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A Study of the effect of Plant Density on Growth and Yield in two varieties of Grain Barley.

A Thesis, presented in partial fulfilment of the requirements for the degree of Master of Agricultural Science at Massey University

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AGROMONY THESIS:

Topic:

The effect of Plant density on growth and yield in two varieties of Grain Barley.

CHAPTER I.

INTRODUCTION:

As a thesis topic, I have chosen to work with a temperate cereal viz: Barley (Hordeum distichum) and to examine in two varieties; Zephyr and Kenia:—

(1) The physiological and growth characters of two Barley varieties differing in grain yield potential.
(2) The effect of plant density on growth and development and on grain yield and its components.

In cereals, as in many crops, an increase in plant density leads to an increase in total dry matter until a level of yield is reached after which increase in density does not lead to a further increase in yield. The data upon which this statement is based often refers to shoot dry matter only. Grain yield on the other hand reaches a maximum with increasing density, after which a further increase in density leads to a fall in grain yield (Holliday, 1960; Donald, 1963). Crop growth, leaf area, tiller initiation and tiller death and other parameters are modified by plant density. Attempts have been made to relate these parameters with grain yield in studies involving the physiological basis of varietal and fertilizer effects upon grain yield. Watson et al have made very full studies and have suggested that high grain yield is dependent upon having high values of leaf area and leaf area duration, especially after ear emergence (Watson, Thorne and French, 1963).

METHODS OF STUDY:

The problem of accounting for variation of yield in terms of growth and development of the crop plant is obviously very complex, for ultimately it involves the effect of external factors on all the physiological processes of the plant, the interrelation between different processes, and their dependence on internal factors determined by the genetical constitution of the plant. There are three main methods of study used by experimenters in sorting out such problems.
(1) Controlled environment with either whole plants or plant parts.

(2) Field studies using Growth Analysis techniques.

(3) Field studies using the energy balance concept.

To discover the physiological basis for variation in crop yield it is necessary to supplement laboratory studies by direct observation on field grown crops, measuring those attributes that are capable of relatively simple physiological interpretation. The disadvantages of any field study is that high variability in the plant population necessitates repetition of each observation on a large number of samples or a smaller number of samples with more frequent sampling intervals.

Growth Analysis is used as a technique in the field of studying related growth parameters in order to give some picture of the effects of density on grain yield, and is based on the principal that the increase in dry weight of plants in a given period is a measure of net photosynthesis. Full analysis of yield requires consideration of the distribution of dry matter and leaf area between the different parts of the plant as well as the total dry weight and leaf area accumulated. Physiological techniques appropriate for laboratory studies are, in general, not suitable for investigations on crops growing in field conditions. One reason for this is that such techniques may themselves change the environment; for example although it is possible to measure directly the gas exchange of plants growing on a field plot, this involves enclosing the plants in an airtight chamber inside which the environmental factors of light temperature, CO₂ concentration and water supply may differ in intensity from those outside.

In early experiments with cereals (Engledow and Wadham, 1923), the procedure followed was to make a census of the growing crop recording at intervals the number of plants/unit area, number of tillers/plant shoot height, and at harvest the number of ears/plant, grains/ear and grain weight; the plant characters assumed to be related to yield. These census studies did not succeed in defining easily measured yield controlling characters that the cereal breeder can use as a basis for selection as the different yield attributes are sometimes inversely correlated. The yield of a field crop is the weight/unit area of the harvested produce or some specific part of it, hence it is more logical to base an analysis of yield on the weight changes that occur during growth than on changes in morphological characters. The first step in developing a procedure for analyzing growth in terms of dry weight change was made by Blackman (1919). Blackman showed that increase in dry weight can be regarded as a process of continuous compound interest, the increment produced
in any interval adding to the "capital" for growth in subsequent periods. The rate of interest, or relative growth rate,
\[ R = \frac{I}{W} \times \frac{dw}{dt} \]
where \( R = \text{growth rate} \)
\( W = \text{dry weight} \)

\[ \log_e W_2 - \log_e W_1 = \frac{t_2 - t_1}{t} \]

The dry matter yield of a plant was considered as dependent on (1) the initial capital, i.e.; the seed weight, (2) the relative growth rate, and (3) the length of the growth period and variations in yield can be analysed in terms of these three quantities.

However, the dry weight of a plant is not all productive capital, for a considerable part of it consists of skeletal material not active in growth. As dry matter increase is attributable to photosynthesis, a better measure of the productive capital or "growing material" of the plant is leaf size. The rate of increase of dry weight per unit leaf area, \((I/L) (dw/dt)\) where \( L \) is the total leaf area of the plant, is a measure of the excess of the rate of photosynthesis over the rate of dry matter loss by respiration. Gregory (1917) suggested the use of this function in the analysis of growth and called it Net Assimilation Rate (NAR), and Briggs, G., Kidd, E. and West, C. developed \( E \) (Unit leaf rate) as an 'efficiency index'. The relative rate of plant growth at any one time, may be taken as an expression of the efficiency of the plant at that time in producing dry matter, or the difference between rates of assimilation and respiration/100 gm dry weight at that time.

Thus NAR and \( E \) is the rate of increase of dry weight per unit leaf area. N.A.R. is capable of relatively simple physiological interpretation, while leaf area is the result of many physiological and environmental processes: genetics of the plant, age, nutritional status, temperature and moisture status, etc. LAI (Leaf area index) is often taken as a measure of the size of the Photosynthetic System, but it is not a perfect measure because parts of the plant other than the leaf laminae are capable of photosynthesis and may sometimes account for an appreciable fraction of the dry matter production. Thus total annual photosynthesis is a function of the size, duration and efficiency of the photosynthetic system. Growth analysis involves sampling or harvesting whole plants at different growth stages over time from a population of similarly treated plants at intervals, in this case weekly intervals were used. Watson (1947) has shown that while \( E \) varies between species grown in the same environment, between varieties of the same species, and between seasons for the
same crop in the same place, variation in E within and between species and between seasons is accompanied by relatively greater variation in leaf area, so that measurement of leaf area is important in the study.

Thus it is clear that the relative growth rate (R.G.R.) is the product of N.A.R. and the ratio of leaf area to total dry weight; this ratio (L/W, leaf area ratio) may be regarded as an index of the amount of 'growing material' per unit dry weight of the plant. Consequently, the progress of dry matter accumulation and its end point yield at harvest can be completely described in terms of the two attributes NAR and leaf area.

It is not practicable to make a continuous record of the changes with time in total dry weight and leaf area; instead, they are measured by taking samples from a population of similarly treated plants at intervals, usually a week or multiples of a week. RGR and NAR are then estimated as mean rates over the successive intervals. Fisher (1921) showed that, if \( W_1 \) and \( W_2 \) are the total dry weights at times \( t_1 \) and \( t_2 \) respectively, the mean value of R.G.R. for the time interval \( t_2 - t_1 \) is given by:

\[
\frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}
\]

and following Gregory (1926) it has been usual to calculate N.A.R. as

\[
NAR = \frac{(W_2 - W_1)(\log_e L_2 - \log_e L_1)}{(t_2 - t_1)(L_2 - L_1)}
\]

For short intervals (1-2 weeks) it appears that this condition is approximately satisfied, and the errors introduced are negligibly small for field crops, in comparison with those due to sampling variation in \( W \) and \( L \).

**Limitations to the concept of N.A.R.**

It is important to bear in mind that N.A.R. is not a pure measure of photosynthesis, but it depends on the excess of dry matter gain by photosynthesis over loss by respiration. Some of the limitations to the concept of N.A.R. are:

1. Photosynthesis occurs mainly in the leaves whereas respiration proceeds throughout the whole plant.
2. N.A.R. is often estimated from plant tops only as roots are difficult to obtain. This will result in an under-estimation of N.A.R., at the times when the root system is increasing in dry weight, i.e. the error introduced may be large in the very early growth stages, later decreasing and becoming negligible.
(3) Another limitation of the NAR concept arises from the fact that photosynthesis is not entirely restricted to the leaf lamina, but occurs also in other parts of the plant difficult to measure, e.g. in stems and petioles, and in the leaf sheaths and ears of cereals.

(4) Photosynthesis may occur at a greater rate in different parts of the plant, e.g. nearly half the dry weight increase of Barley plants after ear emergence is the result of photosynthesis in the ears (Watson and Norman, 1939; Porter, Pal, and Martin, 1950).

(5) NAR varies with changes in the external climatic factors, viz: light and temperature. Weekly values for increase in Dry Weight/Unit leaf area vary more or less about a mean - fluctuations attain increasing amplitude as age of the plant increases e.g: after 8 weeks in maize - (Briggs, Kidd and West, 1920) when sampling errors are largely responsible.

Watson (1952) points out that there can be no ideal basis of reference for NAR that will render it wholly independent of the 'internal factor' or 'growing material' of the plant since NAR depends on both photosynthesis and respiration. The best course seems to be to use a basis of reference appropriate for photosynthesis, since this must be the dominant process whenever increase in dry weight is taking place. Williams (1939) preferred to express NAR on the basis of leaf protein-nitrogen E; although this involves elaborate analytical procedures and it is doubtful of its superiority. Hence it is better to continue to use the leaf area basis for the sake of uniformity.
CHAPTER II.

Uses of Growth Analysis in Cereal Physiology

1. Leaf growth and Crop yield:

The problem of increasing agricultural yield is fundamentally the problem of how to increase the total annual photosynthesis/unit area of crop, hence size of the photosynthetic system must be one of the determinants of crop yield. Total annual photosynthesis is a measure of the size, efficiency and duration of the photosynthetic system. The L.A.I. (sum of the laminae areas/unit area of land) can be taken as a measure of the size of the photosynthetic system.

1. Methods of increasing L.A.I.

(a) Nutritional.

Nitrogen increases leaf area throughout the growth period; phosphate increases leaf area particularly in the early stages of growth, later it hastens leaf senescence, eventually it may decrease leaf area, K tends to delay leaf senescence.

(b) Species.

To secure maximal D.M. production in cereals, high values of L that persist for such a short time should occur when seasonal weather conditions are most favourable for photosynthesis i.e: June and July for annual cereals such as wheat and barley (U.K. conditions), sugar beet and potatoes do not develop a large leaf area until late in the season, (September and October) where E has fallen below its mid-summer maximum. The important point is to increase L at the time of the year when E is high i.e. better synchronisation of the leaf growth curves with the seasonal drift of E without change in the magnitude of L.

Limitations:

As L increases a point is reached where mutual shading of leaves must eventually begin to decrease the rate of photosynthesis of part of the foliage and so to decrease E. If E were independent of L, the rate of increase of D.M. per unit area of land, crop growth rate (E x LAI) would increase indefinitely with L, but mutual shading prevents this. Watson (1954) found that increased LAI caused decreased NAR, and the effect was greater for kale than for sugar beet, probably due to growth forms.
Relative importance of LAI and E as determinants of yield.

The limit to crop growth rate is set primarily by climatic and soil factors e.g. length of the frost free period. Yield is decreased when the growth period is shortened by late planting of spring crops or by early harvest.

A measure of the efficiency of the photosynthetic system is provided by the rate of increase of dry weight per unit leaf area, N.A.R. or E, which can be estimated from successive determinations of dry weight and leaf area at short intervals throughout the growth period. At present this is the only method available for making extensive measurements of mean rates of photosynthesis of field crops for successive periods of the order of 1 week. E varies between species grown in the same environment, between varieties of the same species, and between seasons for the same crop in the same environment, Watson (1947). Variation of E within and between species is accompanied by relatively greater variation in leaf area, and yield of a crop from year to year is more closely correlated with variation in mean leaf area than with mean E. Comparison between species in respect of the relation of yield to L and E are more difficult because the growth period varies in length and in the part of the year that it occupies. However, variation in mean dry weight yield between wheat, barley, sugar beet and potatoes is nearly proportional to the integral of L over the growth period, i.e. the leaf area duration, D.

Variation in nutrient supply over a wide range has little or no effect on E, Watson (1947) compared with the effect on L.A.I. In some cases, water stress decreases E, but it decreases L more consistently Watson (1952). The existence of variation in E within species suggests the possibility of increasing E by breeding and selection, however there is evidence that within each species, E and L are inversely correlated, so that selection for high E will not necessarily increase yield. The main source of variation in E is change in external factors such as light and temperature i.e. E shows a seasonal trend associated with climatic changes, and is maximum in mid summer and falls to zero in Winter.

Heath and Gregory (1938) summarised the available data on N.A.R. mostly derived from pot cultures, but including some field crops over periods ranging from 4 to 14 weeks in order to eliminate the effects of short term variations in climatic conditions. Gregory concluded that the mean N.A.R. during the vegetative phase was approximately constant for all diverse plants and environments investigated. However, Watson (1947) disproved this as E of 4 species tested; sugar beet, potatoes (dicots), wheat and barley (monocots)
differed widely; results were from 15 experiments in 6 years. However, differences in crop yield were attributed to wider differences in E. Of the species tested, barley was the most efficient in E over a short period followed by wheat. Sugar beet and potatoes do not develop a large L until late in the season when E has fallen, due to drop in temperature and solar radiation. The important point is that L should be at a maximum when E is high.

Watson (1952) reported estimates of E for cereals sown on the same day for the period 27 April to 21 June:

<table>
<thead>
<tr>
<th></th>
<th>Wheat</th>
<th>Barley</th>
<th>Oats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean E (gm/m²/wk)</td>
<td>35.8</td>
<td>31.2</td>
<td>28.7 ± 0.65</td>
</tr>
</tbody>
</table>

In wheat, Watson (1947) found no evidence of any differences in E between 3 varieties of winter wheat Square heads Master, Yeoman and Victor, in 2 years. Lupton (1961) presented data for E in 5 varieties of winter wheat and one variety of spring wheat, all autumn sown. For most of the experimental period the spring variety Peko, had a higher E than the winter varieties. This difference between spring and winter wheats was observed by Watson, Thorne and French (1963) where E of spring varieties was about 50% greater. In this instance there were no differences between E of spring varieties Atle and Jufy I, but for much of April and May E of variety Cappelle-Desprez was greater than that of the older winter variety Square heads Master. Differences in E were caused by mutual shading arising from differences in L.A.I., and not changes in leaf physiology. In a field experiment involving 3 barley varieties, Plumage Archer, Herta and Proctor, Watson, Thorne and French (1958) found no differences in E before ear emergence, but in a pot experiment Plumage Archer had a significantly greater E than Kenia, Herta or Proctor for part of the experimental period. Thorne (1963) reported similar rates of apparent photosynthesis in leaves of Plumage Archer and Proctor both before and after ear emergence. Cannell (1967) using seven barley varieties ranging in grain yield potential found no consistent differences in E between the barley varieties. Similarly, in wheat even though variety Atle, one of the older varieties had a consistently lower E than the other cultivated varieties, no association was evident between E and the yielding potential of the series of related varieties. In this study, the stronger relationship between mean leaf area and shoot weight increase support the conclusion of Watson 1952, that dry-matter production can most readily be influenced by adjustments in leaf area. Thus the variation in N.A.R. 'within' species is not great, and the opinion of Gregory (1950) that, 'there is little hope in increasing efficiency of the photosynthetic process 'within species', is
probably justified, unless there can be progress from selection for differences in palisade cell numbers of photosynthetic pathways e.g. the C₄ cycle as in maize and certain tropical grasses.

**Effect of Plant Spacing on Yield and Yield Components.**

Cereal crop yields are remarkably stable over a wide range of densities, and this can be examined by considering the response of yield components to density. The yield components are: the number of plants/unit area, the number of fertile tillers per plant, the number of grains/ear, (this can be sub-divided in wheat and oats into grains/spikelet and spikelets/ear), and finally grain weight.

**Plant Number:**

The first of these components (plant No/unit area) is determined by the experimenter, and is itself little affected by the density of initial establishment, except at extremely high plant density levels. In experiments with wheat (Puckeridge and Donald 1967) the plant number determined shortly after braiding was found to change little throughout the season except at densities of more than 600 plants/m². Kirby (1967) has shown that plant density in barley showed no significant change throughout the season over the range from 100 to 800 plants/m². In oats grown over a comparable range of densities there was some reduction in plant number, but the relative range was the same in all treatments, Jones and Hayes (1967).

**Fertile Ears, panicles per plant:**

All cereals show a marked fall in fertile ears of panicles per plant as plant density is increased. The data taken from the above sited examples over a wide range of environments will serve to illustrate the magnitude of the effect.

**TABLE III.**

<table>
<thead>
<tr>
<th>Cereal Species</th>
<th>Plants/m²</th>
<th>No Ears/Plant</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100</td>
<td>4.1</td>
</tr>
<tr>
<td></td>
<td>200</td>
<td>2.5</td>
</tr>
<tr>
<td>Barley</td>
<td>400</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>800</td>
<td>1.0</td>
</tr>
<tr>
<td></td>
<td>200²</td>
<td>2.1*</td>
</tr>
<tr>
<td>Wheat</td>
<td>600²</td>
<td>0.7*</td>
</tr>
<tr>
<td>Oats</td>
<td>200²</td>
<td>1.75*</td>
</tr>
<tr>
<td></td>
<td>700</td>
<td>0.77*</td>
</tr>
</tbody>
</table>

* = Approx.
An example of the Relation of ear Number per M², Grain Number per ear and 1000 Grain dry weight to plant density. Ex Kirby 1968 - Plant Breeding Institute, Cambridge.
In wheat, at very low densities, where there is almost no interplant competition almost 30 ears/plant are formed, and in barley at 20 cm square 30 or more ears are formed. Increase in ear number per plant with decreasing density partly compensates for the fewer plants at lower densities, but in all experiments for which data is available, the greatest number of ears per unit area is found at the highest density.

Because of intra-plant competition, the greater number of extra ears, greater grain weight and grains per ear at wide spacings compared with narrow spacings is partly off set.

Grains per ear and grain weight:

In barley, which has the simplest inflorescence of the cereal crops, changes in ear size with decreasing density have been shown by Kirby, E.J., (1968) where average number of spikelets/ear falls from 26 at 50 plants/m$^2$ to 16 at 800 plants/m$^2$. In wheat and oats, where there is a further component of grain number/spikelet, the spikelet number falls with increasing density, but the number of florets per spikelet is less affected. The effect of plant density on the number of spikelets per ear reduces still further the effect of plant density on grain yield.

Grain weight is the final yield component to be considered, and the last one to be determined in the life cycle of the plant. Unlike other yield components it is difficult to draw any general conclusions as to the response of 1000 grain weight to plant density. Experiments with wheat, oats and barley indicate that this yield component is least affected by plant density.

Puckeridge (1962) has recorded in detail the effects of plant density on the growth of wheat, although he did not include $N$ levels in his experimental design. Wheat was sown at a range of densities from 5.7 to $3.54 \times 10^3$ plants/acre, an even denser sowing of $19 \times 10^6$ plants per acre could not be maintained.

**Table IV.**

<table>
<thead>
<tr>
<th>Initial Density x $10^3$ plants/acre:</th>
<th>Shoots/Plant: Weeks from sowing (23rd May, 1961)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.7</td>
<td>4 10 14 17 20 24</td>
</tr>
<tr>
<td>28.3</td>
<td>1.8 16.4 24.9 40.5 37.0 33.0</td>
</tr>
<tr>
<td>141.6</td>
<td>1.9 16.1 30.0 29.5 27.0 24.5</td>
</tr>
<tr>
<td>708.2</td>
<td>1.8 13.7 11.9 10.6 9.5 9.9</td>
</tr>
<tr>
<td>3,541.0</td>
<td>2.0 5.5 4.1 3.0 3.0 3.3</td>
</tr>
<tr>
<td></td>
<td>1.3 1.6 1.4 1.2 1.5 1.2</td>
</tr>
</tbody>
</table>
As shown in the above table, with increase in density, the number of shoots per plant begins to decline earlier from week 17 at 5,700 to week 10 at 700,200 plants/acre (a population slightly lower than normal field population). At the highest population shown (over 3 times a satisfactory field population) few tillers are formed and the number varies little. Since the time at which the numbers of shoots per plant were greatest depends on the plant density and the dates of ear emergence are similar to all densities, the decline of shoot numbers is clearly not directly related to some physiological stage of growth or development. Clearly competition between plants affects tiller number per plant as in this experiment, but there must also have been competition between tillers 'within' the individual plants since the number of shoots per plant declined from a maximum even at the widest spacing. Either this is the explanation, or that earlier developed shoots exert a suppressive effect on the later formed tillers at all spacings. If on the other hand tiller numbers are adjusted without recourse to competition by using c.c.c (an anti-gibberellin), Humphries 1962 found that the increase in tiller numbers is associated with a definite decline in yield. This would suggest an 'internal' competition effect for available nutrients required for grain growth.

Tillering and Seed Yield in Cereals:

Introduction:

The life history and longevity of tillering in annual grasses will vary considerably with the time of origin (season) and the environment. In annual cereals, the time trend is such that live tillers reach a peak in spring, falling to a minimum 'before' ear emergence and varying little until final harvest. With wider spacing, or decreased density, late tillering is more pronounced than with denser spacing. This is the pattern in spring wheat (Watson, Thorne and French 1958, Thorne, 1962, Kirby, 1962, and in winter and spring sown wheat, De Silva, 1961, Krishnamurthy, 1963, Watson, Thorne and French, 1963).

Once a tiller has become reproductive it usually survives, and when a reproductive tiller dies, its decline has usually started before the apex begins to elongate, but the morphological development of the apex continues for a long time even though the fate of the tiller is sealed (Krishnamurthy, 1963).
Effect of Nutrients:

(a) Type of Nutrient:

Gregory (1937) summarised the data for barley in their relative importance for tillering \( N \succ P \succ K \). Watson (1947) showed that nitrogen increased shoot number and leaf area per shoot; phosphate increased shoot number but had little effect on leaf area per shoot tending to depress it in later stages of growth by hastening leaf death. Potassium had little effect on shoot number, but increased leaf area per shoot, possibly by prolonging leaf life. This order of importance of nutrients for tillering \( \text{viz: } N \succ P \succ K \) has similarly been found in grasses. Langer (1959) found in Timothy that high \( N \) gave twice the tiller number of low \( N \) at 3 weeks similarly for phosphate at 4 weeks, and for \( K \) these differences were not attained. It is not always clear what level of nitrogen is available to plants or how much the primary responses are distorted by increased competition due to appearance of new tillers and increases in the size of tillers already present. In cocksfoot, Lambert (1966) found that the primary effects of \( N \) were to increase the number of tillers and ears per plant and to accelerate the rate of development of inflorescences; in addition \( N \) advanced the date of initiation of the inflorescences without similarly advancing the date of complete differentiation. Greatest increases in numbers of tillers due to application of \( N \) were in autumn each year when the highest numbers were recorded. Donald and Henson (1969) found in wheat that most of the \( N \) of the plant is taken up via the root system of the main stem and primary tillers with only a small uptake by the roots of the secondary tillers and an almost nil uptake by the tertiary tillers, while loss of \( N \) by senescing tertiary tillers to fertile tillers was small (2.8% of maximum \( N \) content of whole plants).

(b) Periodicity of Tilling.

Aspinall (1961), (1963) in barley, and Langer (1959) in grasses have shown that mineral nutrition affects the number of fertile tillers and the length of time over which new tillers appear:—

Figure 2. Fireline Barley Aspinall (1961)

(a) All nutrients applied before germination
Sln 100% 50% 10% N (3), (2), (1).

(b) 50% 5% 1% N Sln.

Nutrients given weekly.
Tillering and Ear emergence of Piroline Barley under varying nutrient regimes.

The time of onset of the non-tillering and its duration both depend on the nitrogen nutrition of the plants. This has been shown to occur in Timothy maintained at 3 levels of Nitrogen (Langer, 1959), and more recently by Aspinall (1961) in Barley (Fig. 2). In the first case tillering followed a 2 phase pattern, rising at first then levelling off i.e: when nutrients were applied before germination. At low N levels, tillering stopped sooner and after fewer tillers had appeared than those where nutrients were given at full strength. The degree but not the proportion of tiller death also varied with the amount of nutrients applied. Continuous nutrient supply (case B) in Fig. 2 reduced the length of the low tillering phase depending on the level of nutrition, but even a 5% nutrient solution regularly supplied resulted in more continuous tillering than a full strength solution given at the beginning of the experiment. In both series ear emergence occurred much later than the reduction in rate of tiller appearance, which suggests that these two events are not necessarily correlated, although in this context, time of initiation of growth rather than appearance of the tiller would be more meaningful physiologically. Where small doses are given regularly, tillering is almost continuous while large doses of N given regularly cause an almost complete lack of effects of ear emergence on tillering. Watson et al, (1958) showed that in the field, 'Proctor' and 'Herta' Barley but not 'Flumage Archer' continued tillering after ear emergence when N was applied at sowing i.e: varieties do differ in their response patterns to nutrients.

(c) Tiller survival and Ear emergence:

There are two possible phenomena involved in the cessation of tillering on the one hand, and the appearance of the ear and resumption of tillering on the other: viz, internal competition for nutrients (especially N) and apical dominance (and influence from the stem apex) on developing grains.

It is difficult to accept that rapid stem elongation causes tillering to cease; the two events do not occur together. Actively growing meristems clearly exert a more powerful influence than inactive ones, but since tillers develop their own photosynthetic and root systems at an early stage, it is more than doubtful that the distribution of nutrients is the controlling factor, even though it is possible to affect the onset and duration of minimal tillering by application of N.

This problem has been studied in two nearly 'iso-genic' cultivars of barley segregated for male sterility (Laude, Ridley and Suneson, 1967).
The number of living tillers and tiller mortality was similar in fertile and sterile plants alike until 10 days after awn emergence.

These authors state that this senescence is not attributable to the mobilization of nutrients into the developing grains, but that the triggering mechanism for pre-heading shoot senescence appears to be operative at the initial stages of floral development and before mechanical debudding is feasible.

Effects of Nutrients on the resumption of tillering:

The level of mineral supply also affects the resumption of tillering which usually occurs soon after the beginning of ear emergence. In Piroline barley, Aspinall (1961) found that raising the nutrient supply as soon as the first ears had appeared caused an immediate response in tiller production, but in later treatments, resumption of tillering was progressively delayed. In another variety of barley, evidence was obtained that the developing grains are competing strongly for minerals to the detriment of tiller-bud growth (Aspinall 1963). However it required a disproportionately high concentration of external nutrient supply to overcome the influence of the grains i.e. in this case factors other than mineral nutrition are likely to play a part. In the study by Suneson et al. 1967, the shoot mortality prior to awn emergence does not appear to be related to nutrient deficiency since increased tillering following awn emergence occurred in both fertiles and steriles without nutrient addition to the pots.

Aspinall's experiments also show that nitrogen can be taken up after ear emergence by barley in pots, and Gregory's suggestion (1937) that the uptake of N ceased when plants reached the reproductive phase has not been supported by work on field crops, Watson et al. (1958, 1963) Thorne (1962), De Silva (1961), and Bunting (unpubl.).

Apical dominance:

As in most plants, the expansion of lateral buds of cereals into tillers can be encouraged by removing the young inflorescence at a suitable stage thus preventing the shoots from becoming reproductive. Leopold (1949) showed that plants in which the apical region is damaged tiller freely unless IAA is applied to the damaged apex. However, Thorne (1962) showed that removing ears from 'Plumage Archer' and 'Proctor' barley plants on the older shoots had no effect on the production or survival of shoots, while application of auxin to the cut ends also had no effects. Similarly, Aspinall (1963) was unable to demonstrate an effect of these treatments, and suggested that the pattern of growth of the plants was already determined in some way by the
distribution and supply of carbohydrates and nitrogen.

**Inter-tiller relationships.**

That materials for growth can move from one tiller to another has been demonstrated in young wheat plants using tracer C\(^{14}\), Lupton (unpubl.), Qinlan and Sagar (1962), however movement from parent shoots to the younger tillers decreases with age. When surplus tertiary tillers are removed, the yield of the rest of the plant can be increased (Hashimoto et al. 1956), Hirano and Shimada (1960) and I-Shun (1958) and Miller (1949) in wheat, and Tinkler and Jones (1931) in wheat. Recently, Donald and Dawson (1969) showed that sterile tertiary tillers can act as a temporary nutrient reservoir for the fertile plant parts, but they are of little value as the amount of \(\text{N}\) transferred is small. The death of tillers is associated with the movement from them into the parent shoot of minerals and certain carbon compounds; this was shown by Dungan (1931) in maize, by Nakamura (1956) in rice, and by Smith (1933) and Palfi and Dezai (1960) in wheat.

Thorne (1962) noted that when tillers of Plumage Archer barley died there was no check in growth of the whole plant, and concluded that either dry matter was transferred from dying shoots or that other shoots grew faster because competition was less. On the other hand, Krishnamurthy (1963) found that the absolute growth rate of 4 varieties of winter wheat was markedly decreased at the time when tiller numbers were falling. The interruption in the growth curve of the plants as a whole was not reflected in the curve for the main axis, but appeared as a net fall in the weight of tillers. In 1962, in a similar series of observations, the fall in absolute growth rate was much less marked because the losses of tillers were spread over a much longer period.

**Patterns of Tillerina in relation to yield.**

Temperate cereals, barley and wheat exhibit differences in shoot survival, although the generalised time trend is similar in both species; Watson et al. (1958); Thorne (1962); Kirby (1967); Lawde et al. (1967). Exceptions to this generalised time trend were recorded in 'Herta' barley by Watson et al. (1958), where live tiller number continued to increase after ear emergence and in 'Proctor' where no pre-ear emergence decline was apparent, although there was some decline in both varieties by harvest.

Higher survival rates of shoots in newer barley varieties have been observed (Watson et al. 1958; Thorne 1962; Kirby 1967). Bunting and Drennan (1966) draw attention to varietal differences in the proportion of shoots forming ears, and concluded that highest yields are often obtained from varieties in which tillering is limited. Bingham (1967) showed in an
experiment with wheat that this association held in that the 'proportion' of shoots forming ears was least in the older variety 'Holdfast' and greater in the newer varieties 'Professeur Marchal' and 'Cappelle-Desprez'; the varieties differed in yield approximately in the ratio 75: 95: 100, Holdfast, Professeur Marchal and Cappelle Desprez respectively, and the percentage shoots surviving to form ears were 25.8, 28.1 and 34.3. Thorne (1962) found that the lower yielding barley variety 'Plumage Archer' grown in pots produced more shoots than did the higher yielding 'Proctor', but had fewer ears at maturity because some shoots died about 7 days before ear emergence. It is interesting to note that in this study the number and position on the plant of the shoots that died were not always the last to be produced.

Relation of shoot components to yield:

Many workers e.g: Engledow and Wadhams (1923), Thorne (1966) and Cannell (1969) have found that the earlier formed tillers have higher survival rates and contribute most to grain yield. Thorne (1966) made a study of component tillers to yield in pot grown barley. At low level of N, 'Plumage Archer' with a peak of 3.5 shoots/plant and a final number of 1.5 shoots/plant derived most of its final yield from the main stem and the tiller at the second node. In 'Proctor', the maximum shoot number per plant was 3.3 and the final number approx 2.2; the third node tiller contributed more to final grain yield than the second. At high levels of N, Plumage Archer and Proctor had maximum shoot numbers of 6.8 and 5.8 per plant with final values of 4.2 and 5.0 respectively. At this level of N, Plumage Archer derived 96% of its yield from the main stem and from tillers at the 2nd., 3rd., and 4th., nodes, while Proctor derived 82% from the same tillers, but in addition the tiller arising from the axil of the prophyll of the second node tiller provided 14% of the total yield. Krishnamurthy (1963) working with wheat has found higher survival rates in early appearing shoots which also had larger ears. Cannell (1969) compared the two barley varieties Spratt Archer (representing old) and Maris Badger (representing new) under two fertility regimes, low N and high N. The newer variety appeared to be more 'adaptable' in terms of the number of shoots surviving per plant than the older variety. Whereas at a higher level of N there was very little difference in tiller survival—peak values being 6.7 for Spratt Archer and 7.1 shoots per plant for Maris Badger respectively, under low N there was a considerable divergence. Krishnamurthy (1963) found in tiller marking studies in the field with 6 wheat varieties that of 2.2 ears produced per plant from a total of 4.3 shoots, 1.5 were on shoots that appeared before the end of March. The earliest formed tillers not only had a much
higher chance of survival, they also produced larger ears than later formed tillers. Khatri (1965) working with New Zealand bred varieties of wheat found the best yielders to be those with the higher numbers of surviving tillers.

From the evidence cited it would appear that shoot survival is a varietal characteristic that plant breeders cannot afford to overlook when examining yield components of cereals. Studies to explain why more of the early formed tillers survive in the more modern varieties than in the older or less successful varieties are urgently needed. The contrast may well depend on differences smaller than can be detected by infrequent sampling within the period at which the earliest nodes expand. Since this character is affected by the supply of nitrogen it may be associated with differences in the efficiency with which varieties take up and utilize $N$ and hence in biochemical features such as the nitrate-reductase system (Zieserl et al 1963).

Single versus Multi-tiller plants:

The value of the single culm habit in wheat was subjected to preliminary tests in 1967 by Donald, using the semi-dwarf variety 'Pitic'. From pot studies the uni-culm or uni-tiller habit had a clear yield advantage over 3 culm and 2 culm habit plants which did not differ in their productivity. Donald's conclusions were that there was a benefit due to the single-culm habit per se, and one due to more dispersed arrangement permitted by single culms. Perhaps there is less internal competition for growth substances and nutrients during ear and grain development in the uni-tiller case. This is supported by the fact that uni-culm plants had greater numbers of fertile spikelets per ear, grains per spikelet and also smaller percentage and absolute numbers of sterile spikelets than corresponding treatments with 3 culm or 2 culm plants.

<table>
<thead>
<tr>
<th>Effect of Uniculm and Multiculm Habits on Yield and Yield Components.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dispersed 3-culm plants</td>
</tr>
<tr>
<td>Dispersed 1-culm plants</td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>
The total effect of the uniculm habit involving both the uni-culm influence and the increased dispersal which it permits, is best illustrated by comparing dispersed 3-culm and 1-culm plants. Donald (1967) considers that the grain yield increase from the uni-culm habit under pot conditions may have been due to the advantages of greater photosynthetic area at emergence, or more and earlier formed root systems. Other reasons are also suggested such as a longer period of apex differentiation by main stems and better light relationships among the plants.

These findings must be confirmed under field conditions especially with limited water or nutrient supply. This 'ideal' wheat plant may fail when compared with existing cultivars under standard conditions as heavier sowing rates would be needed. Similarly the capacity to grow with its like neighbours with minimal mutual interference may also mean that it is susceptible to competition from weeds, Tanner et al (1966). Thus the concept of seeking a minimal intensity of tiller competition in cereals moderates any significance of high yield per plant. The important aspect is not that a plant grows large but only that it makes good use of its environment above and below ground. If the cereal plant although of low absolute yield is efficient in using its restricted environment within the crop and is of low competitive ability against its neighbours, then high crop yields can be secured simply by increasing the population or density.

Effects of the environment:

(1) Moisture Stress:

Aspinall (1964) has shown in barley that a water stress before stamen initiation in barley is likely to influence only tillering. A single cycle of stress either long or short will slow down tillering rate, but upon rewatering a large temporary increase in tillering ensues. This response is so like that of plants given a divided application of mineral nutrients, Aspinall (1961), that the availability of nutrients, could be postulated as the dominating factor involved in both instances. A temporary increase in vegetative growth above the control rate has often been observed upon rewatering following a stress; Gates (1955) in tomatoes; Owen and Watson 1956 in sugar beet; Robbins and Domingo 1962 in wheat. Although this may be associated with the uptake and distribution of nitrogen Stanhill (1958), tiller buds have also to be in a responsive condition. Stress late in development gives a much smaller increase, if any, in tiller numbers as in nutrient supply, Aspinall (1961). Alternatively the maintenance of apical dominance by major tiller apices may depend on their continued growth, and a temporary check during soil moisture stress may
release the sub-ordinate apices from their control. It is thought that the observations of more rapid R.G.Rs and higher NAR after a period of water stress than before Gates (1955) can be reconciled with the view that since P and N migration is least pronounced in the most active and developing leaves and in meristematic tissue, a removal of the stress further cell division may be stimulated by increased availability of N and P compounds in the vascular system.

Where soil moisture stress is continued for more than one cycle, however, tillering is curtailed by a stress occurring late in development (anthesis). In this case, late tillers which elongate after ear emergence in barley are completely suppressed. The data collected by Aspinall, Nicholls and Hoy (1964), supports the contention that the organ which is growing most rapidly at the time of the stress is the one most affected; as found by Hagen et al in clover. In barley, the effect of reduced tillering by a stress is greater the earlier the period of stress, and is probably related to nutrient uptake and distribution within the plant. Grain number per ear is seriously affected by stress occurring prior to anthesis, an effect probably associated with the process of spikelet initiation and later with the formation of the gametes. Grain size, however, is reduced more by a stress at anthesis and shortly after. Chinoy (1962) concluded that varietal differences in drought resistance in wheat reflected differences in stage of maturity between varieties rather than any genetic difference in resistance to wilting. Wells and Dubetz (1966) concluded that in barley, the effects of stress on grain yield were greatest at or near anthesis. They also showed that this is probably the best stage for differentiating between genotypes for reaction to stress.

In determinate species, the effect of water stress can be quite marked as the reproductive phase is of short duration and the majority of the population flower simultaneously. In wheat and barley, Watson 1952, Asana and Saini and others have shown that continued active photosynthesis after fruit set is also a most important determinant of final yield. Wardlaw (1967), studying the effects of water stress on translocation in relation to photosynthesis and growth during grain development in wheat found that grain growth was unaffected by several days of leaf wilting and this was partly accompanied by a change in the distribution of assimilates from the lower parts of the plants to the grains. The movement of assimilates into the conducting tissue is prolonged in wilted leaves, but the velocity of translocation is little affected by stress. Wardlaw suggested that water stress acts directly on the
leaf rather than indirectly through effects on growth or sugar movement within the conducting tissue.

Asana and Basu (1963) using an Indian wheat Pbc281 subjected to intermittent drought showed that during the early stages of grain development, (the first fortnight after anthesis) although water stress reduced the increase in dry weight of the shoot and inhibited accumulation of sugars in the stem, the increase in grain weight was not affected. During the later stage (between 27 and 34 days later), grain weight was reduced under water stress and this effect was attributed to reduced photosynthetic activity resulting from rapid yellowing of the ear, and depression in the rate of transfer of stem sugars to the ear as indicated by their subsequent higher level in the stem.

For determinate species such as maize there is evidence for a marked critical period of water stress effects on reproductive development. Data of Denneud and Shaw (1960), and Robbins and Domingo (1953) have shown that the tasseling - silking period is most critical. Depletion of moisture to wilting percentage for 1 to 2 days, and for 6 to 8 days during the tasseling period resulted in 22% and 50% grain yield respectively, Robbins and Domingo (1953). Stress applied while the plant is still actively expanding retards enlargement of plant parts. Recovery when the stress is removed is not immediate but growth rate appears to return to normal after a few days. A similar lag period followed by recovery is reported by Hagen et al for Ladino clover and by Van Der Paaw (1949) in oats. Early stress has an indirect effect on grain yield through reducing the size of the assimilatory surface at the time of ear development. A yield reduction of 21% from stress during ear formation, Denneud and Shaw (1960) is largely due to a reduction in the photosynthate produced. Van Der Paaw (1949) found that a critical period for oats was evident at heading and that lower yields were primarily due to barrenness of the inflorescence.

2. Temperature effects on growth in cereals:

The generalized temperature response curve for growth of plants follows closely the shape of an enzyme response curve rising rapidly at the lower temperature range 0° to 15°C and less rapidly at the intermediate temperature range of 15°C to 30°C (Leopold A.G., 1964) and falling off at higher temperatures. This same type of temperature response is known for many plant tissues and includes rates of photosynthesis and growth of coleoptiles, stems, roots, leaves and other plant parts.

The effect of temperature on the growth and distribution in the
plant is indicated for a number of cereal species in the following tables taken from Van Dobben (1962).

**TABLE I.**

Effect of Temperature on Root/Shoot Ratio.

<table>
<thead>
<tr>
<th>Temperature:</th>
<th>Spring Oats</th>
<th>Maize</th>
</tr>
</thead>
<tbody>
<tr>
<td>0°C</td>
<td>Wheat(Peko)</td>
<td>1.5</td>
</tr>
<tr>
<td>10°C</td>
<td>Barley(Herta)</td>
<td>1.7</td>
</tr>
<tr>
<td>16°C</td>
<td>Barley(Herta)</td>
<td>3.0</td>
</tr>
<tr>
<td>25°C</td>
<td>Barley(Herta)</td>
<td>4.0</td>
</tr>
</tbody>
</table>

From the above table it can be concluded that root/shoot ratio generally increases with temperature, (also observed by Khalil; 1956). At temperatures just above zero cereals show ratios between 1 and 2. In the range 10°-16°C much higher values are reached, and between 16° and 25°C several species seem to show a maximum, or at least no further increase. Also there are distinct differences between spring sown temperate crops and sub-tropical crops such as maize. In the latter, the shoot/root ratio and growth rate increase without reaching an optimum value within the range shown. Also, comparisons of Tables I and II show a clear agreement in temperature response between shoot/root ratio and growth rate. This is strong evidence that the growth response to temperature is mainly governed by shifts in the shoot/root ratio.

**TABLE II.**

<table>
<thead>
<tr>
<th>Temperature:</th>
<th>Spring Wheat:</th>
<th>Spring Barley:</th>
<th>Oats:</th>
<th>Maize:</th>
</tr>
</thead>
<tbody>
<tr>
<td>10°C</td>
<td>32</td>
<td>20</td>
<td>23</td>
<td>-</td>
</tr>
<tr>
<td>16°C</td>
<td>22</td>
<td>12</td>
<td>20</td>
<td>19</td>
</tr>
<tr>
<td>25°C</td>
<td>20</td>
<td>11</td>
<td>18</td>
<td>9</td>
</tr>
</tbody>
</table>

Number of days in which the Dry Weight of Juvenile Plants increased 10-fold under Optimal Conditions.

The temperature determines the ultimate size as the result of a mutually independent influence of temperature on growth (increase in dry weight) and development (length of the growth period). For small cereals, the time available for production is reduced by a rise in temperature without being sufficiently compensated by more vigorous growth so that plants remain smaller when the temperature is higher. When the temperature is raised from 10° to 16°C, the rates of growth and development are accelerated stronger than in the range 16°C - 25°C.
TABLE III.

<table>
<thead>
<tr>
<th>Temperature</th>
<th>Spring Rye</th>
<th>Spring Wheat</th>
<th>Spring Barley</th>
<th>Maize</th>
</tr>
</thead>
<tbody>
<tr>
<td>10°C</td>
<td>82</td>
<td>129</td>
<td>99</td>
<td>-</td>
</tr>
<tr>
<td>16°C</td>
<td>51</td>
<td>70</td>
<td>63</td>
<td>87</td>
</tr>
<tr>
<td>25°C</td>
<td>37</td>
<td>57</td>
<td>52</td>
<td>50</td>
</tr>
</tbody>
</table>

TABLE IV.

<table>
<thead>
<tr>
<th>Rise in temperature:</th>
<th>Spring Rye</th>
<th>Spring Wheat</th>
<th>Spring Barley</th>
<th>Maize</th>
</tr>
</thead>
<tbody>
<tr>
<td>10°C-16°C</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Rate of growth</td>
<td>1.4</td>
<td>1.4</td>
<td>1.7</td>
<td>-</td>
</tr>
<tr>
<td>2. &quot; development</td>
<td>1.6</td>
<td>1.8</td>
<td>1.6</td>
<td>-</td>
</tr>
<tr>
<td>16°C-25°C</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Rate of growth</td>
<td>1.1</td>
<td>1.0</td>
<td>1.1</td>
<td>2.1</td>
</tr>
<tr>
<td>2. &quot; development</td>
<td>1.5</td>
<td>1.3</td>
<td>1.2</td>
<td>1.7</td>
</tr>
</tbody>
</table>

Growth = No. of days in which the Dry Weight increased 10-fold at 10°C (16°C) divided by the same value at 16°C (25°C).

TABLE V.

<table>
<thead>
<tr>
<th>Temperature</th>
<th>Spring Rye</th>
<th>Spring Wheat</th>
<th>Spring Barley</th>
<th>Oats</th>
<th>Maize</th>
</tr>
</thead>
<tbody>
<tr>
<td>10°C</td>
<td>8780</td>
<td>16,240</td>
<td>12,000</td>
<td>16,210</td>
<td>-</td>
</tr>
<tr>
<td>16°C</td>
<td>4560</td>
<td>11,100</td>
<td>6,790</td>
<td>9,750</td>
<td>13,600</td>
</tr>
<tr>
<td>25°C</td>
<td>405</td>
<td>7,250</td>
<td>5,400</td>
<td>7,350</td>
<td>35,150</td>
</tr>
</tbody>
</table>

For maize, the reverse relations hold, i.e.: when the temperature rises from 16°C to 25°C growth is accelerated relatively more than development, so that the plants finally become larger, i.e: maize has the ability of compensating and even over compensating for the acceleration of development at higher temperatures by a relatively still greater increase in daily growth rate.

The relative growth (R.G.R.) provides a means of comparing efficiency of growth of plants of widely different size and can be separated into a morphological component, the L.A.R. (A/wp dm$^2$ gm$^{-1}$) and a physiological component $E_a$. An increase in temperature over the range of 10$^\circ$-25$^\circ$C results in higher values of $A/wp$ in Marquis spring wheat (Friend et al. 1965) because of increases in both $A/WL$ (Unit leaf weight, $dm^2$ gm$^{-1}$ - a measure of leaf thickness) and $WL/wp$ (leaf weight ratio, or way in which the assimilates are distributed between leaves and the rest of the plant). Also since $R.G.R. = E_a \times A/wp$, (Hughes 1962) an increase in temperature over the range 15$^\circ$-20$^\circ$C leads to a higher value of $R.G.R.$ in wheat because the increase in $A/wp$ (LAR) more than compensates for a decrease in $E_a$. Above 25$^\circ$C, RGR is reduced by a decline in $A/wp$.

In maize, however, Wilson 1967 showed a linear increase in $E_a$, RGR and LAR over the temperature range 10$^\circ$ to 30$^\circ$C under controlled environments. Also an increase in temperature not only raised the general level of $E_a$, but also steepened the response to radiation. Other multiple regression studies have shown increase in $E_a$ with daily range of temperature in barley, clover and potatoes (Gregory 1926; Black 1955; Watson 1947). $R.G.R.$ ($E_a$) also varies between small cereal species, e.g.: Watson 1947 and declines with time in Barley, even under constant conditions, Thorne 1961.

<table>
<thead>
<tr>
<th>Mean NAR gms/dm$^2$ wk$^{-1}$</th>
<th>wheat</th>
<th>Barley</th>
<th>Oats</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.358</td>
<td>0.312</td>
<td>0.287</td>
</tr>
</tbody>
</table>

The decline in wheat is most rapid at a temperature of 25$^\circ$C, with high light intensities and long day lengths when growth and self-shading are also rapid. Gregory (1926) found that N.A.R. of barley was positively correlated with mean daily maximum temperature and negatively correlated with mean daily minimum. His interpretation was that high night temperature increased respiration loss and so reduced N.A.R. whereas high day temperature increased NAR by increasing photosynthesis. In oats, Stoskopf et al. (1966) found a significant correlation of + 0.691 between NAR and diurnal temperature difference measured at ground level within plots. These authors suggested that since N.A.R. failed to correlate too well with diurnal temperature range, solar energy may be the real cause for variation in N.A.R. and not diurnal temperature range.
Effect of temperature on tillering: leaf production.

In most cereals, maize being the notable exception, the rate of leaf production by a plant depends more on the rate of tillering than on leaf production by an individual shoot. In wheat, a rise in temperature from 20°C to 25°C increases the rate of leaf production to a greater extent than that of tillering; so that apical dominance is greatest at high temperatures (Friend et al. 1962). The close correlation between the ratio of root weight/total plant weight and the degree of apical dominance under a wide range of environmental conditions suggests that increased tillering at low temperatures and high light intensities is brought about by the increased supply of photosynthates. A similar control of tillering in barley is reported by Paleg and Aspinall, 1964. When the temperature is increased from 10°C to 20°C or 25°C, the demand for assimilates by the main axis becomes greater because of stimulation of cell division and the increase in rate of leaf primordium formation. (Friend et al., 1962). In consequence, the supply of assimilates available to tiller buds and roots is restricted and apical dominance is increased. The 'percentage survival' of tillers is not affected over the temperature range 10°C - 30°C and light intensity range of 1000-2000 f.c. However at low temperature although rate of tillering is slow, the duration of increase in tiller numbers continues for longer than at high temperatures because of delayed flowering.

The effect of the environment on leaf growth is of prime importance for growth of cereals. The rate of formation of single ridges, the earliest stage of a leaf primordium increases with increasing temperature over the range 10°C to 25°C in wheat, Friend (1965). An increase in temperature over the range 10°C to 30°C results in narrower and thinner leaves. The leaf length and area increases with increasing temperature over the range 10°C - 20°C or 25°C and declines at 30°C for wheat (Friend et al., 1965).

The Physiological factors associated with Grain Yield in Cereals:

Understanding the control of 'economic yield' in plant physiology involves knowledge of the following factors:

1. Which parts of the photosynthetic system acts as sources of dry matter for economic yield.

2. What internal factors influence their photosynthetic activity and dry matter partitioning.

3. When during the growth period are these sources active.

4. What effect has respiratory losses on the accumulation of economic yield.

5. What part does the environment play.
Sources of Dry Matter Yield:

The evidence is for temperate cereals (wheat, barley) and subtropical rice and maize) that most of the grain dry matter is formed from CO₂ assimilated 'after' the ears emerge as in wheat and barley Thorne (1962), and after flowering as in rice and maize, Watson and Allison (1965). The evidence that sugars formed before ear emergence and stored in the root or shoot contribute little to the grain is indirect and based on the fact that shoot and root do not lose much of their sugar and dry weight while the grain is filling under normal conditions. Loss of sugar from the stems and roots of barley after ear emergence could account for only 20% of the grain and was probably caused mainly by respiration (Archbold and Mukerjee 1942). Again, the CO₂ absorbed after ear emergence by the part of the shoot above the flag-leaf node including the ear accounted for most of the grain dry weight of barley and wheat (Thorne 1963, 1965) i.e: yield is mainly determined by growth after ear emergence, and growth before ear emergence affects grain yield only by affecting (1) the potential surface for photosynthesis after ears emerge, and (2) the number and potential size of the 'sinks' for starch accumulation. Watson et al, 1963 point out the far greater importance of leaf area duration over total LAI is greater than twice that of spring wheat until ear emergence, but yields only 14% more grain as its Dₜ (leaf area duration after ear emergence) was only 17% greater than that of spring wheat. The relationship between grain yield and D can be described conveniently by the ratio between them, called the grain: leaf ratio, G, by Watson et al 1963. G is a measure of the photosynthetic efficiency of the leaves in producing Dₜ for grain in the same way as Eₐ measures the photosynthetic efficiency of the leaves during the vegetative phase. G is fairly constant for differences in yield of any variety within one season and most of the variation within seasons can be explained by variation in radiation and temperature, but there are differences between varieties (Welbank and Witte 1965).

Final Grain Weight W, can be expressed in the following relationship:

\[ W = (PE - RN - Rd) + S. \]

\[ S = D.M. \text{ that moves from the shoot into the ear.} \]

\[ PE = D.M. \text{ contributed by photosynthesis in the ear itself.} \]

\[ RN \text{ and } Rd \text{ are respiration losses by night and day respectively.} \]

These above can be expressed as percentages of final grain weight or of increase in ear weight between anthesis and maturity which equals W because weight of the glumes and rachis does not change after ear emergence in barley
and wheat, Porter et al (1950); Krishnamurthy (1963); Kriedeman (1964).

In maize, photosynthesis in the ear contributes very little to final grain weight, because the surface area of the ear is only about 2% of that of the rest of the plant, Allison (1964). The sheaths also probably contribute little to the grain filling period as they provide only about 18 to 20% of the photosynthetic area, which is much less than in wheat.

Rice resembles wheat in that most of the carbohydrate in the grain is produced by photosynthesis after the ears emerge; however up to a third may be contributed from carbohydrate stored in the shoot, Takeda and Murata (1955), Yin et al (1956), Envi (1962), and in Barley up to 20% from the same.

Methods of study:

A. Ear and Stem shading.
   Leaf removal or shading.

   Contributions of different organs to the grain have been estimated quantitatively from the effects on grain yield of removing organs at ear emergence or shading them after ear emergence.

   Possible discrepancies of shading or leaf removal are:
   (1) Shaded ears may yield less grain because of greater respiration caused by increased temperatures.
   (2) Translocation of carbohydrate from other parts of the plant; e.g. from shoot to grain as a result of shading or leaf removal.
   (3) Greater photosynthesis in other parts of plants.

B. Use of tracer $\mathrm{^{14}C}_2$ in gaseous exchange studies using an infra-red gas analyser.

C. Other methods.

   Buttrose and May (1959, 1962) devised a method of estimating PE (ear Photosynthesis) whereby the weights of grains in comparable positions on ears with different numbers of spikelets are compared with carbohydrate supply from stems restricted by shading.

   \[ W = PE + \frac{R}{n} \]
   where \( W \) = grain wt; \( R \) = total reserves translocated from shaded parts \( n \) = No. of grains compared with controls. Lupton (1961) and Buttrose (1962) used this method with wheat. In wheat, this method gave values of PE of 21–50%.

Comparison of Methods:

The following is a comparison of values obtained for PE for the different methods:
1. Shading and Excision.

<table>
<thead>
<tr>
<th>Crop</th>
<th>Experimenter:</th>
<th>Method:</th>
<th>Value of PE:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat</td>
<td>Thorne G. 1962</td>
<td>Pot Trial</td>
<td>14%</td>
</tr>
<tr>
<td></td>
<td>Quinlan &amp; Sagar 1965</td>
<td>&quot;</td>
<td>25%</td>
</tr>
<tr>
<td></td>
<td>De Silva 1961</td>
<td>Field &quot;</td>
<td>26%</td>
</tr>
<tr>
<td></td>
<td>Boonstra 1929</td>
<td>&quot;</td>
<td>30% &quot;</td>
</tr>
</tbody>
</table>

* = leaves and stem 25% each.

<table>
<thead>
<tr>
<th>Crop</th>
<th>Experimenter:</th>
<th>Method:</th>
<th>Value of PE:</th>
</tr>
</thead>
<tbody>
<tr>
<td>2. Barley</td>
<td>Watson &amp; Norman 1939</td>
<td>Pot trial</td>
<td>25%</td>
</tr>
<tr>
<td></td>
<td>Archbold 1942</td>
<td>&quot;</td>
<td>30%</td>
</tr>
<tr>
<td></td>
<td>Watson et al 1958</td>
<td>&quot;</td>
<td>26%</td>
</tr>
<tr>
<td></td>
<td>Thorne G. 1962</td>
<td>&quot;</td>
<td>10-14%</td>
</tr>
<tr>
<td></td>
<td>&quot; 1963</td>
<td>Field &quot;</td>
<td>15-39%</td>
</tr>
</tbody>
</table>

The lower part of the shoot seems to contribute little to the grain. Grain dry weight of barley was decreased by only 15% by shading the shoot below the base of the flag leaf sheath (Watson et al 1958).

CO₂ Exchange methods:

Contribution of photosynthesis by the ear to the grain can be estimated directly by measuring the gas exchange of the ear with an infra-red CO₂ analyser or by an absorption technique, because auto-radiography shows that CO₂ absorbed by the ear is not translocated to the shoot; Buttrose and May (1959); Lupton (1964). Competition between kernels is not evident, although it can be induced when carbohydrate supply is artificially depleted by shading or spikelet removal. The disadvantages of enclosing organs to measure their CO₂ exchange and the possible bias in the resulting estimate of contributions to the grain are that enclosed organs probably photosynthesize less than unenclosed ones because light intensity is less and temperature greater. But this should not affect comparisons between different organs, or between the same parts of different varieties, provided enclosure affects them all similarly. CO₂ uptake during the day, summed over the life of the ear gives $PE - Rd$, and CO₂ output at night measures $Rn$. $PE$ can be calculated if $Rd$ is measured in the dark and assumed to be the same as in the light.

Results are generally higher for exchange methods than for shading and excision as there is less plant interference to photosynthesis and respiration. Hence these give probably the most reliable estimations than shading methods.
The value of PE for barley is generally higher than that of wheat especially in this method.

**Attributes likely to enhance grain yield.**

1. **Sink Capacity.**

   Grain yield will be increased by increasing the capacity of the plant to produce grain assimilates; only when there is an efficient "sink" to receive it, i.e. when enough grains are able to grow large enough to accept all the grain D.M. that could be formed. Very little is known about the relationship between cereal yield and the capacity of the ear to accumulate dry matter, although Thorne G. (1962, 1963) has shown that it can be increased by shading the ear or decreased by removing some spikelets from ears, Nosberger and Thorne (1965), Wardlaw (1965). Wardlaw found that removal of grains from 2 out of 3 consecutive spikelets reduced the velocity to assimilate movement to the ear from the flag leaf in wheat and increased transfer down the stem to the roots.

   The yield of modern barley varieties seems not to be restricted by the 'capacity' of the ears to accumulate or accept dry matter e.g. 1000 grain weight versus yield increase in N.I.A.B. trials (U.K.) between 1956 and 1963. 1000 grain weight of 12 barley varieties introduced since 1946 increased nearly linearly with yield. Regression coefficients of 1000 grain weight on grain yields were Kenia b = 0.24, Rika b = 0.28, Union b = 0.29, Proctor b = 0.28, Maythorpe b = 0.56.

   ![Graph of 1000 Grain Weight vs. Yield](image)

   There was no curvature towards the yield axis when yield was large, such as would be expected if grains have a limiting maximum size that was approached when growing conditions favoured large yields.
Thorne (unpubl.) found that G became less as the temperature fell and attributed this to a sink effect. Wheat and barley grown at 15°C after ear emergence had a greater D than plants grown at 20°C because the leaves senesced more slowly. But this extra leaf produced little or no extra grain and so G at 15°C was less than half that at 20°C. But a sink effect cannot always be the explanation because G of barley was less at the colder temperature even when the ears were shaded and therefore should have been larger sinks.

Grain yield can be increased by increasing one of the yield components either separately or in combination, but in practice large increases in one are usually accompanied by decreases in the other e.g. N fertilizer often increases yield by increasing the numbers of ears, but grains/ear are usually smaller and fewer.

The main determinant of yield in wheat is grain weight/ear (Bunting et al., 1964) which is correlated with grain size in winter varieties and grain number in spring varieties (Krishnamurthy, 1963) whereas the larger yields of Proctor and Herta barley than that of Plumage Archer depend more on ears/acre (Watson et al., 1958).

Tillering and Tiller survival:

This topic has been dealt with previously (see tillering and seed yield).

Increasing the number of ears should in theory be a good method of increasing yield because the capacity of the system to produce and store grain dry matter should be increased. Producing fewer tillers with higher survival rates seems more economical and is characteristic of better yielding varieties, e.g. Watson and Thorne (1958) found that both Proctor and Herta barley outyielded Plumage Archer by 15% in field plots; while plants of Plumage Archer grown in pots produced more shoots than did Proctor, less ears at maturity were produced by Plumage Archer because some of the shoots died about 7 days before ear emergence. This may not always be a characteristic of higher yielding varieties, e.g. a fairly recent wheat variety 'Professeur Marchal' which yields well produces many more tillers than survive to form ears, Krishnamurthy, (1963). The capacity to produce more tillers than survive may have its advantages; it compensates under conditions which restrict tillering or cause some tillers to die, e.g. attacks of fungal or insect diseases, water shortage after ear emergence N deficiency, etc. The dry matter in the tillers that do die may not entirely be wasted, e.g. all the N and apparently most of the D.M. from the tillers of Plumage Archer barley that died before ear emergence moved to the rest of the plant, Thorne G. (1962); Donald and Rawson (1969) showed this in wheat also.
Size, duration and efficiency of the Photosynthetic surface after flowering and ear emergence:

The most obvious character likely to contribute to large grain yields is ample leaf area after ear emergence. Different yields are often correlated with differences in D, e.g: the increase in grain yield of Herta barley and Fako spring wheat caused by N fertilizer is explicable by the increases in D. D depends on the shape of the curve of leaf area L against time. D will be large when maximum L is large, when maximum L is delayed, and especially when it occurs after the ears emerge, and when L persists for a long time.

Mineral nutrition can affect the change of L with time and hence D and yield. Grain yield and D of winter wheat were increased by giving N fertilizer, giving it early increased maximum L and giving it late delayed senescence Thorne and Watson (1955). Barley loses leaf faster than spring wheat but at least when given N, barley has greater maximum L so that D of spring wheat and barley may be similar although their leaf area curves differ in shape. Grain yields of 3 varieties of wheat were more closely related to the duration after anthesis of the leaf area above the flag leaf node than to the duration after ear emergence of total leaf area, Wellbank et al (1965).

Differences in leaf angle occur in some cereals, but their effect on photosynthetic efficiency has not been investigated; Donald (1963). Increasing the rate of photosynthesis by the leaves that contribute to the grain, should increase grain yield, but although cereals have been found to differ in the rate of photosynthesis of their combined flag leaf lamina and sheath and peduncle, the faster rates were not associated with greater grain yields, Thorne (1965).

Ear photosynthesis differs between species and also between varieties, but the differences cannot often be associated with equivalent differences in yield. Barley ears absorb more CO₂ than those of wheat, but the barley shoot absorbs less because it has a smaller surface area and is less efficient, Thorne (1965). Wheat varieties reported to photosynthesize most in their ears are usually awned ones, Asana and Mani (1950). Awns have chloroplasts and stomata, Grundbacher (1963) and can photosynthesize. Some cereal strains with awns yield better than awnless ones especially in a drought, but not all do. Individual ears of Proctor barley photosynthesize slightly less than those of Plumage Archer, but Proctor has more than enough extra ears to compensate for this, and per acre, ear photosynthesis contributes more to the grain in Proctor than in Plumage Archer. This would seem to account for its greater yield, Thorne (1963).
Greater translocation to the grain of carbohydrate formed in the shoot should increase grain yield, e.g. the faster growth of ears of Proctor than of Plumage Archer could be explained by the greater loss in dry weight from the former in 2 out of 3 experiments. (Thorne 1965).

**Effect of the Environment:**

**Mineral nutrition:**

In wheat, Single W.V., (1964) found that spikelet number per ear was more than doubled between 0 and 8 ppm of applied N. A further increase in N concentration to 56 ppm gave an improvement of less than 20%, suggesting a limited response. In wheat, Single W.V. found that low N had less effect on the number of florets initiated/spikelet than on spikelet number/ear. However, raising the N level at various times until emergence of the flag leaf increased grains/ear to approximately the same number because lack of spikelets in plants treated late was compensated for by greater fertility in the 3rd and 4th florets which otherwise may not have developed.

Time of application is important, for Thorne (1947) showed that grain number/ear responded to N given in spring, but its application at ear emergence had no effect on inflorescences already present. In barley, Gregory (1949) recorded a high proportion of sterile flowers in plants receiving excess N in relation to their P status. Earlier work had shown the importance of adequate food supply at the time when the 5th floret in the spikelet is about to cease developing, Hudson (1934). Not only must external concentration be taken into account, but also the period over which nutrients enter the plant, particularly as the assertion by Gregory F.C. (1937) that barley grown in pots ceases to take up N at the beginning of the reproductive phase has not been substantiated by Aspinall D. (1963) and other workers.

**Temperature and light:**

In wheat and other small cereals, high light intensities or low temperature results in high total plant dry weight at anthesis, Friend et al 1962, with large stems and ears with many spikelets. Ear development can be related to the differential effects of temperature and light intensity on the processes of growth and development. Low temperature retards the rate of development of the ear resulting in larger ears at anthesis. Low light intensity shortens duration of ear development resulting in smaller ears with fewer spikelets. Friend et al (1962) found that at 10°C spikelet number continued to increase, while at 30°C spikelet number stopped increasing at
about the stage of anther development. The increase in number of spikelets on the mature ear at low temperatures is brought about by a larger apex with a higher number of ridges at the time of double ridge formation. Working with 4 varieties of wheat, Langer (unpubl.) confirmed the effect on rate of development of the individual spikelets of photoperiod and showed that temperature was also involved. Plants in continuous light at 24°C produced about 8 spikelets, compared with over 14 in plants exposed to 16 hours of light at 15.5°C. The effect of temperature on rate of spikelet formation depends on light intensity. In general, plants in weak light have more primordia to start with, but as spikelets are initiated more slowly and over a shorter period than in bright light the ears are shorter with fewer spikelets.

Similar effects of day length, light and temperature are reported for phleum, (Langer)

In rice, Ueki K. (1959) found that numbers of tillers and spikelets/unit area decreased as the temperature of the irrigation water rose from 22°C to 30°C. The numbers of grains and grain weight/unit area were greatest in plots in which the mean water temperature was 25-26°C and the maximum temperature was under 30°C.

Working with two Indian wheat varieties, Asana and Saini (1962) found that high temperatures initially increased the rate of grain filling. However, as time went on, rapid yellowing of the ear and stem combined with losses of stem sugars led to a reduction in final grain weight. For every increase of 5°C in the mean of maximum and minimum temperature, the 1000 grain weight was reduced by 13.9 and 17.8% depending on the variety, probably through increased respiration of the grain and decreased photosynthesis. High temperatures had relatively less adverse effect on grain yield development in Pb281 than in NP270 and the difference was associated with slower rate of yellowing of the ear and higher level of stem sugars in Pb281. Asana and Williams (1964) showed in wheat under controlled conditions that grain yield declined by 16% when day temperature was raised from 25°C to 31°C. (Temperatures used were 25°C, 28°C and 31°C by day and 9°C and 12°C by night). Grain weight is clearly a fairly stable varietal character, but the interaction leaves room for a possible differential effect, although not significant in this case. Grains I.E. (1956) studied the interaction of genotype with night temperature in cereals using oats and barley at several locations and concluded that night temperature or some related factor could explain part of the erratic behaviour of oats and barley not due to disease, drought or fertility. While night temperatures cannot influence grain yield directly, the effect is probably indirectly through increased respiration rate.
CHAPTER III.

Materials Methods and Measurements:

This experiment was carried out in the 1968/69 spring-summer period. The two varieties of grain Barley used were Zephyr (high yielding) and Kenia (a lower yielding Barley from Binder x Gold). The experiment was laid out in a randomised block design comprising 2 Varieties x 4 Plant Densities x 6 replicates and plots were split for 12 sequential harvests. This design was used for the growth study, and grain yield data collected consisting of 4 plants per plot from each of 5 replicates.

1. Sowing procedure:

The seeds were sown on the 2nd, 3rd and 4th/11/68 in a square pattern, and the distances between seeds, area of ground per seed and approximate equivalent seed rates are given in Table I. These spacings give a range of densities, the narrowest being close to the usual commercial sowing rate (100-150 lbs. per acre) i.e: about 1.13 to 1.70 millions of seeds per acre:

<table>
<thead>
<tr>
<th>Variety</th>
<th>Spacing cm</th>
<th>Area per Seed cm²</th>
<th>Plants per m²</th>
<th>Seeds per acre (millions)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Zephyr</td>
<td>20 x 20</td>
<td>400</td>
<td>25</td>
<td>0.101</td>
</tr>
<tr>
<td>(2) Kenia</td>
<td>15 x 15</td>
<td>225</td>
<td>45</td>
<td>0.180</td>
</tr>
<tr>
<td>11 x 11</td>
<td>121</td>
<td>83</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7.5 x 7.5</td>
<td>56.2</td>
<td>180</td>
<td></td>
<td>0.720</td>
</tr>
</tbody>
</table>

To avoid "edge effects" all plots were surrounded by a number of guard rows, which varied according to the spacing treatment (2, 3, 3 and 4 rows respectively for the 20 x 20, 15 x 15, 11 x 11 and 7.5 x 7.5 cm spacings). Within plots, the sampling was arranged so that all plants to be sampled were separated by at least the above respective guard plants in the four increasing-ly dense spacings.

The equivalent of 3 cwt. of Super-phosphate per acre, plus 1 cwt. of muriate of Potash was broadcast on to plots at sowing time. Plots were sown by hand using metal frames divided into the appropriate spacing with cotton. One or more seeds were placed at the corner of each division and seeds thinned at emergence to one plant per position.

2. Growth Analysis measurements:

Samples of single plants per plot were harvested on each of 12
occasions commencing after 10 days from sowing and then regularly at 7 day intervals throughout 12 harvests. Measurements of plant material present (W or dry weight) and of the assimilatory surface (A or LAI) were made at each harvest. These measurements enabled relative growth rates RGR, NAR's absolute growth rates and L.A.R.'s to be calculated for each between harvest interval from the following formulae:

Relative Growth rates:

\[ R.G.R. = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \]

Net assimilation Rate NAR, E (Unit leaf rate)

\[ NAR = \frac{1}{A} \times \frac{dw}{dt} \]

For the period \( t_1 \) to \( t_2 \), average NAR = \( \frac{W_2 - W_1}{t_2 - t_1} \)

In these formulae, \( t_1 \) and \( t_2 \) represent two successive harvest dates and \( W_1, L_1, W_2, L_2 \) are respective plant dry weights and leaf weights.

Leaf Area ratio:

\[ L.A.R. = \frac{A}{W} \]

Components of LAR = \( \frac{LW}{W} \times \frac{A}{LW} \), where \( \frac{LW}{W} \) = Leaf weight ratio and \( \frac{A}{LW} \) = Specific Leaf area.

These three expressions are interrelated, and at any instant of time \( T \), the following relationship holds:

\[ \frac{1}{W} \times \frac{dw}{dt} = \frac{1}{A} \times \frac{dw}{dt} \times \frac{A}{W} \]

i.e.: \( RGR = NAR \times LAR \)

Absolute Growth Rate

\[ G.R. = \text{dry weight increment per plant per unit time} = \frac{W_2 - W_1}{t_2 - t_1} \]

where \( W_1 \) and \( W_2 \) are dry weights in gm/plant at times \( t_1 \) and \( t_2 \) respectively.

Leaf Area Duration:

\[ L.A.D. \text{ is the integral of the Leaf Area index over the growth period i.e., the area under the LAI/Time graph.} \]

One other attribute that has often been used in the Analysis of Leaf area changes should be mentioned viz: The Relative Leaf Growth Rate \( \frac{1}{L} \frac{dL}{dt} \); although this was not used in my study. It is useful for comparisons of growth in Leaf area at different times in the growth period and for
EXPERIMENTAL LAYOUT

TREATMENT

1 = 7.5 cm Z
2 = 7.5 cm K
3 = 11 cm K
4 = 11 cm Z
5 = 15 cm Z
6 = 15 cm K
7 = 20 cm K
8 = 20 cm Z

25

4
1
6
2
5
7
3
8

32

33

7
2
6
3
8
4
1
6

40

41

6
1
2

43
correlation of leaf growth rate with external factors as it provides a means of eliminating the effect of varying plant size at different stages of growth. In this experiment LAI has been used instead as an index of leaf area increase.

**Trial Layout**

2 Varieties x 4 Spacings x 6 Replicates

**TABLE II.**

<table>
<thead>
<tr>
<th>No. Harvests allowed for</th>
<th>Spacing cm</th>
<th>No. Guard Rows</th>
<th>Dist. betw. Harv. Plants cm</th>
<th>Plants/ Plot</th>
<th>Plot size ft</th>
</tr>
</thead>
<tbody>
<tr>
<td>18</td>
<td>20</td>
<td>2</td>
<td>60</td>
<td>352</td>
<td>10' x 14'</td>
</tr>
<tr>
<td>16</td>
<td>15</td>
<td>3</td>
<td>60</td>
<td>455</td>
<td>6' x 17'</td>
</tr>
<tr>
<td>16</td>
<td>11</td>
<td>3</td>
<td>44</td>
<td>555</td>
<td>5' x 13'</td>
</tr>
<tr>
<td>16</td>
<td>7.5</td>
<td>4</td>
<td>37.5</td>
<td>828</td>
<td>4' x 11'</td>
</tr>
</tbody>
</table>

**Morphological and Physiological measurements:**

At each harvest the following additional data were collected based on measurements of single plants in each plot at each harvest.

**A. Morphological:**
1. No tillers/plant.
2. Rate of tillering, and tiller mortality.
3. No fertile tillers per plant and heading dates.
4. Rate of leaf appearance.

**B. Measurements of Dry Weight W, and leaf area A on various parts of the plant:**
1. Green leaf (Lamina area) A & W.
2. Dead and Senescent leaf W.
3. Stem A & W.
4. Ear Area and Duration.

**C. Final Harvest:**

Based on 4 Plants per plot.
1. Grain number/Ear.
2. Grain Weight per Plant and per metre$^2$.
3. Number of ears per Plant and per metre$^2$.
4. 1000 Grain Weight.

All measurements for each Density and Variety are the same. Within spacing treatments, area sampled per plot was the same, but differed between density treatments.
Photosynthetic area:

The photosynthetic area was calculated for samples 1 to 11 inclusive. After harvest 10, senescence of leaves and stems made such estimates difficult to obtain. The photosynthetic tissues still present on the plant were stem and ear mainly, and varying amounts of leaf depending on the spacing at this time. Estimates of the lamina area were obtained for the first two harvests using Length x Breadth x Coefficient (0.7). For the remaining harvests estimates were obtained using an Air-flow planimeter, and stem area (Leaf sheath and peduncle when present from length and diameter). Ears and awns were treated as a rectangle and length x breadth measurements made, and a correction factor used from measurements made on ear and awns separately.
STAGES OF GROWTH IN GRAIN BARLEY

PLATE 1

After Sowing showing Barley at the 4 leaf stage

PLATE 2

Barley plants at the 6 leaf stage

PLATE 3

7.5cm Spacing Kenia left
11cm Spacing Zephyr right at 5 weeks
STAGES OF GROWTH IN GRAIN BARLEY

PLATE 4

11cm Spacing, Zephyr Right KENIA Left at 7 weeks.

PLATE 5

7.5cm Spacing Zephyr right
11cm Spacing Kenia Left at 7 weeks

PLATE 6

7.5cm Spacing Zephyr showing Nets for Bird protection at ripening stage
PLATE 7

Foreground, 15cm Spacing Zephyr left 15cm Kenia right, showing Virus infection.

PLATE 8

20cm Spacing Kenia, showing Virus infection

PLATE 9

7.5cm Spacing Kenia Left Zephyr Right ripening stage
CHAPTER IV.

Experimental Results:

Plant Number:

After germination there was no evidence of plants dying during the course of the experiment, and there was no downward trend of plant number with time. There were however, varietal differences in the percentage establishment from the seeds sown. In Zephyr, 92.6% of the seeds planted produced plants, whereas in Kenia only 90.3% establishment was found.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Spacing cm</th>
<th>Mean %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zephyr</td>
<td>7.5</td>
<td>92.2</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>91.7</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>93.3</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>93.1</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>92.5</td>
</tr>
<tr>
<td>Kenia</td>
<td>7.5</td>
<td>89.6</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>89.3</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>90.8</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>91.7</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>90.3</td>
</tr>
</tbody>
</table>

In a preliminary germination test on undusted seed in a germination chamber, no varietal differences were observed, and germination was about 7 to 9% higher than in the field.

Tiller Number:

In most seasons, the tiller number of Barley rises to a maximum, and then falls until just before ear emergence, after which there is little change in tiller number. This trend was observed in spacings 7.5 cm and 11 cm but was not observed in the wider spacings of 15 cm and 20 cm, presumably because at these wider spacings both inter and intra-tiller competition for nutrients light and water was still less than a maximum (see Figures 6 and 7). In the former two spacings, the mean number of live tillers reached a maximum at about Harvest No.4 i.e. well before ear emergence which occurred later at Harvests 6 and 7. At the 15 cm spacing, tiller number reached a peak at about Harvest 9, then levels off. The continued growth of tillers at the widest spacing was attributed to the growth of smaller tillers possibly due to irrigation effects after Harvest No.6, or possibly due to the virus attack effects on tiller growth. This second growth of tillers has been observed in many Barley crops, Kirby (1967) and is a characteristic feature when moist conditions synchronise with later stages of vegetative development. After Harvest No.4 the trend for the tiller numbers to equalise for all densities ceased, and the curves for tiller number ran more or less parallel for the narrowest three spacings; although after Harvest 6 Kenia developed greater numbers of tillers at the widest three spacings than did Zephyr.
Ear emergence:

There were differences in time of ear emergence due both to spacing and variety. The most dense spacings showed ear emergence first about one week to 10 days before the widest spacing, with the intermediate 11 cm and 15 cm spacings more or less equally interspersed. Over the whole experiment all ears had emerged by Harvest No. 9. Dry weights of ears were measured from Harvest 5 i.e. before ear emergence, until Harvest 12, Variety Zephyr emerged about 5 days before the ears of Kenia at equivalent spacings.

Lodging:

Heavy rains soon after ear emergence caused some lodging and again treatment differences were seen. The relative proneness to lodge was for spacing 7.5 cm > 11 cm > 15 cm, and for variety Kenia > Zephyr.

Photosynthetic Area:

The photosynthetic area was calculated from Harvests 1 to 11 inclusive. After Harvest 9, the senescence of leaves and stems and ears made such estimates difficult to obtain, and subject to large errors. Some photosynthetic tissues were however still present on the plant, mostly on the stem and ear. Estimates of lamina area were obtained using an air-flow planimeter, and the stem area (leaf sheath and peduncle when present) from length and diameter measurements. Ear areas were derived from simple length by breadth measurements and multiplied by a correction factor, depending on the variety. The main effect of spacing upon lamina area (see Figures 6 and 7) was that the close spacing, 7.5 cm gave the highest maximum lamina area and this was reached earlier in the season than the wider spacings. Maximum L.A.I. of variety Zephyr was 10.43 at Harvest No. 5 for spacing 7.5 cm, 5.44 at Harvest No. 5 for spacing 11 cm, 3.33 at Harvest No. 6 for spacing of 15 cm, and 2.27 at Harvest No. 6 for spacing of 20 cm. After reaching the maximum, the decline was most rapid in the dense spacings (see Figure 7), so that differences at the last sampling were much smaller (Table No. 3, Appendix I). Maximum L.A.I. for variety Kenia was 8.33 for spacing 7.5 cm at Harvest No. 6, 5.79 at Harvest No. 5 for spacing 11 cm, 4.05 at Harvest No. 6 for spacing of 15 cm, and 3.06 for spacing of 20 cm at Harvest No. 7.

The differences between varieties (Figure 8) is very small and is one of initial size rather than growth rate in the early stages. Variety Zephyr reached the maximum lamina area about one week before Kenia, although the peaks were fairly similar in size. The values obtained for total
photosynthetic area follow similar trends as those for total lamina area, but tended to be rather variable after ear emergence, due to difficulties in estimating stem area and ear area during this period.

Analysis of variance of LAI within Harvests (see Appendix IV) showed that spacings were significant from Harvests 1 to 11 except at Harvest No.10, and varieties only significant at Harvests No.3 and 11.

Leaf Area Duration: (L.A.D.)

L.A.D. is the integral of L.A.I. over the growing season (or the area under the L.A.I./Time graph). To examine the growth of the crop in the period after ear emergence, the parameters D and G were calculated for spacing and variety treatments. These parameters developed by Watson et al (1963) give an integrated measurement of the size of the photosynthetic surface and is analogous to the net assimilation rate. The values for D and G in this experiment are shown in the following tables. D represents total Photosynthetic area of leaves while DE represents the leaf area duration after flag leaf and ear emergence. These values were highest for the narrow spacings and lowest for the wider spacings, while varieties were similar.

1. Variety  
   Zephyr  
   Spacing   DT   DE  Grain  G.
   WKS:  WKS:  Yield/m2  g/m2/wk.
   
   7.5 cm  1  12.68  4.06  1094.6  86.3
   11 cm  2  10.27  3.95  1108.5  107.9
   15 cm  3  9.03  3.34  1042.9  115.5
   20 cm  4  7.22  -  821.2  113.7

2. Variety  
   Kenia  
   Spacing   DT   DE  Grain  G.
   WKS:  WKS:  Yield/m2  g/m2/wk.
   
   7.5 cm  1  12.83  4.46  967.4  75.4
   11 cm  2  11.54  3.68  1040.6  90.2
   15 cm  3  8.63  3.12  974.5  112.9
   20 cm  4  6.36  -  812.0  127.7

DE represents ear area duration, a portion of Watson et al's DF for winter and spring wheats.

Yield and Yield Components:

When the crop was ripe, the yield of Total Dry Matter and the values for the yield components were determined and are summarised for variety and spacing in Appendix I and II.
Variance ratios of the main treatments and Interaction for Dry Matter and grain yields and some of the yield components described in the Text.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Plant Dry Matter</th>
<th>Grain D.A.</th>
<th>Ear No.</th>
<th>Grains /Ear</th>
<th>Harvest Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blocks</td>
<td>0.742 NS</td>
<td>7.33 **</td>
<td>1.07 NS</td>
<td>2.50 NS</td>
<td>1.36 NS</td>
</tr>
<tr>
<td>Varieties</td>
<td>9.295 *</td>
<td>6.60 **</td>
<td>2.87 NS</td>
<td>10.33 **</td>
<td>0.00 NS</td>
</tr>
<tr>
<td>Spacing</td>
<td>29.84 **</td>
<td>18.50 **</td>
<td>39.63 **</td>
<td>66.67 **</td>
<td>1.81 NS</td>
</tr>
<tr>
<td>Var x Spac</td>
<td>4.22 *</td>
<td>0.81 NS</td>
<td>2.65 NS</td>
<td>0.33 NS</td>
<td>1.95 NS</td>
</tr>
</tbody>
</table>

* = Significant at the 5% Level
** = ** = 1% 
NS = Not Significant

Yield Components:

The effect of increasing density was to increase the number of ears, but varieties responded differently to density in this respect. Ear number of variety Kenia was higher at the three widest spacings than that of Zephyr although there were no significant spacing effects. Ear number was almost the same at the narrowest spacing. The possible cause for higher ear numbers of Kenia at the wider spacings could be attributed to the effects on this variety of yellow dwarf virus which caused leaf damage and plant stunting.

Pointings or plant scoring over 4 replicates of plots for relative degree of virus infection on 23/11/68 based on yellowness of the leaf and plant growth stunting showed a significant variety x spacing interaction.

Variety means of degree of virus infection (0-16) scale:

<table>
<thead>
<tr>
<th>Variety</th>
<th>Spacing cm</th>
<th>7.5</th>
<th>11</th>
<th>15</th>
<th>20</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Zephyr</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.50</td>
<td>4.75</td>
<td>10.25</td>
<td>10.00</td>
<td>7.37</td>
<td></td>
</tr>
<tr>
<td>2. Kenia</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>5.00</td>
<td>8.75</td>
<td>12.25</td>
<td>13.25</td>
<td>9.81</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.75</td>
<td>6.75</td>
<td>11.75</td>
<td>11.64</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Variance ratios of the main treatments and Interaction for degree of Virus infection:

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>Sums of Squares</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Sign</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blocks</td>
<td>3</td>
<td>1.75</td>
<td>0.58</td>
<td>1.73</td>
<td>NS</td>
</tr>
<tr>
<td>Varieties</td>
<td>1</td>
<td>36.12</td>
<td>36.12</td>
<td>109.45</td>
<td>***</td>
</tr>
<tr>
<td>Spacings</td>
<td>3</td>
<td>259.25</td>
<td>86.42</td>
<td>261.87</td>
<td>***</td>
</tr>
<tr>
<td>Var x Spec</td>
<td>3</td>
<td>8.63</td>
<td>2.88</td>
<td>8.72</td>
<td>**</td>
</tr>
<tr>
<td>Error</td>
<td>31</td>
<td>10.25</td>
<td>0.33</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Non-virus infected plants would increase in tiller number as inter-plant competition for nutrients light and water would be reduced if neighbouring plants were infected.

**Grain Number/Ear:**

Grain number per ear responded in the opposite manner with increased plant density from that of tiller number i.e: it declined with increased plant density. Both varieties and spacings were highly significant and the results are summarised in the following table:

<table>
<thead>
<tr>
<th>Variety and Spacing means for Grain Number/Ear:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variety</td>
</tr>
<tr>
<td>---------</td>
</tr>
<tr>
<td>1. Zephyr</td>
</tr>
<tr>
<td>2. Kenia</td>
</tr>
<tr>
<td>Mean</td>
</tr>
</tbody>
</table>

Lower grain numbers per ear at the higher density treatments was presumed to be caused by increased inter and intra plant competition by developing grains for the available assimilates.

**1000 Grain Weight:**

This yield component responded in a like manner to grain number/ear with increase in plant density.

There were varietal differences in that variety Kenia at the wider spacings showed a lower 1000 grain weight over that of Zephyr, which was possibly due to greater intra-plant competition at these spacings or from effects of virus infection which was greater in Kenia compared with Zephyr at these spacings.
Mean values and standard errors of Grain Yield Per Plant for Spacing and Variety:

<table>
<thead>
<tr>
<th>Variety:</th>
<th>Spacing cm:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>7.5 cm</td>
</tr>
<tr>
<td>1. Zephyr</td>
<td></td>
</tr>
<tr>
<td>S E</td>
<td>± 0.18</td>
</tr>
<tr>
<td>2. Kenia</td>
<td></td>
</tr>
<tr>
<td>S E</td>
<td>± 0.22</td>
</tr>
</tbody>
</table>

Over the range of densities used in this experiment all varieties yielded the most grain at some intermediate density and considering the mean of all varieties at each density, the highest yield was found at density 11 cm. The fact that the density x variety interaction was not significant indicated that both varieties responded to density in the same way; although grain yield was higher for Zephyr at all spacings than Kenia (see Figure 1) and this was significant at the 5% level only. Since the tiller number between varieties was not significant then the varietal differences in yield must have been due to grain number per ear and possibly 1000 grain weight. Although ear number per plant, spikelet number per ear and weight per grain all fall with increasing density, ear number per unit area and spikelet number per unit area were higher in the dense spacings.

Spikelet Number/m²:

<table>
<thead>
<tr>
<th>Variety:</th>
<th>Spacing:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>7.5 cm</td>
</tr>
<tr>
<td>1. Zephyr</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4518.0</td>
</tr>
<tr>
<td>2. Kenia</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4392.0</td>
</tr>
<tr>
<td>Mean</td>
<td>4455.0</td>
</tr>
</tbody>
</table>

It is only when the yield component grains per ear is considered that reduced yield of grain found with variety Kenia at the highest density is accounted for. Thus at the highest density especially for Kenia there is overproduction of grain relative to the spacing giving maximum yield. Therefore, unless the size of the grain was determined before grain filling, the yield reduction is not due to the smaller size of the 'sink' Thorne (1966).

Harvest Index:

The relation between the response of total yield and grain yield to density may be summarised as a ratio i.e: the migration coefficient, Beavers (1947) or 'harvest index', Stern and Beach (1965). Increasing plant density
had little effect on Harvest Index i.e: the results between density treatments were not significant, neither were the varieties.

Variety and Spacing Means of Harvest Index.

<table>
<thead>
<tr>
<th>Variety</th>
<th>7.5 cm</th>
<th>11 cm</th>
<th>15 cm</th>
<th>20 cm</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Zephyr</td>
<td>0.514</td>
<td>0.509</td>
<td>0.442</td>
<td>0.447</td>
<td>0.478</td>
</tr>
<tr>
<td>2. Kenia</td>
<td>0.462</td>
<td>0.489</td>
<td>0.478</td>
<td>0.474</td>
<td>0.475</td>
</tr>
<tr>
<td>Mean</td>
<td>0.488</td>
<td>0.499</td>
<td>0.460</td>
<td>0.460</td>
<td></td>
</tr>
</tbody>
</table>

Generally, however, the closer spacings especially at 11 cm had slightly higher mean 'harvest indices' than did the wider spacings of 15 cm and 20 cm. In a similar spacing experiment with barley varieties (densities used 3.5, 5, 7 and 10 cm square), Kirby (1967) recorded a maximum Harvest Index at the 10 cm spacing. In this experiment, the effect of increasing density was to significantly reduce this ratio of grain yield to total plant dry weight from 0.42 at the 10 cm spacing to 0.38 at the 3.5 cm spacing. At the 7 cm spacing the Harvest Index was 0.42 and at 5 cm spacing 0.40.

Dry weight:

There was a significant difference in total dry matter between both variety and density treatments (see Appendix IV), but while density treatments were significantly different from Harvest No.2 to Harvest No.12, varieties were significantly different at Harvests No.4 and No.12. Ear dry matter showed similar trends to total dry matter except that the curves were not nearly as steep. Spacings were significantly different from Harvest No.7 onwards, but varieties were not significantly different within harvests until Harvest No.10 i.e: until near grain development and maturation. Zephyr was significantly greater in ear dry matter at least at the two wider spacings.

Leaf dry weight followed similar curves to leaf area, reaching a peak at Harvests 5 to 6 for the closest spacings and 6 to 7 for the widest spacings. Spacings were significantly different from Harvests No.4 to Harvest No.11, but varieties only significantly different at Harvests No.4 and No.11 (see Appendix IV).

Relative Growth Rates:

Of the components of crop growth rate, leaf area has been shown to be much affected by density, and to a much lesser extent by variety (see Figure 8). Relative growth rate showed a gradual decline over Harvests, and mean Relative Growth rates were 0.76 ± 0.07 gm/ga/wk for Zephyr and 0.75 ± 0.09 gm/ga/wk for Kenia. Similarly Growth rates of ears in both varieties showed a gradual
decline over Harvests and there appeared to be little difference between varieties. The mean R.G.R. for the ears of Zephyr was $1.50 \pm 0.14$ gm/gm/wk and for Kenya, the mean ear R.G.R. was $1.47 \pm$ gm/gm/wk. Leaf area ratio was examined in both tabular and graphical forms, (see Figure ; and Appendix III), and while varieties were very similar, spacings were generally higher for the narrowest densities. The other component of Relative Growth rate viz: Net assimilation rate, N.A.R. while it was derived was very similar between varieties.
EFFECT OF DENSITY ON GRAIN YIELD

YIELD in gm/M²

ZEPHYR

KENIA

LSD SPACINGS = 77.5

LSD VARIETIES = 55.8

DENSITY PLANTS / M²
RECIPROCAL OF GRAIN YIELD PER PLANT/PLANT DENSITY

\[ \frac{1}{W} \]

\[ \frac{1}{(\text{Grain Yield})} \]

KENIA -

\[ X = 0.000034 Y \times 0.000434 \]

ZEPHYR

\[ X = 0.000032 Y \times 0.000376 \]
GRAIN NO PER EAR / PLANT DENSITY

GRAIN NUMBER PER EAR

29 28 27 26 25 24 23 22

PLANT DENSITY

20 40 60 80 100 120 140 160 180

LS D SPACINGS
5% LEVEL = 0.50

LS D VARIETIES
5% LEVEL = 0.35

ZEPHIR
KENIA
EFFECT OF DENSITY ON 1000 GRAIN WEIGHT

1000 GRAIN WEIGHT

PLANT DENSITY (Plants / m²)
FIG. 5.

EAR NUMBER/m² / PLANT DENSITY

KENIA -

ZEPHYR -

L.S.D. 5% = 43.8
FOR SPACINGS
LAMINA AREA (LAI) / TIME FOR KENIA.
LAMINA AREA (LAI) / TIME FOR ZEPHYR.

TIME (WEEKS)
LAMINA AREA/TIME FOR VARIETIES

FOR S.E. VALUES SEE APPENDIX

TIME (WEEKS)

TDE (WE~)

ZEPHYR -

KENIA
FIG. 9

EAR AREA PER PLANT/HARVEST INTERVAL

ZEPHYR

Standard errors shown

HARVEST INTERVAL
FIG. 10.

EAR AREA PER PLANT/HARVEST INTERVAL

KENIA

Standard errors shown

EAR AREA PER PLANT (CM²)

HARVEST INTERVAL
FIG. 10 (b).

GRAIN YIELD/LEAF AREA DURATION

GRAIN YIELD
gm/\text{m}^2

ZEPHYR

KENIA

LEAF AREA DURATION (DAYS)
AFTER FLAG LEAF EMERGENCE
FIG. 11.

TILLER NO PER PLANT/HARVEST INTERVAL
ZEPHER

Ear Emergence

HARVEST INTERVAL
FIG. 12.

TILLER NO PER PLANT/HARVEST INTERVAL

KENIA

Ear emergence

TILLER NUMBER/PLANT

HARVEST INTERVAL

20 cm
15 cm
11 cm
7.5 cm
FIG. 14.

PLANT DRY WEIGHT/HARVEST INTERVAL

KENIA

HARVEST INTERVAL (WEEKS)
FIG. 16.

BAN DRY WEIGHT / HARVEST INTERVAL

ZEPHYR

HARVEST INTERVAL (WEEKS)

EAR DRY WEIGHT
FIG. 19.

TOTAL RELATIVE GROWTH RATE/HARVEST INTERVAL

RELATIVE GROWTH RATE g/cm²/yr

HARVEST INTERVAL
CHAPTER V.

DISCUSSION.

Grain Yield:

In my experiment, over the range of densities used, both varieties yielded the most grain at some intermediate density, and considering the mean of both varieties at each density, the highest yield was found at density 11 cm. Both varieties responded to density in a similar way except that there was a greater drop in grain yield of Kenia at the 7.5 cm spacing than in Zephyr at this spacing. Variety Zephyr significantly outyielded Kenia at the closest three spacings i.e.: 7.5, 11 and 15 cm, but varieties were not significantly different at the widest spacing (see Figure 1). The variety x density interaction was not significant.

At high densities Kenia suffered some lodging and this may have caused a greater drop in yield than might otherwise have occurred. Grain yield in Barley may be expressed in terms of its components - plant number, ear number per plant, spikelet number per ear and the weight per grain. The response of the latter three components to a change in plant number will determine the yield of grain. Although ear number per plant spikelet number per ear, and weight per grain all fell with increasing density, ear number per unit area and spikelet number per unit area were higher in the dense spacings. The increase in ear number per plant with decreasing density partly compensates for the fewer plants at low densities but in all experiments for which data is available, the greatest number of ears per unit area is found at the highest density (see Figure 5). The yield component grains per ear is considered responsible for the reduced yield of grain found with Kenia at the highest density. Thus at the highest density there is over-production of grains relative to the spacing giving maximum yield with Kenia, but much less so with Zephyr.

1000 Grain weight increased with decreasing density in both varieties, but Zephyr increased in 1000 grain weight linearly while Kenia showed quite a marked decline at the widest spacing. Internal competition for metabolites for developing grains, or damage to maturing grains done by virus which affected Kenia greater than Zephyr may have caused this drop in grain weight with Kenia at the widest spacing. Internal competition is likely to be a cause, because Kenia had more tillers at the wider spacings than did Zephyr and some of these tillers tended to be secondary late maturing tillers contributing little to final yield but adding more competition for metabolites to developing grains. Unlike the other yield components it is difficult to draw any general conclusions as to the response of 1000 grain weight to plant density. In some
seasons, in Cambridge experiments Kirby (1968), 1000 grain weight declined with increasing density while in others little effect was found. Other experiments with Wheat and Oats also indicate that this component is least affected by plant density.

In an experiment with adapted and exotic varieties of Barley, Kirby (1969) showed that irrigation brought about a mean increase of 50% in ear number, but varieties varied in response; on the one hand Philip showed virtually no increase in ear number, while Algerie 48 almost doubled its ear number. Philip, when irrigated gave only 96% of the yield in unirrigated treatments, while Deba-Abed and Algerie 48 yielded 44 and 40% respectively more than in the unirrigated treatments.

Theoretical considerations and experience with other crops suggest that the nearer the plant arrangement is to a square pattern i.e: with all plants equidistant from each other, the higher will be the yield per unit area. The planting arrangement may be expressed as the ratio r/p of the distance between rows (r) to the distance between plants in the row (p), and where plants are arranged in a square pattern this ratio of course is unity.

Experiments with spring wheat, Fawcett (1964) showed that for any seed rate yield per unit area fell as r/p increased to eighteen. A plant density of 400 plants per m$^2$ arranged in 7.5" rows gives an r/p ratio of 15; with a 4.5" row width as with some drills; with the same plant density, the r/p ratio is 6. Comparisons between the wide and narrow row width has indicated that the latter gives up to 5% greater yields.

**Photosynthetic Area:**

The parameters D and G were calculated for spacing and variety treatments to examine the growth of the crop in the period after ear emergence. The values of D and G in this experiment are shown in the results section. While DT represents total Photosynthetic area, DE represents the leaf (ear) area after flag leaf and ear emergence. These values were highest for the narrow spacings and lowest for the wider spacings, while varieties were similar.

<table>
<thead>
<tr>
<th>Variety</th>
<th>DT: wks</th>
<th>DE: wks</th>
<th>G: gm/m$^2$/wk</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zephyr</td>
<td>9.8</td>
<td>3.78</td>
<td>105.8</td>
</tr>
<tr>
<td>Kenya</td>
<td>9.8</td>
<td>3.75</td>
<td>101.5</td>
</tr>
</tbody>
</table>

The values for G indicate that Zephyr is a more efficient producer of grain dry matter than is Kenya per unit area of ground. In my experiment an account was taken of the size of the ear which is itself an important
contributor to grain dry matter. While no significant differences between varieties were found, because of the inexact method of measurement it is possible that the varietal differences in C which were found were due to ear photosynthesis.

It is therefore difficult to explain the differences in crop growth rate and yield in terms of leaf area and leaf area duration, for in the early part of the season the high density treatments produced a closed canopy which would be expected to intercept the maximum radiation earlier than the low density treatments (the arrangement of plants was such that mutual shading was reduced to a minimum. The greater leaf areas persisted in the high density treatments after ear emergence, although if the photosynthetic area of the ear were taken into account the apparent differences would be reduced. Allowing for these uncertainties it nevertheless seems likely that density affected the efficiency of dry matter production by the leaves, both as measured by the NAR and the grain dry-matter ratio.

Leaf area (L.A.I.) followed a similar pattern over time to leaf dry weights, rising to a maximum at between early and mid December depending on the spacing. The narrowest spacings were first to reach a peak, followed by the wider spacings. Trends were similar in both varieties, and while varieties generally were not significantly different within harvests, spacings were significantly different. The narrowest spacings reached the highest peak in leaf area in both varieties followed by 11 cm, 15 cm, 20 cm spacing.

The initial increase of L.A.I. in Barley is associated with tillering. During this phase, the number of tillers producing leaves increases and tiller number reaches maximum when L.A.I. is still small and many of the younger shoots subsequently die. The large increase in L.A.I. that occurs in late November to mid December for Barley takes place during the phase of stem elongation and is the result of expansion of existing leaves. L.A.I. reaches its maximum at about the time when the shoots have attained half their final height. During the greater part of the life of annual crops sown in rows, L.A.I. has very low values. But in this experiment which was sown in a square pattern, the L.A.I. of the closest spacings reached greater than 6 for a good portion of the growing season. During about three quarters of the growth period the L.A.I. of the 3 widest spacings was less than 5. When the leaf area of a crop is less than the area of land on which it is growing, some of the incident solar radiation cannot be intercepted by the leaves and must fall on bare soil. This situation holds for a large part of the life of annual crops which are sown in rows and accounts in part for their low efficiency of solar radiation interception.
Tiller Number:

Depending on the spacing, tiller number rose to a maximum until just before ear emergence, where it falls and remains little changed for the rest of the life of the crop as with the narrowest two spacings. But with the wider spacings, tillering continued on for much longer, and was attributed to growth of secondary and tertiary tillers promoted by irrigation or reduced competition resulting from virus attack effects. Trenner (1969) showed that in wheat varieties, the presence of a large number of un-productive shoots (tillers) appeared to have only a transitory effect on the growth of productive shoots, and the latter were able to grow rapidly after the death of tillers and caught up with productive shoots which had been subjected to much less inter-tiller competition. Varieties were significantly different in tiller number only at Harvests No. 8 and 9, while spacings were significantly different within harvests from Harvest No. 3 to Harvest No. 12 (see Appendix IV) with Zephyr out-tillering Kania at 20 cm, 15 cm and 11 cm spacings.

Dry Weight:

In general the curves for total plant dry matter were S shaped especially for the closest spacings of 11 cm and 7.5 cm, but failed to reach peaks at the widest spacings probably because of continued tillering at these spacings and hence increased dry matter. Ear dry matter showed similar trends to total dry matter except that the curves were not nearly as steep. Variety Zephyr was significantly greater in ear dry weight at least at the two wider spacings at Harvests No. 10, 11 and 12. Leaf dry weight followed similar curves to lamina area, reaching a peak at Harvests 5 to 6 for the closest spacings and 6 to 7 for the widest spacings. In general varieties were not significantly different within harvests while spacings were significantly different from Harvests No. 4 to Harvest No. 11 (see Appendix IV).

Harvest Index:

Results of this parameter i.e. the relation between the response of total yield and grain yield to density can be compared with those obtained by Kirby (1967) except that spacings and varieties were not significantly different. Kirby (1967) showed that varietal differences in yield in his experiment were due both to differences in total Dry Matter and in the harvest index. Thus the higher yielding Proctor had both a high yield of dry matter and a high index, whereas Moore, a low yielding unadaptable variety had both a low index and a low yield of dry matter. Such differences emerged in a composition of some old and new varieties of Barley by Sandfaer, Jorgensen and Haar (1965).
Kirby (1969) reported differences between varieties in Harvest index when he compared some adaptable and exotic varieties:

<table>
<thead>
<tr>
<th>Variety</th>
<th>Harvest Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Algeria</td>
<td>0.48</td>
</tr>
<tr>
<td>Deba-abad</td>
<td>0.48</td>
</tr>
<tr>
<td>Philip</td>
<td>0.53</td>
</tr>
<tr>
<td>Proctor</td>
<td>0.46</td>
</tr>
<tr>
<td>Yokozuna</td>
<td>0.42</td>
</tr>
<tr>
<td>S.E.</td>
<td>± 0.0088</td>
</tr>
</tbody>
</table>

While Kirby (1967) reported a maximum harvest index at a spacing of 10 cm square, in my experiment maximum Harvest Index was found at a spacing of 11 cm square.

Crop growth rate and Components:

Examination of the components of Relative growth rate, and growth rate itself showed that varieties were very similar both for total relative growth rate, and growth rates of ears. Total plant and relative growth rates of ears showed a similar gradual decline over harvests, and there appeared to be little difference between varieties. Figures for mean values of total R.G.R. of ears are shown in the results section and in Appendix III. The components Leaf area ratio and Net assimilation rate were derived and there was little difference between varieties. Kirby (1967) found in his experiment with 4 Barley varieties Proctor, Plume-dehner and Bomen that the mean N.A.R. was 1.87 mg/cm²/wk and there were significant differences between spacing treatments only.

Calculations based upon published data on respiration rates per unit dry matter of Barley but making large assumptions as to the response of respiration rate to density and age of the plant etc., show that although the calculated gross photosynthesis was greatest in the high density treatments, this was offset by a calculated high respiration rate per unit area of crop, thus resulting in the lowest dry matter increment over the period. Confirmation of this situation by actual measurements of respiration rate both of the crop and of the various parts of the plant under the conditions is obviously needed.

Conclusions:

Cereal plant density affects yield and growth characters of fundamental importance. The experiment is described in which growth, yield and yield components of Barley grown over a wide range of densities were examined. Two varieties, Zephyr and Kenia were grown at densities equivalent to 25, 45, 83 and 180 plants per m². Density was found not to affect seedling establishment or plant survival, but there was a small variety effect on seedling establishment in favour of Zephyr.
Varietal differences were seen in maximum tiller and the percentage of tillers surviving to form ears, as well as spacing differences. The effect of increasing density was to increase the maximum tiller number per unit area, but this was followed by different rates of tiller death until Harvests 6 to 7 after which there was no further compensation for tiller number. Ear emergence was affected by both variety and density. Tiller death was greatest in the narrow spacings, while the amount of secondary tillering was greatest in the wider spacings. Yellow dwarf virus attack affected the amount of tillering and leaf production and stunted plant growth. The effect of virus attack was significantly greater for Kenia than for Zephyr at equivalent spacings.

Total stem and leaf dry matter per plant increased with decreasing density probably because of increased tillering and leaf production at the wider spacings. Ear dry matter showed a similar trend to leaf dry matter except that the curves were not nearly as steep. The general shape of the curves for total dry matter versus time was S shaped especially for the narrow spacings. Varietal differences in ear and total dry weight were not observed until the later stages of growth.

The main effect of spacing upon lamina area was that the closest spacing, 7.5 cm, gave the highest maximum lamina area, and this was reached earlier in the season than the wider spacings. Although values for DT and DE were similar between varieties, spacing values were highest for the narrow spacings, and lowest for the widest spacings. The values for G indicated that Zephyr was a more efficient producer of grain dry matter than was Kenia per unit area of ground.

Relative growth rates, both total and for ears, M.A.R.'s and leaf area ratios were similar between varieties. Total growth rates and relative growth rates of ears showed a decline over harvests as did leaf area ratios.

Both varieties yielded the most grain at some intermediate density viz: 11 cm, and both varieties responded to density in terms of grain yield in a similar manner except that there was a greater drop in yield at the closest spacing, with Kenia than with Zephyr. Zephyr out yielded Kenia over three spacings, viz: 7.5, 11 and 15 cm, but not at the widest spacing. Of the yield components, grains per ear seemed to contribute most to the variation in grain yield. Ear number per unit area rose with density, but grains per ear and 1000 grain weight both declined. Virus infection was considered a cause for the drop in 1000 grain weight at the widest spacing, but internal competition for nutrients may also have been a factor because of increased tillering of variety Kenia at this spacing.
These results are discussed in the light of current theories of yield in cereals, and differences in yield are also examined in terms of leaf area duration and the ratio of leaf area duration to grain yield G.
APENDIX I

ANALYSIS OF VARIANCE GRAIN YIELD AND YIELD COMPONENTS

1. GRAIN YIELD/M²

<table>
<thead>
<tr>
<th>Variety</th>
<th>7.5</th>
<th>11</th>
<th>15</th>
<th>20</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zephyr</td>
<td>1094.6</td>
<td>1108.5</td>
<td>1042.9</td>
<td>821.2</td>
<td>1016.8</td>
</tr>
<tr>
<td>Kenia</td>
<td>967.4</td>
<td>1040.6</td>
<td>974.5</td>
<td>812.0</td>
<td>948.6</td>
</tr>
<tr>
<td>Mean</td>
<td>1030.9</td>
<td>1074.6</td>
<td>1008.7</td>
<td>816.6</td>
<td></td>
</tr>
</tbody>
</table>

ANALYSIS OF VARIANCE

<table>
<thead>
<tr>
<th>Source of Variance</th>
<th>df.</th>
<th>Sum of Squares</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Sign</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between Blocks</td>
<td>4</td>
<td>206,764.76</td>
<td>51,657.5</td>
<td>7.333</td>
<td>***</td>
</tr>
<tr>
<td>Varieties</td>
<td>1</td>
<td>46,471.48</td>
<td>46,471.0</td>
<td>6.608</td>
<td>*</td>
</tr>
<tr>
<td>Spacings</td>
<td>3</td>
<td>390,342.03</td>
<td>130,113.3</td>
<td>18.504</td>
<td>***</td>
</tr>
<tr>
<td>Var x S interaction</td>
<td>3</td>
<td>17,423.03</td>
<td>5,808.3</td>
<td>0.811</td>
<td>NS</td>
</tr>
<tr>
<td>Error</td>
<td>28</td>
<td>200,551.17</td>
<td>7,162.54</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>39</td>
<td>861,053.04</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

L.S.D. (Least Significant Difference)

a) L.S.D. Spacings 5% level and Error df

\[ L.S.D. = t \text{(error df)} \times \sqrt{\frac{2 \times E}{n}} \]

\[ = 77.5 \]

b) L.S.D. Varieties

\[ L.S.D. = t \text{(error df)} \times \sqrt{\frac{2 \times E}{n}} \]

\[ = 55.8 \]

2. EAR NUMBER/M²

<table>
<thead>
<tr>
<th>Variety</th>
<th>7.5</th>
<th>11</th>
<th>15</th>
<th>20</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zephyr</td>
<td>990.0</td>
<td>786.3</td>
<td>781.2</td>
<td>702.5</td>
<td>815.0</td>
</tr>
<tr>
<td>Kenia</td>
<td>943.2</td>
<td>827.9</td>
<td>850.5</td>
<td>739.0</td>
<td>840.1</td>
</tr>
<tr>
<td>Mean</td>
<td>966.6</td>
<td>807.1</td>
<td>815.8</td>
<td>720.7</td>
<td></td>
</tr>
</tbody>
</table>
### Analysis of Variance

<table>
<thead>
<tr>
<th>Source of Variance</th>
<th>d.f.</th>
<th>Sums of Squares</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Sign</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between Blocks</td>
<td>4</td>
<td>11,254.0</td>
<td>2813.5</td>
<td>1.38</td>
<td>NS</td>
</tr>
<tr>
<td>&quot; Varieties</td>
<td>1</td>
<td>7,573.0</td>
<td>7573.0</td>
<td>3.73</td>
<td>NS</td>
</tr>
<tr>
<td>&quot; Spacings</td>
<td>3</td>
<td>313,856.0</td>
<td>104,618.6</td>
<td>51.58</td>
<td>**</td>
</tr>
<tr>
<td>Var x S interaction</td>
<td>3</td>
<td>20,978.0</td>
<td>6992.7</td>
<td>3.45</td>
<td>NS or*</td>
</tr>
<tr>
<td>Error</td>
<td>12</td>
<td>24,342.0</td>
<td>2028.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>39</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- a) L.S.D. Spacings 5% level = 43.88
- b) L.S.D. Varieties 5% level = 31.02
### APPENDIX I.

**MEANS AND STANDARD ERRORS FOR LEAF AREA (LAI)**

1. **Table I**

<table>
<thead>
<tr>
<th>Variety</th>
<th>Spacing</th>
<th>Harvest Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zephyr</td>
<td>MEAN</td>
<td>S.E.</td>
</tr>
<tr>
<td>0.27</td>
<td>0.01</td>
<td>0.11 0.00</td>
</tr>
<tr>
<td>0.95</td>
<td>0.10</td>
<td>0.44 0.03</td>
</tr>
<tr>
<td>4.99</td>
<td>0.41</td>
<td>2.36 0.24</td>
</tr>
<tr>
<td>6.71</td>
<td>0.54</td>
<td>4.34 0.25</td>
</tr>
<tr>
<td>10.43</td>
<td>1.08</td>
<td>5.44 0.30</td>
</tr>
<tr>
<td>7.79</td>
<td>0.76</td>
<td>5.11 0.37</td>
</tr>
<tr>
<td>6.74</td>
<td>0.96</td>
<td>4.70 0.23</td>
</tr>
<tr>
<td>4.69</td>
<td>0.39</td>
<td>3.51 0.18</td>
</tr>
<tr>
<td>2.65</td>
<td>0.24</td>
<td>2.62 0.39</td>
</tr>
<tr>
<td>1.92</td>
<td>0.30</td>
<td>1.52 0.31</td>
</tr>
<tr>
<td>0.11</td>
<td>0.07</td>
<td>0.55 0.15</td>
</tr>
</tbody>
</table>

2. **Table 2**

<table>
<thead>
<tr>
<th>Variety</th>
<th>Spacing</th>
<th>Harvest Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kenia</td>
<td>MEAN</td>
<td>S.E.</td>
</tr>
<tr>
<td>0.24</td>
<td>0.02</td>
<td>0.10 0.00</td>
</tr>
<tr>
<td>1.03</td>
<td>0.10</td>
<td>0.33 0.02</td>
</tr>
<tr>
<td>3.49</td>
<td>0.29</td>
<td>1.49 0.11</td>
</tr>
<tr>
<td>6.49</td>
<td>0.73</td>
<td>3.64 0.29</td>
</tr>
<tr>
<td>7.96</td>
<td>0.79</td>
<td>5.79 0.50</td>
</tr>
<tr>
<td>8.33</td>
<td>0.83</td>
<td>5.43 0.42</td>
</tr>
<tr>
<td>7.10</td>
<td>0.71</td>
<td>4.47 0.37</td>
</tr>
<tr>
<td>4.19</td>
<td>0.42</td>
<td>3.88 0.42</td>
</tr>
<tr>
<td>2.98</td>
<td>0.35</td>
<td>3.57 0.26</td>
</tr>
<tr>
<td>2.06</td>
<td>0.59</td>
<td>1.63 0.21</td>
</tr>
<tr>
<td>0.11</td>
<td>0.05</td>
<td>0.46 0.19</td>
</tr>
</tbody>
</table>
## APPENDIX I

### 3. GRAIN NUMBER/FAR

<table>
<thead>
<tr>
<th>Variety</th>
<th>7.5 cm.</th>
<th>11 cm.</th>
<th>15 cm.</th>
<th>20 cm.</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zephyr</td>
<td>25.1</td>
<td>27.1</td>
<td>27.8</td>
<td>28.4</td>
<td>27.1</td>
</tr>
<tr>
<td>Kenia</td>
<td>24.4</td>
<td>26.9</td>
<td>27.2</td>
<td>27.6</td>
<td>26.5</td>
</tr>
<tr>
<td>Mean</td>
<td>24.7</td>
<td>27.0</td>
<td>27.5</td>
<td>28.0</td>
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</tr>
</tbody>
</table>

Standard errors needed

### ANALYSIS OF Variance

<table>
<thead>
<tr>
<th>Source of Variance</th>
<th>d.f.</th>
<th>Sums of Squares</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Sign</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between Blocks</td>
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<td>3.00</td>
<td>0.75</td>
<td>2.50</td>
<td>N.S.</td>
</tr>
<tr>
<td>Varieties</td>
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<td>3.10</td>
<td>3.10</td>
<td>10.33</td>
<td>**</td>
</tr>
<tr>
<td>Spacings</td>
<td>3</td>
<td>61.85</td>
<td>20.60</td>
<td>68.67</td>
<td>**</td>
</tr>
<tr>
<td>V x S interaction</td>
<td>3</td>
<td>0.50</td>
<td>0.10</td>
<td>0.33</td>
<td>N.S.</td>
</tr>
<tr>
<td>Error</td>
<td>28</td>
<td>8.10</td>
<td>0.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>39</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

L.S.D. Spacings 5% error d.f. = 0.50
L.S.D. Varieties 5% " " = 0.35

### 1000 GRAIN Weight

<table>
<thead>
<tr>
<th>Variety</th>
<th>7.5</th>
<th>11</th>
<th>15</th>
<th>20</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zephyr</td>
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<td>60.27</td>
<td>62.61</td>
<td>64.57</td>
<td>60.20</td>
</tr>
<tr>
<td>Kenia</td>
<td>53.97</td>
<td>58.17</td>
<td>60.98</td>
<td>59.51</td>
<td>58.16</td>
</tr>
<tr>
<td>Mean</td>
<td>53.66</td>
<td>59.22</td>
<td>61.79</td>
<td>62.04</td>
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</table>
APPENDIX I
MEANS AND STANDARD ERRORS FOR LEAF AREA/PLANT

3. Table 3

<table>
<thead>
<tr>
<th>Variety</th>
<th>Spacing</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
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<td>Zephyr</td>
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<td>15.7</td>
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4. Table 4

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<td>116.6</td>
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<td>6.6</td>
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</table>

<table>
<thead>
<tr>
<th>Harvest Number</th>
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<tbody>
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<tr>
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</tr>
<tr>
<td>10</td>
</tr>
<tr>
<td>11</td>
</tr>
<tr>
<td>12</td>
</tr>
</tbody>
</table>
### APPENDIX I

**LAMINA AREA AND TIME FOR VARIETIES**

#### Table 5

<table>
<thead>
<tr>
<th>Variety</th>
<th>Harvest Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zephyr</td>
<td></td>
</tr>
<tr>
<td>MEAN</td>
<td>S.E.</td>
</tr>
<tr>
<td>0.11</td>
<td>0.05</td>
</tr>
<tr>
<td>0.44</td>
<td>0.17</td>
</tr>
<tr>
<td>2.30</td>
<td>0.96</td>
</tr>
<tr>
<td>3.56</td>
<td>1.24</td>
</tr>
<tr>
<td>5.27</td>
<td>1.85</td>
</tr>
<tr>
<td>4.62</td>
<td>1.20</td>
</tr>
<tr>
<td>4.34</td>
<td>0.96</td>
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**Kenia**

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#### Table 6

**EAR AREA**

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APPENDIX II

DRIY WEIGHT DATA

**Table 1. EAR DRY WEIGHT**

1. Variety: Zephyr

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## APPENDIX II

### LEAF DRY WEIGHT

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Stem Dry Weight
## APPENDIX II

### STEM DRY WEIGHT

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### APPENDIX II

#### TOTAL DRY WEIGHT

Table 8

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## APPENDIX II

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**Means and Standard Errors**

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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 III

RELATIVE GROWTH RATES/WEEK

$$\text{R.G.R.} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \text{ gm/gm/wk.}$$

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1. **Zephyr**
   \[
   \text{MEAN RGR} = 0.76 \pm 0.07 \text{ gm/gm/wk}
   \]

2. **Kenia**
   \[
   \text{MEAN RGR} = 0.75 \pm 0.09 \text{ gm/gm/wk}
   \]
# APPENDIX III

**RELATIVE GROWTH RATES**

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1. **Zephyr**
   
   \[
   \text{MEAN RGR} = 1.50 \pm 0.14
   \]

2. **Kenia**
   
   \[
   \text{MEAN RGR} = 1.47 \pm 0.14
   \]
## Appendix III

### Leaf Area Ratio

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   - Zephyr

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Harvest Number indicates the sequence of harvests, with higher numbers representing later harvests.
### APPENDIX III.

**NET ASSIMILATION RATES**

\( \text{gm/cm}^2/\text{day} \)

#### Variety

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**Analysis of Variance**

**Dry Weight Data**

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<td>2.83</td>
<td>4.22 *</td>
</tr>
</tbody>
</table>

**Note:** The table provides F ratios and significance values for the sources of variance, including blocks, varieties, spacings, and variances. The significance levels are indicated by asterisks: * for P < 0.05, ** for P < 0.01, and NS for non-significant differences.
APPENDIX IV  
ANALYSIS OF VARIANCE  
TILLER NUMBER/PLANT  

1. Harvest No.12 Variance Ratios

<table>
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<th>Ratio</th>
<th>Sign</th>
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<td>4.23</td>
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<tr>
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<td>1.35</td>
<td>0.68</td>
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L.S.D. Spacings 5% error df = 1.16

2. Harvest No.11 Variance Ratios

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<th>Ratio</th>
<th>Sign</th>
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<td>1.01</td>
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<td>&quot; Spacings</td>
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L.S.D. Spacings 5% error df = 1.82

3. Harvest No.10 Variance Ratios

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<th>Ratio</th>
<th>Sign</th>
</tr>
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<td>&quot; Varieties</td>
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<td>7.23</td>
<td>7.23</td>
<td>0.98</td>
<td>NS</td>
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<tr>
<td>&quot; Spacings</td>
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<td>2046.88</td>
<td>682.30</td>
<td>92.57</td>
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<td>0.39</td>
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L.S.D. Spacings 5% error df = 2.27
### APPENDIX IV

#### 4. Harvest No. 9 Variance Ratios

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<th>Ratio</th>
<th>Sign</th>
</tr>
</thead>
<tbody>
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<td>Between Blocks</td>
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<td>26.69</td>
<td>5.33</td>
<td>1.87</td>
<td>NS</td>
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<tr>
<td>&quot; Varieties</td>
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<td>46.03</td>
<td>46.03</td>
<td>16.21</td>
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</tr>
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<td>645.69</td>
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</tr>
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<td>7.35</td>
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<td>NS</td>
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<td>Error</td>
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<td>Total</td>
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L.S.D. Spacings 5% error df = 1.52
L.S.D. Varieties 5% " " = 0.97

#### 5. Harvest No. 8 Variance Ratios

<table>
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<th>Square</th>
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<th>Sign</th>
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</thead>
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<td>Between Blocks</td>
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<td>1.98</td>
<td>0.59</td>
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<td>16.33</td>
<td>4.86</td>
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L.S.D. Spacings 5% Error df = 1.52
L.S.D. Varieties 5% " " = 1.07

#### 6. Harvest No. 7 Variance Ratios

<table>
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<th>Sign</th>
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</thead>
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<td>2.09</td>
<td>0.74</td>
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<td>1.38</td>
<td>NS</td>
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<td>99.33</td>
<td>2.84</td>
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L.S.D. Spacing 5% Error df = 1.38
## APPENDIX IV

7. **Harvest No. 6 Variance Ratios**

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<th>Square</th>
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<th>Sign</th>
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</thead>
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<td>3.00</td>
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<td>0.73</td>
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<td>5.15</td>
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L.S.D. Spacing 5% error df = 1.86

8. **Harvest No. 5 Variance Ratios**

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<td>2.52</td>
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<td>138.15</td>
<td>3.94</td>
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L.S.D. Spacing 5% Error df = 1.64

9. **Harvest No. 4 Variance Ratios**

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<th>Ratio</th>
<th>Sign</th>
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<td>15.87</td>
<td>2.76</td>
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<td>3.00</td>
<td>0.52</td>
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<td>17.24</td>
<td>3.00</td>
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L.S.D. Spacing 5% Error df = 1.93
## APPENDIX IV

### 10. Harvest No. 3 Variance Ratios

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<td>8.33</td>
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L.S.D. Spacing 5% Error df = 1.92

### 11. Harvest No. 2 Variance Ratios

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<th>Mean (Square)</th>
<th>F Ratio</th>
<th>Sign</th>
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<td>3.00</td>
<td>0.99</td>
<td>NS</td>
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<td>&quot; Spacings</td>
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<td>0.83</td>
<td>0.27</td>
<td>NS</td>
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### 12. Harvest No. 1 Variance Ratios

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<th>Mean (Square)</th>
<th>F Ratio</th>
<th>Sign</th>
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</thead>
<tbody>
<tr>
<td>Between Blocks</td>
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<td>0.41</td>
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<td>Error</td>
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<td>13.99</td>
<td>0.40</td>
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<td>Total</td>
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</table>
## APPENDIX IV

### ANALYSIS OF VARIANCE LAI

#### WITHIN HARVESTS

#### Harvest No. 1

<table>
<thead>
<tr>
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<th>F</th>
<th>Sign</th>
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</tr>
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<td>0.00110</td>
<td>1.134</td>
<td>NS</td>
</tr>
<tr>
<td>Spacings</td>
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<td>0.12698</td>
<td>130.907</td>
<td>***</td>
</tr>
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<td>Var x Spec</td>
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<td>Error</td>
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L.S.D. Spacings 5% level = 0.026

#### Harvest No. 2

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<th>Sign</th>
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<td>0.01333</td>
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<td>1.83035</td>
<td>125.109</td>
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L.S.D. Spacings 5% level = 0.100

#### Harvest No. 3

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<th>F</th>
<th>Sign</th>
</tr>
</thead>
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<td>35.075</td>
<td>***</td>
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<td>Error</td>
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L.S.D. Spacings 5% level = 0.362

#### Harvest No. 4

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<td>Spacings</td>
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L.S.D. Spacings 5% level = 0.716
## APPENDIX IV

### Harvest No. 5

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L.S.D. Spacings 5% level = 1.112

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L.S.D. Spacings 5% level = 1.030

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L.S.D. Spacings 5% level = 0.967

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L.S.D. Spacings 5% level = 0.566
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L.S.D. Spacings 5% level = 0.520

## Harvest No. 10

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L.S.D. Spacings 5% level = 0.494

## Harvest No. 11

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L.S.D. Spacings 5% level = 0.296
## APPENDIX IV

### ANALYSIS OF VARIANCE

#### EAR AREA

1. **Harvest No. 7 Variance Ratios**

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L.S.D. for spacings = \( t \frac{2 \times \text{EMS}}{n} \)

\[ = 32.9 \]

2. **Harvest No. 8 Variance Ratios**

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L.S.D. for spacing = \( t \frac{2 \times \text{EMS}}{n} \)

\[ = 43.73 \]
APPENDIX IV

3. HARVEST NO.9 VARIANCE RATIOS

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L.S.D. for spacing = t 25 df x \( \frac{2 \times 8.4}{n} \)

= 48.9

4. HARVEST NO.10 VARIANCE RATIOS

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L.S.D. for spacing = t 25 df x \( \frac{2 \times 9.6}{n} \)

= 45.9

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L.S.D. for spacing = t 25 df x \( \frac{2 \times 16.6}{n} \)

= 37.12
BIBLIOGRAPHY:

     Univ. Reading.
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     " " " " Vol.16.
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