the most commonly used functions are those of Table 1 or polynomial regressions. Richards (1969) has reviewed the application of these equations to plant growth. The same author (Richards, 1959, 1969) has shown that the three asymptotic equations, the logistic, the negative exponential, and the Gompertz can be derived as special or limiting cases of a generalized four parameter logistic and Nelder (1961) presents an iterative least-squares method for fitting this function. Since these and other equations have two or more empirical constants they give a flexible description of most observed data, granted the restricted application of the exponential and time-power functions to non-asymptotic cases. Where extended asymptotes occur an ordinary polynomial is inadequate but inverse polynomials (Nelder, 1966) may be used. The empirical description of growth has also been attempted using a combination of several functions, usually exponentials (Hammond and Kirkham, 1949; Hansen and McGregor, 1954; Williams, 1964).

The empirical approach has value in that it summarizes explicitly information which may be otherwise hidden in raw data. Such curves also provide accurate estimates for growth rates in place of geometric and numerical approximations, a use which has been mentioned already in relation to growth analysis. Descriptive curves are in addition useful in directing attention to the reasons underlying the form of a growth curve (Williams, 1964) and in the comparison of treatment effects (Sprent, 1967; Mead, 1970). However in all these cases, as a number of authors have stressed (Thompson, 1942; Weiss and Kavanau, 1957; Bertalanffy, 1960; Putter, Yaron and Bielorai, 1966; Steward, 1968), the use and interpretation of empirical curves must be tempered by a consideration of the underlying biological realities.

## 1.2 THE GROWTH OF WHEAT

In this part of the review physiological aspects of grain yield in wheat, the growth of the wheat plant in relation to yield, and current knowledge on the agronomy and physiology of the short stature dwarf and semidwarf wheats are discussed.

### 1.2.1 Physiological Aspects of Grain Filling in Wheat

There is an extensive literature on the physiology of grain filling in cereals and, particularly, in wheat and barley. Early in the present century the accepted view on this subject was that reserves accumulated during vegetative growth constituted the principal source of carbon in the grain (Brenchley and Hall, 1909; Brenchley, 1912). This idea found expression in the "migration index", the ratio of grain to total shoot weight, which supposedly indicated the efficiency of grain filling (Engledow and Wadham, 1923-24). The same index, stripped of physiological significance, currently appears as the "harvest index" (Donald, 1962). The two lines of research which led to a reconsideration of this concept have been reviewed by Archbold (1945). First, shading and defoliation experiments in wheat (Boonstra, 1929, 1931; Smith, 1933) and barley (Watson and Norman, 1939) demonstrated that a proportion of the grain weight was derived from photosynthesis in the ear and other plant parts, thus confirming much older experiments by Deherain and Dupont (1901 : see Archbold and Mukerjee, 1942). Second, detailed examination of changes in dry weight and chemical composition in barley (Archbold and Mukerjee, 1942; Archbold, 1942) showed that any reserves from vegetative growth were in the nature of surpluses and too small to be of major importance in grain filling.

Current views on grain formation (Thorne, 1966, 1969; Langer, 1967) have developed directly from this point. There is much experimental evidence to show that most of the carbohydrate in the wheat grain is formed from  $\text{CO}_2$  assimilated after ear emergence (Asana and Mani, 1950; Thorne, 1965; Stoy, 1965; Birecka and Dakic-Wlodkowska, 1966; Rawson and Evans, 1970) while the contribution of reserves is minor (Wardlaw and Porter, 1967; Rawson and Hofstra, 1969). All parts of the plant which are photosynthetically active after anthesis, lower leaves, the flag leaf, leaf sheaths, peduncle and the spike itself, contribute to grain formation. In the ear the outer sterile glumes, the flowering glumes, the awns, the grain and the rachis are capable of photosynthesis (Carr and Wardlaw, 1965). Ear photosynthesis involves the assimilation of atmospheric  $\text{CO}_2$  and re-fixation of  $\text{CO}_2$  respired by the ear (Kriedemann,

1966). Grain respiration accounts for some two-thirds of the total ear respiration (Carr and Wardlaw, 1965) and the grains themselves reassimilate most of their respired  $\text{CO}_2$  (Evans and Rawson, 1970). In the intact ear photosynthesis by the rachis and rachillae must presumably serve a similar function. The contribution of ear photosynthesis to grain yield is substantial, particularly in awned wheats (Evans and Rawson, 1970) and may reach as high as 50% of the total requirements for grain filling (Carr and Wardlaw, 1965).

The other major sources of assimilates for grain formation are the photosynthetic parts above the flag leaf node which include the flag leaf lamina, the flag leaf sheath and the exposed part of the peduncle (Asana and Mani, 1950; Quinlan and Sagar, 1965; Voldeng and Simpson, 1967). Among these organs the flag leaf is the most important contributor to grain filling having a net photosynthetic rate approximately twice that of the stem and leaf sheaths in both barley (Thorne, 1959) and wheat (Evans and Rawson, 1970). In wheat the role of assimilates from leaves below the flag leaf node in grain filling is small although photosynthesis in these parts may be of indirect importance to the process (Quinlan and Sagar, 1962; Lupton, 1966). By way of summary the approximate contributions of the ear and other parts to grain formation presented by Thorne (1969) are given in Table 2 (FLN = flag leaf node). These figures can be taken as no more than a rough guide since the actual contributions vary with variety, experimental method and environment (Thorne, 1966; Langer, 1967; Puckridge, 1969), and, in the light of work by Carr and Wardlaw (1965) and Evans and Rawson (1970) they appear to underestimate the importance of ear photosynthesis.

Table 2 Estimates of % of Final Grain Weight from Various Sources (Thorne, 1969).

	%
Ear gross photosynthesis	24
Ear respiration by day	- 28
Ear respiration by night	- 11
Ear net photosynthesis	- 15
Assimilates from above FLN	100
Assimilates from below FLN	15

The economic importance of grain filling has also stimulated much research on the translocation and distribution of assimilates within the plant (Wardlaw, 1968; Milthorpe and Moorby, 1969). This work has shown that translocation from the glumes (Lupton, 1966) and the flag leaf (Euttrose and May, 1959; Lupton, 1968) is largely towards the grain, although the peduncle may act as a temporary sink at anthesis and for some days after (Carr and Wardlaw, 1965; Birecka, 1968; Wardlaw, 1970). Some of the assimilate stored in the peduncle may subsequently be retranslocated to the ear (Wardlaw and Porter, 1967; Rawson and Hofstra, 1969). In the same period there may be downwards translocation from lower leaves to roots (Wardlaw, 1965) and tillers (Rawson and Hofstra, 1969). The complexity of assimilate distribution within the plant during the grain filling period is further shown by the work of Rawson and Evans (1970) and Walpole and Morgan (1970) on the pattern of grain growth within the ear, and that of Euttrose and May (1959) demonstrating changes in assimilate uptake which reflect the synthetic activity of different regions within the caryopsis itself.

The major question yet to be answered is that concerning the nature of limitations to grain yield. Here there are three main possibilities:

- i) inadequacy of assimilate supply;
- ii) inability of the developing grains, the "sink", to utilize available assimilates;
- iii) inefficiencies in translocation between source and sink.

Limitations in grain yield due to inadequate photosynthesis have been suggested by Stoy (1966) and, in the later stages of grain filling, by Walpole and Morgan (1970). On the other hand Evans and Rawson (1970) have shown photosynthesis is adequate for grain filling in a range of varieties, while the work of Evans and Dunstone (1970), which shows that photosynthetic rates per unit leaf area are inversely related to grain yield in lines representing the evolutionary development of modern wheats, does not support the idea that assimilates limit yield, especially since increases in leaf size are accompanied by a proportionate increase in grain size in these lines.

The experimental evidence for and against a sink limitation is also conflicting. In wheat (King, Wardlaw and Evans, 1967) and other species (Neales and Incoll, 1968) the rate of photosynthesis in leaves can be reduced by lowered sink capacity; increases in the rate of photosynthesis in the flag leaf during grain filling have also been shown in some cases

(Birecka and Dakic-Wlodkowska, 1966; Rawson and Hofstra, 1969; Evans and Rawson, 1970). However Lupton (1968) and Birecka, Szczypa and Kozłowska (1969) working on plants with ears removed were not able to show limitations to photosynthetic rates of the flag leaf. Nevertheless there is much evidence that sink size does affect the translocation of assimilates in a regulatory role (Thorne, 1966; Langer, 1967; Wardlaw 1968) and may in this way constitute a limitation to grain yield.

Translocation may also limit grain yield. Doodson, Manners and Myers (1964) and Milthorpe and Moorby (1969) consider that there is little restriction on the movement of assimilates, this being controlled by sinks and sources, while Wardlaw (1965) gives some evidence that the movement of assimilates between the flag leaf and ear is controlled by the vascular anatomy at the flag leaf node. Evans et al. (1970) raise the further possibility that the cross-sectional area of phloem available for translocation may be limiting in modern wheat varieties. There is also evidence of a xylem discontinuity which restricts flow of material from the xylem in the rachilla to that in the pericarp (Zee and O'Brien, 1970) although the physiological significance of this is unknown.

The central problem in deciding which physiological factors may limit yield is one of complexity. In a number of investigations mentioned above apparent limitations were not closely related to yield while in others the limiting factors, if any, were obscure. Evans (1970) has suggested that one source of this difficulty is a buffering effect due to mobilization of reserves or to compensatory changes in the rate of photosynthesis in various parts. In a general discussion of the problem Good (1969) criticizes over-simplification of the "source-sink" concept, pointing out that the sink for assimilates is a complex system representing the whole catabolism of the plant so that simple experimental manipulations are unlikely to yield conclusive answers. This fact appears sometimes to have been overlooked in experiments in which limitations to yield are investigated.

### 1.2.2 The Growth of the Wheat Plant in Relation to Yield.

The growth of the cereal plant is determined by the activity of the apical meristems of the shoot and roots, the lateral meristems of leaves, tillers, nodal roots, and the spike, and the intercalary meristems of leaf sheaths and stem internodes (Bunting and Drennan, 1966). The growth of grain, while affected by many modifying factors, remains primarily an expression of the activity of these meristems. In the following section aspects of the relation of yield to the growth and development of the wheat plant will be considered.

As a consequence of the processes of grain filling described in the preceding section there has arisen the view that grain yield depends primarily on the growth and development of the plant in the period after ear emergence with prior growth of importance only in so far as it affects the size of photosynthetic surfaces available during grain filling and the number and potential size of the kernels themselves (Thorne, 1966, 1969). Support for this view comes largely from growth analysis experiments involving varietal comparisons. In wheat Watson, Thorne and French (1963) showed that varietal differences in the unit leaf rate, prior to ear emergence, were associated with compensatory changes in leaf area index, so that differences in dry matter production were small. In other experiments no association between grain yield and unit leaf rate in the vegetative phase within a range of varieties has been found (Quinlan and Sagar, 1965; Cannell, 1967; Lupton, Ali and Subramaniam, 1967). On the other hand the duration of photosynthetic area after ear emergence, and particularly of area above the flag leaf node (Welbank, French and Witts, 1965), has been shown to be closely related to yield (Watson et al., 1963; Thorne, Ford and Watson, 1967) while leaf area duration prior to heading is not (Thorne, 1966). The apparent efficiency of the photosynthetic area after ear emergence can be measured by the grain leaf ratio,  $G$ , which is the ratio of grain yield to leaf area duration (Watson et al., 1963). Examination of this ratio in varietal comparisons has shown some differences (Watson et al., 1963) but in general the close dependence of grain yield upon duration of photosynthetic structures has been confirmed.

A closer examination of the relationship between plant growth and grain yield reveals however that the importance of the later stages of growth may be overemphasized. Davidson (1965) has shown that leaf removal at ear emergence has no significant effect on grain yield (cf. Stoy, 1965) but leaf area control prior to this decreased grain yield substantially by reducing spikelet number and grain weight. Similar effects have been noted by Lucas and Asana (1968) and Puckridge (1969), while Thorne, Ford and Watson (1968) have shown that differences in grain yield can be related to the effect of early environmental conditions upon grain number.

Further evidence for the importance of the early stages of growth in determining yield comes from work in which the relation of grain yield to plant density has been studied. In wheat and most cereals grain yield exhibits a broad maximum over a range of plant densities

with a tendency for a decrease in the ratio of grain dry matter to total dry matter as density increases (Holliday, 1960; Donald, 1963; Kirby, 1967). The stability of yields over this range of densities may be analysed further in terms of the yield components, the numbers of plants per unit area, of tillers per plant, of spikelets per ear, of grains per spikelet and the weight per grain. These, and particularly the latter four, since plant mortality after establishment is generally low (Puckridge and Donald, 1967), are major yield controlling factors reflecting the determination of grain yield during the growth and development of the plant.

The number of tillers per plant and tiller fertility vary markedly with plant density (e.g. Kirby, 1967) and are related to light interception, crop growth, and thus yield (Puckridge and Donald, 1967). In wheat, and also in barley, tiller number increases early in growth, peaks, and then declines to a relatively stable plateau prior to ear emergence (Thorne, 1962; Watson et al., 1963; Quinlan and Sagar, 1965; Laude, Ridley and Suneson, 1967; Bremner, 1969; Cannell, 1969). This trend is related to the death of late tillers (Thorne, 1962; Cannell, 1969) which depends on internal competition (Aspinall, 1961) and apical effects (Friend, 1966). The effect of late unproductive tillers on ear-bearing shoots appears to be minor and they may in fact contribute to the growth of fertile shoots (Bremner, 1969; Lupton and Pinthus, 1969; Rawson and Donald, 1969). Since the upper limit of tillers on a shoot is determined at spikelet initiation and tiller survival largely prior to ear emergence it is apparent that tiller number per plant depends mainly on the early stages of growth.

Two other yield components, the number of spikelets per ear and number of grains per spikelet, are also determined in the period up to and including anthesis. Spikelet number depends largely on the duration of primordium production (Rawson, 1970; Kirby and Faris, 1970) and this can be affected by a number of environmental factors (Friend, 1966; Langer, 1967) and also by correlations within the apex which may be partly related to internal competition for nutrients (Williams, 1966b; Kirby and Faris, 1970; Rawson, 1970). Floret number, which later sets an upper limit to grain number per spikelet, is determined after spikelet number and the control of this will presumably depend upon similar factors to those affecting spikelet number. Floret fertility is a further determinant of grain yield and there is evidence that this may be fixed early in the growth of the ear by the effects

of internal competition on stamen and carpel growth (Williams, 1966a, 1966b). While failure to set seed at anthesis due to lack of pollination is said to be rarely important in cereals such as wheat (Heslop-Harrison, 1969) it is apparent that a number of florets, particularly those in distal positions, do not set seed even though fertile (Walpole and Morgan, 1970). This may reflect the earlier regulation observed by Williams (loc. cit.) or a competitive disadvantage of later flowering florets (Rawson and Evans, 1970).

Thus, of the yield components, all but one, the weight of the grains (Section 1.2.1), are determined in the period of growth up to anthesis. Growth in this period is therefore of direct consequence to grain yield since it sets the potential which can be realized in the period after flowering.

Grain yield also depends upon root growth. Aspects of the growth of roots in cereals have been reviewed by Brouwer (1966) and Hackett (1969). In wheat and barley, as in most grasses, the proportion of root weight to shoot weight is initially high (Bray, 1963) but declines in time (Williams, 1960; Welbank and Williams, 1968). Nevertheless roots are still active until late in the growth of the plant as evidenced by their apparent sink activity well after anthesis (Wardlaw, 1965). The size, distribution and activity of the root system affects grain yield (Boatwright and Fergusson, 1967; Hurd, 1968) and these factors in turn depend on aspects of shoot growth such as tillering (Pinthus, 1969). Correlations between root and shoot growth (Pope, 1932, Williams, 1960; Brouwer, 1966) serve as a further reminder that above-ground growth leading to grain yield is inseparably linked to that below ground.

### 1.2.3 Short Stature Wheats

The most important agricultural advance for many decades, the so-called "green revolution" of the sixties, has hinged on the exploitation of the superior yielding ability of the new short stature varieties of all the major grain crops. In wheat the new varieties were developed in the United States and at the Rockefeller Foundation in Mexico, using the dwarfing genes found in Japanese strains (Vogel et al., 1956; Borlaug, 1965; Reitz and Salmon, 1968). These have proved phenomenally successful in many countries (Borlaug, 1965, 1968; Swaminathan, 1968; Reitz, 1970).

The agronomic advantages of the dwarf and semidwarf wheats over standard height varieties are attributed to a number of factors.

1. Resistance to lodging, permitting heavier application of water and fertilizer (Woodward, 1966; Syme, 1967; Porter et al., 1964) and contributing to the greater responsiveness to fertilizers (Beech and Norman, 1968).
2. Day length insensitivity (Reitz and Salmon, 1968) leading to earlier flowering and a longer duration of grain growth (Syme, 1967); absence of a vernalization requirement<sup>N<sup>o</sup></sup> (Pugsley, 1964) contributing to earliness. ?
3. Large ear and high ear : straw ratio allowing more photosynthesis and grain set (Syme, 1967). Awedness is an important character here (Vogel et al., 1963).
4. Resistance to disease, particularly rusts (Borlaug, 1965).

The major disadvantage of the short stature wheats appears to be poor seedling emergence (Pugsley, 1964; Sharma, 1968), which is related to their shorter coleoptiles and less rapid coleoptile elongation (Burleigh, Allan and Vogel, 1965). Differences in physiology such as this, and also in phenology, have, in India at least, demanded altered farming practices for these varieties (Sharma, 1968; Swaminathan, 1968).

The physiological features characteristic of short stature wheats do not appear to have been extensively investigated. Dwarf and semidwarf varieties do not respond to gibberellic acid (Allan, Vogel and Craddock, 1959; Radley, 1970) and their response to CCC is negative (Appleby, Kronstad and Rohde, 1966). The reduced stem length which is the characteristic feature of dwarf and semidwarf varieties is due mainly to shorter peduncles and upper internodes (Johnson, 1954; McNeal, Berg and Kages, 1960) and not to fewer internodes (Thorne, Welbank and Blackwood, 1969). Work on the genetics of the short stature character has been reviewed by Powell and Schlehner (1967).

Work at Rothamsted (Thorne et al., 1969) shows semidwarf varieties have a greater apparent grain production efficiency, as measured by the grain leaf ratio for area above flag leaf node, than standard varieties. This was attributed in part at least to greater ear photosynthesis. Evans and Rawson (1970) have demonstrated that ear photosynthesis in awed short stature varieties can be higher than in non-awed standard varieties. There is also evidence (Sharma, 1968; Subbiah et al., 1968)

that the shorter stature wheats have a more extensive and better distributed root system than some normal varieties. High tillering capacity has been cited as another yield advantage of the semidwarf wheats (Vogel et al., 1963; Woodward, 1966; Sharma, 1968) but there is evidence that it may be unimportant (Syme, 1967; Thorne et al., 1969). It is apparent that for this, and other characteristics, environment and variety must play a large part in determining which factors contribute to the yield advantage of the dwarf wheats. Beech and Norman (1968) note, for example, that within the semidwarf wheats they studied, different patterns of development gave equally high yields, whereas Vogel et al., (1963), in another environment, found that any selections differing distinctly from a certain pattern gave much lower yields.

## 2.1 INTRODUCTION

The experimental area was situated in the Agronomy Department demonstration plots on the Massey University Campus, Palmerston North. This area had previously been in mixed pasture species under grazing for six years. The soil is a silt loam of the Ohakea series (J. A. Pollok, pers. comm.).

After normal seed-bed preparation, including the application of 30% potassic superphosphate at a rate of 3 cwt/acre (see Appendix 1), the area was hand raked and laid out in seven blocks with provision for plots of the two varieties, Raven and Pitic 62, at three population densities within each block. The plant densities, 177.77, 44.44 and 11.11 plants  $\text{m}^{-2}$ , corresponded to between-plant spacings of 7.5, 15 and 30 cm on a square grid. The layout was such that within each plot there was provision for at least 20 sample plants fully protected by guard rows; layout details are shown in Appendix 2.

The seeds for the experiment were supplied by Dr. J. M. McEwan of the Crop Research Division, D.S.I.R. The experiment was sown by hand, using string grids to ensure correct positioning of seeds, on 30.9.68, 1.10.68 and 2.10.68. The first of these dates has been taken as day 1 of the experiment.

Emergence occurred from day 9 onwards and establishment counts, shown in Appendix 5, were made on day 26. In this initial period plants were thinned to one per position where necessary. The first sampling was made on day 28 with the others following, at intervals of 5 to 9 days (Appendix 1), until day 145 when the last sampling of low population plants was made.

Over the course of the experiment weed control was maintained by hand cultivation and spraying with herbicides. The plots were also sprayed to control aphids. Details of these treatments appear in Appendix 1. Birds were the most serious environmental hazard during the experiment and sample plants were protected with plastic ('Netlon') and wire netting from mid-December onwards.

The climatic conditions over the experimental period were favourable and rainfall and insolation are summarized in Appendix 3.

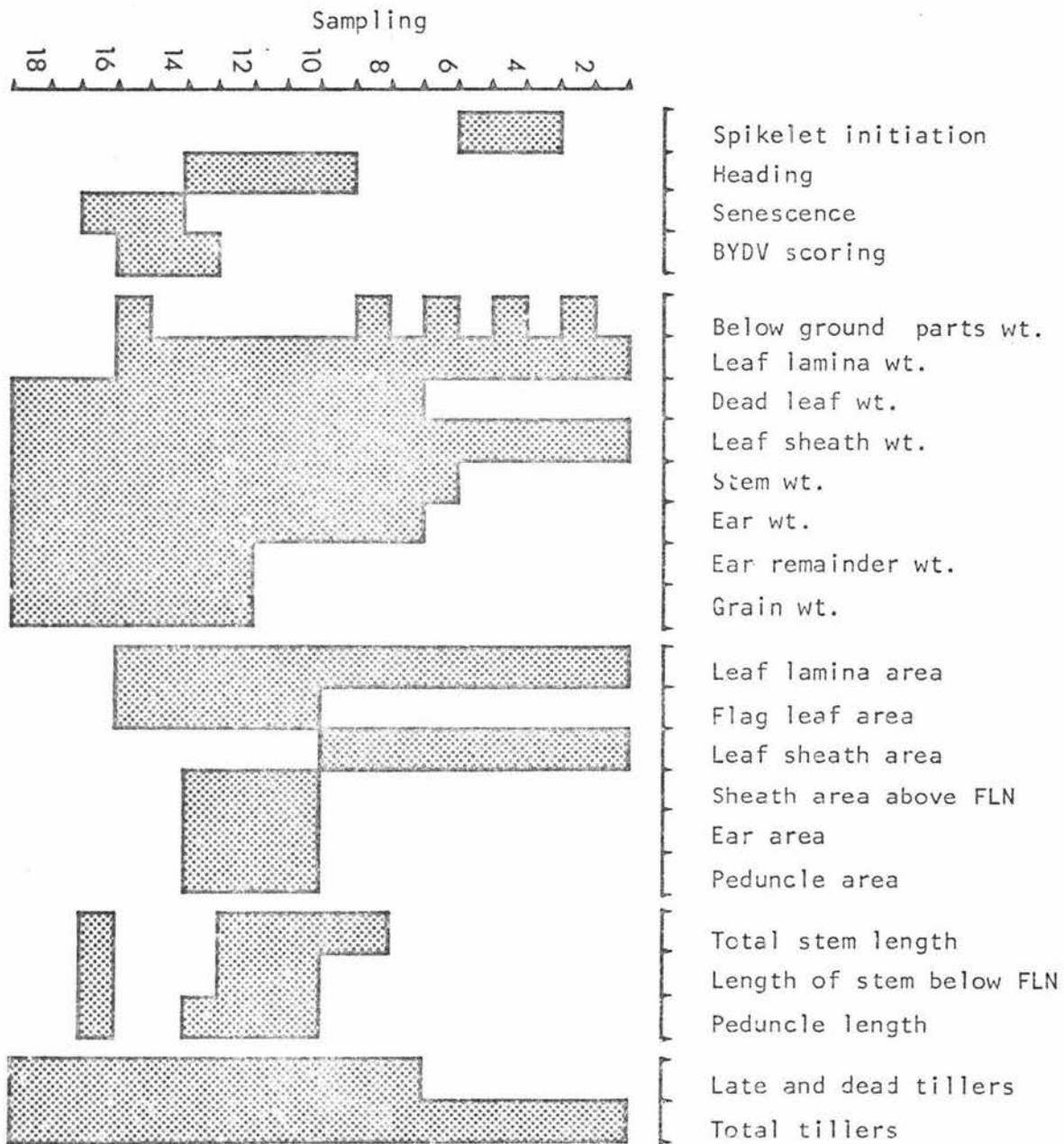
Spray irrigation was applied (0.40 acre-inches) after a dry spell in December but heavy rain fell immediately after this and no further irrigating was done during the experiment.

## 2.2 EXPERIMENTAL METHODS

### 2.2.1 Sampling Procedures

At each sampling one plant from those previously provided for measurement was taken at random from each plot in each replicate. At samplings plants were cut off at ground level and stored in plastic bags in a refrigerator until dissected and measured. Harvests were usually made early in the morning of the day of sampling.

The measurements made on plants at each sampling are summarized in Figure 1. The procedure at a sampling was to separate the plant into tillers and record the data for individual tillers; however, all dry weights were recorded on a whole plant basis. To estimate leaf area at samplings 1 and 2 the length and breadth at the mid-point of all leaves were measured. In later samplings an air flow planimeter was used to measure total leaf area except that after heading (i.e. the emergence of the ear above the ligule of the flag leaf) additional measurements were made of the length and breadth of individual flag leaves. Leaves were taken to be photosynthetically active if more than 50% of their area was green, and were otherwise included in the dead leaf fraction. Until sampling 10 the diameter of the base and the total length of leaf sheath to the ligule of the last fully expanded leaf were recorded. After this only the length and basal diameter of the flag leaf sheath were measured. Stem length was measured from sampling 6 onwards and later the length of the peduncle was recorded separately. After ear emergence the diameter of the peduncle at the ligule of the flag leaf was measured. The number of internodes below the flag leaf node (FLN) was recorded at samplings 11 and 12. Ears were separated after sampling 6. From heading onwards the number of spikelets, their fertility, and the lengths of the diagonals of the 8th spikelet counted from the base of the ear, were recorded for all ears. From sampling 12 the grain was separated from one ear per plant (or from two ears if there were more than 10 tillers on a plant); for the final sampling (17, or 18 in the case of the low plant population plots) grain was separated from all ears. Where ears had been damaged by birds, as occurred in samplings 16, 17 and 18, the ear was discarded; the correction necessitated by this procedure is outlined in Section 2.3.1.



Variable

Figure 1 Variables Measured at Samplings

After these measurements had been made, the separated fractions from all tillers of a plant were bulked, dried at 82°C for 24 hours, and weighed.

### 2.2.2 Recording Other Data

To provide an estimate of the mean date of spikelet initiation in each treatment samples of stem bases (i.e. those parts of leaf sheath and stem below ground level) were taken on days 40, 44 and 50 and preserved in formalin-acetic-alcohol. These samples were later split into separate tiller bases, dissected, and scored for spikelet initiation using Plate 1 in Barnard (1964) as a standard.

In order to estimate the end point of active photosynthesis in organs above the FLN these parts were scored for colour at samplings 14, 15 and 16. The following arbitrary criteria were used to classify specified parts as senescent:

- i) flag leaf area greater than 50% yellow;
- ii) flag leaf sheath or peduncle greater than 50% yellow at their approximate mid-point;
- iii) ear if the 8th spikelet counted from the base was substantially yellowed;
- iv) awns (in the case of Pitic 62) if those on the 8th spikelet were more than 50% yellowed.

To estimate the incidence of a late infection of barley yellow dwarf virus all sampled plants were scored on a zero (no apparent infection) to four (infection in all tillers) scale from harvests 12 to 14. Scoring was based on leaf colouring and was therefore confounded to some degree by leaf senescence.

In parallel with the series of samplings detailed in Section 2.2.1 three plants from each plot in blocks 1, 2, 4 and 6 were scored for leaf appearance and tillering until heading. Leaf appearance was recorded when the tip of the leaf could be seen within the last incompletely expanded leaf. Tiller appearance was recorded when the tip of a tiller appeared above the leaf sheath of its subtending leaf. The appearance of leaves and secondary tillers on the main stem, and of leaves on secondary tillers was recorded. Booting (the stage just before the tip of the ear appears above the ligule of the flag leaf) and heading dates were also recorded for the main stem and secondary tillers. This scoring was done at two day intervals initially and later at semi-weekly and weekly intervals. Recording was aided by

use of rings of remit wire, colour coded for different tillers, placed in the axils of known leaves on each tiller.

## 2.3 STATISTICAL METHODS

### 2.3.1 Preliminary Organisation of Data

The Massey University I.B.M. 1620 Computer was used to process the bulk of the data in the experiment. In most cases raw data were punched directly and programmes written as required to bring them into a form suitable for further analysis.

For the analyses of variance one preliminary missing plot analysis was required. This was calculated, following the method of Snedecor and Cochran (1967), from 2-way tables of means for each sampling. In subsequent analyses of variance (Section 2.3.2) the degrees of freedom for the residual mean square were reduced by one for each missing plot analysis.

Preliminary analysis indicated that for most data variances increased in time with mean values. To stabilize the variance and satisfy the assumptions of the regression models used in analysis of variance the logarithmic transformation

$$X = 100 \log (X + 1)$$

was applied to such data. For the fitting of polynomial growth curves to the data a natural logarithm transformation was used.

Estimates of leaf lamina area and flag leaf area (adaxial surfaces) from length x breadth measurements or air-flow planimeter readings were corrected before further analysis as detailed in Appendix 4. In the regressions used for corrections the length x breadth area, or the air flow planimeter reading, was treated as the dependent variable following the standard practice in calibrations (David and Cody, 1965). Methods used to calculate leaf sheath, peduncle, ear and awn (in Pitic 62) areas are also described in Appendix 4.

Subsampling was not used in the experiment except in the case of the grain fraction where the mean grain : ear remainder ratio from a subsample of ears was used to apportion the total ear weight into grain weight and ear remainder weight. In final samplings these fractions were completely separated so this procedure was not required.

Bird damage to the ripening grains made corrections for grain and ear weights necessary in samplings 16, 17 and 18, and ear total weight, or grain weight for the final sampling was proportionately increased to allow for missing ears. The number and size of corrections required are shown in Table 3.

Table 3 Corrections for Bird Damage.

Sampling	Population	Mean no. of ears per plant	Mean no. of damaged ears	Prop. of damaged ears	No. plants requiring correction	Prop. of plants requiring correction
16	1	3.0	1.0	0.33	1	0.02
	2	-	-	-	-	-
	3	20.8	2.7	0.13	8	0.19
17	1	-	-	-	-	-
	2	7.2	1.7	0.24	4	0.09
	3	22.3	3.9	0.17	11	0.26
18	3	19.1	6.1	0.32	13	0.92

### 2.3.2 Analyses of Variance

Analyses of variance were calculated using the system of computer programmes described by Munford (1970). Initial analyses were computed using completely factorial three or four way designs; the resulting table of mean squares was then adjusted by dropping all interactions involving blocks into the residual mean square term. The data were thus analysed according to a randomized complete block design. The regression models used were

$$Y_{ijkl} = m + t_i + p_j + v_k + (tp)_{ij} + (tv)_{ik} + (pv)_{jk} + (tpv)_{ijk} + b_l + e_{ijkl}$$

where  $Y_{ijkl}$  is the observed quantity,

$m$  is the mean of  $Y$  over all treatments,

$t_i$  is the effect of the  $i$ th time interval ( $i = 1, 2, \dots, 17$ ),

$p_j$  is the effect of the  $j$ th population ( $j = 1, 2, 3$ ),

$v_k$  is the varietal effect ( $k = 1, 2$ ),

$b_l$  is the block effect ( $l = 1, 2, \dots, 7$ ),

$e_{ijkl}$  is a random error element and,

$(tp)_{ij}$  etc., the terms in parentheses, are the various interactions,

or, in the two-way case,

$$Y_{jkl} = m + p_j + v_k + (pv)_{jk} + b_l + e_{jkl}$$

Mixed model analyses of variance in which  $t_i$  and  $p_j$  are random effects and  $v_k$  is fixed were derived from these regressions. The F-ratios used to test the main effects and interactions, obtained following Henderson (1960), are showed in Table 4. The coefficients of variance components have been omitted in this table.

Table 4 Expected Values and F-ratios for Three-way Mixed Model Randomized Complete Block Analysis of Variance

Source		Expected value of MS	F
Blocks	B	$6^2_w + 6^2_b$	
Time	T	$6^2_w + 6^2_{tp} + 6^2_t$	
Population	P	$6^2_w + 6^2_{tp} + 6^2_p$	
Variety	V	$6^2_w + 6^2_{tpv} + 6^2_{pv} + 6^2_{tv} + 6^2_v$	
TP		$6^2_w + 6^2_{tp}$	
TV		$6^2_w + 6^2_{tpv} + 6^2_{tv}$	
PV		$6^2_w + 6^2_{tpv} + 6^2_{pv}$	
TPV		$6^2_w + 6^2_{tpv}$	
Residual		$6^2_w$	

As indicated there is no appropriate test for the variety mean square. An approximate F-test for V was provided by

$$F = \frac{V' + TPV'}{TV' + PV'}$$

where  $V'$ ,  $TPV'$ ,  $TV'$  and  $PV'$  denote the mean squares corresponding to the sources of variation shown in Table 4. The approximate degrees of freedom for this ratio were estimated from

$$n_1 = \frac{(V' + TPV')^2}{(V')^2/f_v + (TPV')^2/f_{tpv}}$$

and

$$n_2 = \frac{(TPV' + TV')^2}{(TV')^2/f_{tv} + (PV')^2/f_{pv}}$$

where  $f$  subscript represents the appropriate degrees of freedom for each mean square (Snedecor and Cochran, 1967). In the two-way analyses of variance the varietal effect was tested against the PV interaction and the population effect against the residual variance.

### 2.3.3 Curve Fitting

Polynomials of degree  $k$  in time were fitted to the means of the natural logarithms of dry weight and photosynthetic area data and to the arithmetic means of stem length data. The computer programmes for this procedure were written by Mr. V. J. Thomas of the Applied Mathematics Division, D.S.I.R. A description of the method follows.

If plants with dry weights  $W_{ij}$  are harvested from  $r$  replicates at  $p$  occasions over the experimental period it is assumed that the observed value of  $\log_e W_{ij}$  for the  $i$ th sampling from the  $j$ th plot can be represented by

$$\log_e W_{ij} = B_0 + B_1 t + B_2 t^2 \dots + B_k t^k + \epsilon_{ij}$$

where  $B_0, B_1, \dots, B_k$  are the polynomial coefficients of the successive powers,  $t, t^2, \dots, t^k$  of time, and  $\epsilon_{ij}$  represents the random deviation from the true value. Curves of this type were fitted to the observed values using a multiple regression model. Writing  $y_{ij}$  for  $\log_e W_{ij}$  the general form of this model is

$$y_{ij} = \mu + \beta_1 (T - \bar{T}) + \beta_2 (T - \bar{T})^2 \dots + \beta_k (T - \bar{T})^k + \epsilon_{ij}$$

where  $\mu$  is the mean value of  $y$ , and

$\beta_1, \beta_2, \dots, \beta_k$  are partial regression coefficients.

The model is initially fitted as a polynomial of degree  $k = 0$

$$y_{ij} = \mu + \delta_{i.0} + \epsilon_{ij}$$

where  $\delta_{i.0}$  is a residual including all terms in  $(T - \bar{T})$  of order greater than zero. The analysis of variance of the fitted equation

$$y_{ij} = \bar{y} + d_{i.0} + e_{ij} \quad \text{----- } M_0$$

is given in Table 5.

Table 5 Analysis of Variance for  $M_0$

Source	SS	df	MS	F
Improvement with $M_0$ over $y = 0$	$SSB_0$	1	$MSB_0 = SSB_0$	$MSB_0/s^2$
Residual	$SSE_0$	$(p-2)$	$MSE_0 = SSE_0/(p-2)$	$MSE_0/s^2$
Within group	SSW	$p(r-1)$	$s^2 = SSW/p(r-1)$	

The F-ratios  $MSB_0/s^2$  and  $MSE_0/s^2$  provide tests of the improvement due to  $M_0$  and the lack of fit of this model respectively. Models

of higher degree in  $k$  are then fitted successively. The general form of these models is

$$y_{ij} = \bar{y} + \sum_{k=1}^m (\hat{\beta}_m t^k) + d_{i.m} + e_{ij} \quad \text{----- } M_m$$

where  $d_{i.m}$  represents all terms in  $t$  of order greater than  $m$  and  $t$  is written for  $(T - \bar{T})$ . The resultant partitioning of the total sum of squares of  $y$  is shown in Table 6.

Table 6 Partitioning of Total SS in Successive Models

Model	Improvement over $y = 0$	df	Residual	Improvement with extra term
$M_0$	$SSB_0$	1	$SSE_0$	$SSB_0$
$M_1$	$SSB_1$	2	$SSE_1$	$SSE_0 - SSE_1$
$M_{m-1}$	$SSB_{m-1}$	$m-1$	$SSE_{m-1}$	$SSE_{m-2} - SSE_{m-1}$
$M_m$	$SSB_m$	$m$	$SSE_m$	$SSE_{m-1} - SSE_m$

At each stage a comparison of  $M_m$  with  $M_{m-1}$  using analysis of variance reveals the improvement in fit of  $M_m$  over  $M_{m-1}$  and the lack of fit of  $M_m$ . This analysis of variance provides a test of the null hypothesis that residual variance due to terms in  $t$  of order greater than  $m$  is zero,  $MSE_m/s^2$ , and measures the improvement of fit as  $MSB_{m-(m-1)}/s^2$  as shown in Table 7. For this experiment the procedure outlined above was continued until the improvement of fit due to a model of higher degree was not significant except in some cases where, in the interest of subsequent growth analysis, an insignificant term was included or, more rarely, a significant term excluded.

Table 7 Analysis of Variance for  $M_m$

Source	SS	df	MS	F
$m$ th fixed variate $t^m$	$SSE_{m-1} - SSE_m$	1	$MSB_{m-(m-1)}$	$MSB_{m-(m-1)}/s^2$
Residual, $d_{i.m}$	$SSE_m$	$p-m-1$	$MSE_m$	$MSE_m/s^2$
Within group	SSW	$p(r-1)$	$s^2$	

### 2.3.4 Growth Analysis

Quadratic polynomials were found to give an adequate description of the changes of total dry weight, leaf area and total photosynthetic area in time. These were

$$W = \exp (B_0 + B_1 t + B_2 t^2)$$

and 
$$A = \exp (C_0 + C_1 t + C_2 t^2)$$

where  $B_0$ ,  $B_1$ ,  $B_2$ ,  $C_0$ ,  $C_1$  and  $C_2$  are polynomial coefficients. The significant growth analysis quantities were derived from these equations using the computer. For the above equations the following relationships hold:

1. The relative growth rate at any instant of time is

$$R = \frac{1}{W} \frac{dW}{dt} = B_1 + 2B_2 t$$

2. The leaf area ratio is

$$LAR = A / W = \exp (\log_e A - \log_e W)$$

3. The unit leaf rate is

$$E_A = R / LAR = (B_1 + 2B_2 t) \cdot \exp (\log_e W - \log_e A)$$

The crop growth rate and indices such as the leaf area index were similarly derived from fitted curves. At any instant of time the crop growth rate is

$$\begin{aligned} C &= \rho \cdot \frac{dW}{dt} \\ &= \rho \cdot \frac{1}{W} \cdot \frac{dW}{dt} \cdot W \\ &= \rho \cdot (B_1 + 2B_2 t) \cdot W \end{aligned}$$

where  $\rho$  is plant density (plants. unit area<sup>-1</sup>). The leaf area index is instantaneously

$$LAI = \rho \cdot \exp (\log_e A)$$

In the experiment total photosynthetic areas based on the sum of leaf lamina and sheath areas, ear area and peduncle area were also calculated and used in growth analyses. By analogy with  $E_A$ , LAR and LAI, the equivalent quantities on a total photosynthetic area basis are symbolized  $E_{PA}$ , PAR and PAI.

To calculate leaf area duration (LAD) or photosynthetic area duration (PAD) estimates of the days of 50% heading and senescence of photosynthetic parts were required. These were determined from 2 x r chi-square analyses of proportions in which the overall chi-square

value was partitioned into components due to, and deviating from, weighted regressions of proportion on time as described by Maxwell (1961). (The same method was also used to estimate the day of 50% spikelet initiation.) LAD or PAD between heading and senescence was then obtained by integrating LAI or PAI between these limits.

### 3.1 PERFORMANCE OF THE TWO VARIETIES ON AN AREA BASIS

#### 3.1.1 Grain Yield and Yield Components

The mean grain yields of the two varieties at each plant population are given in Table 8 and are plotted in Figure 2 against density on a logarithmic scale. On average Pitic 62 outyielded Raven by 32%. The means given are indirect estimates based on the grain weights of individual plants taken at the final samplings and errors of estimates are high (coefficient of variation 7 to 19%). Analysis of variance (Appendix 7) showed that there were significant differences between populations but not between varieties.

Yield components corresponding to these yields appear in Table 8 and Figure 3. Analyses of variance (Appendix 7) indicated that the numbers of ears per unit area and of spikelets per ear with one or more florets setting seed (fertile spikelets) showed highly significant trends ( $P < 0.01$ ) with increasing plant density while no population effect occurred for grains per spikelet and weight per grain. Total spikelet number per ear showed a small effect ( $0.05 > P > 0.01$ ) due to density which appears to arise from the higher spikelet numbers at the intermediate density, population 2. Total spikelet number per ear and grain number per spikelet were significantly higher for Pitic 62 than Raven. The varietal differences in ear number per unit area, spikelet fertility and grain weight shown in Figure 3 were not statistically significant although the latter just failed to reach the 5% level of probability.

#### 3.1.2 Growth Analysis on an Area Basis

Crop growth rates calculated from curves fitted to total dry weight data (Section 3.2.1) appear in Figure 4. For both varieties maximum growth rates were reached in the period just after heading and this peak was smaller and occurred progressively later as plant density decreased. At each density the growth rates of the two varieties were similar.

Leaf area indices, based on leaf lamina area, and total photosynthetic area indices, based on leaf lamina, leaf sheath, peduncle and ear areas, derived from fitted curves are also presented in Figure 4. For both varieties maximum LAI occurred at or slightly before the day of 50% ear emergence while maximum PAI occurred a few

Table 8

Means of Grain Yield and Yield Components  
for Varieties within Populations

Variable	Variety	Population			S.E.(V-V)
		1	2	3	
Grain Yield (g.m <sup>-2</sup> )	Raven	714.7	498.9	278.4	73.80
	Pitic 62	928.2	584.5	413.3	
S.E.(P-P)		90.38			
Ears.m <sup>-2</sup>	Raven	634.9	361.9	211.0	44.32
	Pitic 62	660.3	368.2	212.6	
S.E.(P-P)		54.28			
Total spikelets.ear <sup>-1</sup>	Raven	16.51	17.01	16.21	0.247
	Pitic 62	18.77	20.14	19.73	
S.E.(P-P)		0.303			
Fertile spikelets.ear <sup>-1</sup>	Raven	13.74	15.61	14.45	0.452
	Pitic 62	14.91	17.45	17.95	
S.E.(P-P)		0.553			
Grains spikelet <sup>-1</sup>	Raven	1.855	2.065	1.910	0.0989
	Pitic 62	2.584	2.872	3.051	
S.E.(P-P)		0.1212			
Weight.grain <sup>-1</sup> (x 10 <sup>2</sup> g)	Raven	4.274	4.134	4.602	
	Pitic 62	3.671	3.050	3.118	
S.E.(P-P)		0.1972			

S.E.(P-P) = standard error of difference between populations.

S.E.(V-V) = standard errors of difference between varieties.

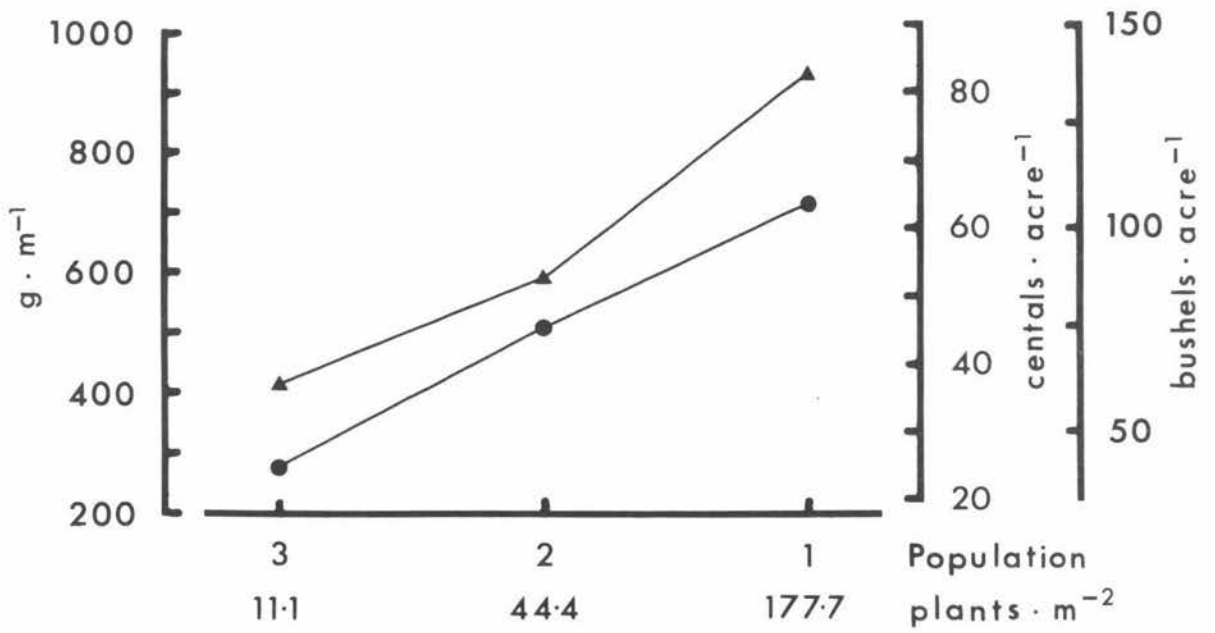


Figure 2 Mean Grain Yield

- Raven
- ▲ Pitic 62

Figure 3

Mean Yield Components for Varieties  
at Each Population.

Identification of curves:

- A : Ears.  $m^{-2}$   
B : Total spikelets.  $ear^{-1}$  \_\_\_\_\_  
Fertile spikelets.  $ear^{-1}$  -----  
C : Grains.  $spikelet^{-1}$   
D : Weight.  $grain^{-1}$

Identification of varieties:

- = Raven  
▲ = Pitic 62

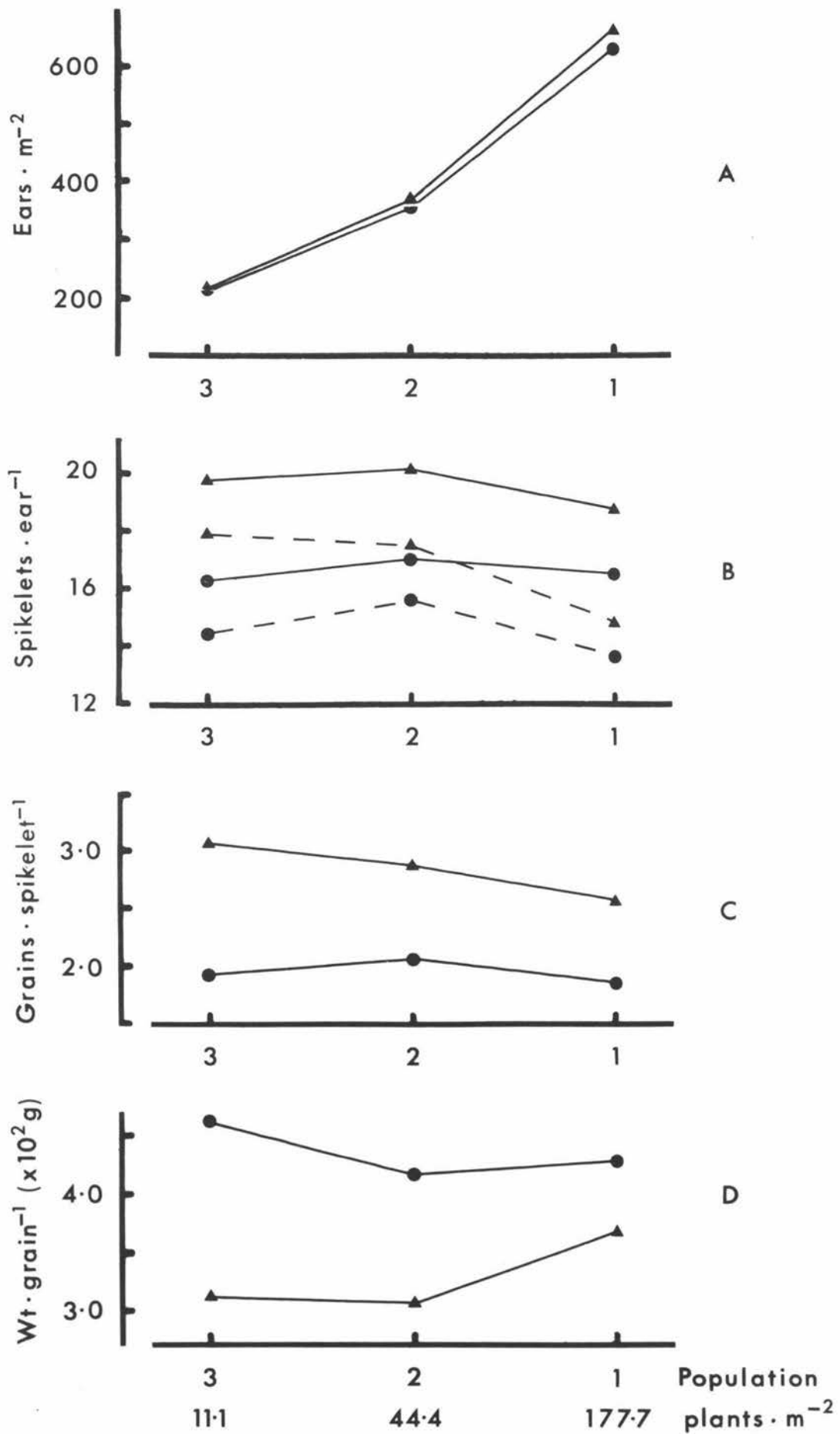


Figure 4

Crop Growth Rates and  
Photosynthetic Area Indices.

Identification of curves:

- A : Leaf Area Indices
- B : Total Photosynthetic Area Indices
- C\* : Crop Growth Rates

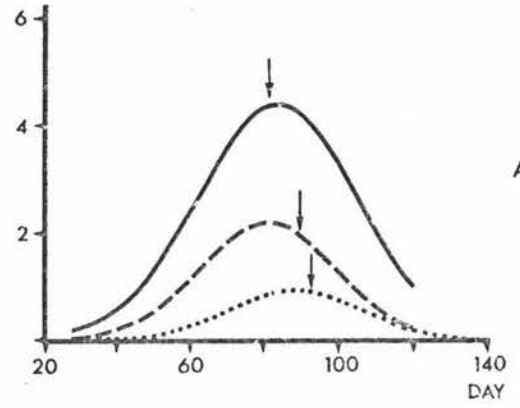
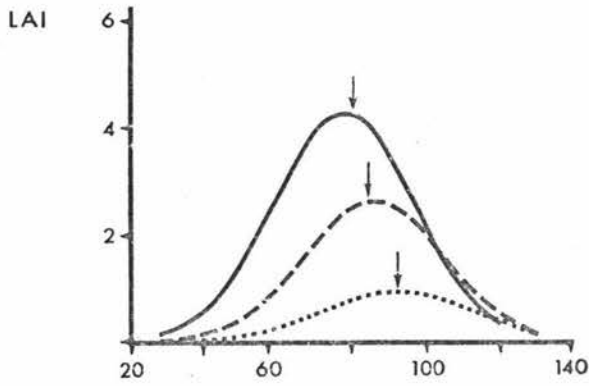
Identification of populations:

- \_\_\_\_\_ 177.7 plants. m<sup>-2</sup>
- 44.4 plants. m<sup>-2</sup>
- ..... 11.1 plants. m<sup>-2</sup>

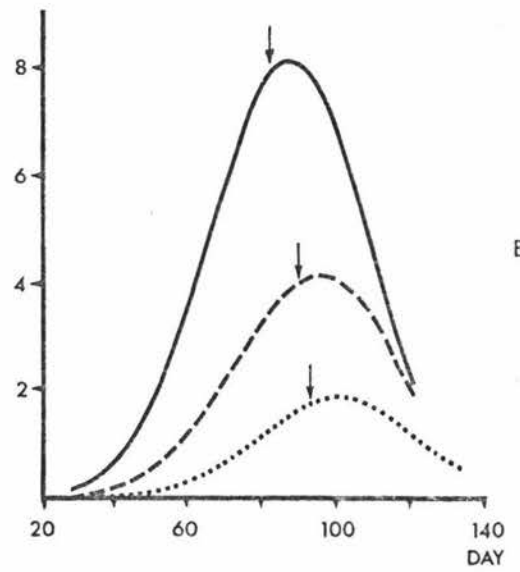
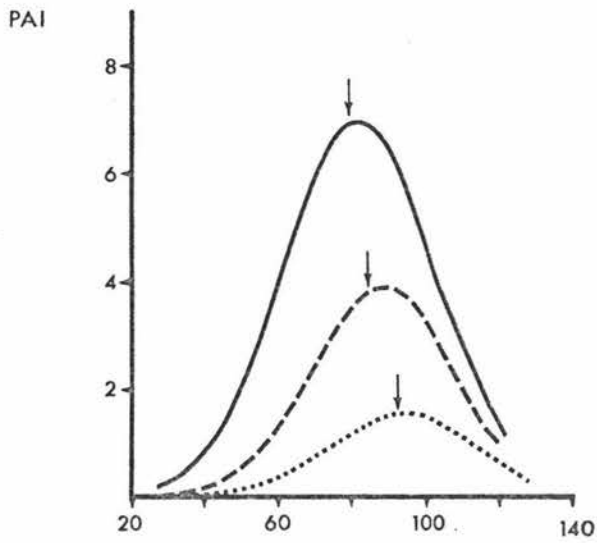
↓ Day of 50% ear emergence.

RAVEN

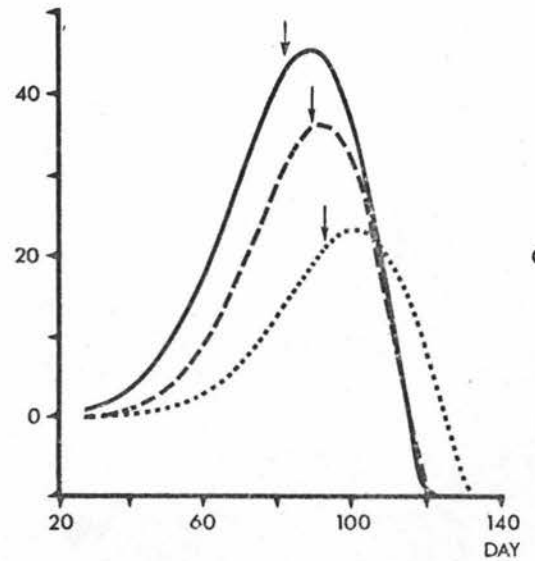
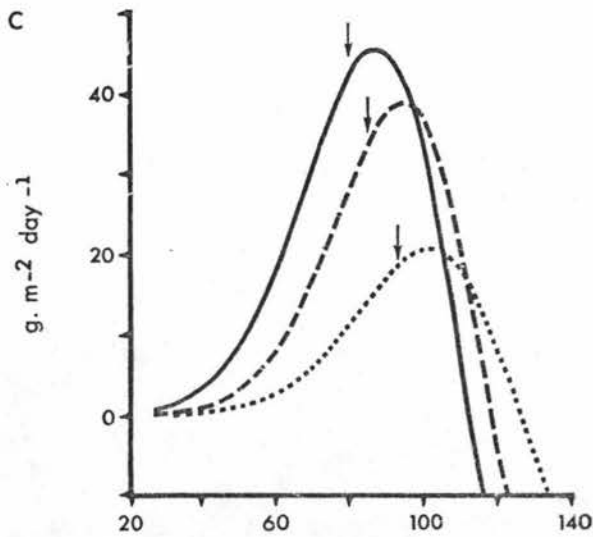
PITIC 62



A



B



C\*

days later. There were no consistent differences in LAI between varieties but the total photosynthetic area indices were greater for Pitic 62; this reflected differences in ear area.

The durations of photosynthetic areas between heading and senescence, obtained by integration as described in Section 2.3.4, are given in Table 9. For the high and intermediate plant densities  $LAD_{\text{flag leaf}}$  was higher for Raven than Pitic 62 while for the lowest plant density the durations were similar. These differences arose partly from the earlier senescence of flag leaves in Pitic 62 (Table 14) and partly from differences in LAI (Figure 4). The advantage of Pitic 62 over Raven in duration of parts above the FLN (flag leaf sheath and lamina, peduncle and ear),  $PAD_{\text{FLN}}$ , and in total photosynthetic area duration,  $PAD_{\text{total}}$ , were largely due to the greater areas of these parts in Pitic 62. Since these durations were derived from fitted curves they are not directly comparable within a variety. Thus  $PAD_{\text{total}}$  minus  $PAD_{\text{FLN}}$  does not give the duration of remaining leaves or parts below the FLN as might be expected. Valid comparisons can only be made between varieties and populations.

Table 9 Durations of Photosynthetic Areas (D) after Ear Emergence and Grain Leaf Ratios (G).

	D (days)			G ( $\text{g}\cdot\text{m}^{-2}\cdot\text{day}$ )		
	Flag leaf	Above FLN	Total area	Flag leaf	Above FLN	Total area
Raven 1	42	126	184	17.0	5.7	3.9
Pitic 1	22	171	240	42.2	5.4	3.9
Raven 2	14	68	98	35.6	7.3	5.1
Pitic 2	9	65	117	64.9	9.0	5.0
Raven 3	8	32	45	34.8	8.7	6.2
Pitic 3	7	48	60	58.9	8.6	6.8

Grain leaf ratios (see Section 1.2.2) are also presented in Table 9. These figures were derived from the mean grain yields of Table 8 and the durations of Table 9. In all cases the grain leaf ratio calculated using  $LAD_{\text{flag leaf}}$  was higher for Pitic 62 than Raven. These differences disappeared when either  $PAD_{\text{FLN}}$  or  $PAD_{\text{total}}$  was used in place of  $LAD_{\text{flag leaf}}$ .

### 3.2 THE GROWTH AND DEVELOPMENT OF THE TWO VARIETIES ON A PLANT BASIS

#### 3.2.1 Analyses of Variance for Dry Weight and Photosynthetic Area Data

Analyses of variance for the dry weights of the various parts of individual plants appear in Appendix 8. These indicate that significant time trends occurred in the weight of all fractions except the ear remainder (rachis, rachillae, glumes and awns). Highly significant population effects emerged for all fractions as expected for analyses based on weight per plant. Significant differences between the two varieties appeared only for the stem, ear remainder and ear total weight fractions. On average the weight of the stem fraction in Raven exceeded that of Pitic 62 by 43% while the ear remainder and ear total weights of Pitic 62 were respectively 29 and 14% greater than those of Raven.

Analyses of variance for the areas of photosynthetic parts appear in Appendix 9. In these analyses time trends were significant in all cases except for flag leaf area. The analyses for flag leaf area, ear area and peduncle area are confounded by tiller number since these variables were measured on tillers which had headed at given samplings. Population effects were significant for all areas except those of the ear and peduncle. The only significant F-test between varieties was for peduncle area, this being on average 1.4 times greater in Raven than Pitic 62. Although the difference was not statistically significant with the analysis of variance used, the ear area of Pitic 62 was 112% that of Raven. This difference arose from the contribution of awns to ear area in Pitic 62 (Table 13).

In both sets of analyses a number of interactions were significant. These probably arose largely from highly significant main effects. Since all data were transformed such interactions are in any case difficult to interpret.

#### 3.2.2 Curves Fitted to Weight and Area Data

The coefficients of polynomials fitted to dry weights and photosynthetic areas appear in Appendices 13 and 14. For uniformity in subsequent analysis of the weight fractions polynomials of the same degree have been used for a given fraction in all cases. Where this has required a polynomial of a degree higher or lower than that which was statistically significant the change has been indicated in the appendix using asterisks. In the case of curves fitted to the area data the same procedure has been followed except for flag leaf area,

ear area and area above the flag leaf node. For these fractions consistency in the degree of polynomial used could only be maintained for varieties within populations. Computer plots and analyses of variance of the polynomial curves fitted to the data for Raven 2 are given as examples in Appendix 6. In the same appendix arithmetic plots of curves for leaf area and total photosynthetic area with corresponding data points are presented. It should be noted that these latter curves were not fitted to the data points plotted but were derived from polynomials fitted to the natural logarithms of the data.

### 3.2.3 Growth Analysis

Relative growth rates of the total weight of above ground parts are shown in Figure 5. There was a tendency for higher relative growth rates at low population densities and the time drift was similar for all populations. There were no large varietal differences.

The components of relative growth rate are shown in Figure 6 where unit photosynthetic rates and the corresponding area to weight ratios are plotted for leaf area and total photosynthetic area. There were similar trends in  $E_A$  for the two varieties particularly before ear emergence. The peak values of  $E_A$  reached after heading were associated with the high growth rates and declining LAI in this period (Figure 4). Maximum values of  $E_A$  were higher for Pitic 62 than Raven at the intermediate and low plant densities. This reflected the more rapid leaf senescence in Pitic 62 at these densities.  $E_A$  also increased in both varieties as density decreased. This trend can be related to the lower LAI at low densities (Figure 4).

Unit photosynthetic rates for total photosynthetic areas,  $E_{PA}$ , exhibited similar differences for populations but the varietal difference was reversed. The higher  $E_{PA}$  for Raven was a reflection of the smaller total photosynthetic area in this variety. In the curves for  $E_{PA}$  the pronounced maximum after heading, seen in  $E_A$ , did not appear since total photosynthetic area was not declining as rapidly as leaf area.

### 3.2.4 Distribution of Dry Matter within Plants

Cumulative logarithmic plots of the changes in dry weights of various plant parts derived from polynomials fitted to each fraction (see Appendix 6) are presented in Figure 7. The main feature of these graphs is the difference in the proportion of grain to straw (weight of

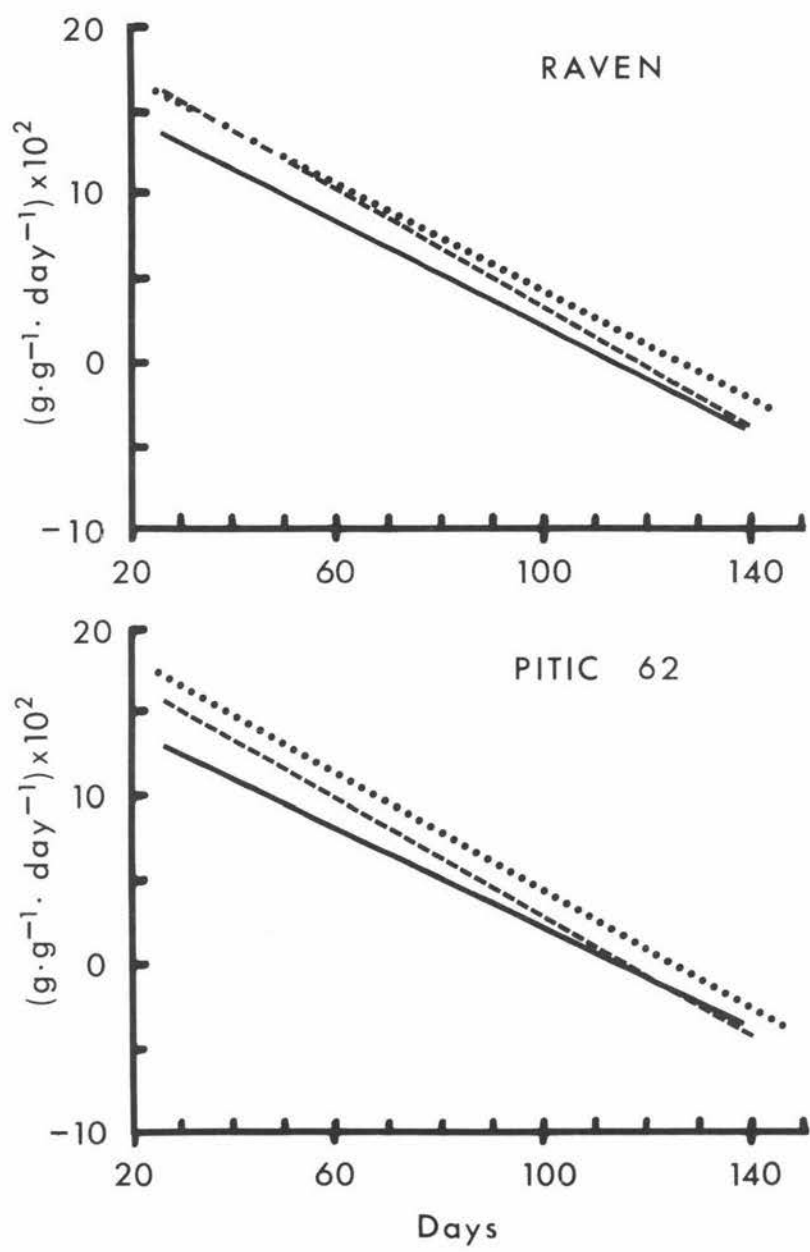


Figure 5 Relative Growth Rates

Population 1 ———  
 Population 2 - - - -  
 Population 3 ······

Figure 6

Unit Photosynthetic Rates and  
Photosynthetic Area Ratios.

Identification of curves:

- A : Unit Leaf Rates
- B : Leaf Area Ratios
- C : Unit Leaf Rates (Based on  
Total Photosynthetic Area)
- D : Total Photosynthetic Area  
Ratios

Identification of populations:

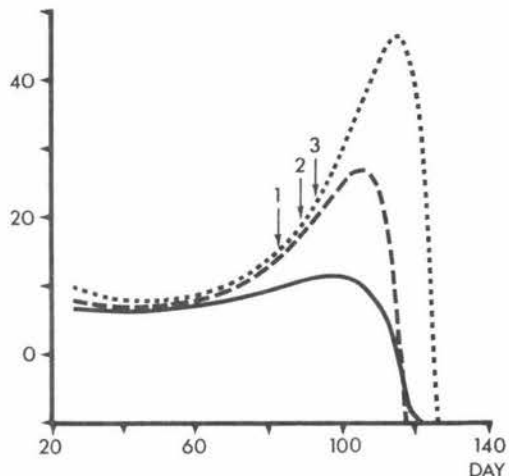
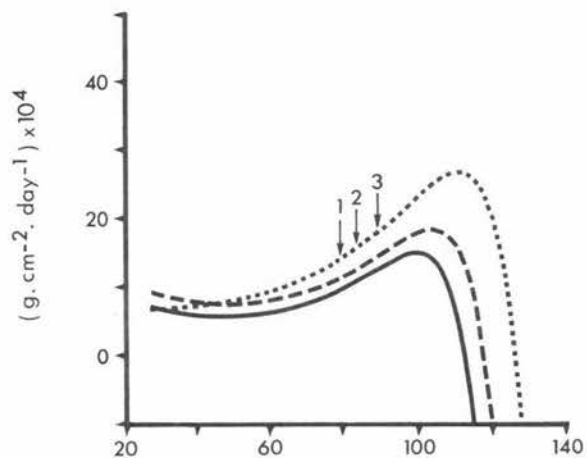
- \_\_\_\_\_ 177.7 plants.  $m^{-2}$  Population 1.
- 44.4 plants.  $m^{-2}$  Population 2.
- ..... 11.1 plants.  $m^{-2}$  Population 3.

↓ Day of 50% ear emergence.

RAVEN

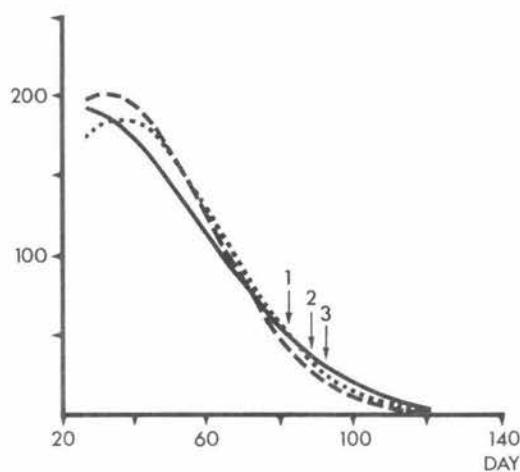
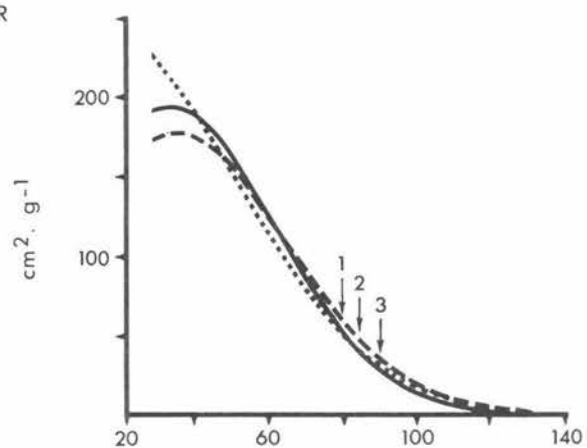
PITIC 62

$E_A$



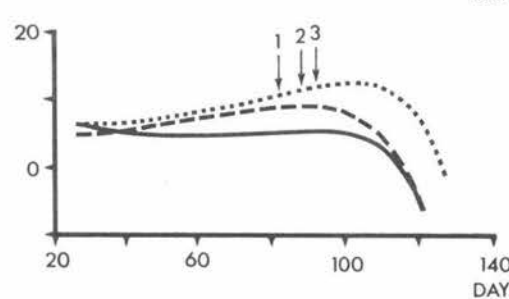
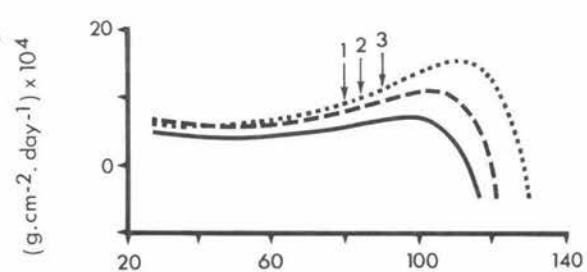
A

LAR



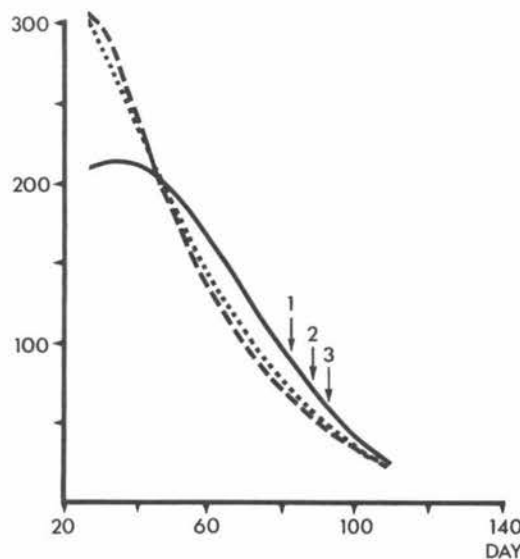
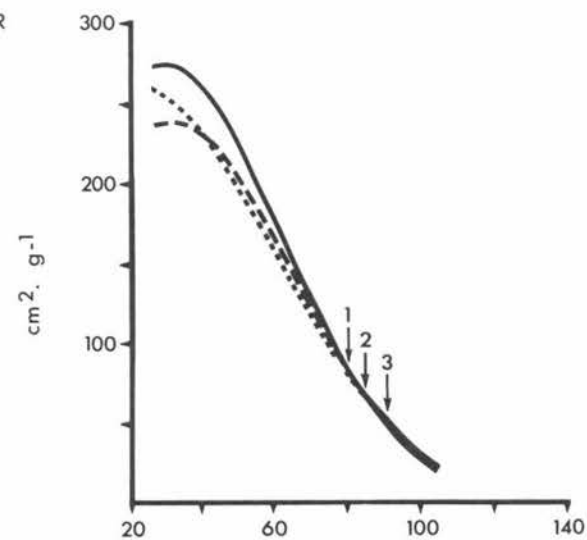
B

$E_{PA}$



C

PAR



D

Figure 7

Cumulative Logarithmic Plots of  
Dry Weight Fractions.

Identification of populations:

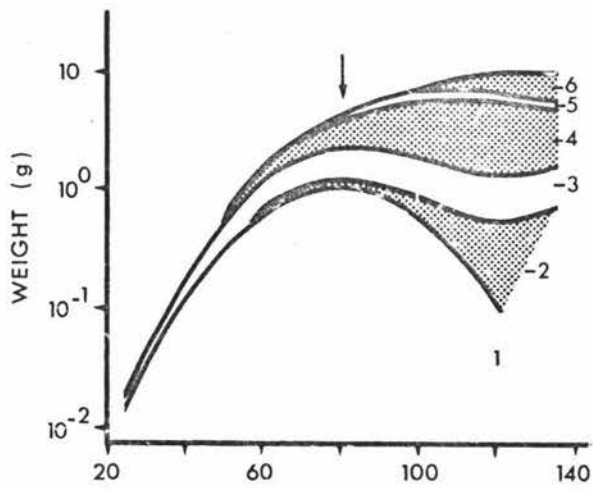
- A : 177.7 plants. m<sup>-2</sup>
- B : 44.4 plants. m<sup>-2</sup>
- C : 11.1 plants. m<sup>-2</sup>

Identification of dry weight fractions:

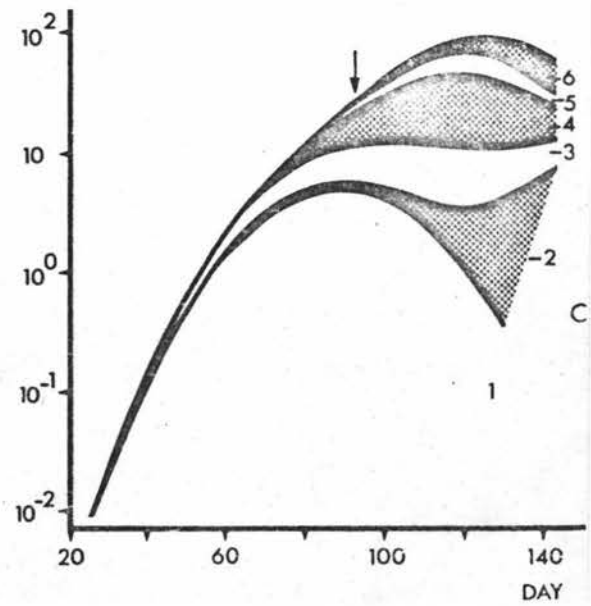
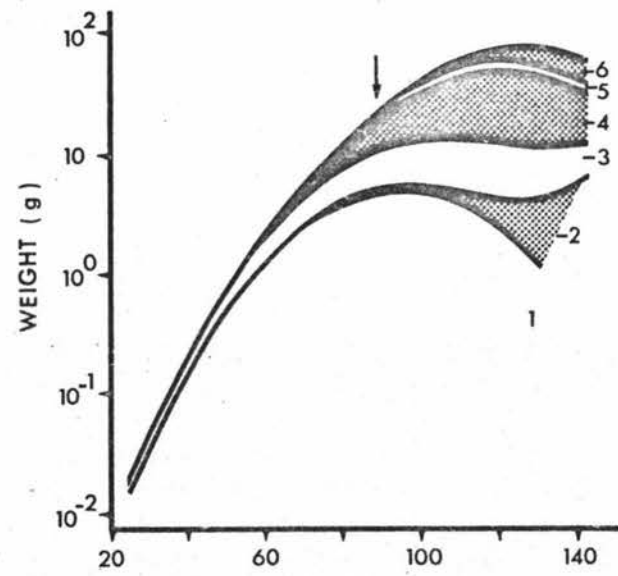
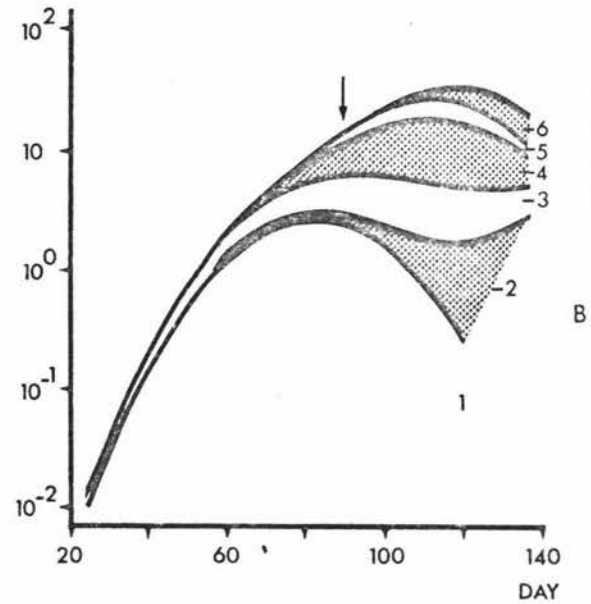
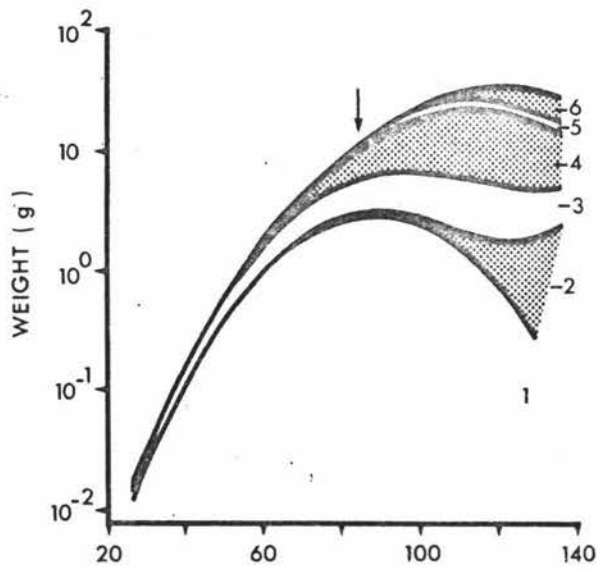
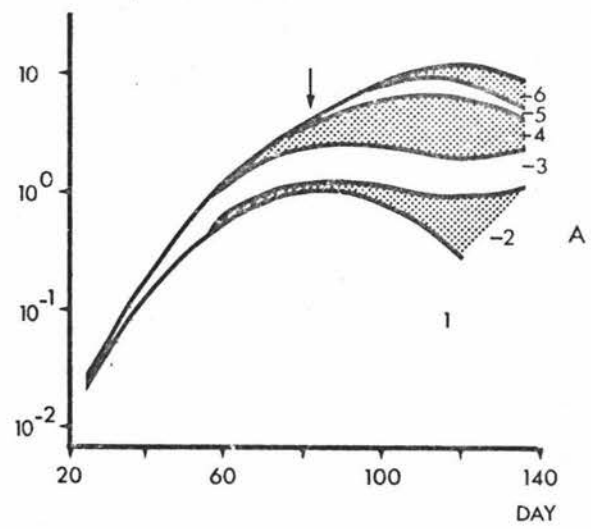
- 1 = leaf
- 2 = dead leaf
- 3 = leaf sheath
- 4 = stem
- 5 = ear remainder
- 6 = grain

↓ Day of 50% ear emergence

RAVEN



PITIC 62



all remaining parts) in Raven and Pitic 62. The mean grain to straw ratios at the final sampling are shown in Table 10. Analysis of variance (Table 11) shows there were significant differences in this ratio between varieties but not between populations. The percentage distribution of dry matter within the plant during development is shown in Figure 8 for the high and low densities. The curves in this figure are derived from the polynomials curves for each fraction as in Figure 7.

Table 10 Mean Grain : Straw Ratios.

Variable	Variety	Population			S.E.(V-V)
		1	2	3	
G : S ratio	Raven	0.552	0.533	0.608	0.043
	Pitic 62	0.781	0.709	0.867	
S.E.(P-P)		0.057			

Table 11 Analysis of Variance for Grain : Straw Ratios.

Variable	Source	df	MS	F
G : S ratio	Blocks	6	$1.942 \times 10^6$	
	Population	2	$4.831 \times 10^6$	2.388 ns
	Variety	1	$5.138 \times 10^7$	$8.266 \times 10$ *
	FV	2	$6.216 \times 10^5$	$3.073 \times 10^{-1}$ ns
	Residual	30	$2.023 \times 10^6$	

### 3.2.5 Area of Photosynthetic Parts

Cumulative logarithmic plots of the areas of photosynthetic parts of the plant are plotted in Figure 9. These curves are derived from polynomials fitted to the area data for individual fractions. The percentage contributions of each photosynthetic part to total area on specified days are shown in Table 12. This table shows that the proportionate contribution to total photosynthetic area of leaf area declined while those of the ear and peduncle increased as the plants matured. In Raven the peduncle made a relatively greater contribution

Figure 8

Percentage Distribution of Dry Matter

Identification of populations:

A : 177.7 plants . m<sup>-2</sup>

B : 11.1 plants . m<sup>-2</sup>

Identification of dry weight fractions:

1 = leaf

2 = dead leaf

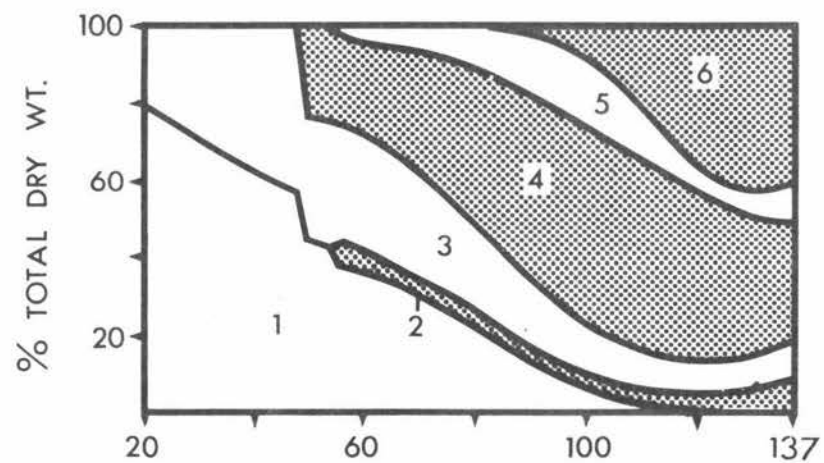
3 = leaf sheath

4 = stem

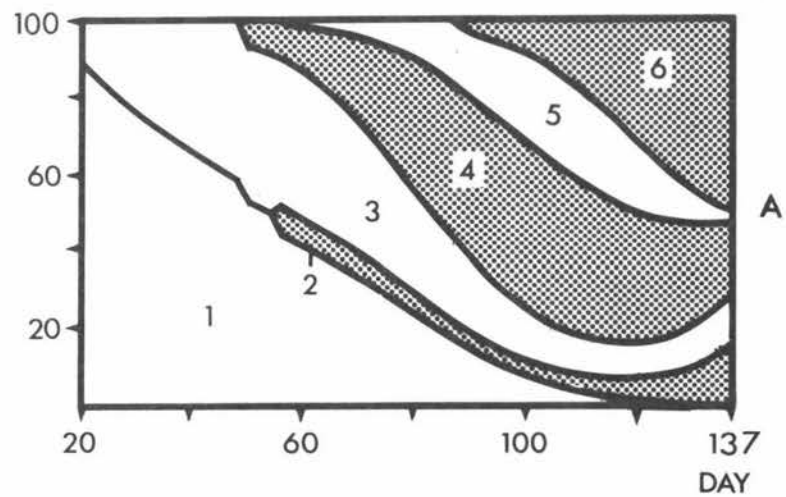
5 = ear remainder

6 = grain

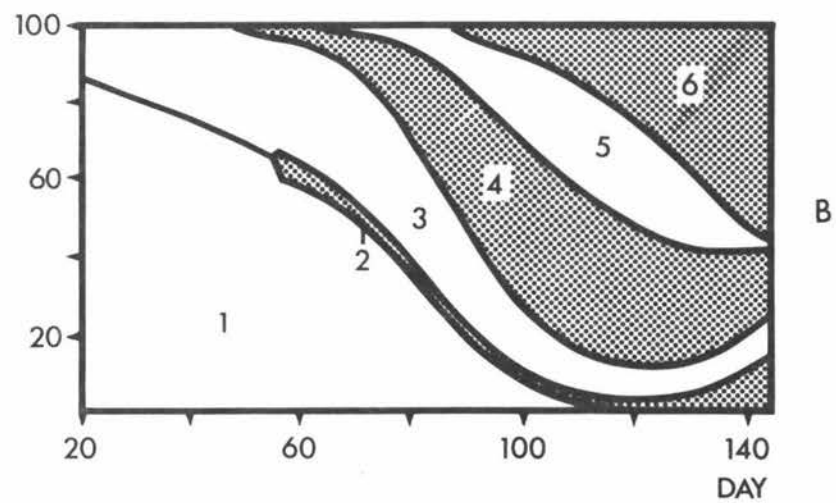
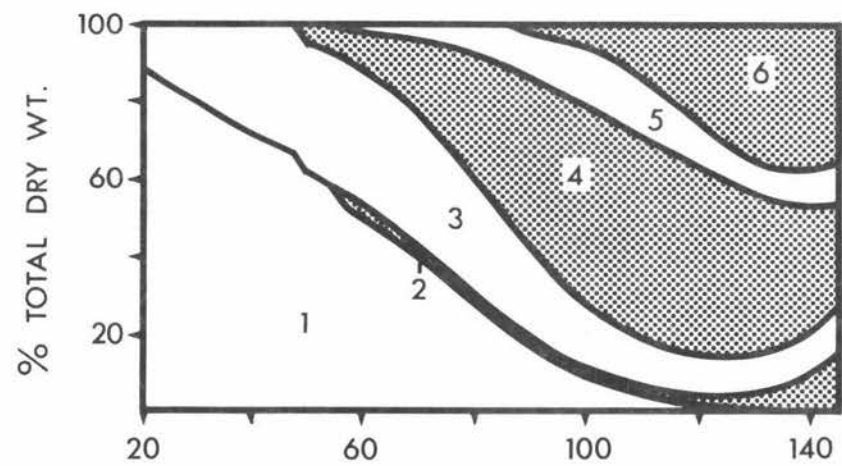
RAVEN



PITIC 62



A



B

Figure 9

Cumulative Logarithmic Plots of Areas  
of Photosynthetic Parts.

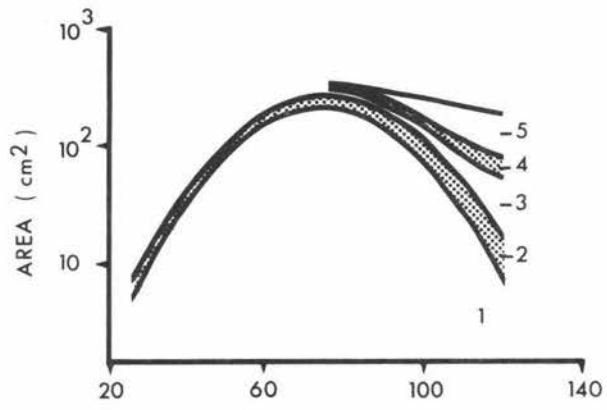
Identification of populations:

A	:	177.7 plants . m <sup>-2</sup>
B	:	44.4 plants . m <sup>-2</sup>
C	:	11.1 plants . m <sup>-2</sup>

Identification of photosynthetic parts:

1	=	area of lower leaves
2	=	leaf sheath area
3	=	flag leaf area
4	=	ear area
5	=	peduncle area

RAVEN



PITIC 62

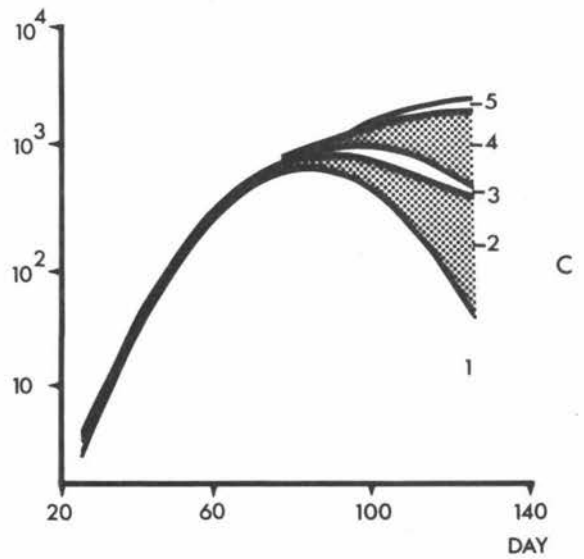
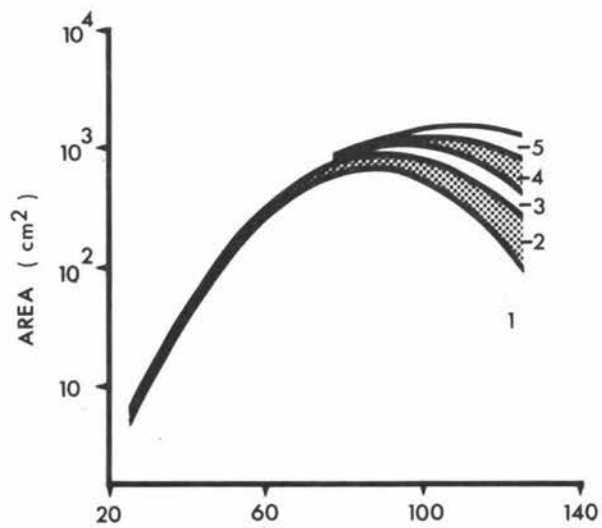
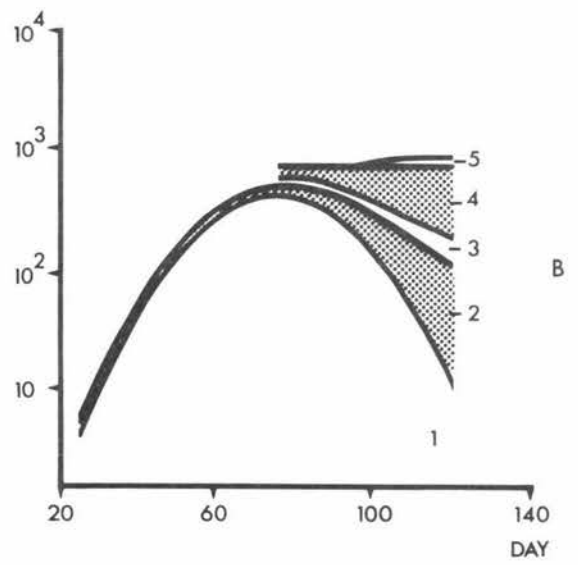
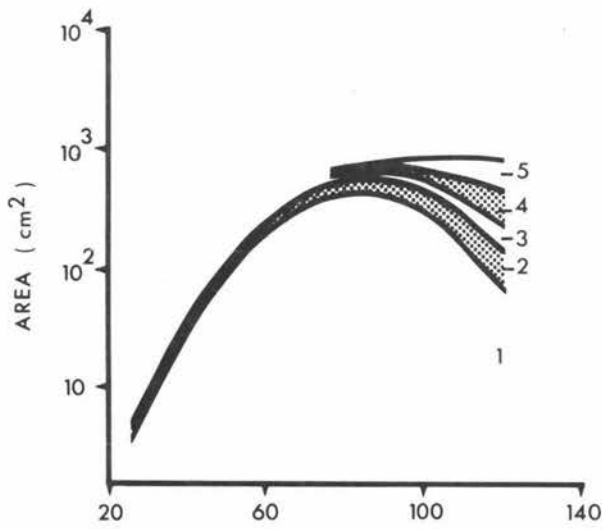
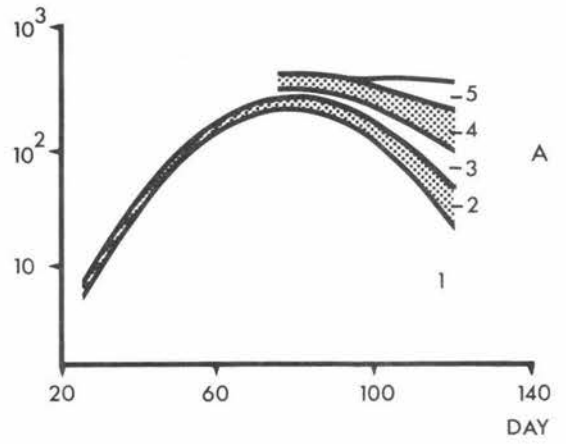


Table 12

Total Photosynthetic Area and %  
Contributions of Photosynthetic Parts

	Day	% contribution of part to total area					Total area (cm <sup>2</sup> )
		Lower leaves	Leaf sheath	Flag leaf	Ear	Peduncle	
Raven 1	40	78	22	-	-	-	42.7
	60	80	20	-	-	-	196.6
	80	60	18	10	0	4	352.3
	100	30	16	13	12	29	261.5
	115	0	10	0	21	69	155.1
Pitic 1	40	79	21	-	-	-	39.1
	60	81	19	-	-	-	172.0
	80	47	13	11	26	4	466.1
	100	29	14	13	29	16	408.7
	115	0	11	0	42	47	285.2
Raven 2	40	79	21	-	-	-	37.1
	60	80	20	-	-	-	249.7
	90	51	21	11	10	7	812.5
	100	33	18	10	14	25	909.8
	120	0	12	0	32	56	695.5
Pitic 2	40	81	19	-	-	-	50.8
	60	85	15	-	-	-	324.5
	90	37	19	10	30	4	817.6
	100	18	19	10	42	11	848.7
	120	0	13	0	70	17	827.1
Raven 3	40	80	20	-	-	-	50.4
	60	81	19	-	-	-	337.3
	90	54	22	12	7	6	1267.7
	100	36	20	16	11	17	1558.6
	120	12	16	13	29	31	1469.9
Pitic 3	40	80	20	-	-	-	36.0
	60	85	15	-	-	-	315.7
	90	52	21	9	17	1	1264.2
	100	26	20	14	31	10	1786.3
	120	0	15	0	67	17	1626.0

to total area than in Pitic 62 but the converse held for ear area. The latter difference arose from the large awn surface area in Pitic 62. The estimated contribution of awn area, calculated as described in Appendix 4, to ear total area is given in Table 13.

Table 13 Percentage Contribution of Awn Area to Ear Area in Pitic 62

Sampling	Population		
	1	2	3
10	64.5	63.2	-
11	65.2	58.0	57.4
12	63.7	59.8	56.7
13	57.6	56.2	50.8
14	57.4	48.7	47.4

Table 14 Estimated Mid-point of Senescence of Photosynthetic Parts.

Variety	Part	Mid-point day		
		Pop. 1	Pop. 2	Pop. 3
Raven	flag leaf	115	120	123
	f-leaf sheath	120	119	126
	peduncle	117	119	126
	ear	118	121	126
Pitic 62	flag leaf	(104)	114	118
	f-leaf sheath	119	120	129
	peduncle	119	121	(137)
	ear	118	121	127
	awns	109	117	122

Estimates of the mid-point of senescence of photosynthetic parts appear in Table 14. These were derived from the chi-square analyses shown in Appendix 12. The general trend shown by these data was delayed senescence as density decreased. Leaf persistence was shorter

in Pitic 62 than Raven and the awns of this variety senesced earlier than other parts. Values for the mid-point of senescence in the peduncles of Pitic 62 at the low density, and the flag leaves of the same variety at the high density, are unreliable since the estimate was made outside the range of the independent fixed variable in the regression equations. The curves in Figure 9 have not been altered to allow for the earlier senescence of some parts so that the flag leaves and lower leaves appear in this figure after the estimated mid-point of senescence.

### 3.2.6 Plant Development

The course of tillering is shown in Figure 10. There were pronounced and highly significant differences in total tiller number per plant between populations but differences between varieties were not significant (Appendix 11). These differences began to appear between days 40 and 50 which coincided with the appearance of tertiary tillers (Table 16) and nodal roots, and the initiation of spikelet primordia (Table 17). After heading there was an increase in total tiller number at the low plant populations but not at the intermediate and high populations. This increase was associated with the production of late tillers at the lower plant densities.

The number of tillers which were dead or non-fertile at each of the later samplings also appear in Figure 10. Differences between populations in this number arose from non-fertile rather than dead tillers (Appendix 11). Although differences between varieties in these categories were not statistically significant the number of dead tillers in plants of Pitic 62 was higher than in those of Raven.

The appearance of secondary tillers and of leaves on these tillers and the main stem are recorded in Table 15. In this table the mean day of tiller appearance was the day on which the first leaf of that tiller appeared. In both varieties at all populations the appearance of leaves on the main stem was regular and occurred over much the same period of time; however Pitic 62 produced more leaves than Raven. The appearance of leaves on secondary tillers was also regular and for these tillers, and the main stem, the rate of leaf appearance could be described using linear regressions. These regressions were in all cases highly significant and did not differ significantly for tillers within a variety and population (analyses not presented). Thus the phyllochron was similar for early and late secondary tillers and convergence of development towards a relatively uniform date of heading

Figure 10

Mean Tiller Numbers at Samplings.

Identification of curves:

———— Total Tiller Number  
----- Total Tiller Number Minus  
Number of Dead and Non-  
elongating Tillers.

Identification of populations:

1 = 177.7 plants . m<sup>-2</sup>  
2 = 44.4 plants . m<sup>-2</sup>  
3 = 11.1 plants . m<sup>-2</sup>

I Standard errors for means of total  
tiller numbers at samplings 3, 6, 9  
12, 15, 17 for population 2.

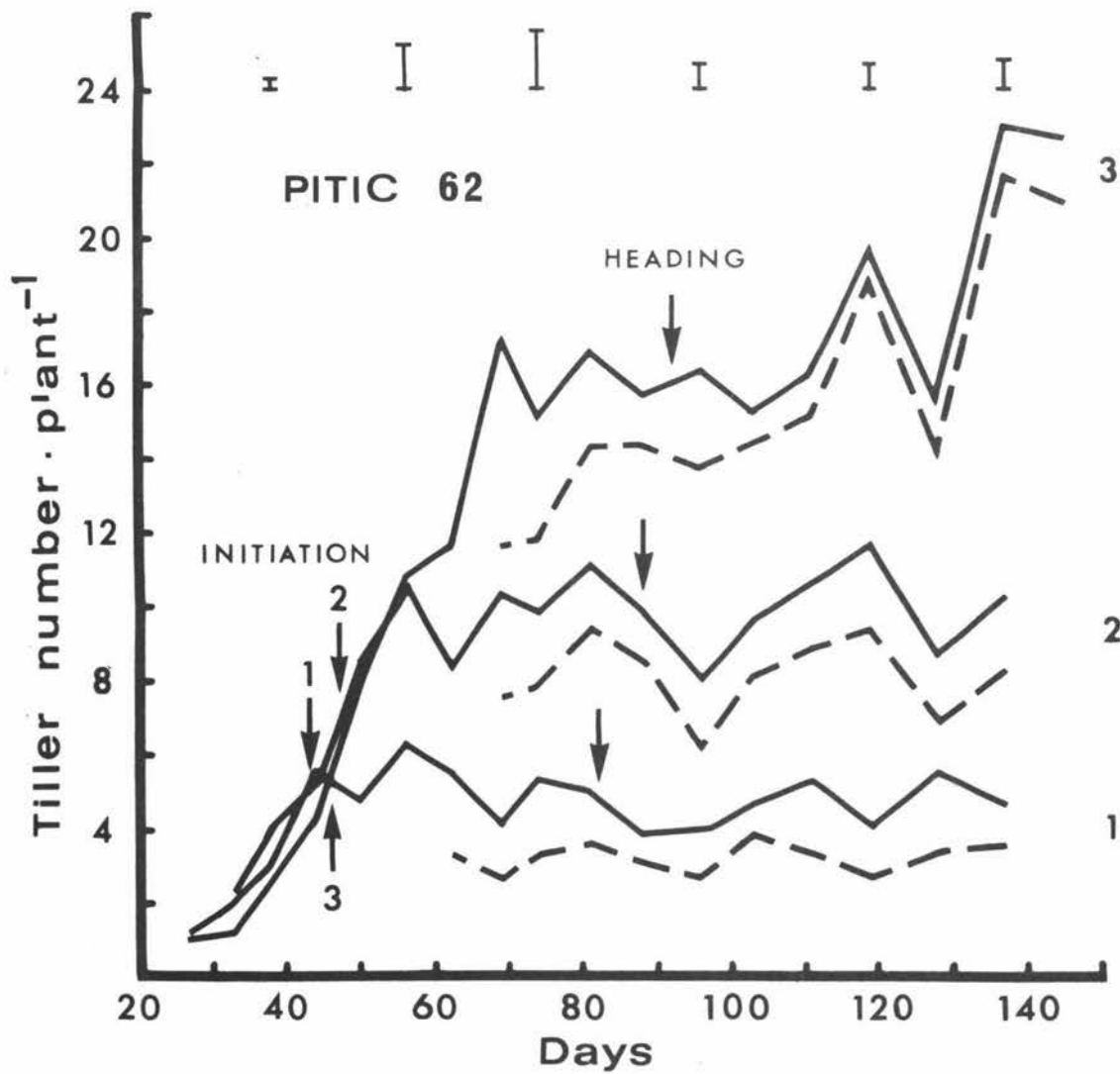
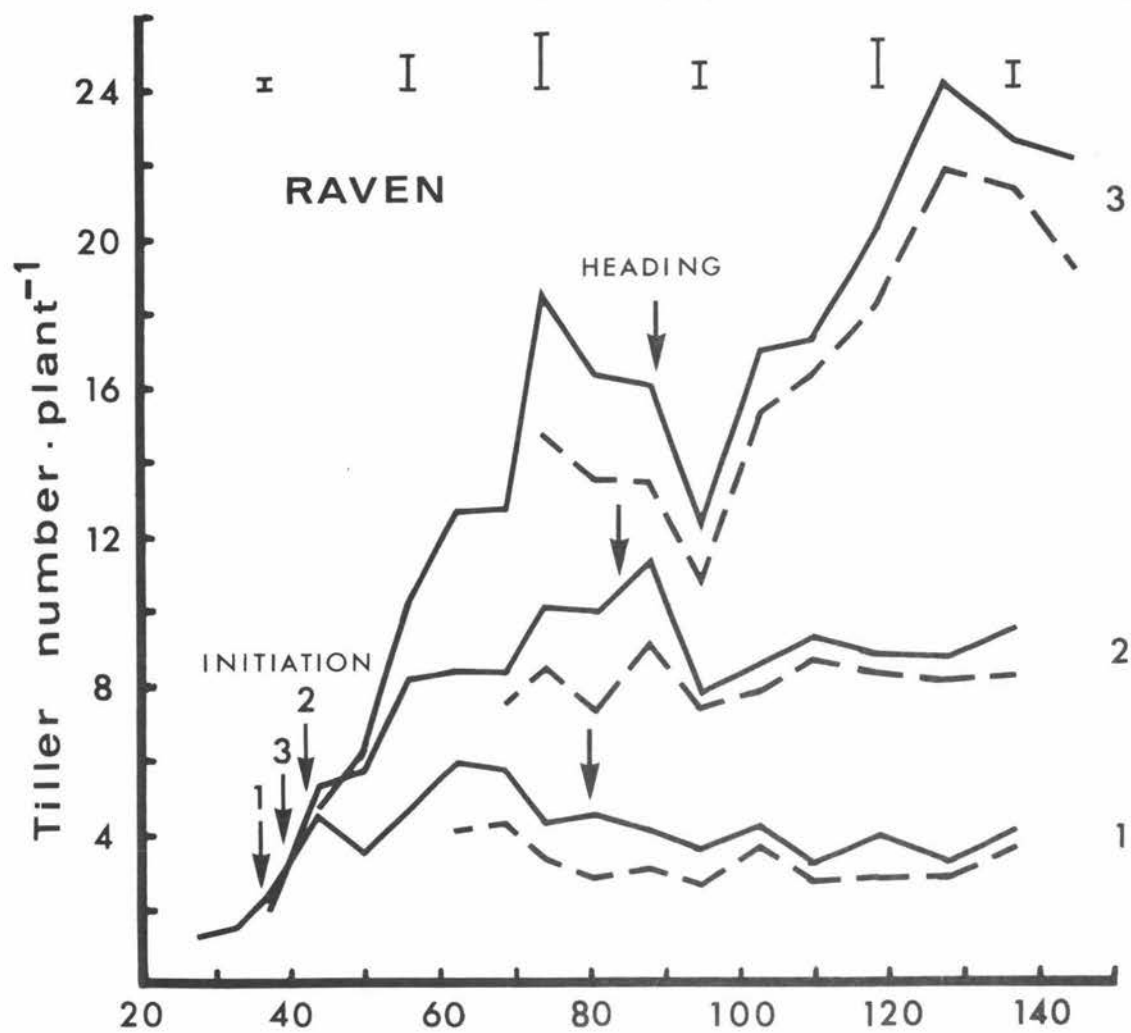


Table 15

Leaf and Tiller Appearance on the  
Main Stem and Secondary Tillers

The mean day of leaf appearance on the main stem, of secondary tiller appearance, of flag leaf appearance and of booting and heading are shown. Tiller identification is as follows:

MS = main stem

CN = coleoptile node tiller

1L = tiller in axis of 1st leaf and so on.

Main stem leaf	Day of leaf appearance	Tiller	Day of tiller appearance	No. of leaves on tiller	Day of flag leaf appearance	Day of booting	Day of heading
Raven 1.							
		MS	-	8.0	55.6	71.6	75.1
		CN	29.0	6.0	63.0	72.5	77.3
1st	-	1L	29.4	5.5	60.0	74.0	77.3
2nd	19.2	2L	34.3	5.0	58.5		
3rd	23.0	3L	38.3	4.0	62.0		
4th	28.9						
5th	36.0						
6th	41.4						
7th	-						
8th	55.6						
Pitic 1.							
		MS	-	9.2	56.7	74.0	77.6
		CN	28.9	7.0	-	76.6	81.0
1st	-	1L	28.6	6.8	61.7	78.8	82.2
2nd	18.7	2L	32.7	6.1	63.2	78.0	82.5
3rd	21.7	3L	38.2	5.0	62.0		
4th	27.9						
5th	32.9						
6th	38.0						
7th	42.5						
8th	51.0						
9th	56.7						

Table 15 (continued)

Main stem leaf	Day of leaf appearance	Tiller	Day of tiller appearance	No. of leaves on tiller	Day of flag leaf appearance	Day of booting	Day of heading
Raven 2							
		MS	-	8.3	63.0	75.0	77.8
		CN	31.6	7.0	64.3	76.1	80.1
1st	-	1L	30.6	6.1	65.0	78.0	81.7
2nd	19.3	2L	34.8	5.2	66.0	79.0	82.6
3rd	23.9	3L	39.8	4.0	68.0	-	83.5
4th	30.3	4L	53.4	4.0	67.8		
5th	35.9						
6th	41.2						
7th	50.0						
8th	57.5						
9th	63.0						
Pitic 2							
		MS	-	10.1	61.1	75.0	80.7
		CN	29.5	7.8	63.4	77.4	79.5
1st	-	1L	29.4	7.2	60.0	77.0	81.8
2nd	18.7	2L	33.5	6.4	64.3	78.9	82.4
3rd	22.2	3L	37.6	5.6	64.7	82.2	84.0
4th	28.4	4L	46.0	4.8	70.0		
5th	33.6	5L	59.5				
6th	36.5						
7th	42.2						
8th	-						
9th	58.3						
10th	61.1						

Table 15 (continued)

Main stem leaf	Day of leaf appearance	Tiller	Day of tiller appearance	No. of leaves on tiller	Day of flag leaf appearance	Day of booting	Day of heading
Raven 3							
		MS	-	8.1	57.7	74.5	78.1
		CN	31.3	6.0	59.5	75.6	80.6
1st	-	1L	30.9	5.6	61.3	77.7	81.3
2nd	18.9	2L	34.9	4.8	62.6	80.1	81.3
3rd	23.7	3L	40.7	4.5	64.3	82.0	84.0
4th	30.3	4L	55.4	3.6	71.6		
5th	36.3						
6th	41.8						
7th	-						
8th	57.7						
Pitic 3							
		MS	-	10.0	63.1	77.4	82.8
		CN	31.4	7.5	65.7	79.2	81.5
1st	-	1L	30.0	7.3	64.0	79.6	82.2
2nd	19.0	2L	33.9	6.4	64.6	80.5	82.5
3rd	22.4	3L	38.9	5.8	67.3	81.0	85.3
4th	28.7	4L	49.5	5.0	67.6	84.3	88.0
5th	33.7	5L	54.6	4.6	74.4		
6th	38.6	6L	61.0	4.0	77.0		
7th	46.7						
8th	54.0						
9th	57.6						
10th	63.1						

(Table 15) was achieved mainly by the reduction in leaf number on later tillers. The tendency for Pitic 62 to produce more leaves than Raven over a similar time span also appeared in secondary tillers.

The rate of booting and of heading on the main stem and secondary tillers could also be described using linear regressions. These did not differ significantly between populations and varieties (analyses not presented).

The production of secondary tillers on the main stem started at about the 4-leaf stage in both varieties at all populations. The first two tillers to arise, those from the coleoptile and first leaf nodes, did so more or less simultaneously (Table 15). Coleoptile node tillers appeared on average in 41 and 42% of the scored plants of Raven and Pitic 62 respectively, this percentage varying inversely with plant density. After emergence of the first two tillers other secondary tillers appeared at gradually increasing intervals. At lower plant densities Pitic 62 produced one or two more secondary tillers than Raven although these late tillers did not head.

The appearance of the first tertiary tillers on specified secondary tillers is shown in Table 16. As density increased tertiary tiller production was reduced. At high density Pitic 62 tended to produce more tertiary tillers than Raven but in both cases the surviving tillers at maturity at this density were usually the main stem and earlier secondary tillers. Tertiary tiller appearance on secondary tillers began approximately one phyllochron earlier than secondary tiller production on the main stem.

Table 16                      Appearance of Tertiary Tillers.

The mean day of appearance of the first tertiary tiller on specified secondary tillers is shown. Secondary tillers are identified as

CN = coleoptile node tiller

LL = tiller in axis of 1st leaf of main stem  
and so on.

	Secondary tiller			
	CN	1L	2L	3L
Raven 1	-	37.3	-	-
Pitic 1	40.0	37.8	41.0	-
Raven 2	41.8	38.2	45.8	55.0
Pitic 2	38.3	36.7	40.5	56.7
Raven 3	42.2	38.8	47.5	53.0
Pitic 3	41.0	37.7	44.0	51.0

The middle points of spikelet primordia initiation and of heading, estimated as shown in Appendix 12, are given in Table 17. This table shows that initiation and heading tended to be hastened at the high plant population and that the interval between these events was also shorter at this density. These differences reflected the heterogeneity of the tiller populations of plants at low densities since the mean heading dates for main stem and secondary tillers (Table 15) were earlier than the estimates for the entire tiller population (Table 17).

The mean dates of anthesis for varieties and populations were not established in this experiment because flowering is variable and difficult to score. From observation it appeared that anthesis occurred from 4 to 8 days after heading. There were no apparent differences between varieties or populations in this respect.

Table 17 Estimated Mid-points of Spikelet Initiation and Ear Emergence.

Variety	Process	Mid-point day		
		Pop. 1	Pop. 2	Pop. 3
Raven	initiation	36	42	39
	heading	80	84	89
Pitic 62	initiation	43	47	46
	heading	82	88	92

### 3.2.7 Stem Growth

Analyses of variance for the lengths of parts of the stems appear in Appendix 10. The analysis for total stem length showed highly significant time effects, population effects and first, order interactions, and a varietal effect significant at the 5% level. These differences can be seen in Figure 11 where polynomial curves fitted to stem length data are drawn. (The coefficients of these polynomials appear in Appendix 15). The average maximum lengths of tillers were 30%, 32% and 17% greater for Raven than those of Pitic 62 at the high, medium and low populations respectively. Since the ratio of total length of lower internodes to peduncle length was almost constant at 0.9 for both varieties at all populations it is apparent that these parts contributed equally to the differences in total stem length. Analysis of variance (Appendix 10) shows both peduncle length and length of lower internodes

Figure 11

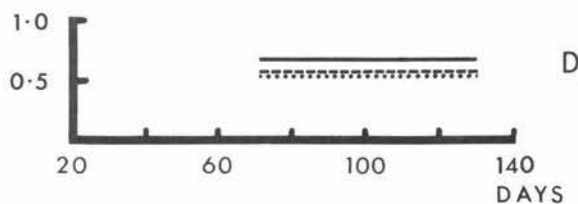
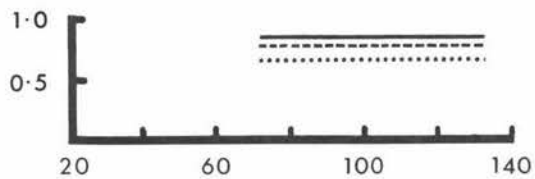
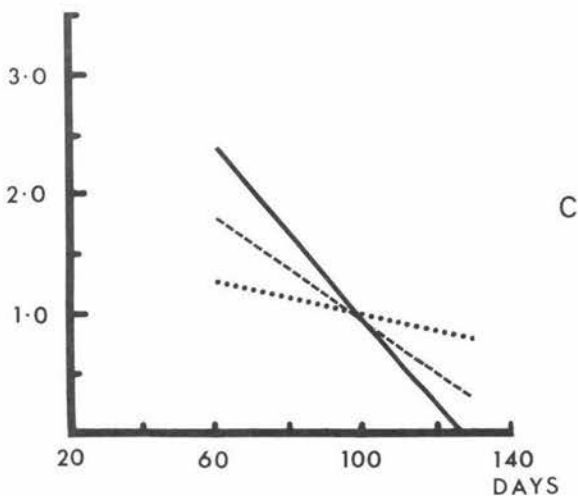
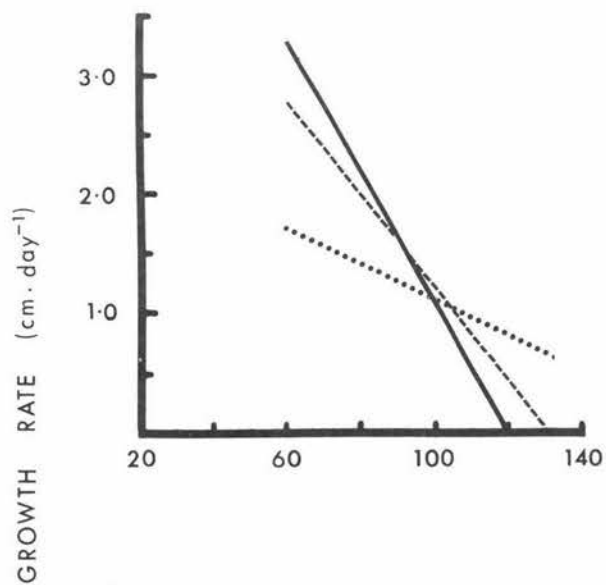
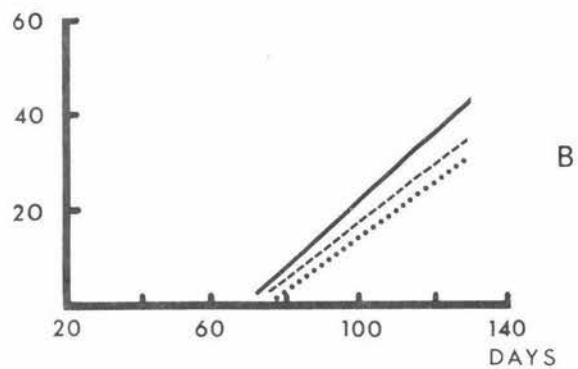
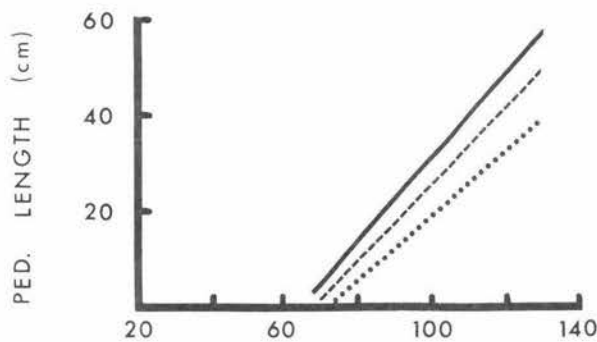
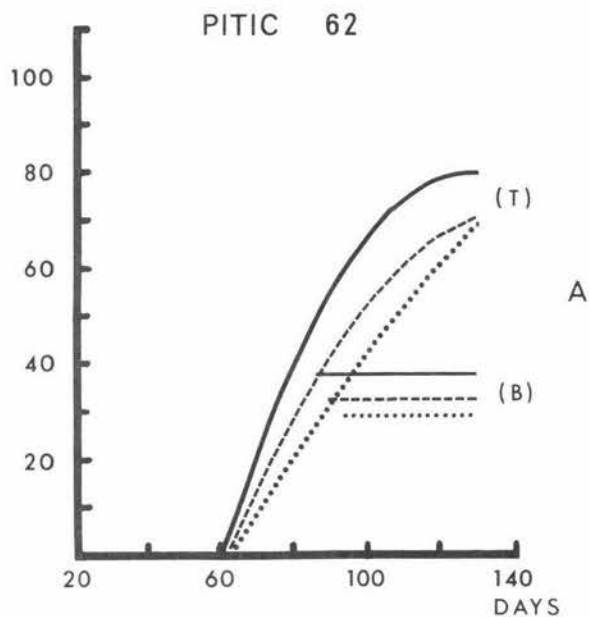
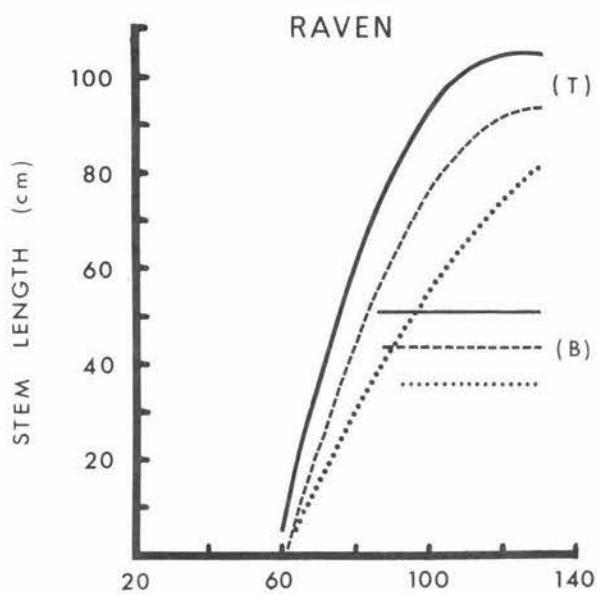
Stem Lengths and Growth Rates.

Identification of curves:

- A : Total Stem Length (T) and  
Length of Internodes below FLN (B).
- B : Peduncle Lengths.
- C : Stem Growth Rates.
- D : Peduncle Growth Rates.

Identification of populations:

- \_\_\_\_\_ 177.7 plants . m<sup>-2</sup>
- 44.4 plants . m<sup>-2</sup>
- ..... 11.1 plants . m<sup>-2</sup>



differed significantly between varieties. These are plotted in Figure 11. Differences between the two varieties in length of stem did not arise from the number of internodes (Appendix 10) although Pitic 62 had on average a slightly higher number of elongated internodes above ground level than did Raven (Table 18). This may be related to the higher leaf number in Pitic 62 (Table 15). The numbers of elongated internodes were similar on all tillers in plants in spite of age differences (analyses not presented).

Table 18 Mean Number of Internodes Below the FLN.

Variable	Variety	Population			S.E. (V-V)
		1	2	3	
Internodes	Raven	3.29	2.99	2.88	0.19
	Pitic 62	3.40	3.17	3.23	
S.E. (P-P)		0.24			

Stem and peduncle elongation rates are also plotted in Figure 11. In both varieties the growth rate for the whole stem declined as population density fell while the differences in peduncle growth rate were smaller. Raven had markedly higher elongation rates for both the whole stem and the peduncle.

#### 4.1 COMPARATIVE YIELD PERFORMANCE OF THE TWO VARIETIES

##### 4.1.1 Grain Yield

Although the yield advantage of Pitic 62 over Raven was statistically non-significant the difference was large and, considerations of grain quality aside, economically important. The lack of significance appears to arise from the substantial errors associated with the indirect estimates of yield used. Acceptance of the null hypothesis under these conditions does not necessarily imply that yields are equal, or even closely similar, since biologically real differences do not automatically lead to significant F-tests (Henderson, 1960). That the yields were in fact different is suggested by the significant ( $0.05 > P > 0.01$ ) difference between variety mean yields which appeared when the data were analysed according to a fixed effects model. This model is less sensitive to experimental variation than the mixed model used in the analysis of variance presented in Appendix 7.

One factor contributing to the experimental errors in the final yield estimates was the small sample size dictated by bird damage to plots. With larger samples, and direct measurement of grain weight per unit area, variation could have been reduced.

Another factor leading to errors was the incidence of barley yellow dwarf virus (BYDV) infection. The symptoms of this disease appeared after ear emergence indicating that infection occurred at a time when effects upon subsequent yield can be severe (Smith and Wright, 1964). The summary of scores for BYDV presented in Table 19 shows that on average 25% of the Raven tillers and 50% of the Pitic 62 tillers appeared to be infected. In spite of this level of infection grain yields were high. However from data on the grain weight of individual tillers (not presented) it was apparent that the BYDV increased the heterogeneity of samples and thus the experimental errors. The data of Table 19 also suggest that Pitic 62 was more susceptible to BYDV than Raven. This would tend to obscure yield differences between the varieties.

The comparison of the yields of the varieties appearing in Figure 2 shows Pitic 62 outyielded Raven at each plant density. The tendency to convergence of yields at the intermediate plant density may in part reflect the relatively low incidence of BYDV in Raven and the higher incidence in Pitic 62 at this density (Table 19). The largest yield

difference appeared at the highest plant density. This suggests that Pitic 62 may have a higher optimum plant density than Raven but to test this effect an experiment with more plant populations extending to much higher densities would be required.

Table 19 Summary of BYDV Scores

Scoring Scale: 0 represents no apparent infection; 1, 2, 3 and 4 represent respectively infection of 25%, 50%, 75% and 100% of the tillers on a plant. Data are mean scores for plants at specified samplings.

Sampling	R1	P1	R2	P2	R3	P3
12	0	1.0	0.3	1.7	0	2.6
13	0	2.1	1.6	2.3	0.7	2.2
14	1.1	1.8	0.6	3.0	2.1	2.8

#### 4.1.2 Yield Components

The components of yield presented in Table 8 and Figure 3 show the sources of differences in yield between the varieties. Since ear numbers per unit area were closely similar in both varieties it is evident that the yield advantage of Pitic 62 must lie in the other yield components. Of these grain number per spikelet and, to a lesser degree, spikelet number and spikelet fertility were the most important. Together these gave Pitic 62 a higher grain number per ear which more than compensated for the lower grain weight in this variety. Similar results have been recorded in other semidwarf wheat varieties by Johnson, Schmidt and Mekasha (1966) and Rawson and Evans (1970). A factor which contributed to the higher grain number per ear in Pitic 62 was the occurrence of two or three additional spikelets on basal nodes of the rachis in about 20-30% of the ears. These spikelets usually contained fertile florets which set seed (cf. Kozhevnikov, 1964).

Similar changes in yield components with changing plant population were observed for both varieties in this experiment. It is apparent that the number of ears per unit area was the major determinant of grain yield at each plant density as is usually the case (Kirby, 1967; Puckridge and Donald, 1967). Trends in other yield components tended to compensate for those in ear number leading to larger ears at the lowest density. The single exception was in Raven at the intermediate population where ear size was greater than that at either extreme, largely

because of a higher number of fertile spikelets per ear. This may reflect the relatively low incidence of BYDV in Raven at the intermediate density since spikelet fertility is one yield component affected by the disease (Doodson and Saunders, 1970). Alternatively the effect may have arisen from an interaction between inter-plant competition and intra-plant competition (Donald, 1963; Puckridge and Donald, 1967) such that there was a maximum ear size at or about this density. If this is the case the inverse relationship between fertile spikelet number and grain size apparent in Haven and, to a lesser degree, in Pitic 62 at the intermediate density, could reflect differing levels of inter-plant and intra-plant competition during early and late periods of growth. However the same relationship could arise simply because with a higher fertile spikelet number there were more small grains (Rawson and Evans, 1970) and mean weights were correspondingly lower. Similarly the inverse relationship between fertile spikelet number and grain size in Pitic 62 at the high plant density may not reflect internal compensation so much as the fact that the tillers remaining at harvest in plants at this density were early tillers which characteristically have larger ears (Engledow and Wadham, 1923-24; Cannell, 1969). This illustrates the problem of heterogeneity which underlies the investigation of yield in wheat. Only with elaborate standardization (e.g. Walpole and Morgan, 1970) can this diversity be reduced to the point where the yield components are physiologically rather than statistically comparable.

#### 4.2 GROWTH OF THE VARIETIES IN RELATION TO YIELD.

##### 4.2.1 Accumulation and Distribution of Dry Matter

The major differences between the varieties in the accumulation of above ground dry matter lay in the stem and ear weights. The stem weight of Pitic 62 was less than that of Raven but this was offset by a greater ear weight (Figure 8) so that total plant weights were virtually identical in both varieties (Figure 7). Differences between varieties in the weights of other plant fractions were not statistically significant. However when the data were analysed using a fixed effects analysis of variance significant differences appeared in leaf lamina weight, dead leaf weight and grain weight. A comparison of this analysis and the experimental mixed model analysis appears in Table 20. The appearance of significant varietal differences using the more restrictive analysis of variance raises the possibility that there were real differences for these fractions. In the cases of the leaves

Table 20

Comparison of F-tests of Population and Variety Differences using Fixed Effects and Mixed Model Analyses of Variance.

\*\* =  $P < 0.01$

\* =  $0.05 > P > 0.01$

ns =  $P > 0.05$

Variable	Variety		Population	
	Fixed effects	Mixed model	Fixed effects	Mixed model
Weight fractions				
leaf lamina	**	ns	**	**
dead leaf	**	ns	**	**
leaf sheath	ns	ns	**	**
stem	**	**	**	**
ear remainder	**	**	**	**
grain	**	ns	**	**
ear total	**	*	**	**
total	ns	ns	**	**
Areas				
leaf lamina	*	ns	**	**
leaf sheath	ns	ns	**	**
flag leaf	**	ns	**	*
ear	**	ns	**	ns
peduncle	**	*	**	ns
above FLN	*	ns	**	**
total	ns	ns	**	**

however, the higher leaf lamina weight of Raven was offset by a greater dead leaf dry weight in Pitic 62 so that total dry weights of active and dead leaves were similar. A comparison of the time trends for the accumulation of dead leaf weight using the regression coefficients of Appendix 13, or the distributions of dry matter shown in Figure 8, suggests that earlier senescence in Pitic 62 was responsible for this pattern.

The differences in grain weight per plant between varieties were probably real although not statistically significant for while total dry weights were similar in each variety the grain to straw ratios of Pitic 62 were greater than those of Raven. The higher grain to straw ratio found in Pitic 62 arose from the differences in stem and ear weight discussed above and is characteristic of semidwarf wheats (Syme, 1967; Thorne et al. 1969). The grain to straw ratios in this experiment varied with density suggesting that in more competitive environments a greater proportion of the total plant dry matter was devoted to supporting tissues such as stem, and a smaller proportion to reproduction.

#### 4.2.2 Changes in Photosynthetic Areas

In this experiment surface area measurements were used to assess the importance of photosynthetic parts. This procedure is arbitrary since the spatial distribution of assimilatory surfaces is at least as important as their size (Loomis and Williams, 1969). Further, gross area measurements can take no account of the heterogeneity of samples arising from age and environmental differences, or, especially in the case of ears, of the true complexity of photosynthetic surfaces. Nevertheless there are no better simple alternatives. Surface area measurements used alongside each other also imply that the photosynthetic activities of parts are similar which is not the case (Thorne 1959; Evans and Rawson, 1970). However correction of leaf sheath or peduncle area to an equivalent leaf area (Fischer and Kohn, 1966) is arbitrary and in this experiment total areas were obtained by summing areas of component parts without correction (Quinlan and Sagar, 1965; Welbank et al. 1966; Simpson, 1968).

The following were the main features of the development of assimilatory surfaces during the growth of the two varieties. Until ear emergence total photosynthetic areas were similar for both varieties but the contributions of leaf sheaths to total area became slightly greater in Raven as stem elongation occurred (Table 12). After ear

emergence a different pattern appeared. Although the total photosynthetic areas of the varieties did not differ significantly that of Pitic 62 was, in all cases, greater than that of Raven after heading (Figure 9). This was reflected in the higher PAI (Figure 4) and longer PAD (Table 9) of Pitic 62 during grain filling. The difference arose from the greater ear area of Pitic 62 and was only partly offset by the smaller contribution of peduncle area (Table 12) and the more rapid leaf senescence in this variety. The area above the FLN thus tended to be greater in Pitic 62. Awns made an important contribution to ear area in Pitic 62 (Table 13).

Although the areas of photosynthetic organs, with the exception of that of peduncles, did not differ significantly there were nevertheless large differences between varieties which were significant when a more restrictive analysis of variance was used (Table 20). It is apparent that non-foliar surfaces, and especially the ear, were important in Pitic 62. In Raven leaves and the peduncle made large contributions to total area. The relatively greater importance of peduncle area in Raven was related to stem length. A similar effect has been noted by Quinlan and Sagar (1965) in a comparison of wheat varieties differing in straw production. The faster leaf senescence in Pitic 62 may be due to BYDV infection but there is also the possibility that leaf turnover may be more rapid in this variety (Section 4.2.4). Thorne et al. (1969) have also found that leaf area in semidwarf wheats is less than that of standard wheats after ear emergence.

As already noted the awns of Pitic 62 made a major contribution to the difference in ear areas between the varieties; without these the ear areas of both varieties would be similar since awn area made up 50% or more of the calculated ear area in Pitic 62. The decline in the contribution of awns to ear area with time appears to have been related to an increase in spikelet area presumably associated with grain growth (cf. Buttrose, 1962). Likewise the differences in awn contribution with density may have depended on increased spikelet area in the larger ears at low densities. Besides these apparent decreases in the contributions of awns to total area there was also an early senescence of awns. Thus persistence of awns in a physiologically active state while other organs senesce, which has been suggested as an advantage of awnedness (Vervelde, 1953; Lamb, 1967), did not occur in this experiment. Again BYDV may have been responsible. Nevertheless awns did make a large contribution to ear area early in grain filling and were probably a source of the yield advantage of Pitic 62 since Evans

and Rawson (1970) have shown that ear photosynthesis is high in this variety and have related this to awedness.

In both Raven and Pitic 62 leaf senescence was associated with tiller senescence and occurred relatively sooner after heading than in other photosynthetic parts. The large contributions of stem, leaf sheath and ear areas to total area serve to emphasize the possible importance of these parts. Similar contributions have been found in other cases (Strebeyko, Wislocka and Krzywacka, 1963; Penka and Srpova, 1965; Quinlan and Sagar, 1965; Ross and Nilson, 1967). Differences between the varieties in the major non-leaf components of total photosynthetic area may also be important in relation to the overall assimilation of the plants. In Pitic 62, a variety in which ear photosynthesis meets a high proportion of grain requirements (Evans and Rawson, 1970), ear area was high and peduncle area low. On the other hand in Raven, where ear photosynthesis is probably less important (cf. results for var. Gabo obtained by Evans and Rawson, 1970), the peduncle and sheath make up a larger proportion of extra-foliar area and thus could potentially contribute more to grain filling.

#### 4.2.3 Growth Analysis

Growth rates and photosynthetic rates reported in this experiment are based upon the weight of above ground parts and are therefore underestimates of the actual rates. Root samples washed from soil blocks weighed on average 104% of the shoot weight at the second sampling and 64% at the eighth sampling. Stem base weight was 30% that of the tops at the second sampling and 8% at the fifteenth sampling. Thus the reported rates could be considerably at variance with true rates, particularly at early samplings.

Crop growth rates calculated in this experiment reached maximum values just after ear emergence. A similar pattern appears in the work of Friend, Helson and Fisher (1962) on wheat, but Pope (1932) found maximum growth rates in barley occurred before ear emergence. The values for the maximum crop growth rates at high densities in both Pitic 62 and Raven are among the highest recorded for any species (Loomis and Williams, 1963). Although wheat is capable of crop growth rates of this magnitude (Hodanova, 1967; King and Evans, 1967) the high values in this experiment could arise from the method of calculation used to obtain C (see below). However mean crop growth rates over the whole season for the high density populations of Raven and Pitic 62 were

respectively 18.8 and 19.9 g.m<sup>-2</sup>. day<sup>-1</sup> and these are not unreasonable in view of the grain yields obtained.

While population differences in crop growth rates were large varietal differences were small. This arose because the curves fitted to total dry weight data for the varieties at each population were similar. Such differences as did exist between varieties appeared towards the end of the life cycle and may thus reflect the relative incidence of BYDV.

Analysis of trends in crop growth rates is complicated by the fact that C and its components, LAI and E<sub>A</sub> or PAI and E<sub>PA</sub>, were derived from only two fitted polynomials, those for total dry weight and leaf area or total dry weight and total photosynthetic area. Physiological inferences from growth analysis must therefore be made with caution since components were not estimated independently and relied heavily on the adequacy of description of the original data.

The similarity of trends in C and LAI and particularly in C and PAI, were reflected in the resultant curves for E<sub>A</sub> and E<sub>PA</sub>. During the first part of growth, crop growth rates depended mainly on LAI as is usually the case (Watson, 1947; Donald, 1963). Apparent increases in leaf assimilatory efficiency (E<sub>A</sub>) from around ear emergence were probably not real but reflected the inadequacy of lamina area as the putative basis for weight increments during grain filling. Differences between varieties during this period depended on differing rates of leaf senescence. Calculation of unit photosynthetic rates on the basis of total photosynthetic areas rather than leaf areas, gave values in which varietal differences after ear emergence were reduced. This arose because the PAI of Pitic 62 were greater than those of Raven after ear emergence. This implies in a phenomenological manner that the ears of Pitic 62 (which gave rise to the higher PAI) were of importance as assimilatory organs but can in no way be taken as a demonstration of this probability. Although calculated E<sub>PA</sub> values did not show the apparent large increase in leaf efficiency during leaf senescence appearing in E<sub>A</sub>, the unit photosynthetic rate cannot be considered any more adequate than the unit leaf rate in elucidating growth patterns. Both the unit leaf rates and the unit photosynthetic rates calculated in this experiment have descriptive value but little more; explanations for changes in growth must be sought at a more fundamental level.

Growth analysis based upon relative growth rate and its components showed much the same effects as that based on the crop growth rate.

The rates of decline of relative growth rates in time were alike for varieties and population. Ballard and Petrie (1936) and Friend, Helson and Fisher (1962) have shown similar time trends in  $R$  in wheat.  $LAR$  and  $PAR$  also fell in time. Small differences in the time trends of these quantities, and in  $R$ , were sufficient to account for the differences in  $E_A$  and  $E_{PA}$  between varieties and populations.

A problem with the use of growth analysis in cereal growth is the indirect dependence of yield upon leaf area. Values of the grain leaf ratio,  $G$ , calculated in this experiment highlight this problem. For Pitic 62 where flag leaf area duration was shorter than Raven grain leaf ratios were high. This finding parallels that of Thorne et al. (1969) for other semidwarf wheats and is in agreement with the high  $E_A$  values for Pitic 62. Since variation in  $G$  could arise from differences in leaf or ear photosynthesis or in the proportion of assimilates from various sources moving to the grain (Watson et al. 1963), possibilities which are not distinguishable here, varietal differences in this ratio have small explanatory value. Calculation of similar ratios based on photosynthetic area above the flag leaf node, or upon total photosynthetic area, removed varietal differences but this does not permit any definite statement about the relative efficiencies of the varieties except in the crudest terms. Without better bases than the duration of photosynthetic surfaces and final grain yield, growth analysis cannot be expected to give a clearer picture.

The regression technique chosen for growth analysis in this experiment proved useful in that it permitted estimates of growth parameters with small frequent samples. Large within-sample variation and small between-sample differences would not normally permit the use of growth analysis in an experiment such as this. The cosmetic value of curve fitting should not however obscure the real difficulties of the technique. Polynomials cannot improve the quality of data and the confidence limits of fitted curves, if calculated, depend upon within sample variation as well as the degree of polynomial used. Thus the fiducial limits for fitted curves, and particularly derived curves, are wide where sampling variation is large and/or polynomials of relatively high degree are required for adequate description of data. Besides this uncertainty, there is the added problem that the shapes of derived curves are determined mainly by the degree of the polynomial fitted to primary data. This can result in biologically meaningless growth rates if high degree polynomials are used, and oversimplification if lower degree polynomials prove statistically adequate. An example of the first situation does

not occur in this thesis but would have arisen had growth rates been calculated from the third degree polynomials used to describe the accumulation of leaf sheath dry weight. The second situation is exemplified by the absence of a decline in peduncle elongation rates consequent upon the use of first degree polynomials to describe the length increase of these parts (Figure 11).

A related difficulty arises where polynomials are fitted to transformed data and growth parameters are then calculated from detransformed quantities. For example if a natural logarithm transformation is applied to  $n$  observations of dry weight,  $W$ , the sum of squares minimized to obtain the polynomial of best fit is

$$\sum_{i=1}^n (\log_e W_i - \widehat{\log_e W_i})^2$$

The first derivative of this curve is then the relative growth rate. An equation for the absolute growth rate can also be obtained from this polynomial mathematically by taking the exponent and differentiating. Alternatively the absolute growth rate could be calculated from a polynomial fitted to untransformed data. The sum of squares minimized is then

$$\sum_{i=1}^n (W_i - \widehat{W_i})^2$$

The first derivative of the resulting curve gives a second estimate of the absolute growth rate. These estimates of growth rate will not however be the same, for, although the source polynomials are mathematically equivalent, they differ statistically in that different sums of squares are minimized. Thus different biological inferences could be drawn from the growth rates depending on the method used. For this reason it is possible that the high crop growth rates appearing in this experiment were in fact artefacts of the method of calculation.

A further problem with the regression technique is that of discontinuities in growth due to environmental conditions (e.g. Brougham, 1959) or, on a finer scale, growth correlations (e.g. Williams, 1964) and diurnal variation (e.g. Allison, 1963; Johnson, 1967). These cannot be encompassed by polynomials so that curve fitting may obscure real fluctuations of biological interest. This difficulty is particularly relevant where polynomials are used to describe growth over extended periods such as the whole growing season as in this experiment. However under field conditions simple causes for observed fluctuations are rarely identifiable so that the information lost in fitting smoothed curves is probably not great.

#### 4.2.4 Plant Development in Relation to Yield

Although the numbers of tillers produced by Raven and Pitic 62 in this experiment were similar there were slight differences in the pattern of tillering. In Pitic 62 early tiller production was faster but this was later offset by a higher number of dead and non-fertile tillers (Figure 10) so that fertile tiller numbers were nearly identical in both varieties (Figure 3). The greater early tiller production of Pitic 62 was due to a faster rate of tillering (Table 15) and possibly to earlier and more rapid tertiary tiller production (Table 16). Differences in tiller number could also have arisen because with the later transition of apices from the vegetative to the reproductive phase in Pitic 62 (Table 17) more leaf primordia were produced.

The higher rate of tiller production in Pitic 62 was paralleled by a faster rate of leaf appearance on tillers of this variety (Table 15). Since the total leaf areas of the two varieties were similar this implies either that the leaves of Pitic 62 were smaller or that the rate of senescence was faster. The first explanation is unlikely since the mean sizes of leaves and flag leaves used in calculating length x breadth regressions were similar in both varieties. Evidence for more rapid leaf senescence in Pitic 62 has been discussed in Sections 4.2.1 and 4.2.2.

Differences between populations in the mid-point of spikelet initiation were recorded in this experiment. These may in part be related to competitive effects which would presumably be for water or nutrients, since LAI in this period were low. The appearance of population differences in tiller number in the period around initiation is suggestive of competition but, on the other hand, there were few differences in leaf appearance between populations during this period. However differences in initiation could have arisen mainly from the heterogeneity of tillers appearing in samples from the low density plots, since there did not appear to be marked differences in the stage of development of main stem apices between populations. Kirby and Faris (1970) report a similar finding for barley grown at a wider range of densities. Some of the apparent difference in spikelet initiation between varieties could also have arisen from sampling since Pitic 62 tended to have more tillers (Figure 10), and therefore potentially more diversity, than Raven during the period in which initiation was estimated.

Although spikelet initiation occurred slightly later in Pitic 62 than in Raven the varieties had similar heading dates. The higher

spikelet numbers on ears of Pitic 62 may therefore have resulted from a higher rate of spikelet initiation. If floret number parallels grain number, as was probably the case, the rate of floret primordia production in Pitic 62 may also have been faster than that of Raven.

The possible higher rate of spikelet production in Pitic 62 may also be related to the stem growth of this variety. Since ear and stem growth are synchronous it is possible that the more rapid elongation of stems in Raven may have an adverse effect on spikelet initiation and contribute to a lower spikelet number. Correlations such as this have appeared in the work of Williams (1964, 1966b) and Kirby and Faris (1970). There is also the possibility that the higher spikelet number in Pitic 62 may arise from differences in the pattern of apex development, for unanalysed data on the length of ears showed that the rachis of Pitic 62 were on average 30% longer than those of Raven. Thus in Pitic 62 slower stem elongation appeared to be accompanied by more rapid ear elongation. This suggests that a closer study of the growth of the apex during ear development and particularly, in the light of work by Radley (1970) on the metabolism of gibberellin in semidwarf wheats, of the hormonal control of ear initiation and growth in Pitic 62, could be fruitful.

The overall pattern of development in the two varieties differed then in two respects. In Raven elongation rates of stem parts, with the possible exception of the rachis, were more rapid. In Pitic 62 there appeared to be a higher rate of primordia formation as shown by tillering, leaf appearance, spikelet number and grain number. Since stems constitute a competing sink for assimilates it is possible that the high stem and peduncle growth rates may affect both ear size and grain filling more in Raven than in Pitic 62. Likewise a higher rate of primordia production in Pitic 62 could reflect lowered competition due to slower stem elongation. This in turn could lead to a larger ear size in the semidwarf wheat with probable advantages both in sink size and assimilatory capacity.

### 4.3 CONCLUSIONS

Although this experiment did not demonstrate that Pitic 62 was clearly superior to Raven it did show that there was probably a yield advantage in favour of the semidwarf variety. Given disease-free plants and higher densities than were used in this experiment it seems likely that Pitic 62 would outyield Raven by a considerable amount. The sources of varietal yield differences in this experiment were the higher grain number per spikelet and spikelet number per ear in Pitic 62 and these more than offset the lower grain weight in this variety. Since the relative importance of yield components differed in Raven and Pitic 62 it is possible that different environmental conditions could be required for maximum yields in these wheats. If the results of this experiment hold in other seasons and environments Pitic 62 might be relatively more sensitive than Raven to environmental conditions between initiation and anthesis, when grain number is established, and less sensitive during grain filling.

Growth analysis in this experiment showed only small varietal differences in growth rate and assimilation rate at each density and these were not obviously related to yield differences. It is apparent that growth analysis is of limited value in cereals where yield is only an indirect expression of total dry matter accumulation. Explanations for observed differences must therefore be sought at a more fundamental level.

The experiment showed that the grain to straw ratio of Pitic 62 was greater than that of Raven and that this difference was related to the growth pattern of the two varieties. In particular there seemed to be varietal differences in the relative activity of apical and intercalary meristems which led to larger ears and shorter stems in Pitic 62. These require confirmation in more detailed experiments which should include a consideration of root growth.

The two varieties in this experiment were both high yielding but the question of which factors were responsible for this, or for yield differences between varieties, remains open. Pitic 62 exhibits a number of the characters (short straw, large ear size, erect ears and awns) which have been proposed for a model wheat plant (Donald, 1968a, 1968b) but it also possesses others (high leaf and tiller numbers, leaves not conspicuously erect) which are specifically excluded from this ideotype. Raven has few of the characters included in the model wheat plant. This experiment suggests that morphological characters

such as appear in Donald's ideotype are related to yield in much the same way as the yield components; they reflect the underlying factors which regulate yield without themselves determining it. (There are of course exceptions to this generalization e.g. leaf angle.) A similar conclusion can be reached from the more extensive study of growth parameters by Lupton, Ali and Subramaniam (1967), while Finlay (1968) stresses the point that high yielding, widely adapted wheat varieties differ markedly in plant form and pattern of growth. Until there is a deeper understanding of the physiological regulation of the growth processes leading to grain yield it seems unlikely that information of much use to plant breeders could be offered on the basis of differences in plant form and growth patterns. The work reported in this thesis has identified some areas in which further research on the physiological regulation of growth processes could be rewarding.

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A P P E N D I C E S

\*\* = ,P < 0.01

\* = 0.05 > P > 0.01

ns = not significant at the 5% level

## Appendix 1

## Chronology

<u>Date</u>	<u>Day</u>	<u>Event</u>
23. 8.68		Ploughing
29. 8.68		Rolling, discing
16. 9.68		Discing
25. 9.68		Harrowing, levelling
29. 9.68		3 cwt 30% K superphosphate applied
30. 9.68	1	) Block 1 sown
1.10.68	2	) Blocks 2, 3, 4 sown
2.10.68	3	) Blocks 5, 6, 7 sown
9.10.68	10	)
15.10.68	16	) Emergence
20.10.68	21	Thinning, hand cultivation
25.10.68	26	Establishment counts
27.10.68	28	1st sampling
1.11.68	33	2nd sampling
6.11.68	38	3rd sampling
12.11.68	44	4th sampling
16.11.68	48	Hand cultivation
18.11.68	50	5th sampling
21.11.68	53	Sprayed 1 pt. 2,4-D/acre
24.11.68	56	6th sampling
28.11.68	60	Sprayed 2 pt. 2,4-D/acre + Malathion
30.11.68	62	7th sampling
7.12.68	69	8th sampling
12.12.68	74	9th sampling
19.12.68	81	10th sampling
23.12.68	85	Irrigation ca. 0.40 acre.inches
26.12.68	88	11th sampling
28.12.68	90	Sprayed 16 fl. ozs./acre Metasystox
2. 1.69	95	12th sampling
10. 1.69	103	13th sampling
18. 1.69	111	14th sampling
26. 1.69	119	15th sampling
4. 2.69	128	16th sampling
13. 2.69	137	17th sampling
21. 2.69	145	18th sampling

Appendix 2

Experimental Layout

Layout: 7 blocks

3 plant populations

1 = 177.77 plants . m<sup>-2</sup>

2 = 44.44 plants . m<sup>-2</sup>

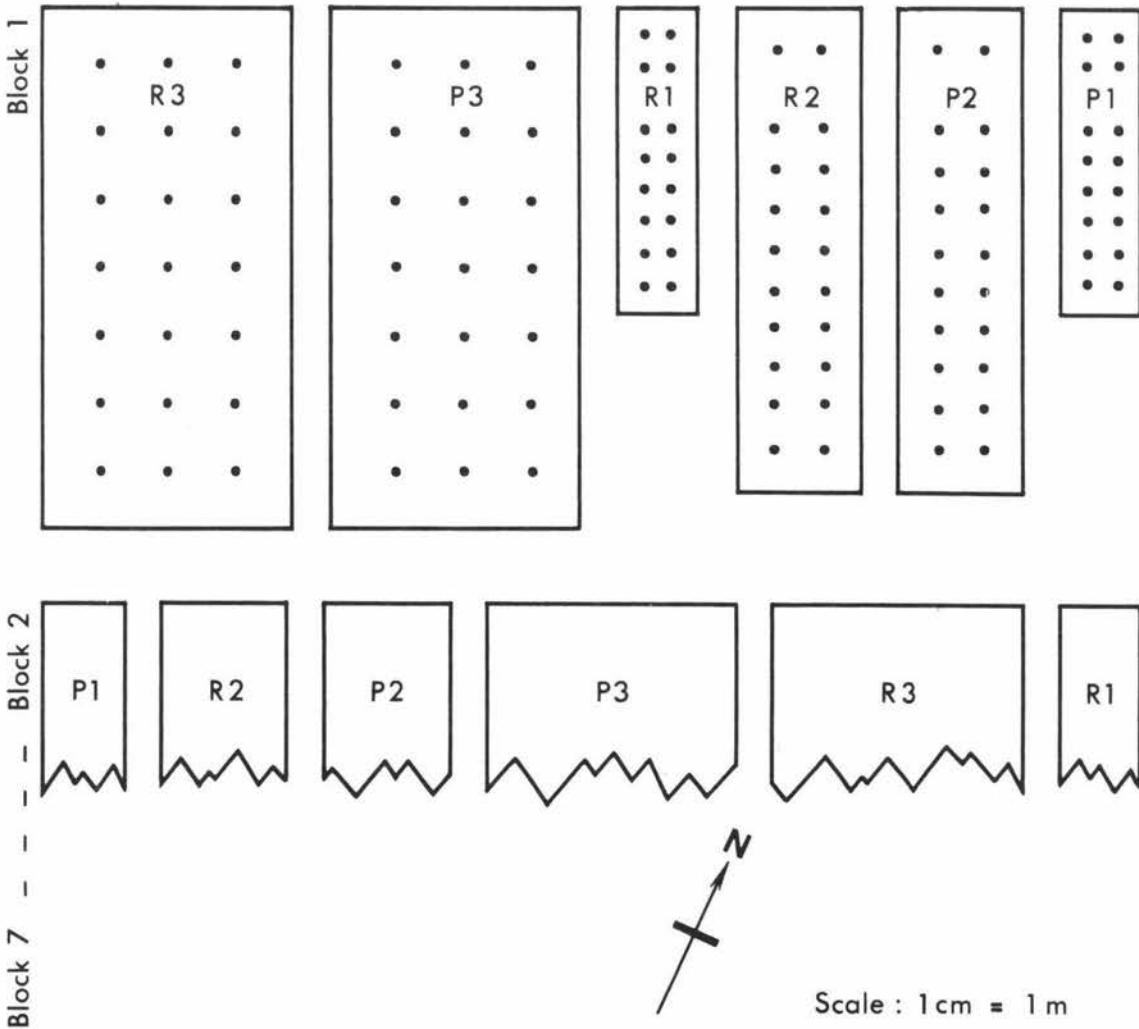
3 = 11.11 plants . m<sup>-2</sup>

2 varieties

R = Raven

P = Pitic 62

20/21 sampling positions consisting of one plant guarded on all sides by 4, 3 and 2 rows of plants in populations 1, 2 and 3 respectively.

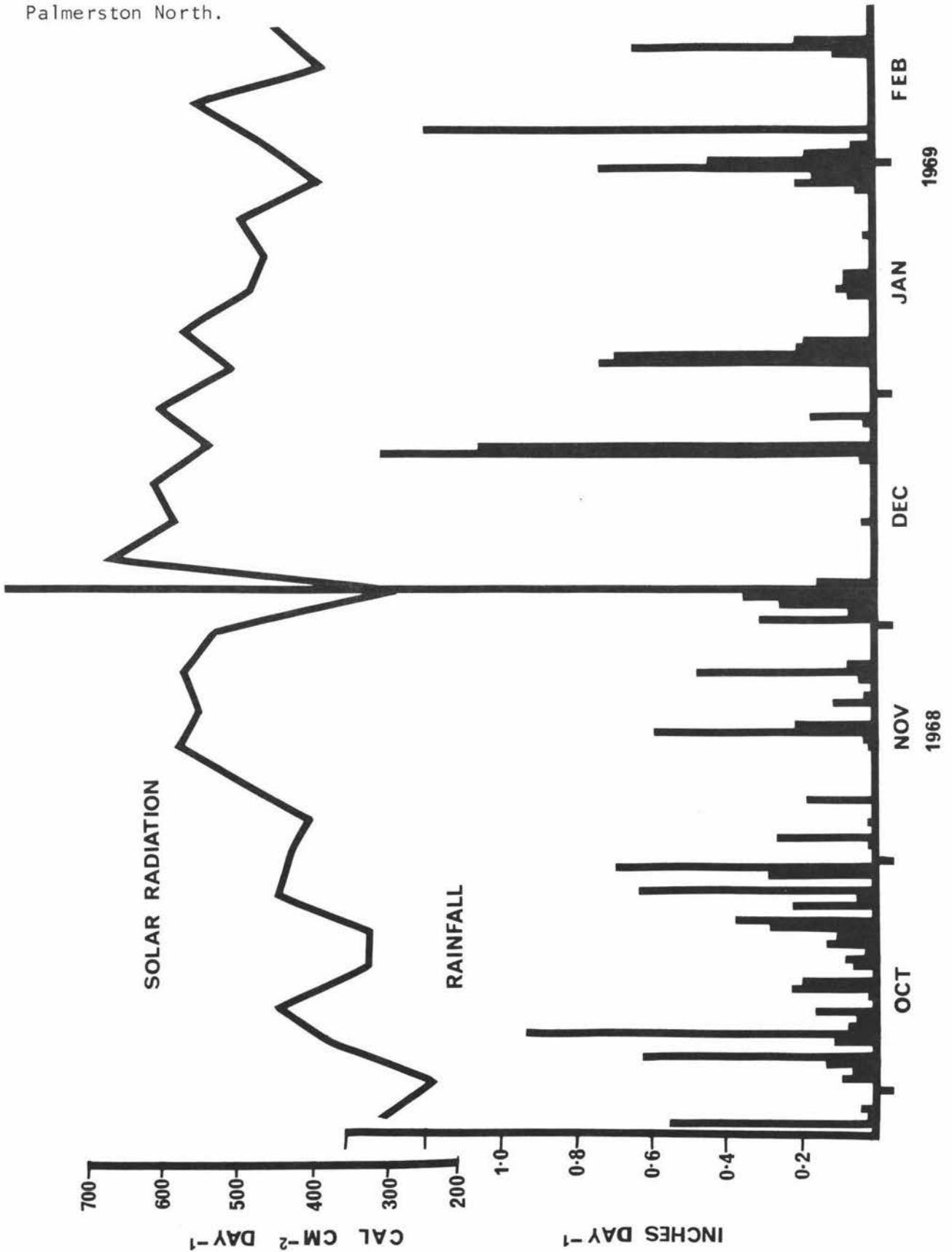


## Appendix 3.

Rainfall and Solar Radiation  
During Experiment.

Daily rainfall recorded at Grasslands Division, D.S.I.R., Palmerston North, using standard meteorological rain-gauge.

Solar radiation measured with an Eppley pyrheliometer presented as 5 day averages. Records from Plant Physiology Division, D.S.I.R., Palmerston North.



## Appendix 4 Estimation of Areas of Photosynthetic Parts

(a) Corrections for Leaf Lamina Area

In samplings 1 and 2 areas of a subsample of leaves were measured from outline tracings. Regressions of areas estimated by length x breadth on actual area were then calculated. Analysis of covariance (p.95) showed separate regressions were required for first leaves, not fully expanded (NFE) leaves, and other leaves (2nd to 5th) but not for varieties (analysis not presented). Leaf areas were individually corrected on this basis.

For the remaining samplings an air flow planimeter was used to measure leaf area. The air flow planimeter readings were corrected by use of regressions of planimeter readings of area on that of paper standards. Analysis of covariance (p. 96) showed these regressions differed significantly at different samplings.

(b) Correction for Flag Leaf Area

Flag leaf area length x breadth measurements were corrected using a regression of l x b on corrected air flow planimeter readings for the same leaves. The regression was

$$y = 5.021 + 1.301x$$

## Analysis of Covariance

Source	SS	df	MS	F
Total	$6.882 \times 10^3$	58	$1.186 \times 10^2$	
Regression	$5.693 \times 10^3$	1	$5.693 \times 10^3$	$2.729 \times 10^2$ **
Deviations	$1.188 \times 10^3$	57	$2.085 \times 10$	

(c) Estimation of Leaf Sheath and Peduncle Areas

Leaf sheath and peduncle areas were calculated from the product of length x basal circumference. It was assumed that leaf sheath below the flag leaf node ceased to be effective after sampling 10 (day 81) so that leaf sheath area was calculated from dimensions above the FLN only after this time.

(d) Estimation of Ear Area

Ear area was estimated from

## Appendix 4 (continued).

$$(1 \times b)_{8\text{th spikelet}} \times \text{number of fertile spikelets}$$

where 1 and b are the lengths of the diagonals of the diamond shaped spikelets. The accuracy of this estimate was checked by projecting the outline of 100 glumes of Raven and of Pitic 62 onto paper with a magnification of 16 and weighing the cut-out areas. A comparison of mean weights of cut-outs showed no significant differences between varieties in glume area.

	Mean weight (g)	S.E. (g)	Equivalent area (cm <sup>2</sup> glume <sup>-1</sup> )
Raven	$2.935 \times 10^{-3}$	$5.677 \times 10^{-4}$	$1.529 \times 10^{-1}$
Pitic 62	$3.044 \times 10^{-3}$	$5.093 \times 10^{-4}$	$1.474 \times 10^{-1}$
			<sup>t</sup> <sub>100</sub>
Difference	$1.090 \times 10^{-4}$	$7.601 \times 10^{-5}$	1.434 ns

The equivalent area per glume was multiplied by glume number per ear to give ear area. Ear area was estimated with errors using both methods for an ear of Raven with 16 fertile spikelets, 76 glumes and 8th spikelet dimensions of 0.13 cm by 0.11 cm ; the estimates were

(i)  $(22.8 \pm 7.6) \text{ cm}^2$  based on spikelet number and dimensions

(ii)  $(11.6 \pm 3.0) \text{ cm}^2$  based on glume area and number

Since both methods are arbitrary, and of similar apparent accuracy, the simpler, method (i), was preferred although it gave higher estimates.

(e) Estimation of Awn Area/Spikelet in Pitic 62

A sample of 10 ears of Pitic 62 was taken on day 122 and all awns were removed. The number of awns in the length classes 0-30 mm, 30-60 mm and 60+ were counted and the length of 5 awns in each class measured. An estimate of awn diameter for each ear was made by measuring the width at the midpoint of 2 sets of 10 awns laid side by side. The awn area per spikelet was then calculated from

$$(\pi \bar{d} \sum_{i=1}^3 (n_i \cdot \bar{l}_i)) / sn$$

## Appendix 4 (continued)

where  $\bar{d}$  is mean awn diameter,

sn is number of spikelets,

$n_i$  is number of awns in the  $i$ th length class and

$\bar{l}_i$  is their mean length.

The resulting mean estimate for 10 ears of  $(1.759 \pm 0.095)$  cm<sup>2</sup> of awn area per spikelet was then used in conjunction with number of fertile spikelets to estimate total awn area on all ears of Pitic 62.

Appendix 4  
(continued)

Comparison of Regressions of Leaf  
Length x Breadth on Measured Area.

Source	df	$\sum x^2$	$\sum xy$	$\sum y^2$	$\hat{b}$	Dev. SS	df	Dev. MS	
First leaves	10	$2.047 \times 10^5$	$2.303 \times 10^5$	$2.776 \times 10^5$	1.125	$1.846 \times 10^4$	9	$2.051 \times 10^3$	
NFE leaves	8	$1.309 \times 10^6$	$1.807 \times 10^6$	$2.507 \times 10^6$	1.380	$1.341 \times 10^4$	7	$1.916 \times 10^3$	
Other leaves	26	$7.142 \times 10^5$	$1.149 \times 10^6$	$2.053 \times 10^6$	1.608	$2.051 \times 10^5$	25	$7.891 \times 10^3$	
Pooled within groups	44	Pooled deviations from individual regressions.					$2.370 \times 10^5$	41	$5.781 \times 10^3$
		$2.228 \times 10^5$	$3.186 \times 10^6$	$4.839 \times 10^6$	1.430	$2.821 \times 10^5$	43	$6.561 \times 10^3$	
		Between individual group regressions.					$4.508 \times 10^4$	2	$2.254 \times 10^4$
<p>Between slopes <math>F_{2,41} = \frac{\text{Between individual group regression MS}}{\text{Pooled deviations from individual regression MS}}</math>  <math>= 3.89^*</math></p>									

Appendix 4  
(continued)

Comparison of Regressions of Air Flow  
Planimeter Readings on Standard Areas.

Source	df	$\sum x^2$	$\sum xy$	$\sum y^2$	$\hat{b}$	Dev. SS	df	Dev. MS
Sampling 3	16	$1.020 \times 10^4$	$8.134 \times 10^3$	$6.498 \times 10^3$	0.797	$1.088 \times 10$	15	$7.253 \times 10^{-1}$
Sampling 4	16	$1.020 \times 10^4$	$7.824 \times 10^3$	$6.009 \times 10^3$	0.767	6.762	15	$4.508 \times 10^{-1}$
Sampling 5	16	$1.020 \times 10^4$	$8.879 \times 10^3$	$7.735 \times 10^3$	0.870	4.235	15	$2.823 \times 10^{-1}$
Samplings 6-7	16	$1.020 \times 10^4$	$9.214 \times 10^3$	$8.329 \times 10^3$	0.903	3.939	15	$2.626 \times 10^{-1}$
Samplings 8-12	21	$2.213 \times 10^4$	$1.970 \times 10^4$	$1.756 \times 10^4$	0.890	$2.076 \times 10$	20	1.038
Samplings 13-15	33	$8.181 \times 10^4$	$6.649 \times 10^4$	$5.409 \times 10^4$	0.812	$4.560 \times 10$	32	1.425
Pooled deviations from individual regressions.						$9.218 \times 10$	112	$8.231 \times 10^{-1}$
Pooled within group	118	$1.447 \times 10^5$	$1.202 \times 10^5$	$1.002 \times 10^5$	0.830	$3.198 \times 10^2$	117	2.733
		Between individual group regressions.				$2.227 \times 10^2$		5
<p>Between slopes <math>F_{5,112} = \frac{\text{Between individual group regression MS}}{\text{Pooled deviations from individual regression MS}}</math>  <math>= 5.531 \times 10^{**}</math></p>								

## Appendix 5

Establishment Counts and Analysis  
of Variance.Percentage Establishment at Day 26.

Data presented as means of angular transformations with corresponding S.E. for population and variety differences. Detransformed means in brackets.

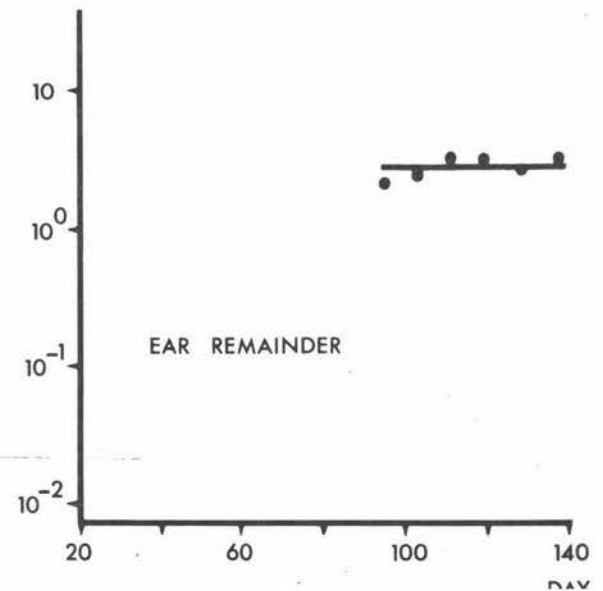
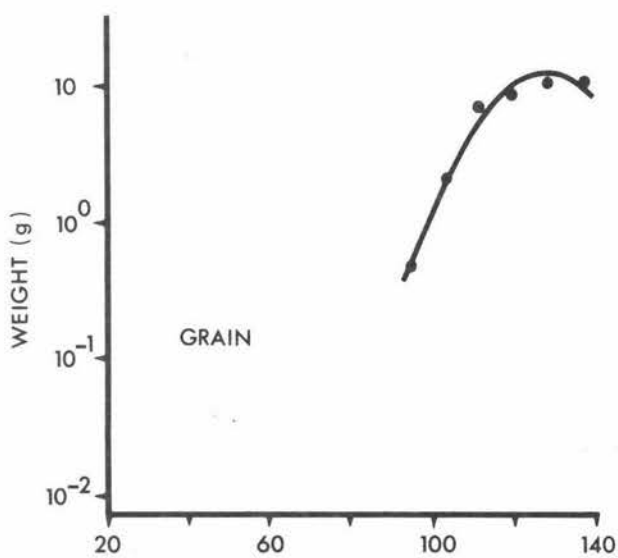
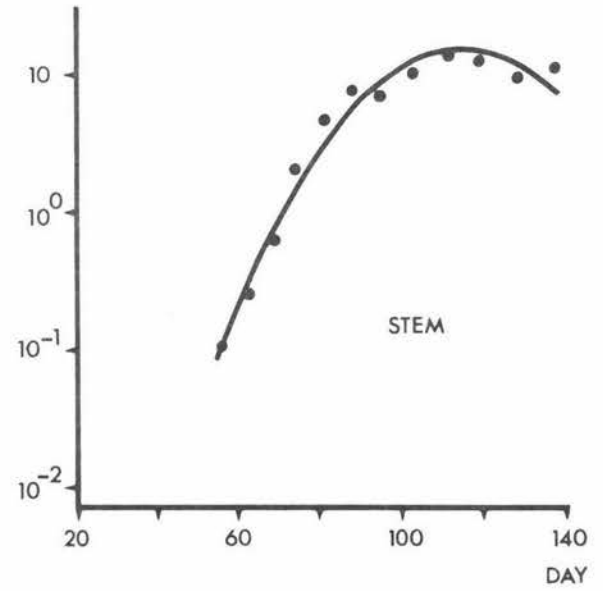
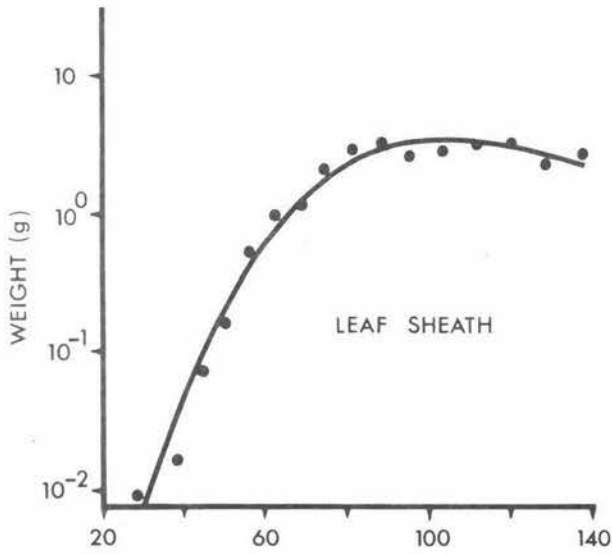
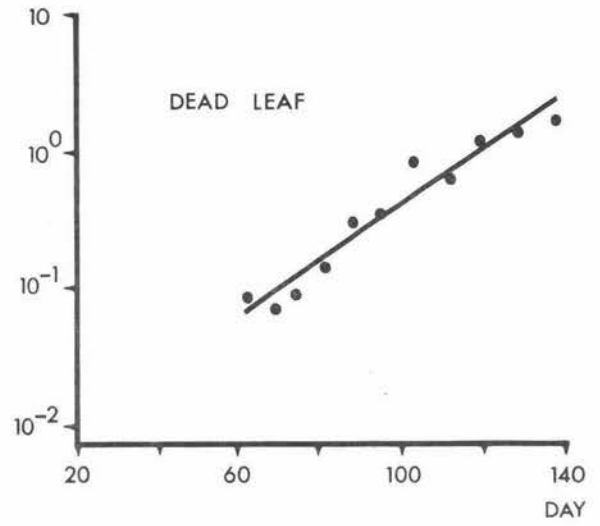
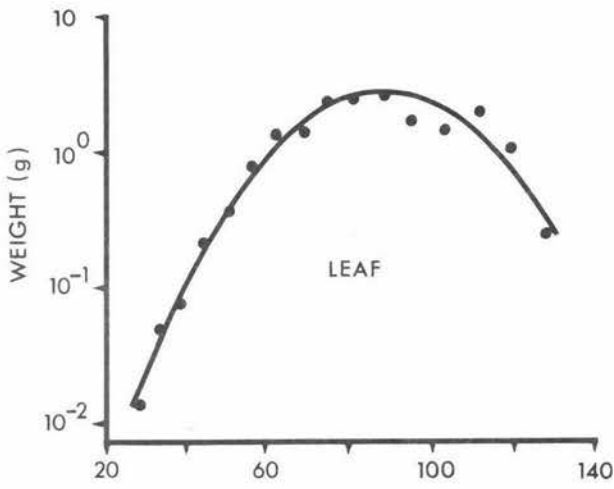
Variable	Variety	Population			S.E. (V-V)
		1	2	3	
Percentage establishment	Raven	73.05 (91.5)	71.05 (89.5)	75.70 (93.9)	3.36
	Pitic	68.91 (87.1)	68.24 (86.3)	70.56 (88.9)	
S.E. (P-P)		4.12			

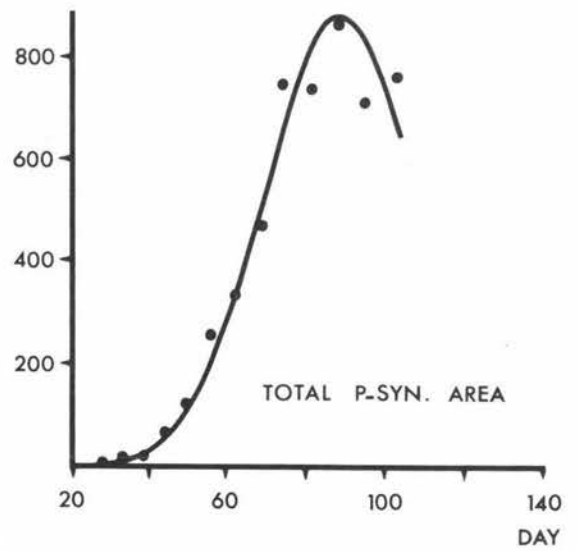
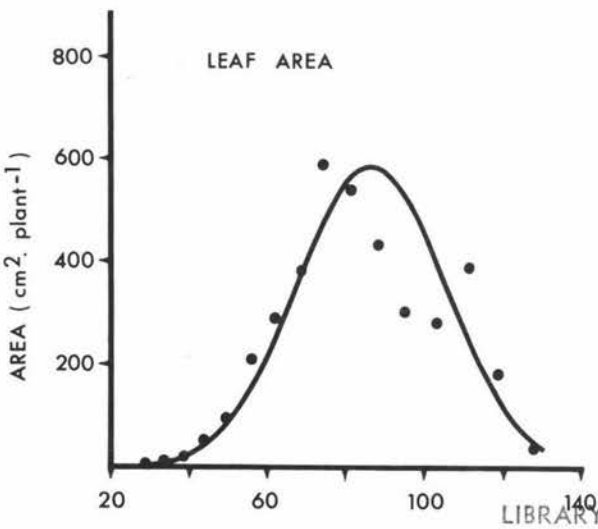
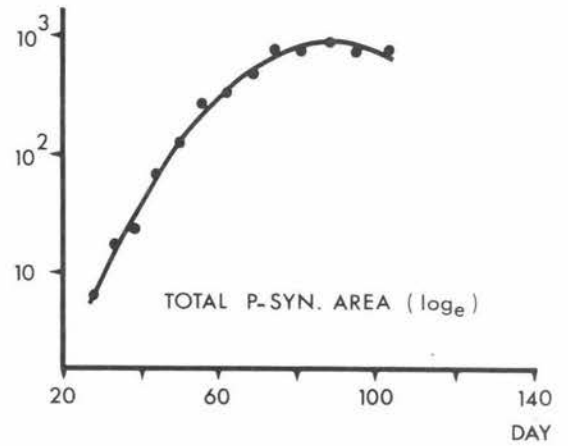
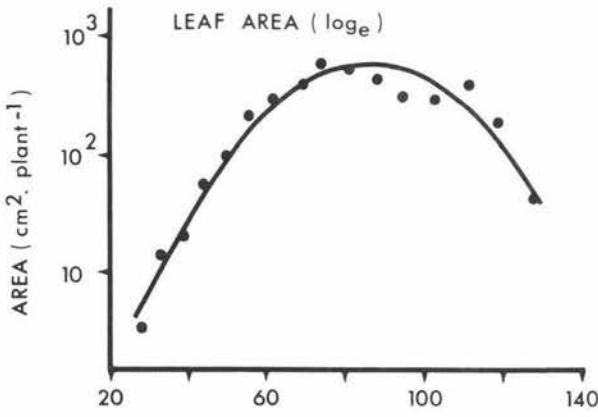
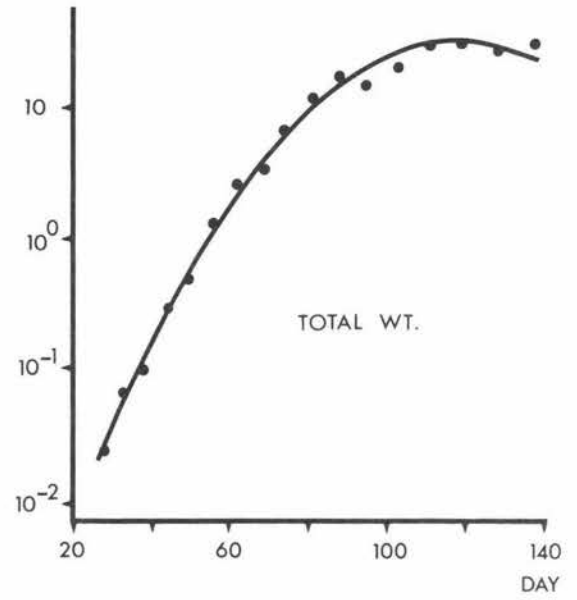
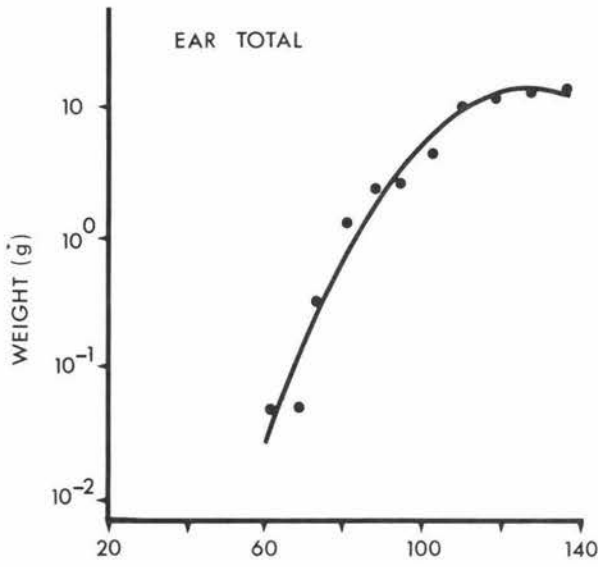
Analysis of Variance of Angular  
Transformed Data.

Variable	Source	df	MS	F
Percentage establishment at day 26	Blocks	6	$4.326 \times 10^5$	
	Population	2	$4.643 \times 10^5$	$3.895 \times 10^{-1}$ ns
	Variety	1	$1.706 \times 10^6$	$3.565 \times 10^0$ *
	PV	2	$4.785 \times 10^4$	$4.014 \times 10^{-2}$ ns
	Residual	30	$1.191 \times 10^6$	

Appendix 6.

Examples of Polynomial Curves Fitted to Dry Weight and Area Data: Raven 2





## Appendix 6 (continued)

Analyses of Variance for Polynomial Curves  
Fitted to Dry Weight and Area Data: Raven 2

Fraction	Source	df	MS	F	
Leaf lamina	mean	1	$6.508 \times 10^2$	$1.994 \times 10^3$	
	linear	1	$1.517 \times 10$	$4.649 \times 10$	
	quadratic	1	$2.207 \times 10$	$6.763 \times 10$	**
	lack of fit	13	$6.520 \times 10^2$	$1.998 \times 10^{-1}$	ns
	cubic	1	$4.722 \times 10^{-2}$	$1.462 \times 10^{-1}$	ns
	within group	91	$3.263 \times 10^{-1}$		
Dead leaf	mean	1	$3.889 \times 10^2$	$6.978 \times 10^2$	
	linear	1	$1.336 \times 10$	$2.397 \times 10$	**
	lack of fit	9	$9.577 \times 10^{-2}$	$1.718 \times 10^{-1}$	ns
	quadratic	1	$1.885 \times 10^{-1}$	$3.383 \times 10^{-1}$	ns
	within group	57	$5.573 \times 10^{-1}$		
Leaf sheath	mean	1	$7.063 \times 10^2$	$1.573 \times 10^3$	
	linear	1	$5.218 \times 10$	$1.162 \times 10^2$	
	quadratic	1	$1.958 \times 10$	$4.362 \times 10$	**
	cubic	1	$6.961 \times 10^{-1}$	1.550	ns
	lack of fit	13	$1.061 \times 10^{-1}$	$2.364 \times 10^{-1}$	ns
	within group	102	$4.489 \times 10^{-1}$		
Stem	mean	1	$8.102 \times 10^2$	$2.055 \times 10^3$	
	linear	1	$2.208 \times 10$	$5.602 \times 10$	
	quadratic	1	7.803	$1.979 \times 10$	**
	lack of fit	9	$9.212 \times 10^{-2}$	$2.337 \times 10^{-1}$	ns
	cubic	1	$4.112 \times 10^{-1}$	1.043	ns
	within group	68	$3.941 \times 10^{-1}$		
Grain	mean	1	$4.246 \times 10^2$	$4.201 \times 10^3$	
	linear	1	5.875	$5.812 \times 10$	
	quadratic	1	1.652	$1.634 \times 10$	**
	lack of fit	3	$4.344 \times 10^2$	$4.297 \times 10^{-1}$	ns
	cubic	1	$7.416 \times 10^{-2}$	$7.337 \times 10^{-1}$	ns
	within group	36	$1.010 \times 10^{-1}$		

## Appendix 6 (continued)

Fraction	Source	df	MS	F	
Ear remainder	mean	1	$3.881 \times 10^2$	$3.687 \times 10^3$	**
	lack of fit	5	$3.265 \times 10^{-2}$	$3.101 \times 10^{-1}$	ns
	linear	1	$8.448 \times 10^{-2}$	$8.024 \times 10^{-1}$	ns
	within group	36	$1.052 \times 10^{-1}$		
Ear total	mean	1	$6.295 \times 10^2$	$2.412 \times 10^3$	
	linear	1	$3.747 \times 10$	$1.435 \times 10^2$	
	quadratic	1	5.220	$2.000 \times 10$	**
	lack of fit	8	$2.001 \times 10^{-1}$	$7.671 \times 10^{-1}$	ns
	cubic	1	$7.718 \times 10^{-2}$	$2.957 \times 10^{-1}$	ns
	within group	62	$2.609 \times 10^{-1}$		
Total	mean	1	$1.100 \times 10^3$	$4.490 \times 10^3$	
	linear	1	$7.868 \times 10$	$3.210 \times 10^2$	
	quadratic	1	$1.306 \times 10$	$5.331 \times 10$	**
	lack of fit	14	$3.588 \times 10^{-2}$	$1.464 \times 10^{-1}$	ns
	cubic	1	$1.472 \times 10^{-1}$	$6.008 \times 10^{-1}$	ns
	within group	102	$2.450 \times 10^{-1}$		
Leaf lamina area	mean	1	$1.427 \times 10^3$	$4.169 \times 10^3$	
	linear	1	$1.085 \times 10$	$3.171 \times 10$	
	quadratic	1	$2.261 \times 10$	$6.605 \times 10$	**
	lack of fit	13	$9.491 \times 10^{-2}$	$2.772 \times 10^{-1}$	ns
	cubic	1	$1.748 \times 10^{-1}$	$5.106 \times 10^{-1}$	ns
	within group	91	$3.423 \times 10^{-1}$		
Total area	mean	1	$1.250 \times 10^3$	$4.812 \times 10^3$	
	linear	1	$2.842 \times 10$	$1.094 \times 10^2$	
	quadratic	1	5.407	$2.081 \times 10$	**
	lack of fit	10	$1.964 \times 10^{-2}$	$7.562 \times 10^{-2}$	ns
	cubic	1	$1.618 \times 10^{-2}$	$6.229 \times 10^{-2}$	ns
	within group	78	$2.597 \times 10^{-1}$		

Appendix 7      Analyses of Variance for Grain Yield  
and Yield Components

Variable	Source	df	MS	F	
Grain yield $\text{g.m}^{-2}$	Blocks	6	$6.155 \times 10^4$		
	Population	2	$7.999 \times 10^5$	$1.399 \times 10$	**
	Variety	1	$2.198 \times 10^5$	$1.509 \times 10$	ns
	PV	2	$1.456 \times 10^4$	$2.546 \times 10^{-1}$	ns
	Residual	30	$5.719 \times 10^4$		
Ears. $\text{m}^{-2}$	Blocks	6	$1.447 \times 10^4$		
	Population	2	$6.840 \times 10^5$	$3.314 \times 10$	**
	Variety	1	$1.296 \times 10^3$	2.334	ns
	PV	2	$5.553 \times 10^2$	$2.690 \times 10^{-2}$	ns
	Residual	30	$2.063 \times 10^4$		
Total spikelets. $\text{ear}^{-1}$	Blocks	6	$5.985 \times 10^{-1}$		
	Population	2	3.181	4.942	*
	Variety	1	$9.276 \times 10$	$6.317 \times 10$	*
	PV	2	1.468	2.280	ns
	Residual	30	$6.436 \times 10^{-1}$		
Fertile spikelets. $\text{ear}^{-1}$	Blocks	6	2.114		
	Population	2	$1.980 \times 10$	9.224	**
	Variety	1	$4.939 \times 10$	9.805	ns
	PV	2	5.038	2.346	ns
	Residual	30	2.147		
Grains. spikelet $^{-1}$	Blocks	6	$5.548 \times 10^{-2}$		
	Population	2	$3.039 \times 10^{-1}$	2.944	ns
	Variety	1	8.361	$4.970 \times 10$	*
	PV	2	$1.682 \times 10^{-1}$	1.629	ns
	Residual	30	$1.032 \times 10^{-1}$		
Weight.grain $^{-1}$	Blocks	6	$7.527 \times 10^{-1}$		
	Population	2	$5.358 \times 10^{-1}$	1.965	ns
	Variety	1	$1.173 \times 10$	$1.721 \times 10$	ns
	PV	2	$6.817 \times 10^{-1}$	2.500	ns
	Residual	30	$2.726 \times 10^{-1}$		

## Appendix 8

Analyses of Variance for Dry weights of  
Plant Fractions and Total Dry Weight  
(Log Transformed Data)

Fraction	Source	df	MS	F	
Leaf lamina	Blocks	6	$1.777 \times 10^3$		
	Time	15	$2.552 \times 10^5$	$1.070 \times 10$	**
	Population	2	$2.786 \times 10^5$	$1.168 \times 10$	**
	Variety	1	$2.219 \times 10^4$		
	TP	30	$2.383 \times 10^4$	$1.334 \times 10$	**
	TV	15	$9.706 \times 10^3$	3.227	**
	PV	2	$3.350 \times 10$	$1.114 \times 10^{-2}$	ns
	TPV	30	$3.007 \times 10^3$	1.684	*
	Residual	560	$1.785 \times 10^3$		
	V + TPV	1.3	$2.520 \times 10^4$	2.587	ns
	TV + PV	15.1	$9.739 \times 10^3$		
Dead leaf	Blocks	6	$7.838 \times 10^3$		
	Time	10	$1.537 \times 10^5$	$2.273 \times 10$	**
	Population	2	$4.614 \times 10^4$	6.821	**
	Variety	1	$8.835 \times 10^4$		
	TP	20	$6.764 \times 10^3$	2.289	**
	TV	10	$5.596 \times 10^3$	$9.819 \times 10^{-1}$	ns
	PV	2	$1.190 \times 10^4$	2.089	ns
	TPV	20	$5.699 \times 10^3$	1.928	*
	Residual	379	$2.955 \times 10^3$		
	V + TPV	1.1	$9.405 \times 10^4$	5.372	ns
	TV + PV	4.1	$1.750 \times 10^4$		
Leaf sheath	Blocks	6	$3.438 \times 10^3$		
	Time	16	$3.457 \times 10^5$	$4.553 \times 10$	**
	Population	2	$1.054 \times 10^5$	$1.388 \times 10$	**
	Variety	1	$9.100 \times 10^2$		
	TP	32	$7.592 \times 10^3$	$1.075 \times 10$	**
	TV	16	$1.359 \times 10^3$	1.884	ns
	PV	2	$1.202 \times 10^3$	1.666	ns
	TPV	32	$7.211 \times 10^2$	1.022	ns
	Residual	589	$7.056 \times 10^2$		
	V + TPV	3.2	$1.631 \times 10^3$	$6.369 \times 10^{-1}$	ns
	TV + PV	7.8	$2.561 \times 10^3$		

## Appendix 8 (continued)

Fraction	Source	df	MS	F	
Stem	Blocks	6	$9.135 \times 10^3$		
	Time	11	$3.207 \times 10^5$	$4.034 \times 10$	**
	Population	2	$9.686 \times 10^4$	$1.218 \times 10$	**
	Variety	1	$3.029 \times 10^4$		
	TP	22	$7.949 \times 10^3$	5.764	**
	TV	11	$1.712 \times 10^3$	1.886	ns
	PV	2	$4.275 \times 10^2$	$4.712 \times 10^{-1}$	ns
	TPV	22	$9.073 \times 10^2$	$6.578 \times 10^{-1}$	ns
	Residual	414	$1.379 \times 10^3$		
	V + TPV	1.1	$3.120 \times 10^4$	$1.458 \times 10$	**
	TV + PV	12.8	$2.139 \times 10^3$		
Ear remainder	Blocks	6	$2.633 \times 10^2$		
	Time	5	$1.886 \times 10^3$	2.546	ns
	Population	2	$7.369 \times 10^4$	$9.951 \times 10$	**
	Variety	1	$7.743 \times 10^3$		
	TP	10	$7.405 \times 10^2$	4.482	**
	TV	5	$3.909 \times 10^2$	2.377	ns
	PV	2	$1.779 \times 10^2$	1.082	ns
	TPV	10	$1.644 \times 10^2$	$9.948 \times 10^{-1}$	ns
	Residual	204	$1.652 \times 10^2$		
	V + TPV	1.0	$7.907 \times 10^3$	$1.390 \times 10$	**
	TV + PV	11.9	$5.688 \times 10^2$		
Grain	Blocks	6	$3.169 \times 10^2$		
	Time	5	$4.698 \times 10^4$	$2.257 \times 10$	**
	Population	2	$6.662 \times 10^4$	$3.201 \times 10$	**
	Variety	1	$2.021 \times 10^3$		
	TP	10	$2.081 \times 10^3$	$1.358 \times 10$	**
	TV	5	$2.373 \times 10^2$	2.268	ns
	PV	2	$5.408 \times 10^2$	5.170	*
	TPV	10	$1.046 \times 10^2$	$6.824 \times 10^{-1}$	ns
	Residual	204	$1.532 \times 10^2$		
	V + TPV	1.1	$2.126 \times 10^3$	2.732	ns
	TV + PV	3.8	$7.782 \times 10^2$		

## Appendix 8 (continued)

Fraction	Source	df	MS	F	
Ear total	Blocks	6	$4.832 \times 10^2$		
	Time	10	$8.274 \times 10^4$	$2.153 \times 10$	**
	Population	2	$6.887 \times 10^4$	$1.792 \times 10$	**
	Variety	1	$3.797 \times 10^3$		
	TP	20	$3.842 \times 10^3$	$1.866 \times 10$	**
	TV	10	$5.349 \times 10^2$	3.295	*
	PV	2	$1.434 \times 10^2$	$8.835 \times 10^{-1}$	ns
	TPV	20	$1.623 \times 10^2$	$7.883 \times 10^{-1}$	ns
	Residual	289	$2.058 \times 10^2$		
	V + TPV	1.1	$3.959 \times 10^3$	5.836	*
	TV + PV	11.8	$6.783 \times 10^2$		
Total	Blocks	6	$2.597 \times 10^3$		
	Time	16	$4.165 \times 10^5$	$8.376 \times 10$	**
	Population	2	$1.096 \times 10^5$	$2.204 \times 10$	**
	Variety	1	$1.303 \times 10^3$		
	TP	32	$4.972 \times 10^3$	$1.180 \times 10$	**
	TV	16	$7.223 \times 10^2$	1.222	ns
	PV	2	$2.620 \times 10^2$	$4.432 \times 10^{-1}$	ns
	TPV	32	$5.911 \times 10^2$	1.401	ns
	Residual	589	$4.217 \times 10^2$		
	V + TPV	2.1	$1.894 \times 10^3$	1.924	ns
	TV + PV	14.5	$9.843 \times 10^2$		

## Appendix 9

Analyses of Variance for Areas of  
Photosynthetic Parts (Log Transformed Data)

Fraction	Source	df	MS	F	
Leaf lamina area	Blocks	6	$8.944 \times 10^2$		
	Time	14	$9.558 \times 10^4$	$1.422 \times 10$	**
	Population	2	$8.332 \times 10^4$	$1.240 \times 10$	**
	Variety	1	$3.091 \times 10^3$		
	TP	28	$6.718 \times 10^3$	$1.252 \times 10$	**
	TV	14	$2.103 \times 10^3$	2.454	*
	PV	2	$4.051 \times 10^2$	$4.727 \times 10^{-1}$	ns
	TPV	28	$8.570 \times 10^2$	1.597	*
	Residual	520	$5.364 \times 10^2$		
	V + TPV	1.6	$3.948 \times 10^3$	$5.542 \times 10^{-1}$	ns
	TP + PV	29.9	$7.123 \times 10^3$		
Leaf sheath area	Blocks	6	$3.060 \times 10^3$		
	Time	12	$1.474 \times 10^5$	$3.204 \times 10$	**
	Population	2	$3.744 \times 10^4$	8.137	**
	Variety	1	$1.009 \times 10^3$		
	TP	24	$4.602 \times 10^3$	8.482	**
	TV	12	$8.928 \times 10^2$	1.674	ns
	PV	2	$7.495 \times 10^2$	1.406	ns
	TPV	24	$5.330 \times 10^2$	$9.826 \times 10^{-1}$	ns
	Residual	449	$5.425 \times 10^2$		
	V + TPV	2.3	$1.542 \times 10^3$	$2.882 \times 10^{-1}$	ns
	TP + PV	24.6	$5.351 \times 10^3$		
Flag leaf area	Blocks	6	$1.247 \times 10^3$		
	Time	5	$2.820 \times 10^4$	2.658	ns
	Population	2	$5.780 \times 10^4$	5.449	*
	Variety	1	$9.127 \times 10^3$		
	TP	10	$1.060 \times 10^4$	$1.122 \times 10$	**
	TV	5	$1.991 \times 10^3$	3.300	ns
	PV	2	$3.280 \times 10^3$	5.436	*
	TPV	10	$6.034 \times 10^2$	$6.384 \times 10^{-1}$	ns
	Residual	204	$9.452 \times 10^2$		
	V + TPV	1.1	$9.730 \times 10^3$	$7.006 \times 10^{-1}$	ns
	TP + PV	11.5	$1.388 \times 10^4$		

## Appendix 9 (continued)

Fraction	Source	df	MS	F	
Ear area	Blocks	6	$4.656 \times 10^3$		
	Time	4	$1.637 \times 10^5$	$1.029 \times 10$	**
	Population	2	$2.405 \times 10^4$	1.512	ns
	Variety	1	$5.193 \times 10^4$		
	TP	8	$1.590 \times 10^4$	8.970	**
	TV	4	$1.822 \times 10^4$	$1.803 \times 10$	**
	PV	2	$2.217 \times 10^3$	2.194	ns
	TPV	8	$1.010 \times 10^3$	$5.700 \times 10^{-1}$	ns
	Residual	169	$1.773 \times 10^3$		
	V + TPV	1.0	$5.294 \times 10^4$	2.922	ns
	TV + PV	18.2	$1.812 \times 10^4$		
Peduncle area	Blocks	6	$4.713 \times 10^3$		
	Time	3	$2.687 \times 10^5$	$3.867 \times 10$	**
	Population	2	$7.100 \times 10^3$	1.021	ns
	Variety	1	$5.660 \times 10^4$		
	TP	6	$6.948 \times 10^3$	6.711	**
	TV	3	$3.439 \times 10^3$	6.568	*
	PV	2	$1.400 \times 10^3$	2.674	ns
	TPV	6	$5.235 \times 10^2$	$5.057 \times 10^{-1}$	ns
	Residual	134	$1.035 \times 10^3$		
	V + TPV	1.0	$5.715 \times 10^4$	6.850	*
	TV + PV	7.7	$8.348 \times 10^3$		
Area above FLN	Blocks	6	$5.860 \times 10^2$		
	Time	3	$1.891 \times 10^4$	$2.121 \times 10$	**
	Population	2	$3.360 \times 10^4$	$3.769 \times 10$	**
	Variety	1	$2.422 \times 10^3$		
	TP	6	$8.915 \times 10^2$	1.797	ns
	TV	3	$6.190 \times 10^2$	3.951	ns
	PV	2	$3.605 \times 10^2$	2.301	ns
	TPV	6	$1.566 \times 10^2$	$3.159 \times 10^{-1}$	ns
	Residual	134	$4.959 \times 10^2$		
	V + TPV	1.1	$2.578 \times 10^3$	2.059	ns
	TV + PV	7.9	$1.252 \times 10^3$		

## Appendix 9 (continued)

Fraction	Source	df	MS	F	
Total area	Blocks	6	$1.764 \times 10^3$		
	Time	12	$1.867 \times 10^5$	$5.857 \times 10$	**
	Population	2	$3.004 \times 10^4$	9.422	**
	Variety	1	$2.750 \times 10^2$		
	TP	24	$3.188 \times 10^3$	6.638	**
	TV	12	$8.842 \times 10^2$	1.328	ns
	PV	2	$1.099 \times 10^3$	1.651	ns
	TPV	24	$6.655 \times 10^2$	1.385	ns
	Residual	449	$4.803 \times 10^2$		
	V + TPV	9.4	$9.405 \times 10^2$	$2.194 \times 10^{-1}$	ns
	TV + PV	17.8	$4.287 \times 10^3$		

Appendix 10      Analyses of Variance for Stem Lengths and  
Number of Internodes.

Fraction	Source	df	MS	F	
Length of stem below FLN after heading	Blocks	6	$8.606 \times 10^3$		
	Time	2	$7.207 \times 10^3$	$2.875 \times 10^{-1}$	ns
	Population	2	$1.589 \times 10^5$	6.340	ns
	Variety	1	$3.071 \times 10^5$		
	TP	4	$2.506 \times 10^4$	9.848	**
	TV	2	$1.044 \times 10^3$	$4.656 \times 10^{-1}$	ns
	PV	2	$1.184 \times 10^4$	5.279	ns
	TPV	4	$2.243 \times 10^3$	$8.814 \times 10^{-1}$	ns
	Residual	99	$2.545 \times 10^3$		
	V + TPV	1.0	$3.093 \times 10^5$	8.382	*
	TP + PV	5.9	$3.690 \times 10^4$		
	Number of internodes below FLN	Blocks	6	$1.416 \times 10^{-1}$	
Population		2	$7.255 \times 10^{-1}$	8.773	**
Variety		1	$9.324 \times 10^{-1}$	9.333	ns
PV		2	$9.990 \times 10^{-2}$	1.208	ns
Residual		72	$8.269 \times 10^{-1}$		
Peduncle length	Blocks	6	$1.160 \times 10^4$		
	Time	5	$8.129 \times 10^5$	$8.510 \times 10$	**
	Population	2	$1.695 \times 10^5$	$1.775 \times 10$	**
	Variety	1	$2.935 \times 10^5$		
	TP	10	$9.551 \times 10^3$	8.402	**
	TV	5	$1.126 \times 10^4$	6.719	**
	PV	2	$1.262 \times 10^4$	7.528	*
	TPV	10	$1.677 \times 10^3$	1.475	ns
	Residual	198	$1.136 \times 10^3$		
	V + TPV	1.0	$2.952 \times 10^5$	$1.331 \times 10$	**
TP + PV	5.5	$2.217 \times 10^4$			

## Appendix 10 (continued)

Fraction	Source	df	MS	F	
Total stem length	Blocks	6	$6.860 \times 10^4$		
	Time	6	$3.064 \times 10^6$	$9.350 \times 10$	**
	Population	2	$1.058 \times 10^6$	$3.231 \times 10$	**
	Variety	1	$1.247 \times 10^6$		
	TP	12	$3.276 \times 10^4$	6.782	**
	TV	6	$4.287 \times 10^4$	$1.157 \times 10$	**
	PV	2	$6.685 \times 10^4$	$1.804 \times 10$	**
	TPV	12	$3.705 \times 10^3$	$7.669 \times 10^{-1}$	ns
	Residual	239	$4.831 \times 10^3$		
	V + TPV	1.0	$1.251 \times 10^6$	$1.256 \times 10$	*
	TP + PV	4.2	$9.962 \times 10^4$		

## Appendix 11

Analyses of Variance for Tiller Data  
(Log Transformed Data)

Variate	Source	df	MS	F	
Total tiller number	Blocks	6	$4.908 \times 10^2$		
	Time	16	$1.975 \times 10^4$	9.665	**
	Population	2	$7.192 \times 10^4$	$3.518 \times 10$	**
	Variety	1	$1.903 \times 10^3$		
	TP	32	$2.044 \times 10^3$	$1.263 \times 10$	**
	TV	16	$2.192 \times 10^2$	$8.661 \times 10^{-1}$	ns
	PV	2	$7.844 \times 10^2$	3.098	ns
	TPV	32	$2.531 \times 10^2$	1.564	ns
	Residual	599	$1.618 \times 10^2$		
	V + TPV	1.3	$2.156 \times 10^3$	$7.623 \times 10^{-1}$	ns
TP + PV	18.2	$2.828 \times 10^3$			
Number of non- elongated live tillers	Blocks	6	$6.351 \times 10^2$		
	Time	10	$1.809 \times 10^4$	$2.447 \times 10$	**
	Population	2	$1.898 \times 10^4$	$2.567 \times 10$	**
	Variety	1	$1.022 \times 10^3$		
	TP	20	$7.394 \times 10^2$	2.202	**
	TV	10	$6.247 \times 10^2$	2.432	*
	PV	2	$4.563 \times 10^2$	1.776	ns
	TPV	20	$2.568 \times 10^2$	$7.651 \times 10^{-1}$	ns
	Residual	379	$3.357 \times 10^2$		
	V + TPV	1.6	$1.279 \times 10^3$	1.069	ns
TP + PV	10.9	$1.195 \times 10^3$			
Dead tillers	Blocks	6	$2.015 \times 10^2$		
	Time	7	$3.394 \times 10^3$	8.481	**
	Population	2	$2.879 \times 10^2$	$7.195 \times 10^{-1}$	ns
	Variety	1	$5.180 \times 10^3$		
	TP	14	$4.001 \times 10^2$	1.179	ns
	TV	7	$1.070 \times 10^3$	2.895	*
	PV	2	$7.949 \times 10^2$	2.149	ns
	TPV	14	$3.697 \times 10^2$	1.090	ns
	Residual	274	$3.391 \times 10^2$		
	V + TPV	1.1	$5.550 \times 10^3$	4.644	ns
TP + PV	4.4	$1.195 \times 10^3$			

Appendix 12  $\chi^2$  Analyses for Regressions of Proportions

(a) Regressions of Proportions of Tillers with Spikelet Primordia on Time.

Source	$\hat{b}$	$\hat{c}$	Overall $\chi^2$	df	$\chi^2$ due to regression	
R1	0.027	-0.481	3.931 *	2	3.568	ns
P1	0.074	-2.768	31.278 **	2	26.153	**
R2	0.050	-1.616	17.126 **	2	16.803	**
P2	0.081	-3.222	55.733 **	2	56.415	**
R3	0.039	-1.061	16.680 **	2	15.349	**
P3	0.067	-2.603	31.687 **	2	27.304	**

(b) Regressions of Proportions of Tillers Heading on Time.

Source	$\hat{b}$	$\hat{c}$	Overall $\chi^2$	df	$\chi^2$ due to regression	
R1	0.069	-5.063	42.069 **	2	41.677	**
P1	0.065	-4.894	56.024 **	2	48.229	**
R2	0.047	-3.486	146.849 **	2	137.718	**
P2	0.062	-5.042	87.222 **	2	83.351	**
R3	0.040	-3.109	183.711 **	3	176.327	**
P3	0.043	-3.509	210.904 **	3	206.219	**

## (c) Regressions of Proportions of Tillers with Senescent Photosynthetic Parts on Time.

Source	$\hat{b}$	$\hat{c}$	Overall $\chi^2$	df	$\chi^2$ due to regression
R1 flag leaf	0.042	-0.154	22.539 **	2	21.707 **
R1 leaf sheath	0.049	-0.465	28.599 **	2	26.541 **
R1 peduncle	0.056	-0.466	50.032 **	2	38.314 **
R1 ear	0.057	-0.550	40.685 **	2	37.393 **
P1 flag leaf	0.019	0.427	9.541 **	2	8.996 **
P1 leaf sheath	0.051	-0.471	40.749 **	2	37.008 **
P1 peduncle	0.058	-0.644	49.047 **	2	49.058 **
P1 ear	0.058	-0.522	52.499 **	2	48.941 **
P1 awns	0.029	0.223	19.090 **	2	17.797 **
R2 flag leaf	0.047	-0.446	78.759 **	2	78.154 **
R2 leaf sheath	0.054	-0.567	103.183 **	2	101.433 **
R2 peduncle	0.058	-0.637	117.932 **	2	117.660 **
R2 ear	0.054	-0.632	106.429 **	2	103.962 **
P2 flag leaf	0.041	-0.074	66.577 **	2	61.705 **
P2 leaf sheath	0.058	-0.653	109.815 **	2	108.275 **
P2 peduncle	0.058	-0.717	126.983 **	2	109.516 **
P2 ear	0.057	-0.729	134.107 **	2	110.434 **
P2 awns	0.048	-0.336	76.237 **	2	77.225 **
R3 flag leaf	0.033	-0.266	226.787 **	2	220.501 **
R3 leaf sheath	0.037	-0.464	134.714 **	2	136.505 **
R3 peduncle	0.035	-0.426	117.576 **	2	122.956 **
R3 ear	0.034	-0.398	107.243 **	2	113.069 **
P3 flag leaf	0.024	0.056	130.893 **	3	110.612 **
P3 leaf sheath	0.030	-0.383	83.512 **	2	72.901 **
P3 peduncle	0.021	-0.290	79.384 **	2	54.496 **
P3 ear	0.032	-0.374	74.858 **	2	71.458 **
P3 awn	0.042	-0.437	108.818 **	2	97.529 **

Appendix 13      Coefficients of Polynomials Fitted to  
Dry Weight Data.

The polynomial coefficients in equations of the form

$$\log_e W = B_0 + B_1 t + B_2 t^2 + B_3 t^3$$

are tabulated.

Fraction	$B_0$	$B_1$	$B_2$	$B_3$
Raven 1				
Leaf lamina	-2.032	$2.253 \times 10^{-1}$	$-1.411 \times 10^{-3}$	
Dead leaf	2.859	$2.717 \times 10^{-2}$		
Leaf sheath	-6.602	$4.053 \times 10^{-1}$	$-3.940 \times 10^{-3}$	$1.239 \times 10^{-5}$
Stem	-2.470	$1.900 \times 10^{-1}$	$-8.306 \times 10^{-4}$	
Ear remainder	6.908			
Grain	$-3.293 \times 10$	$6.363 \times 10^{-1}$	$-2.456 \times 10^{-3}$	
Ear Total	-7.344	$2.368 \times 10^{-1}$	$-8.886 \times 10^{-4}$	
Total	$-6.621 \times 10^{-1}$	$1.763 \times 10^{-1}$	$-7.815 \times 10^{-4}$	
Pitic 1				
Leaf lamina	$-7.219 \times 10^{-1}$	$1.817 \times 10^{-1}$	$-1.074 \times 10^{-3}$	
Dead leaf	2.710	$3.193 \times 10^{-2}$		
Leaf sheath	-6.001	$3.734 \times 10^{-1}$	$-3.466 \times 10^{-3}$	$1.045 \times 10^{-5}$
Stem	-8.114	$2.961 \times 10^{-1}$	$-1.325 \times 10^{-3}$	
Ear remainder	7.252			
Grain *	$-2.527 \times 10$	$5.122 \times 10^{-1}$	$-1.949 \times 10^{-3}$	
Ear Total	$-1.453 \times 10$	$3.765 \times 10^{-1}$	$-1.528 \times 10^{-3}$	
Total	$-4.061 \times 10^{-1}$	$1.687 \times 10^{-1}$	$-7.323 \times 10^{-4}$	
Raven 2				
Leaf lamina	-2.850	$2.454 \times 10^{-1}$	$-1.392 \times 10^{-3}$	
Dead leaf	1.462	$4.659 \times 10^{-2}$		
Leaf sheath *	-6.234	$3.551 \times 10^{-1}$	$-2.815 \times 10^{-3}$	$7.083 \times 10^{-6}$
Stem	8.902	$3.250 \times 10^{-1}$	$-1.415 \times 10^{-3}$	
Ear remainder	8.043			
Grain	$-3.896 \times 10$	$7.585 \times 10^{-1}$	$-2.977 \times 10^{-3}$	
Ear Total	$-1.293 \times 10$	$3.549 \times 10^{-1}$	$-1.397 \times 10^{-3}$	
Total	-1.772	$2.074 \times 10^{-1}$	$-8.804 \times 10^{-4}$	

## Appendix 13 (continued)

Fraction	$B_0$	$B_1$	$B_2$	$B_3$
Pitic 2				
Leaf lamina	-3.218	$2.720 \times 10^{-1}$	$-1.658 \times 10^{-3}$	
Dead leaf	3.054	$3.634 \times 10^{-2}$		
Leaf sheath *	-5.517	$3.319 \times 10^{-1}$	$-2.543 \times 10^{-3}$	$6.044 \times 10^{-6}$
Stem	$-1.151 \times 10$	$3.775 \times 10^{-1}$	$-1.692 \times 10^{-3}$	
Ear remainder	8.338			
Grain	$-3.301 \times 10$	$6.599 \times 10^{-1}$	$-2.565 \times 10^{-3}$	
Ear total	$-2.054 \times 10$	$5.049 \times 10^{-1}$	$-2.089 \times 10^{-3}$	
Total	-1.445	$2.040 \times 10^{-1}$	$-8.796 \times 10^{-4}$	
Raven 3				
Leaf lamina	-1.875	$2.201 \times 10^{-1}$	$-1.163 \times 10^{-3}$	
Dead leaf	1.076	$5.425 \times 10^{-2}$		
Leaf sheath *	-6.005	$3.410 \times 10^{-1}$	$-2.500 \times 10^{-3}$	$5.862 \times 10^{-6}$
Stem	$-1.032 \times 10$	$3.464 \times 10^{-1}$	$-1.433 \times 10^{-3}$	
Ear remainder	8.775			
Grain	$-3.283 \times 10$	$6.443 \times 10^{-1}$	$-2.409 \times 10^{-3}$	
Ear total	$-1.358 \times 10$	$3.631 \times 10^{-1}$	$-1.372 \times 10^{-3}$	
Total	-1.403	$2.005 \times 10^{-1}$	$-7.941 \times 10^{-4}$	
Pitic 3				
Leaf lamina	-3.972	$2.830 \times 10^{-1}$	$-1.597 \times 10^{-3}$	
Dead leaf	2.236	$4.706 \times 10^{-2}$		
Leaf sheath *	-7.593	$3.841 \times 10^{-1}$	$-276 \times 10^{-3}$	$6.906 \times 10^{-6}$
Stem **	-1.398	$4.108 \times 10^{-1}$	$-1.726 \times 10^{-3}$	
Ear remainder	9.195			
Grain	$-2.403 \times 10$	$5.070 \times 10^{-1}$	$-1.862 \times 10^{-3}$	
Ear total **	$-2.048 \times 10$	$4.908 \times 10^{-1}$	$-1.920 \times 10^{-3}$	
Total	-2.300	$2.179 \times 10^{-1}$	$-8.713 \times 10^{-4}$	

\* Polynomial of higher degree than statistically significant polynomial.

\*\* Polynomial of lower degree than statistically significant polynomial.

## Appendix 14

Coefficients of Polynomials Fitted  
to Photosynthetic Area Data.

The polynomial coefficients in equations of the form

$$\log_e A = B_0 + B_1 t + B_2 t^2$$

are tabulated.

Fraction	$B_0$	$B_1$	$B_2$
Raven 1.			
Leaf lamina area	1.626	$2.168 \times 10^{-1}$	$-1.388 \times 10^{-3}$
Leaf sheath area	1.366	$1.829 \times 10^{-1}$	$-1.131 \times 10^{-3}$
Flag leaf area	8.118		
Ear area	8.076		
Peduncle area	$9.571 \times 10^{-2}$	$8.831 \times 10^{-2}$	
Area above FLN	9.837		
Total area	2.219	$2.050 \times 10^{-1}$	$-1.255 \times 10^{-3}$
Pitic 1.			
Leaf lamina area	2.371	$1.856 \times 10^{-1}$	$-1.111 \times 10^{-3}$
Leaf sheath area	1.815	$1.581 \times 10^{-1}$	$-8.977 \times 10^{-4}$
Flag leaf area **	8.541		
Ear area	9.384		
Peduncle area **	-9.528	$1.830 \times 10^{-1}$	
Area above FLN	$1.014 \times 10$		
Total area	2.193	$1.955 \times 10^{-1}$	$-1.118 \times 10^{-3}$
Raven 2			
Leaf lamina area	$4.963 \times 10^{-1}$	$2.431 \times 10^{-1}$	$-1.409 \times 10^{-3}$
Leaf sheath area	$2.278 \times 10^{-1}$	2.041	$-1.092 \times 10^{-3}$
Flag leaf area	9.109		
Ear area	4.619	$4.816 \times 10^{-2}$	
Peduncle area	-3.464	$1.350 \times 10^{-1}$	
Area above FLN	$1.072 \times 10$		
Total area	$9.679 \times 10^{-1}$	$2.352 \times 10^{-1}$	$-1.327 \times 10^{-3}$

## Appendix 14 (continued)

Fraction	$B_0$	$B_1$	$B_2$
Pitic 2.			
Leaf lamina area	$8.920 \times 10^{-1}$	$2.453 \times 10^{-1}$	$-1.516 \times 10^{-3}$
Leaf sheath area	1.654	$1.645 \times 10^{-1}$	$-8.394 \times 10^{-4}$
Flag leaf area	9.005		
Ear area	6.528	$3.960 \times 10^{-2}$	
Peduncle area	$-7.582 \times 10^{-1}$	$9.908 \times 10^{-2}$	
Area above FLN	$1.080 \times 10$		
Total area	2.636	$1.852 \times 10^{-1}$	$-9.734 \times 10^{-4}$
Raven 3.			
Leaf lamina area	1.769	$2.077 \times 10^{-1}$	$-1.125 \times 10^{-3}$
Leaf sheath area	$9.578 \times 10^{-1}$	$1.849 \times 10^{-1}$	$-9.100 \times 10^{-4}$
Flag leaf area	$-1.407 \times 10$	$4.535 \times 10^{-1}$	$-2.118 \times 10^{-3}$
Ear area	2.409	$7.379 \times 10^{-2}$	
Peduncle area	$-2.756$	$1.295 \times 10^{-1}$	
Area above FLN	5.682	$5.827 \times 10^{-2}$	
Total area	1.706	$2.153 \times 10^{-1}$	$-1.142 \times 10^{-3}$
Pitic 3.			
Leaf lamina area	$-1.948 \times 10^{-1}$	$2.633 \times 10^{-1}$	$-1.499 \times 10^{-3}$
Leaf sheath area	$9.757 \times 10^{-1}$	$1.695 \times 10^{-1}$	$-7.450 \times 10^{-4}$
Flag leaf area	$-2.819 \times 10$	$7.259 \times 10^{-1}$	$-3.427 \times 10^{-3}$
Ear area	1.197	$9.721 \times 10^{-2}$	
Peduncle area	$-1.483 \times 10$	$2.458 \times 10^{-1}$	
Area above FLN	4.131	$7.661 \times 10^{-2}$	
Total area	1.427	$2.103 \times 10^{-1}$	$-1.040 \times 10^{-3}$

\*\* Polynomial of lower degree than statistically significant polynomial.

Appendix 15      Coefficients of Polynomials Fitted  
to Stem Length Data

Coefficients in equations of the form

$$L = B_0 + B_1 t + B_2 t^2$$

are tabulated.

Fraction	$B_0$	$B_1$	$B_2$
Raven 1			
Stem below FLN	$5.132 \times 10^2$		
Peduncle length	$-5.571 \times 10^2$	8.648	
Total length	$-2.903 \times 10^3$	$6.545 \times 10$	$-2.718 \times 10^{-1}$
Pitic 1			
Stem below FLN	$3.852 \times 10^2$		
Peduncle length	$-4.768 \times 10^2$	6.929	
Total length	$-2.100 \times 10^3$	$4.545 \times 10$	$-1.781 \times 10^{-1}$
Raven 2			
Stem below FLN	$4.394 \times 10^2$		
Peduncle length	$-5.274 \times 10^2$	7.959	
Total length	$-2.431 \times 10^3$	$5.134 \times 10$	$-1.959 \times 10^{-1}$
Pitic 2			
Stem below FLN	$3.333 \times 10^2$		
Peduncle length	$-4.216 \times 10^2$	5.905	
Total length	$-1.511 \times 10^3$	$3.117 \times 10$	$-1.086 \times 10^{-1}$

## Appendix 15 (continued)

Fraction	$B_0$	$B_1$	$B_2$
Raven			
Stem below FLN	$3.572 \times 10^2$		
Peduncle length	$-4.726 \times 10^2$	6.630	
Total length *	$-1.319 \times 10^3$	$2.611 \times 10$	$-7.496 \times 10^{-2}$
Pitic 3			
Stem below FLN	$2.951 \times 10^2$		
Peduncle length	$-4.223 \times 10^2$	5.679	
Total length *	$-9.251 \times 10^2$	$1.688 \times 10$	$-3.420 \times 10^{-2}$

\* Polynomial of higher degree than statistically significant polynomial.