A COMPARATIVE STUDY OF SEMI-DWARF AND CONVENTIONAL CULTIVARS OF WHEAT AND BARLEY

by

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SUMMARY

Semi-dwarf varieties of wheat and barley were compared with conventional varieties under a range of husbandry treatments. In the barley study, two semi-dwarf varieties were compared with three conventional varieties in each of two seasons. Five rates of nitrogen and five seed rates were applied as treatments. The performance of the varieties was compared in yield and the principal yield components. Large differences were found between the years of the experiment as the weather in the second season promoted tiller production which could not be utilised due to the lack of sunshine in the post-anthesis period. The performance of two of the varieties, Golden Promise and one of the dwarfs (6262Co/N/44) was affected less by this difference between seasons due to their economy of tiller production. Variation in response to the husbandry treatments among the semi-dwarf varieties was similar to the variation in the conventional varieties. The semi-dwarf varieties did not give a greater response to increase in nitrogen or seed rates but their delayed lodging increased the range of these treatments over which maximum yield could be achieved before lodging caused yield reduction.

A smaller field trial was carried out in 1972 on a sandy soil in an endeavour to examine the effect of drought on three varieties, one of which was a semi-dwarf. The principal aim of this study was defeated by a wet spring so no further conclusions could be drawn.

Study of the growth of roots of two barley varieties was undertaken in one season. Extensive root growth occurred in the first weeks of growth after which the size of the root system was maintained until after anthesis before any reduction in the amount of root was recorded. Golden Promise, the shorter strawed of the two varieties examined showed slightly poorer root growth in the early season and an earlier reduction in the amount of root in the soil from which it was concluded, this variety could be at risk in dry seasons if the same rooting pattern was developed.

The wheat study was a combined agronomic and physiological study, over two seasons, of three semi-dwarf and two conventional varieties under five rates of nitrogen. Yield and its components were measured. Total leaf lamina area and dry weight were measured at several dates in the first season and total photosynthetic area above the flag leaf node after anthesis in the second. A fuller understanding of the mechanisms of yield production was sought by relating these measures. Root growth of four of the cultivars was studied in the early part of one season but no significant differences were found between the varieties. A detailed study of the rates and duration of grain filling in the different parts of the ear was also undertaken and the findings of this study were related to the measures of yield and crop growth.

Two of the dwarf varieties, TL363/30 and TL365a/34, gave yields similar to, or greater than Maris Nimrod, the standard variety. No differences were found in the yield response of the varieties to nitrogen but a reduction in the efficiency of the leaf area in grain production at high nitrogen rates was found in all varieties. From the leaf and grain yield studies it was concluded that this reduction in efficiency was due to mutual shading of the leaves at high leaf areas and not to a shortage of total sink capacity. It was found that grains in different parts of the ear grew at different rates with the slowest growing grains being in the distal florets. The pattern of grain filling was the same in all varieties and the rate of individual grain filling was unaffected by nitrogen rate. It was suggested that the rate of grain filling of a variety could impose a limit on the amount of carbohydrate utilised in grain filling.

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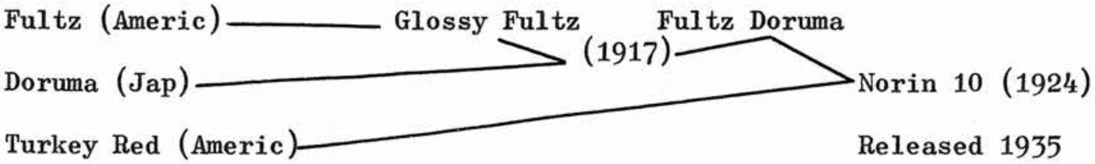
CHAPTER 1

HISTORICAL REVIEW OF LITERATURE

In wheat and barley breeding there has been a steady progression towards shorter strawed varieties which have a greater resistance to lodging (Berbigier, 1968; Vogel et al, 1956). In barley breeding the progression has been accelerated in recent years by the creation of mutants with short straw resulting from a shortening of the internodes (Berbigier, 1968).

The wheat breeding of the world has been changed by the discovery and use of a number of dwarf and semi-dwarf varieties. These include Norin 10, Seu Seun 27 and Suwon 92. Of these, the one to have the greatest impact on the wheat breeding of the world has been Norin 10. This cultivar was originally bred in Japan in 1924 (Reitz and Salmon, 1968). The breeding of this variety was:



(Reitz and Salmon, 1968).

In 1946 this cultivar was taken to the United States of America where it was used in crosses with conventional varieties to produce short-strawed cultivars. The dwarfing character of Norin 10 and Suwon 92 is believed to be carried on one major recessive gene and its effect is modified by other genes to a greater or lesser extent (Briggle and Vogel, 1968). The first variety to be produced in the U.S.A. using gene plasma from Norin 10 was Gaines, which was a very successful variety in the Pacific North-West area of the United States. The production of this variety attracted the attention of breeders throughout the world, who began to show interest in the semi-dwarf character. Italian and Balkan dwarf varieties which have not had such world wide acclaim can also trace their origin to the same source (Reitz and Salmon, 1968).

About the same time as breeding was started in the United States, breeders in Mexico also began to investigate the new semi-dwarfism with remarkable success. In the early 1960's, a number of very useful semi-dwarf cultivars were produced by CIMMYT in Mexico. These cultivars had the great advantage of being neutral in reaction to day length. They included Sonora 64, Lerma Rojo, and Mexico 120. The usefulness of these cultivars was fully realised in 1964 when they were grown in India and gave yields which were quite outstanding in that part of the world (IARI, 1968). Within a few years the 'Green Revolution' was fully mounted and very large quantities of the Mexican cultivars were being grown in India, Pakistan and a number of other Near-Eastern countries. Record harvests were recorded in every country where the introduction of the wheats was made (CIMMYT, 1970). By 1971 however, the picture was somewhat less attractive. Yields in India had been falling for two years, in Pakistan yields were also on the decline and in the Near East a similar picture was developing (CIMMYT, 1972, Hafiz, 1972). The large yield reductions are due to serious attacks by diseases (Noble, Personal Communication). Inadequate screening of the imported seed against seed-borne diseases has been largely responsible. A lack of knowledge of the indigenous races of leaf-borne diseases has also been a contributory factor as resistance against these races was not sought, nor was the reaction of the imported cultivars to these races known. Large areas were sown with one or two of these imported varieties without taking these disease factors into consideration and drastic yield losses have resulted (Noble, Personal Communication). More attention is being paid to disease races now, but the confidence of the farmers in the underdeveloped countries has been seriously shaken by this carelessness on the part of the scientists involved.

Within the United States, breeding programmes have been carried out in every wheat growing region to try to incorporate the dwarfing character in the indigenous type. These programmes have not met with conspicuous success in every case. For example in the central regions, durum wheats, with the dwarf character, have been produced but these are very susceptible to disease, (Briggle and Vogel, 1968). The disease problem is thus widespread, but with increased awareness of the causes, and diligent use of sources of resistance available, this problem can be kept at bay. In addition to the dwarf varieties of wheat derived from the Norin 10 source, some dwarf varieties of wheat have been produced by mutation, by irradiation in the same way as some barley dwarfs have been produced (Briggle and Vogel, 1968), (Konsak et al, 1969).

Different classifications of varieties by stature, have been attempted, to avoid confusion. Borojevic (1968) suggested a height classification whereby the categories of wheat became;

Stunted (grass clump)	<30 cm late maturing, part or complete sterility
Dwarf	30-50 cm
Semi-dwarf	50-70 cm
Short strawed	70-90 cm

Medium high	90-110 cm
Tall	> 110 cm

The usefulness of such a classification has been questioned (Briggle and Vogel, 1968) as height expression is very greatly dependent on the environmental conditions. The extent of this dependence is shown by Johnson (1953). Other workers in the field have classified dwarf varieties by the number of dwarfing genes having an additive effect in reducing the height of the plants.

Characteristics of Semi-Dwarf and Dwarf Cultivars

Several studies have been undertaken in which the dwarf varieties were examined to establish the mechanism by which the dwarfing was manifest and to evaluate the varieties for any other associated changes in plant characters which might make the dwarf varieties unsuitable for general use (Allan, et al, 1965; Borojevic, 1968; Burleigh, et al, 1965; CIMMYT, 1970, 1972; Gupta, et al, 1968; IARI, 1968; Johnson, et al, 1966; McNeal, et al, 1960; Paquet, 1968; Thorne, et al, 1969; Vogel, et al, 1956, 1963).

In general, these studies found little change in the various test weights and measurements made other than variation which would normally be found between conventional varieties. Several workers however, found that coleoptile length was shortened, as well as the expected shortening of internodes and peduncle. The shortening of the coleoptile can lead to poor emergence and stand establishment among the dwarfs (Allan, et al, 1965; Burleigh, et al, 1965; Feather, et al, 1968; Gupta, et al, 1968; Thorne, et al, 1969). Other workers reported increased tillering in the semi-dwarf selections which could be a result of the poorer establishment (Paquet, 1968; Roy, et al, 1969). The short coleoptile of the Norin 10 dwarfs, while not a very serious disadvantage, has been overcome in some breeding programmes (Briggle and Vogel, 1968; Konsak, et al, 1969), by the use of other dwarfing sources e.g. the irradiation of the variety Burt. In addition to these studies of the characters of the dwarf wheats, the suitability of the dwarfs for many regions of the world has been evaluated (Beech and Norman, 1968; CIMMYT, 1970, 1972; IARI, 1968; Paquet, 1969; Porter, et al, 1964; Vogel, et al, 1963). Where disease susceptibility did not affect the results of these experiments, the dwarf cultivars were, in general, adequate performers in the situations in which they were tested. In other parts of the world crosses with indigenous cultivars have been made before the introduction of the dwarf varieties. This imparts greater disease resistance and a better adaptation to the climate of the region, before widespread introductions of the new cultivars (Lupton, et al, 1970).

More detailed reviews of the behaviour of semi-dwarf varieties in terms of physiological development and root growth will be given in later chapters (Chapters 3, 4 and 5). Likewise the effect of husbandry on the development of semi-dwarf wheat will be dealt with in Chapter 3 and the effect on barley in Chapter 2.

CHAPTER 2

BARLEY EXPERIMENTS 1970, 71 and 72

2A Introduction

In view of the recent interest in the production of semi-dwarf varieties of barley (Berbigier, A.1968), it was considered desirable to investigate the behaviour of such varieties under different husbandry treatments and to compare this behaviour with that of more conventional varieties. The very different stature of these varieties, led to the hypothesis that the two different types may respond differently to such husbandry treatments as, seed rate and nitrogen level to such an extent as to materially bias the results of variety trials which included these varieties. In addition, if this was the case, it would be desirable to establish the extent of any differences in response to enable changes in the recommended rates of fertiliser and seet rates to be quantified and made available to those using the new varieties.

The dwarf varieties already in use, or nearing release from the breeders, have been exhibiting higher performance (Berbigier, A.1968) and in the light of this finding, an investigation into the mechanism by which this increase in yield was brought about, in terms of yield components was thought desirable, as a knowledge of the sources of increased performance could lead to more efficient breeding methods orientated towards improvement of those parameters which are most readily influenced and which lead to the most effective increases in yield.

2B The influence of variety, nitrogen fertilizer and seed rate on the growth of barley.

i The morphological growth of Barley.

The growth of barley can be divided into four stages;

1. The germination stage
2. The vegetative stage
3. The reproductive stage
4. The seed stage.

In a strict botanical sense the germination stage lasts from imbibition of moisture to the elongation of the radicle but in agricultural terms the emergence of the coleoptile above the soil can be considered as the end of this stage and the start of the vegetative stage. (Wellington,1966) During this stage the seminal root system is developed and the plumule elongates towards the soil surface. As the plumule elongates the more permanent adventitious root system starts to develop from the coleoptilar node. The plumule elongation is caused by a lengthening of the internodes which make up the main axis at this stage. The number of internodes which elongate and the extent of this elongation is dependent on the depth of planting. The external environment also influences the rate at which development occurs. Growth at this stage is supported by the starch stored in the endosperm and by the mineral contribution provided by the root system as it develops. The coleoptile is pushed up towards the soil surface together with the apex and its associated groups of nodes and unexpanded internodes with buds and associated leaves. When the coleoptile emerges from the soil the vegetative phase is deemed to begin. During the vegetative phase the leaves, tillers and the root system are developed and this stage lasts until the first double ridge is formed on the apex. It is during this stage that the husbandry treatments such as the provision of fertiliser and manipulation of the population by seed rate changes have the greatest effect. Varietal differences in behaviour during this stage have a large bearing on the subsequent performance which ultimately affects yield.

The pattern of development followed during this stage is the same in both wheat and barley. The coleoptile tip emerges above the soil as a transparent tube containing the true leaves which rapidly turn green and start to elongate. The leaves each consist of a lamina and a sheath which is curved into a cylinder around the growing point and the sheaths of subsequently developed leaves. In the axil of each of the leaves is a bud which can develop into a tiller. Tillers themselves can produce second and third order tillers but these occur only seldom and very rarely in a field situation. Tillers develop throughout this phase though the plant is capable of developing new tillers during the reproductive phase. Development of established tillers continues in the reproductive phase though at a reduced rate (Bunting and Drennan, 1966). The structure of tillers is identical to that of the main stem. The development which takes place in the root system during this stage in the plants development will be reviewed elsewhere. (Chapter 4:ii).

With the appearance of the first double ridge in the apex the reproductive stage is deemed to begin. This stage will be dealt with in greater detail with particular reference to the development of the wheat spike in a later chapter. (Chapter 5). Cereal plants' reproductive development is responsible for the production of a sink for the carbohydrate produced by the leaves of the plant. This sink is responsible for the establishment of the next generation. Barley differs from wheat in that the barley spike is not determinate and can in theory continue to develop new spikelets without restraint. Wheat however produces a terminal spikelet which is inserted perpendicular to the earlier spikelets. Each barley spikelet however is determinate and has only one floret. There are three spikelets at each node of which one or more develop. In "two-row" barleys only one of the spikelets at each node develops but in "six-row" barleys all three spikelets develop but the lateral spikelets are generally smaller than the central one. In the wheat spike however the spikelets are capable of producing any number of florets within each spikelet. The development of the spike in barley is described by Bonnett (1935). The reproductive phase ends at anthesis.

In the seed stage the embryo and the endosperm of the grain are formed and the grain and the whole plant gradually senesce and loose moisture. This outline of the development of the barley plant serves as a basis against which differences in the development caused by different husbandry or environmental influences are manifest.

ii The influence of husbandry on the development of barley.

In growing the barley plant in a crop situation a strong competitive stress is placed on the individual plants which make up the crop. The essence of the development described above occurs with all the plants in the crop but the full potential of each plant is not realised. Donald (1963) described a healthy crop as one made up of subnormal individuals. When plants were sown at a density of 1.4 plants/sq.m. the yield of each plant was 33.2 g. but when sown at the spacing for maximum yield per unit area 35 plants/m2.the yield of each plant was reduced to 7.1 g. The cultural practices which were applied to the crop in the experiments described later in this section have been shown to have a profound effect on the growth of the barley crop.

iii The effect of nitrogen on the growth of barley.

The primary effect of nitrogen on the growth of barley is on leaf growth (Langer, 1966) measured as total foliage area. This parameter is a compound of the number of leaves present at any time and the size of each leaf. Each of these can be further broken down to the more meaningful parameters namely; the number of leaf bearing tillers and the rates of production and senescence of the leaves on each tiller make up the first parameter while the size of each leaf is dependent on the rate of expansion of the leaf and the duration of this expansion. These parameters have not been widely examined but the influence of nitrogen on the growth of the foliage system in barley has been well documented (Langer, 1966). Nitrogen has been shown to increase the mean leaf area per shoot in barley (Watson et al., 1958) but the effect of this increase was smaller than the effect of the increase in shoot number. It appears that the number of leaves on a shoot and the duration of these leaves, have a smaller effect on the total leaf area than the number of shoots (Langer, 1966), though they show some effect of change in nutrient supply. The effect of nitrogen on the control of the tiller number at various stages in the growth of the plant has been thoroughly examined by Aspinall (1961 and 1963). In the first of these papers the tillering pattern was established when the plant was provided with all the nutrients at an early stage. This pattern was an increase in the number of tillers for a period which was dependent on the amount of nutrients supplied. This period was followed by a period in which no new tillers were formed but this was not due to a lack of tiller buds. This phase could be terminated at any time by the application of more nutrient though, if this raising of the nutrient supply was delayed for a time after ear emergence, the onset of renewed tillering was delayed progressively. The second paper looked at the effect on tiller bud growth of applied nutrients during the ear development phase. The principal finding to emerge was that grains and tiller buds competed for nutrients at this stage. The effect of the grains could be overcome by increased nitrogen but an excessively large amount was required to overcome the effect of the grains, implying a further control in the form of a growth substance from the grains inhibiting tiller bud development. Tiller buds are also subject to competition from developing tillers in the earlier stages of growth and the tillers seem to have a greater priority for nutrients than tiller buds. (Aspinall, 1961). The degree of independence achieved by tillers is subject to some doubt. Tillers produce root and leaf systems of their own but transport of nutrient from the main stem to the tillers has been demonstrated by C_{14} studies in wheat and rice (Bunting and Drennan, 1966) though Lupton (1968) found that, after stem elongation in the tiller, it became independent of the parent.

When nutrient supply is continuous the growth of new tillers continues without any break. Initially the growth is exponential but the growth rate reduces to a constant increase in the number of tillers being produced (Aspinall, 1961).

The primary mechanism by which nitrogen affects the growth of the barley plant thus appears to be through the manipulation of the leaf area by the production of tillers. (Bunting and Drennan, 1966 and Langer, 1966). These single plant studies allow a fuller understanding of the mechanisms by which crop yields are obtained in response to fertiliser.

For high yields to be achieved a high application of nitrogen is required. (van Dobben, 1966). This however results in lodging under most conditions and a consequent loss in yield. While a large number of experiments have been conducted to examine the effect of nitrogen on yield very few of these have taken note of how the yield increases came about in terms of yield components.

Experiments of this type include those of Widdowson and Penny (1968 and 69) Moffat and Widdowson (1967), Harvey (1964) and Lessels and Webber (1965). In all these experiments an increase in yield with increasing nitrogen over the low part of the range was recorded but at the highest levels of nitrogen reductions in yield were recorded in a number of these experiments but only Moffatt and Widdowson (1967) accounted for the yield loss in terms of lodging on very fertile sites.

A number of other papers examined the effect of nitrogen coupled with water shortage (van Dobben, 1966, and Leubs and Lang, 1969). These papers emphasise the need for adequate water supply for the utilisation of nitrogen as an increase in leaf area caused by nitrogen application also increases the transpiration of water which in areas of water shortage results in reduced yields. In this case the yield reduction is caused by a reduction in ear numbers and in grain numbers on the ears.

The time of nitrogen application to barley has been shown to have an effect on the utilisation and effectiveness of the nutrient. van Dobben (1966) advocated the use of late application, i.e. up to and just beyond earing as this tends to prolong the period of post anthesis leaf area duration which results in an increased yield. Early application results in an increase in tiller number and in straw length and increases the likelyhood of lodging. The late application is only beneficial when the fertility is adequate to provide a large enough plant to utilise the late application. If this is not the case, van Dobben (1966) suggested a split dressing which provides a large enough plant at the second dressing to fully utilise the late application of fertiliser in prolonging the leaf area duration. The effect of nitrogen on the yield components was examined in the experiment of Oswald (1970) who found that the first application of nitrogen (25 units per acre) gave a marked increase in tiller number, 1000 grain weight, number of grains per ear and yield but that this increase was not sustained with a further application of nitrogen though a slight increase in all the components was noted. It was concluded that competition between tillers became more intense at the higher nitrogen level which prevented any further increase in yield of tillers or of the crop as a whole. (Oswald, 1970).

iv Effect of seed rate on growth of barley.

The plant population of a crop has a profound influence on the individual plants as described earlier (Donald, 1963) and the object in varying the seed rate is to find the population which will give the best yield of all the plants taken together and not the optimum yield of the individual plants. The establishment of a crop does not only depend on the number of seeds sown but on how many of these survive to produce plants and on the propensity of these plants to produce tillers. The overriding consideration when discussing population in barley is not the number of plants but the number of tillers per unit area. (Holliday, 1960)

In an extensive review of the effect of plant population on crop yield, Holliday (1960) found a very large variation in the optimum seed rate for the various cereals. When the fertile tiller population was taken into account the variation was considerably reduced. This confirms that the seed rate is an inadequate measure of the plant population but Holliday found that the response of yield to increase in seed rate was parabolic and thus there is a wide range in plant population in which yield is only slightly affected.

The effect of increased seed rate on the individual plants was recorded by Kirby (1968) in terms of yield components. As seed rate increases the number of plants per unit area changes only slightly. Similarly Holliday (1960) found that the number of plants per seed sown reduced as density increased. The number of tillers per plant was found to be reduced but the greater numbers of ears per unit area are found at high density. The number of grains per ear was reduced by high density but again the number of grains per unit area is only affected a little by changes in density. The final component of yield, the weight of the individual grains was only slightly affected by an increase in density. (Kirby, 1968). Similar findings have been reported by other workers who have looked at the components of the yield (Bengtsson, 1972 and Oswald, 1970). The relationship between the number of tillers per unit area and the yield with increased density was considered to be more than coincidental by Holliday (1960) in that, with a larger number of ears the contribution of the upper parts of the plant to the total dry matter production of the crop becomes greater. Thorne (1965) showed the main part of the grain weight was provided by the upper part of the plant and as this part has an increased contribution a larger grain yield would be expected. Several workers have reported an interaction effect of seed rate and nitrogen though in all cases this has not reached a significant level. (Holliday, 1960; van Dobben, 1966; Bengtsson, 1972; Holmes et al., 1971). In the absence of lodging this interaction is positive but when lodging occurs the interaction is negative. (Holliday, 1960)

The arrangement of the plants in the crop has been shown to have an effect on the response to increase in crop density. (Holliday, 1963; Angus et al., 1972; Donald, 1963; Moffat and Widdowson, 1967; van Dobben, 1966; Holmes et al., 1971). In all cases a yield advantage has been achieved with narrow row spacing of barley when compared with a wider row spacing as this allows the plants to utilise the space around them more effectively. Yield advantage has however been slight when compared to the effects of increased plant density and the addition of more nitrogen.

Finally varieties respond differently to changes in the crop environment caused by such changes as seed rate and nitrogen manipulation. Varietal characteristics such as propensity to tillering, leaf width, leaf inclination, plant height and straw strength affect the way in which a variety will respond to an increased competitive stress. As an example, Angus et al. (1972) compared two barley varieties of differing leaf inclinations at two densities. One variety had erect leaves and responded to an increase in density by an increase in dry matter production and yield while the other variety which had long lax leaves responded with a decrease in dry matter production and grain yield. Watson et al. (1958) examined the difference between old and new varieties of barley and found that the new varieties appeared to be more efficient in photosynthesis and partitioned their assimilates more efficiently than the older varieties. In addition the new varieties did not lodge while the old varieties did. The net result was a 10-15% higher yield in the new varieties, illustrating the extent to which the variety is responsible for differences in yield when the husbandry treatments are the same.

In light of the increasing use of short statured varieties of barley (Berbigier, 1968) a fuller understanding of the response of such varieties to changes in husbandry practice would be desirable. In addition, should the reaction of such varieties be markedly different in response to husbandry treatments, modification of the variety testing procedures may also be required to avoid a bias against varieties of a different type.

v Influence of the environment and the weather on the growth of barley.

The growth and development of the crop in the field is dependent on a number of stimuli, from the environment, e.g. photoperiod and is also dependent on the environment for the provision of essential elements for its growth such as light, moisture and a suitable temperature. These factors which influence the plant growth are largely outwith the control of the farmer though irrigation and shelter from the wind can be provided to some effect (Milthorpe, 1955)

Throughout the growing season the environment imposes limitations on the growth and development of the crop. (Monteith, 1966, i) At germination the processes of imbibition and growth are restricted by temperature. At temperatures between 15° and 25° C germination proceeds at its fastest while at temperatures below 3° C the process stops completely (Monteith, 1966, i). The effect of low temperatures, i.e. temperatures in the range 10°-5° C, at this stage however does not appear to be particularly damaging as within this range germination proceeds at a reasonable pace (Smith. 1967).

During the next phase of growth, the leaf expansion phase, the temperature again exercises the greatest influence through the soil temperature. This must be adequate to enable the root activity, essential for the provision of nutrients to the expanding leaves, to be sustained. Humidity also influences the plant development at this stage as a good flow of water through the plant is essential for the provision of nutrients but if transpiration is too rapid, water stress in the leaves becomes limiting and leaf expansion is slowed (Monteith, 1966, i).

The process of photosynthesis is essential to the production of the plant but is very much at the mercy of the elements. The most important factors of the environment on this process are the concentration of carbon dioxide in the atmosphere near the leaves and the incident light. In bright radiation the carbon dioxide becomes limiting and the radiation is in part wasted. A similar situation develops at low temperatures (i.e. below 10^{o} C) when the permeability of the leaves to carbon dioxide is reduced. (Monteith, 1966, i)

The process of respiration is also affected by the environment in that it is increased with increase in temperature and more of the carbohydrate produced by the photosynthesis of the leaves is lost to the production of the crop product, i.e. the grains in barley. Respiration is also dependent on translocation and thus on the supply of moisture (Monteith, 1966, ii).

The initiation of the flowering phase and the rate of development in this phase are dependent on photoperiod and temperature (Monteith, 1966, ii). The final phase of growth when the grains are filling is dependent for high production on the activity and the duration of the activity of the photosynthetic area provided by earlier growth. (Thorne, 1965) High temperature affects the duration of this phase by hastening senescence (Thorne, et al., 1967) and moisture shortage at this stage has a similar effect. (Black and Watson, 1960).

When the effect of the weather on the production of the barley crop as a whole is examined the optimum season for barley yield would appear to be one in which a cool spring (cool air temperature) preceeded by low winter rain and a warm dry period for sowing is followed by a moderate rainfall during the shooting period and dry periods interspersed with light rain during the reproductive phase. There should be abundant sunshine throughout (Smith, 1967). This conclusion was reached from a wide ranging study of the conditions found in a large number of field experiments.

The influence of the environment is thus considerable and further complicates the assessment of the production of different varieties under different husbandry treatments.

2C Materials and methods. An experiment was carried out in 1970 and repeated, with minor adjustments, in 1971 in which five varieties of barley of different stature were compared at five seed rates and under five rates of nitrogen. The varieties which were studied in these experiments were;

1970 261/34 (Dwarf B) from Guiness barley research, Warminster.
6262Co/N/44 (Dwarf A) Dwarf from P.B.I. Aberystwyth.
Golden Promise a semi-dwarf variety in commercial use.
Zephyr a medium straw length variety in commerial use.
Clermont a tall "six-row" variety in commercial use.

1971 The first four named above were grown in the second year but Clermont was replaced by Julia a medium straw length variety in commercial use.

The design of the experiment was a randomised block design with the three way interaction confounded to allow a block size of 25 plots. There were two replicates of the experiment.

The seed rates in both years were;

S_1 - 45 kg/ha.	S_2 - 101 kg/ha.
S_3 - 157 "	S_4 - 213 "
S_5 - 269 "	

The nitrogen rate was increased in the second year as shown below. This change was made as there was no lodging in the first year even at the highest level of nitrogen. The rates of the two years were;

1970	N_0 - 0 kg/ha.	1971	N_0 - 0 kg/ha.
	N_1 - 38 "		N_1 - 44 "
	N_2 - 75 "		N_2 - 88 "
	N_3 - 113 "		N_3 - 132 "
	N_4 - 151 "		N_4 - 176 "

The experiments were carried out on the farms of the Edinburgh School of Agriculture.

In 1972 the experiment was carried out on Saltcoats Farm Gullane. The object was to test the response of the varieties under conditions of water shortage and the Gullane farm is on very sandy soil which was thought to be suitable for this purpose. Only three of the varieties used in previous years were used at Gullane. These were; Golden Promise, 6262Co/N/44 (Dwarf A) and Zephyr. Three nitrogen rates were applied. The design was completely randomised with six replicates. No zero nitrogen rate was used as the inherent fertility of the sandy soil was thought to be too low to promote adequate growth to prevent such a treatment attracting animal pests.

The nitrogen rates used were;

N_1 - 50 kg/ha, N_2 - 100 kg/ha. N_3 - 150 kg/ha.

All three experiments were sown with a commercial Norsted seed drill in plots 2.6 m wide and approximately 16.5 m long. The drills were 11.5 cm apart. The experiments of 1970 and 1971 were grown on a sand loam gley soil of the Macmerry series (Soil Survey of Scotland) and that of 1972 on a loamy sand soil.

The sowing dates, dates of nitrogen application and dates of weed control sprays were;

	1970	1971	1972
Sowing date	3 April	14 April	16 March
Nitrogen applied Nitro-chalk (21%N)	18-19 May	12-13 May	13 April
MCPA Spray	None *	3 June	25 April

* Some plots were hand weeded in 1970.

No phosphorus or potassium was applied in the first two years but in 1972 200 kg/ha of a 0-20-20 compound fertiliser were sown on the experimental area the day before sowing.

In the first year no anti-mildew treatment was applied but in 1971 the experiment was sprayed with 'Lucel' on the 28 June. In 1972 the seed was treated with 'Milstem' before sowing as protection against mildew as the variety Golden Promise is very susceptible to this disease. Emergence counts were made on three blocks in 1970 and on one whole replicate in 1971 on the 21 May and the 11-12 May respectively. A mildew assessment was made in 1970 and also in 1971 before the spray was applied. Ear emergence dates were scored in 1970 and 1972. Height of straw was measured by sighting each year.

A sample of all the plants enclosed by a frame of area 3715 sq cm was taken from one replicate of the experiment in 1970 and 1971. Yield component measurements were made on this sample. These were;

Number of plants	1970	Number of tillers	1971
Number of tillers/plant	1970		
Number of grains/ear	1970-71		
Weight of 1000 grains	1970-71		
Dry weight of straw	1970-71		
Dry weight of grain	1970-71		
Nitrogen content of straw	1970-71		
Nitrogen content of grain	1970-71		
The weight of grain of four size categories	1970		

No comparable sample was taken in 1972 but the weight of 1000 grains was determined. Plot maturity varied considerably in the first two years of the experiment as a result of the different treatments applied and harvesting was thus staggered and only plots which were deemed ripe were harvested on several dates after 10 September 1970 and 7 September 1971. Maturity was more even in 1972 so all plots were harvested on 21 August.

2D i Results of barley experiments 1970-72.

The overall mean yield of the three years' experiments were 1970 - 3777 kg/ha (4311) 1971 - 3161 kg/ha (3614) 1972 - 6288 kg/ha (6288). The mean yield of the three varieties common to all years are in brackets.

The difference in yield between the years is considerable, reflecting the large differences between the seasons and/or the site in which the crops were grown. Weather data for Bush Estate and Dunbar are presented (Appendix 1) which will be used to discuss probable causes of differences in both yield and the yield components. In the succeeding discussion of the results only effects which were significant at the 95% level and above will be discussed.

D ii Response of yield to Nitrogen.

Yield response to nitrogen differed in the first two years of the experiment (Tables 2:1; 2:2 and Fig 2:1). In the first year the highest yield over all varieties and all seed rates was achieved at 113 kgN/ha. Yield rose sharply with the first 38 kgN/ha after which there was a slight further rise to 113 kg/ha. A slight decline was noted between 113 and 151 kgN/ha. In 1971 the mean yield increased between 0 kgN/ha and 44 kgN/ha but with further increase in nitrogen the yield declined almost to the level found in the absence of nitrogen. The yield increased very steeply to 150 kgN/ha in the 1972 experiment with no decline in the response apparent. The response in 1972 was very much greater than in the previous years (Table 2:3).

Diii The response of yield to seed rate.

The effect of change in seed rate in 1970 and 1971 when this factor was examined was similar (Tables 2:1; 2:2; Fig 2:3). The highest yield was achieved at 213 kg/ha though there was little difference between yield at 157 kg/ha and 213 kg/ha. In 1970 there was a slight decline in yield at the highest seed rate 269 kg/ha which was not found in 1971. Higher seed rates than the maximum of 269 kg/ha of this experiment seem to be required to achieve a decline in yield in response to seed rate, in agreement with the findings of Holliday (1960).

D iv Response of yield to variety.

The order in which the varieties were placed in terms of yield differed between the first two years of the experiment as shown. (Tables 2:1-3)

<u>Chapter 2</u> Where Standard Errors (SE) are quoted the first figure is for comparisons within the Table and the second for comparisons of mean.

Table 2:1 2-way Table of yield 1970 (Kg per Ha).

a. Variety x Nitrogen

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
N_0	4245	4099	4000	4044	3544	3986
N_1	4204	4484	4413	4356	3941	4280
N_2	4138	4309	4468	4506	4130	4310
N_3	4186	4287	4592	4542	4080	4337
N_4	4243	4157	4470	4262	4098	4246
Mean	4203	4267	4389	4342	3958	4232

b. Variety x Seed Rate

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
S_1	3290	3329	3457	3454	3491	3405
S_2	4049	4211	4355	4364	3837	4163
S_3	4403	4359	4723	4606	4288	4476
S_4	4740	4723	4826	4617	4113	4604
S_5	4533	4714	4582	4669	4064	4512
Mean	4203	4267	4389	4342	3958	4232

c. Seed rate x Nitrogen

	S_1	S_2	S_3	S_4	S_4	Mean
N_0	3444	4000	4234	4085	4168	3986
N_1	3481	4208	4655	4521	4533	4280
N_2	3520	4165	4498	4882	4484	4310
N_3	3447	4067	4547	4945	4680	4337
N_4	3130	4374	4444	4586	4696	4246
Mean	3405	4163	4476	4604	4512	

SE 135.2 60.38

Significant effects.

NL ** NQ **

SL ** SQ **

CV ***

N x S *

Table 2:2 Two-way Tables of Yield 1971

a. Variety x Nitrogen

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
N_0	3411	3176	3216	3134	3355	3259
N_1	4126	4059	3622	3886	3874	3914
N_2	4118	3402	3606	3874	3594	3719
N_3	3623	3227	3532	3908	3305	3519
N_4	3275	3501	3302	3570	2872	3304
Mean	3711	3473	3456	3674	3400	3543

b. Variety x Seed Rate

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
S_1	3088	3037	2892	3179	2899	3019
S_2	3586	3250	3255	3726	3412	3446
S_3	3844	3647	3749	3810	3607	3732
S_4	3893	3670	3661	3920	3664	3762
S_5	4143	3761	3722	3738	3417	3756
Mean	3711	3473	3456	3674	3400	3543

c. Seed Rate x Nitrogen

	S_1	S_2	S_3	S_4	S_5	Mean
N_0	2993	3173	3376	3260	3490	3259
N_1	3085	3857	4118	4249	4259	3914
N_2	3207	3496	3894	4101	3895	3719
N_3	2970	3389	3689	3745	3805	3519
N_4	2839	3316	3581	3453	3331	3304
Mean	3019	3446	3732	3762	3756	3543

SE 119.36 53.38

Significant Effects NQ** NC** N_4*

SL** SQ**

CV*

NQ x SL** CV x NL**

CV x NQ* N x CV*

Table 2:3 Two-way Table of Yield 1972

Variety x Nitrogen

	Dwarf A	Zephyr	Golden Promise	Mean
N_1	5027	5482	5507	5339
N_2	6263	6782	6028	6357
N_3	6986	7107	7411	7168
Mean	6092	6457	6516	6288

Significant effects. N **

Figure 2:1 Effect of Nitrogen on Yield and 1000 gr wt.

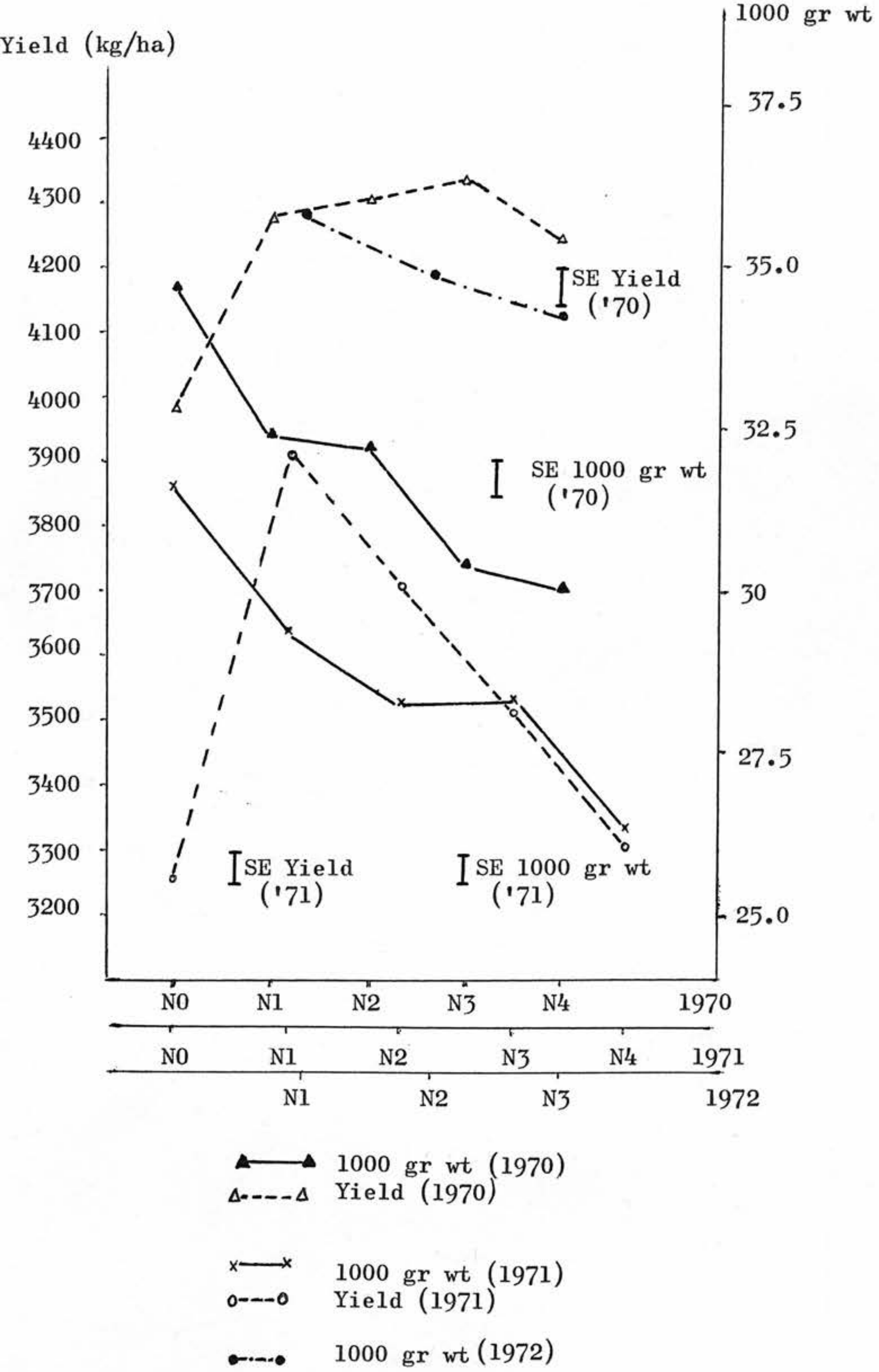


Figure 2:2 Effect of Nitrogen on Tiller Number and number of grains/ear

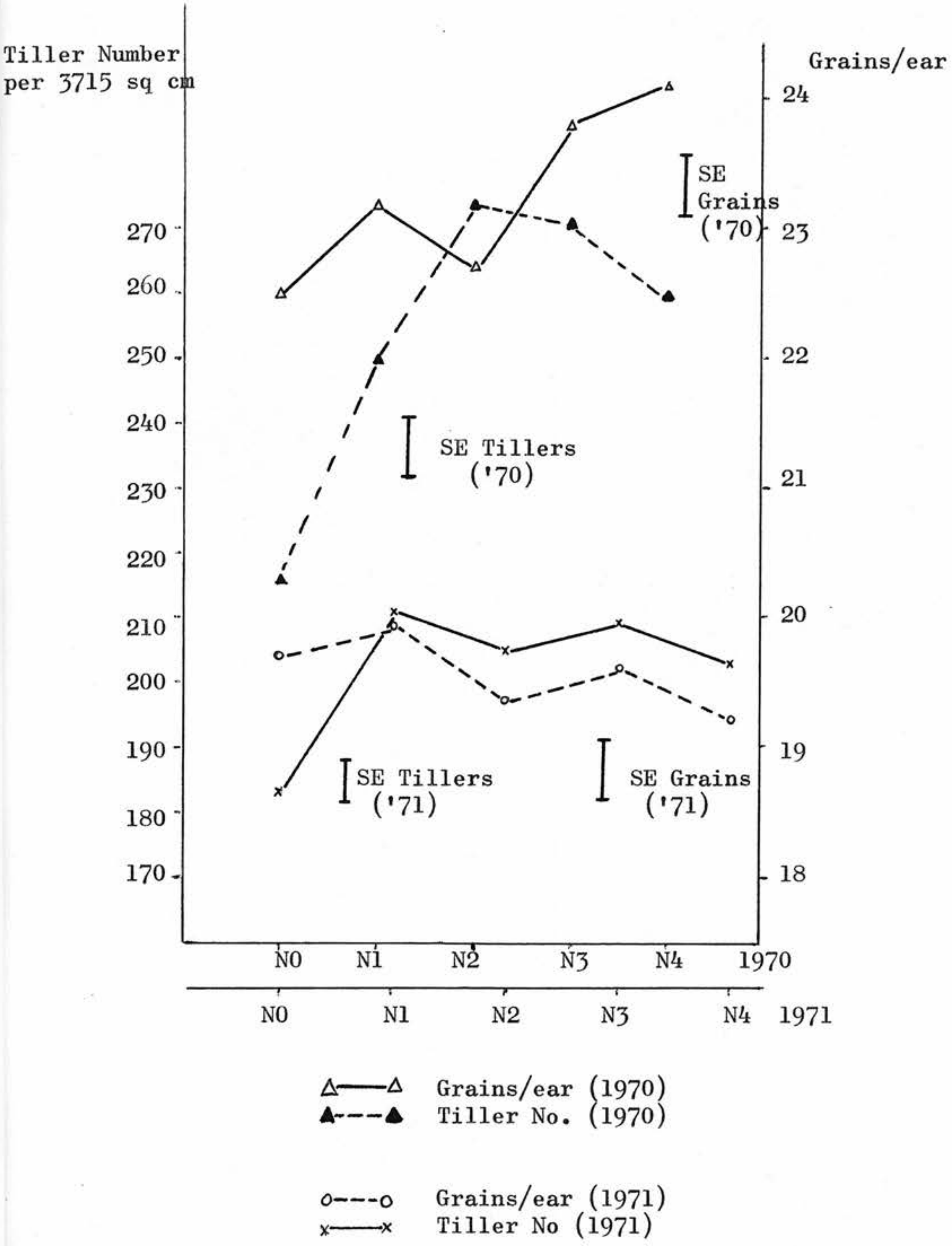


Figure 2:3 The Effect of Seed Rate on Yield, 1000 gr wt and Grain Number/m^2

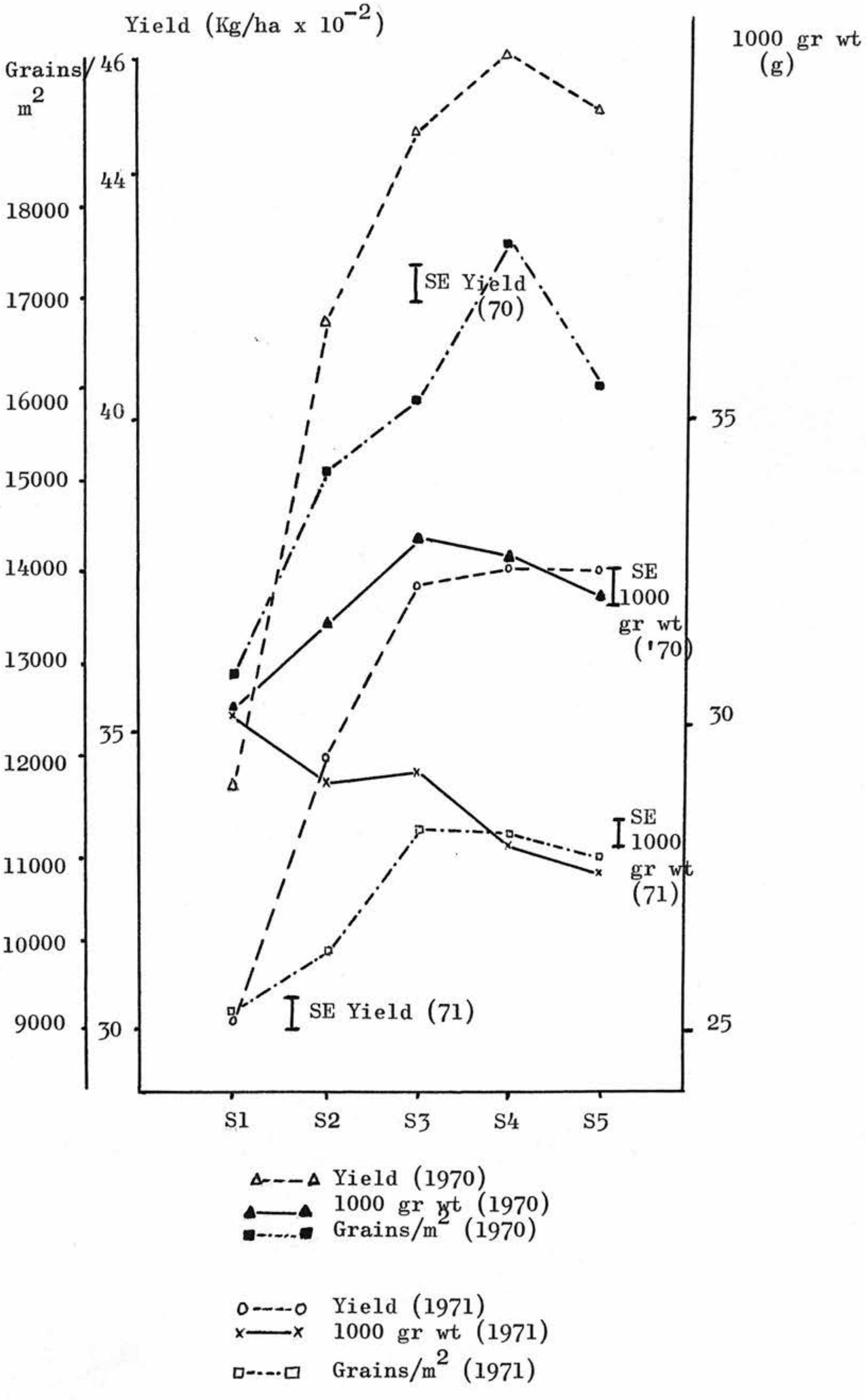
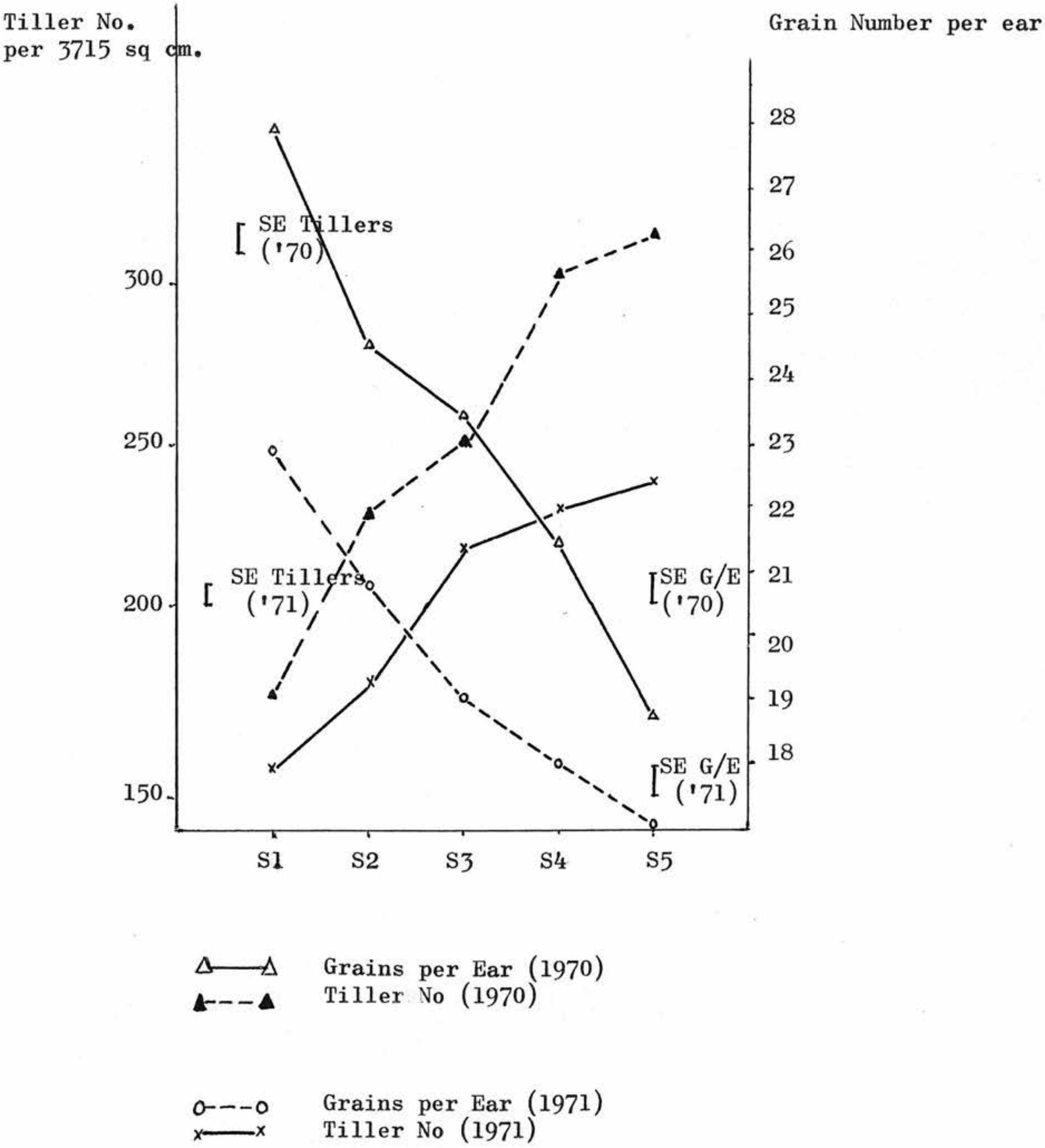


Figure 2:4 The Effect of Seed Rate on Tiller Number and Grain Number per ear



The degree of lodging in the second year could account for part of the change in the yield placings in that Zephyr showed fairly extensive lodging in 1971

Lodging (1971)	Julia	Zephyr	Golden Promise	Dwarf A	Dwarf B
No. plots slight lodging	9	6	2	-	-
No. plots extensive lodging	5	3	-	-	-

Score made on 25 plots per variety.

In 1972 differences in yield between the varieties were nonsignificant.

D v Interactions of Nitrogen, seed rate and variety on yield.

The interaction of nitrogen and variety (1971) could have either of two explanations. (Table 2:2) Firstly, the varieties can be divided into two types in terms of their response to increased nitrogen. Zephyr and Golden Promise were found to sustain their peak level of yield over the range 44 to 132 kgN/ha. before a sharp decline at the highest rate of nitrogen. Dwarf B and Julia had a peak of yield at 44 kgN/ha which was followed by a decline over the next two rates of nitrogen, Dwarf B showed a recovery at 176 kgN/ha however. The fifth variety, Dwarf A, was intermediate in the duration of the peak yield with increasing nitrogen as it maintained the peak yield over the range 44 to 88 kgN/ha before declining. The second explanation could be that the two varieties, Julia and Dwarf A, had a lower yield at 176 kg/ha than with no nitrogen, while the other three varieties did not show such an extreme decline in yield at the highest rates of nitrogen. Thus no clear cut distinction can be drawn between the dwarf and the tall varieties in their response, in yield, to the treatments applied in this experiment.

Figure 2:5 Effect of Seed and Nitrogen Rate on Yield of Barley (1970)

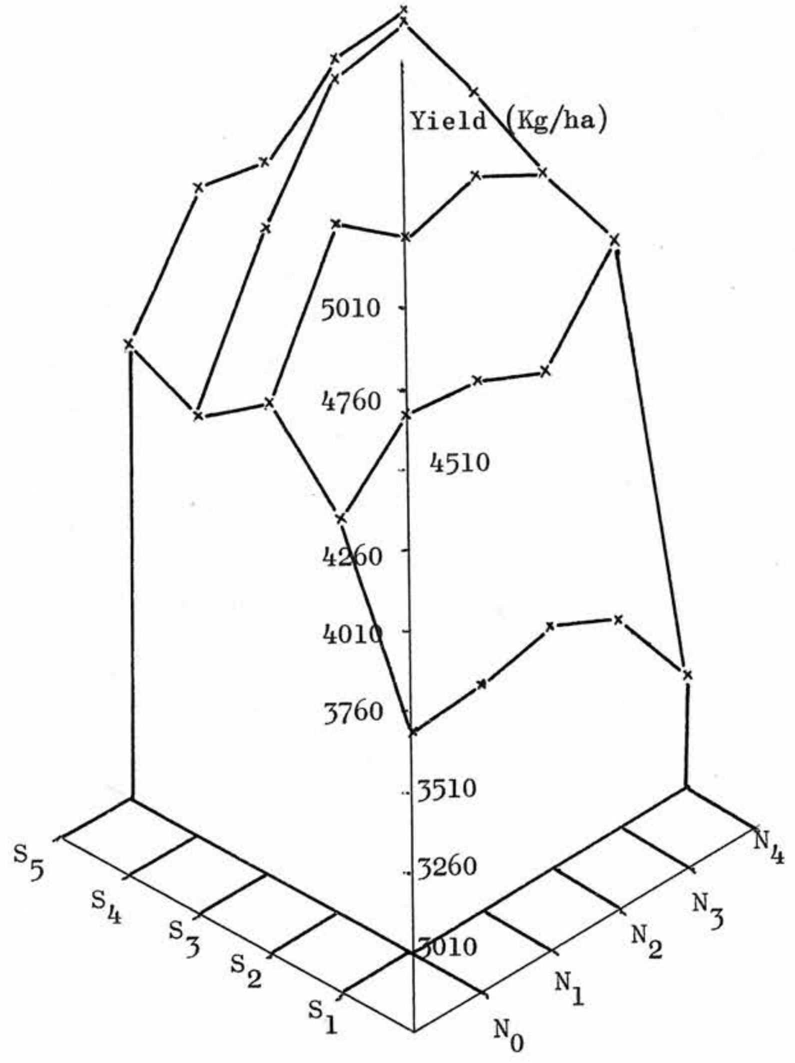
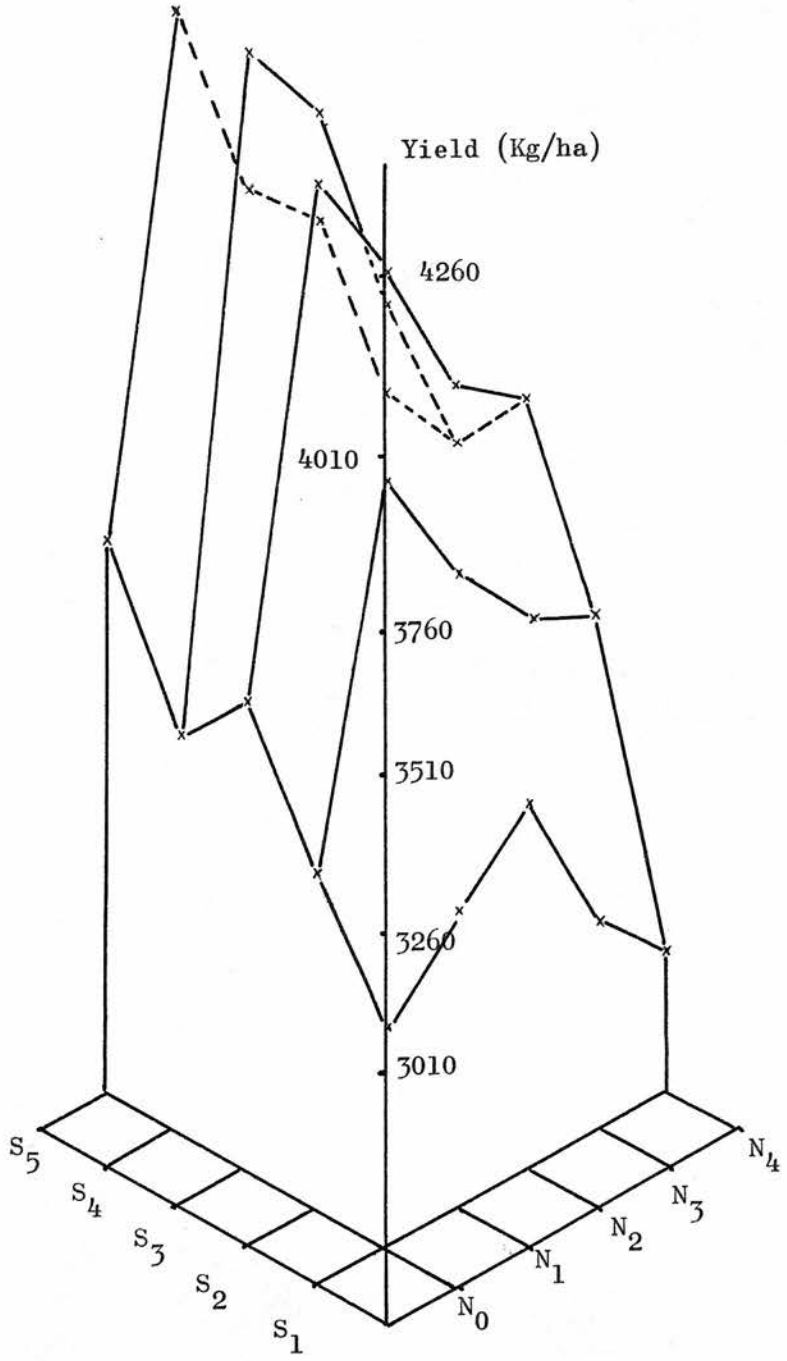


Figure 2:6 Effect of Seed and Nitrogen rate on Yield of Barley (1971)



The nitrogen seed rate interaction is different in the two years. (Figs 2:5-6; Tables 2:1-2). In 1970 the highest response to nitrogen fertiliser was found at high seed rates and the greatest response to seed rate at high N rates but in 1971 the response to seed rate was greatest at intermediate levels of nitrogen, though the highest nitrogen response was still at the highest level of seed rate.

D vi The effect of nitrogen on yield components.

The main effects of nitrogen in the two years are shown in Table 2:4

Table 2:4 Effect of nitrogen on yield components.

1970

Nitrogen	N_0	N_1	N_2	N_3	N_4	Mean	SE	Signif
KgN/ha	0	38	75	113	151			
Grain/ear	22.55	23.22	22.74	23.80	24.12	23.29	.459	Lin *
Tiller No	216.8	249.9	274.2	271.3	260.1	254.5	9.15	lin ** quad **
No grains/sq m	13160	15620	16780	17380	16890			
Straw wt. (g)	147.0	165.9	169.4	184.0	179.4	169.2	5.365	lin **
200 gr wt. (g)	6.96	6.49	6.46	6.09	6.02	6.41	.106	lin **
Gr/straw rat	.964	.915	.901	.828	.821	.886	.033	lin **
% gr N	1.77	1.90	2.01	2.18	2.26	2.02	.040	lin **
% straw N	.68	.82	.95	1.13	1.26	.97	.040	lin **
Sample grain yield (g)	137.4	146.6	149.6	149.2	146.0	145.8	5.038	NS

1971

Nitrogen	N_0	N_1	N_2	N_3	N_4	Mean	SE	Signif
KgN/ha	0	44	88	132	176			
Grain/ear	19.73	19.98	19.36	19.62	19.20	19.58	.464	NS
Tiller No	183	211	205	209	203	202	6.3	quad *
No grains/sq m	9720	11350	10680	11040	10490			
Straw wt (g)	173.1	194.4	205.7	206.8	210.4	198.1	5.85	lin ** quad*

Nitrogen	N_0	N_1	N_2	N_3	N_4	Mean	SE	Signif
KgN/ha	0	44	88	132	176			
200 gr wt (g)	6.33	5.88	5.66	5.67	5.27	5.76	.084	lin ** cub *
Gr/straw rat	.590	.527	.432	.453	.381	.477	.0175	lin ** 4 *
% gr N	1.84	1.93	2.01	2.05	2.18	2.00	.031	lin **
% straw N	.64	.82	1.08	1.08	1.30	.98	.042	lin **
Sample grain yield (g)	99.6	102.1	88.8	93.1	80.0	92.7	3.91	lin **
<u>1972</u>		N	N	N				
		N_1	N_2	N_3				
KgN/ha		50	100	150				
200 gr wt (g)		7.17	6.98	6.86				**
% grain N		1.48	1.68	1.94				**

In 1970 a distinction was made between the number of tillers per plant and the number of plants. Distinction between a tiller and a plant at this stage was very difficult and the results are therefore suspect. The total number of fertile ears calculated from these two measures will however be accurate and directly comparable with the results of 1971. The number of ears in 1970 (254.5) was very much greater than in 1971 (202) measured as the total number on the sample area of 3715 sq. cm.

The straw weight in 1971 was greater than in 1970 though all other yield components were lower in 1971.

The grain weight of the sample, a comparable parameter to the grain yield, was only taken on one replicate of the experiment and was taken from a small sample area (3715 sq. cm). It was therefore subject to a greater experimental error than the total yield. In 1970 the sample yield followed the same pattern as the total yield in response to increased nitrogen (cf. Table 2:4 and Table 2:1) but in 1971 the yield at high levels of nitrogen dropped below that with no nitrogen which is a more exaggerated response than that recorded for the total yield (cf. Tables 2:4 and 2:2).

As a result of the changes in grain and straw weights the grain to straw ratio decreased in value in both years with increase in nitrogen. Values in 1970 were much higher than in 1971 (Table 2:4).

D vii The effect of seed rate on the yield components.

The main effects of seed rate are shown in Table 2:5. The yield components measured were the same as those of the previous section though the seed rate was only varied in the first two years of the experiment.

Table 2:5 Effect of seed rate on the yield components measured.

1970

Seed rate	S_1	S_2	S_3	S_4	S_5	Mean	SE	Signif
Kg/ha	45	101	157	213	269			
Grain/ear	27.93	24.69	23.48	21.55	18.79	23.29	.459	lin **
Tiller No	172.3	228.4	251.7	303.0	316.8	254.5	9.15	lin **
No grains/sq m	12950	15180	15910	17580	16020			
Straw wt (g)	178.9	170.2	162.8	171.0	162.9	169.2	5.365	NS
200 gr wt (g)	6.06	6.34	6.62	6.56	6.49	6.41	.106	lin** quad **
gr/straw rat	.680	.838	.948	.993	.969	.886	.033	lin ** quad **
% gr N	2.18	2.04	1.99	1.93	1.98	2.02	.040	lin *
% straw N	1.20	1.05	0.89	0.84	0.86	0.97	.040	lin **
Sample grain yield	114.4	136.7	153.4	168.6	155.7	145.8	5.038	lin ** quad **

1971

Seed rate	S_1	S_2	S_3	S_4	S_5	Mean	SE	Signif
Kg/ha	45	101	157	213	269			
Grain/ear	22.94	20.81	19.09	18.02	17.02	19.58	.464	lin **
Tiller No	149	176	218	230	238	202	6.3	lin ** quad **
No grains/sq m	9200	9860	11200	11160	10900			
Straw wt (g)	194.1	189.2	207.2	202.3	196.9	198.1	5.85	NS
200 gr wt (g)	6.03	5.81	5.85	5.62	5.51	5.76	.084	lin **
Gr/straw rat	.436	.475	.499	.501	.473	.477	.0175	quad **
% gr N	2.05	2.02	1.98	.2.02	1.95	2.00	.031	NS
% straw N	1.08	1.05	0.96	0.91	0.92	0.98	.042	NS
Sample grain yield (g)	84.2	86.6	100.9	99.3	92.7	92.7	3.91	lin * quad *

The pattern of the sample grain yield was similar to the grain yield of the whole plot except that the decline at the highest seed rate was more marked in the sample.

The response of 1000 grain weight differed in the two years of the experiment (Table 2:5 and Fig 2:3). In 1970 the weight of each grain increased with seed rate up to 157 kg/ha before a slight decline but in 1971 the weight declined throughout the range of seed rates as seed rate increased.

Dviii Interaction of seed rate and nitrogen on yield components.

In 1970 this interaction was not significant in any of the yield components measured but in 1971 several interactions were significant which will be described here.

The number of fertile tillers responded by increasing with increase in nitrogen at low seed rates but with higher seed rates the response to nitrogen was reduced with the peak tiller number achieved with low nitrogen usage. (Appendix Table 2:8). Similarly with 1000 grain weight the response to increased nitrogen was greater at low seed rates than at high (Appendix Table 2:10) though here the response to nitrogen was a decline in 1000 grain weight. The response to seed rate is similarly greatest at low levels of nitrogen with the reduction in 1000 grain weight being greater at the lower nitrogen rates.

Straw weight behaved differently from the two components above as the response to nitrogen was not so great at low seed rates as it was at high. The straw weight at different levels of nitrogen fluctuated over a wide range in response to seed rate changes but not in any consistent fashion. The response to seed rate as a main effect was not significant due to this fluctuation. (Appendix table 2:9).

D ix Response of the yield components to variety.

Some of the varieties used in the experiments were changed after each year. Clermont and Julia were each grown for only one year and Dwarf B only for two. Clermont, the six-row variety, behaved in a different way to the other varieties in terms of yield components. The number of grains per ear was very much greater than the two-row varieties while the number of ears per sample area was very much less and the yield was smaller. As this variety was so different the variety sum of squares was broken down into three parts in 1970

i.e.1.variation between two and six-row varieties.

2.variation between tall and dwarf two-rows

3. variation within tall and dwarf varieties.

Comparison of Julia with the other varieties is only possible in 1971 and it cannot be compared between years. Thus Dwarf A, Zephyr, Golden Promise and Dwarf B will be the varieties discussed at greatest length in this section and they will be compared over the two years in which the yield components were measured.

In 1970 Clermont differed from the other varieties in grain number per ear. In 1971 this component was not significantly influenced by variety (Table 2:6).

Table 2:6 The main effect of variety on the yield components.

1970

Variety	Cler	Zephyr	G.P.	A	B	Mean	SE	Signif
Grain/ear	37.17	19.85	19.00	21.45	18.97	23.29	.459	**
Tiller No	123.4	263.5	287.6	277.5	320.3	254.5	9.15	**
Straw wt (g)	146.9	193.8	151.7	179.6	173.7	169.2	5.365	**
200 gr wt (g)	6.89	7.12	6.26	5.89	5.86	6.41	.106	**
Gr/sr rat	.847	.835	.978	.855	.915	.886	.033	*
% gr N	2.11	1.97	2.05	2.00	2.00	2.02	.040	NS
% straw N	.79	.92	1.02	1.11	.99	.97	.040	*
Sample Grain yield (g)	122.3	159.8	148.7	146.8	151.2	145.8	5.038	**

1971

Variety	Julia	Zephyr	G.P.	A	B	Mean	SE	Signif
Grain/ear	20.05	19.00	19.17	20.39	19.28	19.58	.464	NS
Tiller No	181	162	203	231	234	202	6.3	**
Straw wt (g)	217.9	185.4	175.8	210.2	201.0	198.1	5.85	**
200 gr wt (g)	6.10	6.37	5.54	5.58	5.23	5.76	.084	**
Gr/str rat	.439	.444	.503	.505	.493	.477	.0175	*
% gr N	2.06	1.96	2.03	1.95	1.99	2.00	.031	NS
% straw N	.91	.95	.90	1.06	1.10	.98	.042	*
Sample Grain yield (g)	94.8	80.9	87.3	104.2	96.5	92.7	3.91	*

1972

Variety	Julia	Zephyr	G.P.	A	B	Mean	SE	Signif
200 gr wt	-	7.20	6.56	7.24	-	7.00		**
% gr N	-	1.78	1.68	1.62	-	1.69		**

In both years Dwarf B gave the greatest number of tillers and Zephyr the least. In all varieties the number was much less in 1971 than in 1970 but the drop between years was the least in Dwarf A which meant that Dwarf A nearly equalled Dwarf B in this parameter in the second year (Table 2:6). The straw weight was greater in all varieties except Zephyr in 1971. Dwarf A and B both had a greater weight of straw in 1971 than Zephyr, a reversal of the position in 1970. G.P. had the lowest straw weight of the varieties in both years.

The grain yield of the sample was comparable to that of the plot in 1970 in that the relative yields of the varieties were similar except that Dwarf B gave a strangely high sample yield. This could have been a result of the heterogenous nature of this variety as it had a large number of late maturing tillers which may have contributed to the yield in the sample but would not in the main plot as the small grains would be cleaned out in the combine harvester. In 1971 also, Dwarf B and Julia gave a surprisingly high sample yield. The same explanation could apply to Julia which had a wide range of maturity of the ears of the sample due in part to extensive lodging slowing maturity. Golden Promise on the other hand had a relatively lower sample yield than the yield from the whole plot but this variety was very prone to grain shedding during handling of the sample which could account for the smallness of the sample yield. Apart from these slight differences the yield of the sample reflected the yield of the whole plot with reasonable accuracy (cf. Table 2:6 and Table 2:2).

The resultant grain to straw ratio (Table 2:6) showed a large change in the two years. The ratio was much reduced in all varieties in the second year as grain yield dropped and straw yield increased in 1971. Golden Promise had the highest ratio in 1970 with the Dwarfs A and B well below and Zephyr with a still lower value. In 1971 however, while Zephyr was still the lowest, the other three varieties common to the two years all had comparable values in this ratio (Table 2:6).

D x The interaction of cultivar with nitrogen and with seed rate. The seed rate/cultivar interaction on the number of grains per ear was the only one to be significant in 1970. Here again the difference between Clermont and the two-row varieties was the probable cause of this interaction being significant.

In 1971 however a number of interactions were significant. In tiller number two varieties, Dwarf A and Golden Promise gave a considerable positive response to increased nitrogen but none of the other varieties gave such a response. (Appendix Table 2:8). Julia showed no response to nitrogen in straw weight either, while all the other varieties gave a considerable increase in this component with increased nitrogen accounting for the significance of the ~~cultivar~~ quadratic nitrogen interaction on straw weight (Appendix Table 2:9).

Julia and Zephyr had a much more marked negative response to seed rate in 1000 grain weight than the other three varieties (Appendix Table 2:10). Finally Julia gave a lesser response, than the other varieties, in establishment of seed, to increased seed rate (Appendix Table 2:13), i.e. emergence percentage declined more in Julia.

2E Discussion of barley results Before a meaningful discussion of the effects of husbandry treatments,in the different seasons,on the growth of the varieties under examination can be undertaken,the influence of the weather on the three season's crops, must be examined (Appendix 1). Adverse weather conditions at particular stages in the crop growth cycle can be very damaging to the yield (Monteith, 1966, i). The components of yield which were measured i.e. grain number per ear, ear number per unit area and the weight of the grains are determined at different stages in the growth of the crop. The first two of these are determined early in the season and combine to give the number of grains per unit area to the crop. Tillers which are likely to become fertile and contribute to yield are formed early while later formed tillers are unlikely to mature. The weather in the three seasons of the experiment at the tiller-forming stage differed. In 1971 conditions were best of the three years in that the weather was dry and sunny after a wet spell which would provide adequate moisture. 1970 and 1972 had less sunshine but other conditions were adequate. Shortly after the tillers are initiated the grains are initiated on the ears of the tillers and the grain number per ear is determined. This stage just preceeds extension of the stem and ear emergence. Poor conditions at this stage can result in whole ears being infertile as well as reduced numbers of grains on the fertile ears. Conditions were again adequate in 1970 and 1972 but 1971 was lacking in sunshine at this stage (June) and temperatures were lower than average. The next important period in the growth cycle is the period from anthesis to maturity when the grain weight is determined. 1972 had the best conditions of all three years during this phase having plenty of sunshine. Sunshine in the other two years was below average though particularly so in 1971. These seasonal differences are apparent in both the yield and the yield components of the three years.

Nitrogen applied to the barley crop in the early season has been shown to promote the development of tillers (Aspinall, 1961) and thus increase the number of grains per unit area and increase yield. In these experiments yield was increased with the first rate of nitrogen in 1971, with the first three rates in 1970 and throughout the range of nitrogen usage in 1972. The increase in the number of grains per unit area by an increase in tiller number is not automatic but depends on the maintenance of a constant number of grains on each of the larger number of ears. Competition between tillers for light and nutrients becomes more intense as their number increases and grain number per ear is likely to be affected. Tiller number increased with the first two increments in nitrogen in 1970 and with the first in 1971 but numbers of grains per square metre increased over a greater range in 1970.

No. grains/m^2						
1970	13160	15620	16780	17380	16890	
1971	9720	11350	10680	11040	10490	
% redn between years	26	27	36	36	38	100 x (1970-
% redn in tiller no.	16	16	25	23	22	1971) 1970
% redn in gr/ear	13	14	15	18	20	

Thus although conditions appeared better for tiller production in 1971 the tiller number was reduced by harvest time and the number of grains per square metre was also reduced both by reduction in tiller numbers and by reduction in the number of grains per ear. Conditions at grain formation in 1970 were better than in 1971 so the reduction in grain number per ear in the latter is understandable. The reduction in tiller number must have been the result of either the death of a large number of the tillers produced or a lower number produced in the first place.

The reduced response to nitrogen in tiller number in the second year would thus have been due to competition for necessary factors for tiller production, other than nitrogen. Similar competitive stresses acted on the crop in 1970 also but greater nitrogen utilisation was possible before the other constraints became limiting as the peak tiller number was maintained at a higher level over a wider range of nitrogen usage.

Straw weight was also measured in both years and was greater in 1971 than in 1970 although fertile tiller number was less. This suggests that, rather than a cessation in the production of tillers in 1971, there was a reduction in the number which were fertile of a larger number produced. With a large number produced the competition between tillers would become intense at a lower nitrogen rate and fertile tiller response to nitrogen would cease at a lower nitrogen rate which was the observed response when compared with 1970. Competition would also be more intense at the grain initiatinn stage which would result in a reduction in grain number per ear which was again the observed response.

The effect of these changes on the number of grains per square metre has been shown (Table 2:4). In 1970 response to nitrogen was sustained up to 113 kgN/ha but in 1971 it was only sustained to 44 kgN/ha due to greater inter-tiller competition from infertile tillers.

The other principal determinant of yield is the weight of each grain. This is determined by the growth in the period between anthesis and maturity. Grain weight was less in 1971 than in 1970 and this would be due principally to the poorer weather during this growth stage in 1971 and possibly to continued competition from the infertile tillers. Grain weight in 1972 was very much greater than in either of the previous years reflecting the improved post-anthesis conditions. Increased nitrogen led to a reduction in grain weight which balanced the increase in grain number due to competition between grains for nutrient. The yield, being the product of grain number and grain weight, gave a response to nitrogen which was tempered by the competitive effects described in that the response was sustained to a high level in 1970 as the grain number increase more than balanced the reduction in the grain weight. In 1971 the grain number did not increase over such a wide range of nitrogen rates, the grain weight again declined with increased nitrogen and so the yield declined after the first rate of nitrogen. Lodging at high rates of nitrogen in 1971 would also have the effect of accelerating the reduction in the grain size which would reduce the yield further.

Lodging 1971	N_0	N_1	N_2	N_3	N_4	
No plots, extensive lodging	0	0	0	2	6	25 plots per nitrogen level.
No plots, slight lodging	0	1	2	4	2	
Total no. plots lodged	0	1	2	6	8	

A reduction in the grain to straw ratio with increase in nitrogen was noted in both years. At all rates of nitrogen the ratio was much less in 1971 than in 1970 reflecting the larger straw weight coupled with the smaller grain yield in the second year. The efficiency of the straw in producing grain was thus much less in the secondyear, partly due to the lack of sunshine during the grain filling stage of growth and partly, it is proposed, through an increase in the competition experienced from unproductive tillers.

The yield in 1972 was much higher than in either of the previous years and showed little reduction in response to nitrogen at the highest rates.

Fertility of the soil, on which this crop was grown, was thought to be less by its sandy nature. This hypothesis, was borne out by the magnitude of the response to nitrogen. The season, in which the crop was grown, also had a profound bearing on the yield increase over the previous years, as the weather throughout closely matched the ideal conditions described by Smith (1967) (sect. 2B v). The object of growing the crop on a light soil, which was to study the effect of moisture stress in the vegetative phase, was defeated by the moist spring of 1972. A little lodging was noted in this experiment at the highest rates of nitrogen. Without knowledge of the yield components no further conclusions can be drawn about the growth of the crop in 1972.

The growth of the two crops (1970 and 1971) which was described in the discussion of the effect of nitrogen is applicable to the discussion of the effect of seed rate on the crop growth. Peak yield was achieved at the same seed rate in both years namely at 213 kg/ha. Yield increased rapidly with the first two increases in seed rate after which the response to increased seed rate was reduced,especially in 1971. (Tables 2:1 and 2:2)

In both years, the tiller number increased with the increased seed rate and the number of grains per ear declined. The resultant number of grains per unit area increased to 213 kg/ha in 1970 and to 157 kg/ha in 1971 (see below).

No. grains per sq. metre	S_1	S_2	S_3	S_4	S_5
1970	12950	15180	15910	17580	16020
1971	9200	9860	11200	11160	10900

Thousand grain weight was the only yield component to respond differently in the two experiments. In 1970, thousand grain weight increased with seed rate to 157 kg/ha before declining, while in 1971, the thousand grain weight declined throughout the range of seed rates. Neither the increase in thousand grain weight in 1970, nor its decline in 1971 were large responses, whereas, the changes in the number of grains per ear and in tiller number were considerable. These three components of yield are all interdependent and are also dependent on the weather. The difference in the response in 1970, from the more usual response of thousand grain weight to change in population (Willey and Holliday, 1971) observed in 1971, was probably the result of a small change in the relative numbers of tillers and grains on each tiller. Such changes would occur in response to population changes which altered maturity dates, resulting in some treatments experiencing slightly different conditions at the critical stages in their development.

The number of fertile tillers, in 1971, was much less than in 1970 but straw weight was greater. Competition was as intense in the second year, however, as shown by the lower grain number per ear and the lower grain weight. This supports the theory proposed earlier that there were a large number of infertile tillers produced in the second year, which increased competition.

In 1971, lodging at the highest seed rates would also be responsible for the earlier reduction in the response, of yield, to increased seed rates.

No. of lodged plots 1971	S_1	S_2	S_3	S_4	S_5	
Extensive	0	1	1	3	3	of 25 plots
Slight	1	0	2	2	4	per seed
Total	1	1	3	5	7	rate.

The number of plants established, per seed sown, has been shown to decrease as the seed rate increases (Holliday, 1960; Oswald, 1970; Holmes et al, 1971), due to some form of competition between the seeds.

In this experiment however, the effect of seed rate on establishment, was only slight in 1970 and the opposite effect was observed in 1971, i.e. emergence per seed sown increased as seed rate increased. Whether there is competition between seeds at emergence is doubtful.

No. of plants emerged per Kg seed sown per Ha.	S_1	S_2	S_3	S_4	S_5
1970	19.6	19.3	19.7	18.6	18.9
1971	17.6	17.0	17.0	17.6	17.5

Small differences, at this stage of growth, are unlikely to have an effect on the later growth of the crop however, as differences in the degree of tillering can quickly compensate for small differences in emergence.

The interaction of nitrogen and seed rate on yield (Tables 2:1 and 2:2), which was significant in both years, was the same interaction reported by Holliday, (1960) and Holmes et al. (1971). It is a positive interaction of nitrogen and seed rate, i.e. the response, of yield, to increased nitrogen, is greater at high seed rates than at low. A similar positive interaction between nitrogen and seed rate was noted in straw weight in 1971. This could be due to the better moisture retention properties of a dense crop (high seed rate), allowing greater utilisation of the nitrogen applied to the crop.

A negative interaction, between nitrogen and seed rate, was recorded in the same year, in both fertile tiller number (Appendix Table 2:8) and thousand grain weight (Appendix Table 2:10). This would be the expected response, as, at low seed rates, the competitive effects of increased nitrogen would not affect these components until higher rates were used and thus, the response to increased nitrogen would be greater at low seed rates.

The varieties grown varied in stature and growth habit.

Height (cm) Cultivar	1970	1971	1972
Clermont	91.4	-	-
Julia	-	94.0	-
Zephyr	86.1	91.7	85.9
Golden Promise	74.3	81.6	71.7
Dwarf A	77.0	75.4	65.8
Dwarf B	71.4	73.3	-

Clermont and Golden Promise are both very erect cultivars, Julia and Zephyr both grow with an erect habit but their heads droop near harvest time, while the two dwarf varieties have a rosette habit for the early part of the season before throwing up flowering heads. The two dwarf varieties were not 'fixed' varieties but were breeder's material which was still heterozygous. As a result, the maturity of these varieties showed a greater degree of variation than a normal selected variety.

The effects of variety on yield were significant in 1970 and 1971 only. The order, in which the varieties were placed, in terms of yield, changed considerably between years. (Tables 2:1 and 2:2) Dwarf A was the lowest yielder in 1970 and the highest in 1971, while Zephyr, which was the highest yielder in 1970, was the lowest in 1971. This change in Zephyr, is probably due, in part, to the more extensive lodging in Zephyr in 1971 (see 2D iv). The change in the position of Dwarf A will be more easily expressed with reference to the differences in the yield components of the varieties, between the two years.

% change in yield and yield components between 1970 and 1971 (% of 1970 values)	Zephyr	Golden Promise	Dwarf A	Dwarf B
Yield	-21.3	-15.4	-11.7	-18.6
Grains per ear	- 4.3	+ 0.9	- 4.9	+ 1.6
Tiller number/sample	-38.4	-29.2	-16.6	-26.9
Grains/sq m	-41.1	-28.8	-20.8	-25.8
1000 gr wt	-10.5	-11.5	- 5.3	-10.8
Straw weight	- 4.3	+15.9	+17.9	+15.7

The largest difference between the two years, is in the number of fertile tillers and thus, in the number of grains per unit area. Dwarf A showed the smallest change in these parameters and Zephyr the largest. The reduction in tiller number could arise due to either, a reduction in the number of tillers produced during the tillering phase or, the failure of a proportion of the tillers produced to reach harvest as fertile tillers

The former, is less likely due to the better weather in the tillering phase in 1971, but if large numbers of tillers were produced, the competition during the poor weather of the ear development phase in this season, would be responsible for the abortion of large numbers of tillers. The competitive stress between tillers was not relieved by improved weather later in the season so the changes of recovery of smaller tillers, would be slight. All varieties would be similarly affected by the weather conditions so the variety differences must have been due to some further factor. The lodging, in Zephyr, could have been the additional factor in the very large reduction in fertile tiller number in this variety, although it produced the fewest tillers in the earlier year when tiller survival was probably greater. Lodging is implicated in the yield reduction of Golden Promise while the large drop in yield in Dwarf B is probably the result of a larger degree of tiller competition in this variety, which produced the largest tiller population in the favourable year.

All varieties showed an increase, or, in Zephyr only, a very slight decline in straw weight between the two years, which supports the suggestion that there were a large number of tillers produced which did not reach maturity in the second year.

The change in grain number per ear between years was slight, as was the difference between varieties within each year. Grain weight however, was reduced in the second year in all varieties. The reduction was least in Dwarf A although it had the greatest number of grains on each ear in each year of the experiment and also, had the greatest number of grains per unit area in the second year. These findings indicate that this variety was more efficient in partitioning the assimilates from photosynthetic activity to the grains than the other varieties. This greater efficiency in the second year is also reflected in the lower reduction in the grain to straw ratio of this variety between years.

Nitrogen uptake by the grain and straw was less in 1971 than in the previous year and the partitioning of the nitrogen between grain and straw changed between years.

	Zephyr	Golden Promise	A	B
% of total N in grain 1970	63.5(4.88)	66.0(3.6)	59.6(4.93)	63.7(4.74)
% of total N in grain 1971	47.5(3.35)	52.8(3.35)	47.6(4.26)	46.5(4.13)

() wt of grain and straw N (g/3175 sq cm).

See also Appendix Tables 2:14 to 2:17

The change in the partitioning was least in Golden Promise and Dwarf A, suggesting a greater degree of independence, of adverse conditions, by these varieties. The total nitrogen taken up by these varieties did not change much between years.

The greater efficiency of Golden Promise and Dwarf A suggested by these findings, is supported by the different responses of the varieties to increase in nitrogen in terms of straw weight (Appendix Table 2: 9) and tiller number (Appendix Table 2:8). Both of these interactions were significant in 1971. With increased nitrogen, Dwarf A and Golden Promise gave a positive response in tiller number, while the other two varieties did not. In straw weight, all the varieties except Julia gave an increase in weight with increased nitrogen. Thus Zephyr and Dwarf B gave an increase in straw weight without a similar increase in fertile tiller number in response to nitrogen which suggests a higher number of infertile tillers in these two varieties at high nitrogen rates. This wasteful production of tillers, would account for the poor partitioning of assimilates to the ear in these two varieties when compared to Golden Promise and Dwarf A, that is, if efficiency is measured in both nitrogen partitioning and in grain to straw ratio. The positional changes in yield between the two years could thus be largely due to the increased competition from infertile tillers in Zephyr and Dwarf B in the second year. Zephyr also showed a greater decline in thousand grain weight (Appendix Table 2:10) with increased seed rate than the other varieties in 1971, possibly due to increased lodging at high seed rates or increased tiller competition.

In the first year of the experiment, the prevailing weather conditions allowed the production of a substantial tiller population which was not placed under a great competitive stress by shortage of light and free tillering varieties were not at a disadvantage. In 1971, however, the evidence suggests, that those varieties which were economical in tiller production were at an advantage over the free tillering varieties which suffered from shortage of light in the later stages of growth in this duller season. The third season's yields suggest that conditions approached the optimum for barley growth and varietal differences were slight, though no yield component data is available to allow a study of the means by which the good yields of the 1972 crop were achieved.

From the comparison of the first two years' results it appears that Zephyr and Dwarf B were more susceptible to the poor conditions of the 1971 season, in that, they appeared to over-produce tillers, which competed with each other to the detriment of the yield. The other two varieties showed a greater stability of yield in the varied conditions under which the three crops were grown. The variation among semi-dwarf varieties thus, seems to be as great as that within conventional varieties in response to different nitrogen and seed rates. Dramatic yield increases resulting from the introduction of dwarf varieties are therefore unlikely. The pattern of response of the semi-dwarf varieties to the changes in fertiliser and seed rate were similar to those of conventional varieties and thus, changes in husbandry practice resulting from the introduction of these varieties, will not be necessary, nor will new testing procedures.

The two dwarf varieties used in these experiments have not been selected for further development. Dwarf A showed pronounced susceptibility to Rynchosporium, while Dwarf B was not sufficiently outstanding to warrant further development, though both are being used in further breeding programmes (Davies and Hayes; Personnal communication).

CHAPTER 3

WHEAT

3(A) Physiology of Grain Production in Wheat. The useable end product of the wheat crop i.e. the grain,represents only a part of the productive effort of the crop. Before any attempt to increase the production of the crop can be made the sources of the grain production must be known.

The grain is made up largely of carbohydrate produced by the photosynthetic system of the plant and transported to the grain by the translocation system. The important aspects of the productive cycle are (1) the source of carbohydrate for the grain, (2) the influence of the sinks in the plant in altering the course of carbohydrate through the plant to the different sinks, and (3) the ability of the sink to accommodate the carbohydrate it receives.

The sources of carbohydrate for the grain in wheat appear to be the photosynthetic tissues above the flag leaf node (Thorne, 1966) which include the flag leaf lamina, the flag leaf sheath, the peduncle and the photosynthetic parts of the ear. This finding has been based on a number of experiments using different techniques. Most of these experiments also attempted to establish the relative contributions of these parts of the plant to the grain yield.

The methods used in these studies were; (1) shading a part of the plant and measuring the reduction in the yield over the yield of a control and thus by subtraction finding the contribution of the part which was shaded, (Thorne, 1965 Quinlan and Sagar, 1962); (2) by introducing carbon dioxide labelled with the Carbon-14 isotope into the separate parts of the plant and measuring the radioactivity of the parts of the plant after a short period of time, during which, the carbohydrate produced using the C_{14} was redistributed through the plant and thus, the sources of the carbohydrate for the grain were found (Rawson and Hofstra, 1969; Marshall and Wardlaw, 1973; Wardlaw and Porter 1967; Patrick, 1972) (3) by using gas exchange chambers which measure the CO_2 used by the various plant parts, (Evans and Rawson, 1970). That the photosynthetic area above the flag leaf node is responsible for filling the grain does not mean that the other leaves are superfluous. The leaves produced earlier are responsible for the provision of the sink for the photosynthetic tissues above the flag leaf node in that they provide the nutrients for the ear in its early development before anthesis and are also responsible for determining the number of ears and grains at anthesis. In addition the flag leaf itself is dependent on the leaves below it in its early expansion stage (Rawson and Hofstra, 1969; Wardlaw, 1968). From the production of the first true leaf, each successive leaf is supported by the leaf, or leaves, below it until it reaches about half of its full size. After it reaches its full size, it, in turn, exports to the leaves being formed above it as well as supplying photosynthate to the roots and to other tillers. (Doodson et al., 1964) The export of carbohydrate from leaves has been well documented at all stages in the growth of the plant but the recurring question remains namely, what factors control the destination of the carbohydrate?

Patrick (1972) studied the pattern of assimilate movement during the stem elongation phase of growth of the wheat plant and concluded that transport down the stem was easier than in the opposite direction, which was consistent with the arrangement of the seive elements in the phloem. He also found that leaf growth was supported by the leaf two below the one being supplied. The largest sinks during this phase of growth were the elongating internodes on either side of the exporting leaf. The upper three leaves were responsible for supplying the developing ear up to anthesis after which the flag leaf was the only one to supply this sink. He concluded that the destination of the assimilates was determined by the size of the sink, its proximity to the source of supply and was constrained by the structure of the vascular system. Rawson and Hofstra (1969) came to a similar conclusion regarding the proximity of the sink to the source of supply. They concluded however that the lower leaves exported downwards preferentially and supported the tillers and roots while the upper leaves supported the stem and ear growth. The supply to roots is secondary to that of shoots if a shortage develops (Wardlaw, 1968). In times of surplus production after the start of stem extension the assimilates can be stored in the stem and can be utilised by the grain at a later stage. (Wardlaw and Porter, 1967; Wardlaw, 1968). The extent of the contribution of the leaves below the flag leaf to the grain either directly (Lupton, 1966) or indirectly via stem storage (Wardlaw, 1968) is generally agreed to be less than 10% of the total ear carbohydrate.

The early growth pattern described shows the pattern of supply of assimilates to various sinks in the main culm of the wheat plant. The number of ears produced in a crop also helps to determine the yield of the crop and so the supply of assimilates to tillers becomes important. The degree of independence of the main stem achieved by tillers in wheat is not clear. Lupton (1966) showed the tillers in his experiment to be entirely autotrophic and even dying tillers did not transfer any assimilate back to the main stem. Rawson and Hofstra (1969) found however that tillers never became independent of the main culm and that photosynthate from the lower leaves of the main shoot was finally incorporated in the ears of the tillers. The proportion of the grain weight made up of carbohydrate from this source was however very small. The effect of tillers on the production of the main culm has been variously reported as detrimental to the main culm (Lupton,1966; Wardlaw and Porter,1967), having no effect on the main culm (Thorne,1966; Bremner,1969), as the carbohydrate and nitrogen of the dying tillers which do not contribute to yield are transferred to the main culm and to surviving tillers, or complimentary to the plant growth in that they improve root development to the benefit of all culms (Stoy,1965). All are agreed however, that the best varieties in recent years have had a large proportion of the tillers produced surviving until maturity and contributing to yield. (Lupton,1966; Thorne,1966: Stoy,1965) The differences found in the dependence of tillers on the main culm could be due to varietal differences (Thorne,1966) or differences in the environmental conditions prevailing.

The size of the ear and the number of ears present are dependent on the early leaves, though the partitioning of assimilates between the various sinks in the early stages of growth is still not clear and the control of this partitioning, whether by demand of the sink or due to supply of the source is likewise not fully understood.

The final yield of grain, assuming an adequate size of ear, is dependent on the activity of the parts of the plant above the flag leaf node, the efficiency of this activity, its duration and the partitioning of the assimilates of this activity (Thorne,1966). Stoy (1965) also pointed out that the respiration of the ear had a large bearing on the final yield of grain as 40% of the total photosynthetic production is respired again.

There are differences in the proportion of the grain weight derived from each of the sources (within the photosynthetic tissues above the flag leaf node). The contribution of the ear in awned wheats is much greater than that of awnless wheat but the photosynthetic area is also much greater and generally the size of the flag leaf is reduced in awned wheat. (Stoy, 1965) Awns can be as much as 46% of the chlorophyll containing ear surface area. (Teare and Peterson, 1971) Estimates of the contribution of the flag leaf, ear, sheath and peduncle to the yield of the grain differ markedly between workers. Thorne (1966) in a review of this topic concluded that in awnless wheats, the type most commonly grown in the United Kingdom, the contributions of the various parts were thus: Ear 0-10%; Flag leaf and Sheath 80-90%; other parts 10-15%. The contribution of the ear may in fact be negative in that the respiration of the ear may be greater than the photosynthesis by its green tissues (Thorne, 1965). Stoy (1965) however argues that the ear contribution could be greater than that suggested by Thorne (1965) on the evidence of Krishnamurthy (1963 and Drennan and Krishnamurthy, 1964) and from calculations based on his own results and those of Gabrielsen (1942). The rates of photosynthesis of the various components of this part of the plant appear to be quite different. The lamina of the flag leaf and the ear seem to have considerably higher rates of true photosynthesis than the sheath and peduncle. All are capable of rapid rates of photosynthesis however. (Stoy, 1965).

The efficiency of the activity of the crop is measured by the net assimilation rate (NAR) which is the dry matter production per unit leaf area. (Watson, 1952) This parameter is largely dependent on the leaf area index of the crop at the time of measurement (Stoy, 1965) as the efficiency is dependent on the degree of mutual shading in the crop.

Differences in NAR between cultivars are small however and only between species are differences large (Watson,1968). This parameter measures changes in the weight of the foliage parts of the crop as well as the grain and another parameter was devised to measure the photosynthetic efficiency in terms of grain production. This is the grain/leaf ratio (G)(Thorne,1966) which measures the increase in grain weight per unit leaf area index of photosynthetic area above the flag leaf node. Differences between varieties are apparent in this measure but these could be due to differences in sink size affecting the partitioning of assimilates (Thorne,1966). More direct evidence that sink size could affect the partitioning of assimilates is given by Evans and Rawson (1970) who deduced that grain growth was not limited by the supply of assimilates, which was found to be adequate at all times after anthesis. Indirect evidence for such an effect of sink size is given by Buttrose and May (1959) in barley and by Welbank et al. (1965) for wheat.

As well as differences in partitioning of assimilates differences in the rate of photosynthesis between varieties are possible (Stoy,1965). The reasons for differences in the grain/leaf ratio are therefore obscure but that differences do exist is certain and in itself is justification for further examination of varieties' performance in this character with a view to seeking improvement in yield through improvement in G.

The largest difference in yield between varieties appears to arise from differences in the magnitude and duration of the leaf area after anthesis i.e. in LAD. (Thorne,1966). This appears to apply particularly to leaf area above the flag leaf node (Welbank et al. 1965). Variety differences in yield could be closely correlated to differences in the duration of the leaf area above the flag leaf node in Welbank's (1965) experiments.

Similarly, Thorne (1966), explained differences in the yield between winter and spring varieties of wheat by differences in LAD. The pattern of leaf growth of the two types was very different as the winter variety had a greater maximum leaf area but a shorter duration than the spring variety.

The partitioning of assimilates has been touched on earlier and it seems that the size of the sink can influence the pattern of assimilate movement through the plant and if the sink size is inadequate yield losses can result (Evans and Rawson,1970). The development of the ear and the environmental and cultural influences on this development will be dealt with fully in chapter 5. The mechanisms controlling partitioning of assimilates at this stage of growth are as obscure as the mechanisms in the earlier growth stages of the crop. The influence of the sink, on the partitioning of the supply from the source is not clear but the proximity of the sink to the source of supply appears to have a considerable bearing on the destination of the assimilates (Wardlaw, 1968). The demand of the sink also influences the pattern of movement and it appears that reproductive sinks have priority over purely vegetative ones (Wardlaw,1968). The drawing power of a sink also seems to be considerable when the supply is limited as Marshall and Wardlaw (1973) reported an increase in the movement of carbohydrate and phosphate from the penultimate leaf to the grain in plants where the culm was partly shaded which reduced the supply. Willey and Holliday (1971) also suggest that sink size can be an important limiting factor to yield. The interactions of this source/sink relationship are at present too complex for firm conclusions to be drawn.

Finally, in this study of factors influencing supply of photosynthate to the grain, the influence of the respiration rate on the available carbohydrate must be considerable (Stoy, 1965). Differences in the rate of respiration have not been examined to any extent due to the difficulty in finding a suitable reference basis for the measurement. Considerable varietal differences have been reported within the cereal species as well as differences between the species which may be another important factor in the determination of the grain yield of cereals. (Stoy, 1965)

Of all the factors examined the most important seems to be the LAD of leaf area above the flag leaf node and to prolong this gives a marked improvement in the yield. The influence of the other factors can be considerable but the true extent of their influence is as yet uncertain due to the difficulty of examining the effect of each factor in isolation but the circumstantial evidence gathered to date suggests that the source/sink relationship could in certain circumstances be of primary importance.

3(Aii) The effect of the Environment and Nitrogen Fertiliser on the Growth of Wheat The grain producing system is dependent on the provision of sinks, the duration of the post anthesis leaf area, the influence of the environment and of cultural treatments on those processes in the plant which have the greatest effect on the yield of the crop. (Thorne, 1966)

Moisture provision, temperature, gaseous exchange and disease all have a marked bearing on the efficiency of the leaves in the crop. Moisture provision affects the early growth of the crop by its influence on tillering. As tiller number is the largest factor to influence leaf area in the early stages of the crop, (Campbell and Read, 1968) the effect of moisture is also noticed in the leaf area. The influence of moisture on the crop at this stage is probably through the effect on the uptake of nutrients. Nitrogen is the most influential of these nutrients and its effects on leaf growth and tiller growth are considerable in both wheat and barley (Chapter 2). Temperature also influences tiller production but the response to temperature seems to be dependent on the daylength response of the variety (Kirby, 1969).

Increased light intensity increases the number of tillers produced while low temperature likewise encourages tillering (Friend, 1966). The translocation system seems to be little affected by moisture but translocation of assimilates out of a wilted leaf is less than out of a turgid one (Wardlaw, 1967).

At the later stages of the growth cycle reduction in moisture and high temperature accelerate senescence which reduces the LAD with a consequent reduction in yield (Thorne, 1966). Wilting of a leaf rapidly reduces the rate of photosynthesis but grain growth seems to be little affected by a short period of wilting (Wardlaw, 1967).

Individual leaves do not utilise light of high intensity to the full but the light passes through to lower levels in the crop (Wilson, 1960). The peak of efficiency appears to be around a mean intensity of 800 foot candles. The intensity of a leaf surface is dependent on the angle at which the light hits the leaf and thus differences in the utilisation of light by varieties with differing leaf inclinations would be expected. Such an effect was noticed by Tanner et al (1966) and Angus et al (1972) with barley and by Vogel et al (1963) with wheat. Upright leaf types were found to be more efficient in utilising light. In saturation light conditions the floppy leaf type should be more efficient as intensity at the leaf surface will not be so great. Findings in support of the latter effect are being made at Cambridge (Ford, Personal Communication). Increase in the density of the top layer of the canopy should lead to a more efficient light utilisation for grain production as the photosynthetic products of this layer are moved to the grain.

Utilisation of light depends on the availability of carbon dioxide. Puckridge (1971) found differences between varieties in the uptake of CO_2 but the predominant influence on the uptake was the leaf area index. There was a close relation between LAI and CO_2 uptake. In another experiment the uptake of CO_2 was predicted from the LAI and the measured respiration which gave a good relation with the actual photosynthesis (Puckridge and Rathowsky,1971). In the latter experiment there was no difference in the photosynthesis of the two varieties although one had upright leaves and the other floppy leaves. The total photosynthesis was measured in this experiment. At the same LAI there need be no difference in total photosynthesis though partitioning of assimilates may very well be different. Thus the proportion of carbohydrate moving to the grain may be different. At peak levels of light intensity the supply of CO_2 can become limiting leading to inefficient utilisation of the light (Monteith, 1966)

Total leaf area can be increased with nitrogen but excess causes lodging which results in a marked loss in yield.

Little alteration can be made to the effects of environmental conditions. Delay in leaf senescence after anthesis would bring the crop into a period of shorter days with lower light intensities which would not give as great a yield advantage as might be expected and harvesting difficulties would also be increased. Earlier anthesis would however have a beneficial effect in this country as this would bring the grain growth period nearer to coincidence with the period of maximum daily radiation but provision would still have to be made for an adequate sink. Control of leaf growth by fertiliser and by plant population manipulation remain the principal means by which yield can be influenced.

3(Aiii) The Growth and Yield of Dwarf and Semi-Dwarf Wheats

Since the first successful variety, Gaines, with semi-dwarf growth habit was introduced in U.S.A., breeders throughout the world have bred other semi-dwarf varieties which have been tried and tested against tall varieties in their own region. In other parts of the world where breeding is not so advanced semi-dwarf varieties have been imported and compared directly with the indigenous varieties. These studies have for the most part dealt with the yield of the varieties and the main yield components with little further physiological study which might have further improved the understanding of any differences found and could have revealed hidden potential in these varieties.

In the United States several such experiments have been conducted which have attempted to evaluate the semi-dwarf growth habit for the different regions of wheat production. Briggle and Vogel (1968) reviewed a number of such evaluation experiments and reported that semi-dwarf varieties were being grown successfully in the Pacific North West region and in the Eastern soft wheat region though difficulty was being encountered in the Central States. This difficulty arose through the lack of suitable sources of disease resistance and drought tolerance. Successful semi-dwarf varieties have been produced in some of the Western States (Johnson et al.,1966 and Porter et al.,1964) and in some Eastern States (Vogel et al.,1963). In Australia even under the extreme conditions of the Ord river valley where wheat is ripening in increasing temperatures, semi-dwarf varieties imported from Mexico have been grown with success (Beech and Norman,1968). Mexican varieties were also imported by India and the countries of the Near East and were grown with success with irrigation and nitrogen fertiliser though disease problems are now becoming more acute in these regions (IARI,1968; CIMMYT, 1970 and 72).

No consistent behaviour in terms of yield components emerged from these studies. Some workers found grain size to be small in the semi-dwarf varieties (Johnson et al., 1966; Misra et al., 1968) while others found grains to be larger than conventional varieties (Berbigier, 1968). The variation among the semi-dwarf varieties seems to be as great as that in the conventional varieties. In all trials where nitrogen rate was varied the semi-dwarf varieties exhibited a greater degree of lodging resistance than the control varieties (IARI, 1968; Porter et al., 1964; Vogel et al., 1963; Paquet, 1968 etc.) The shortness of the coleoptile which is associated with semi-dwarfism, and the overcoming of this drawback have been discussed (Chapter 1).

Studies in slightly greater depth carried out in India (IARI, 1968 and Asana and Chattopadhyay, 1970) showed that the yield advantage of Sonara 64 (Mexican) over NP876 (Indian) was almost entirely due to the resistance of the former variety to lodging under highly fertile conditions. Slight differences were noted in the rate of tiller production and in the rate of ear filling but these were too small to affect the yield.

In two Australian studies, those of Beech and Norman (1968) and Syme (1967), the yield advantage of the semi-dwarfs was attributed to a longer period of growth between anthesis and maturity.

In the United Kingdom both imported and home bred semi-dwarf varieties have been studied in comprehensive physiological experiments. (Thorne et al., 1968,69,70 and 71; Lupton et al., 1970,71 and 72). The series of experiments carried out at Rothamsted (Thorne et al., 1968,69,70 and 71) used imported cultivars. Three spring wheats were studied; Mexico 120, Lerma Rojo 64 (both Mexican semi-dwarf) and Kloka (European commercial variety) and two winter wheats; Gaines (American semi-dwarf) and Cappelle. In the early experiments more semi-dwarf material was used but this was dropped for the later study. The semi-dwarf varieties yielded as well as the conventional varieties although they had smaller leaf areas and were susceptible to diseases. The mechanism of this apparent increase in efficiency was sought and it appeared from early experiments that the semi-dwarf varieties were more efficient in utilising the product of the leaf area after anthesis for grain production. Plant density was varied to achieve the same leaf area in both semi-dwarf and conventional varieties and it was found that at the same leaf area the proportion of the photosynthetic product utilised in grain production was the same in both the semi-dwarf and conventional varieties and that the greater apparent efficiency of the semi-dwarf cultivars was derived from a reduction in mutual shading at lower light intensity when leaf area index of the dwarfs was lower than the conventional varieties in the previous experiments, (Thorne, 1970). Any residual improvement in efficiency was accounted for by the fact that the semi-dwarf varieties had awns which were absent in the European cultivar. In the most recent experiment comparing Penjambo 62 (Mexican semi-dwarfs) and Kloka at Rothamsted (Thorne, 1972) the increased efficiency of the semi-dwarf was not apparent.

Experiments at Cambridge using home bred semi-dwarf cultivars and thus avoiding the danger of large differences in disease susceptibility, showed that the semi-dwarfs had a greater rate of photosynthesis at the same LAI than the control varieties (Lupton et al.,1970,71, 72). A greater proportion of the leaf area after anthesis in the semi-dwarf cultivars was in the form of leaf lamina area which has been shown to photosynthesise at a greater rate than leaf sheaths or ears (Stoy, 1965). While the photosynthetic efficiency was greater there was no apparent difference in the proportion which was used in the production of grain.

These varieties had no awns and are thus not directly comparable with those which were studied by Thorne and her co-workers at Rothamsted. The semi-dwarf cultivars grown by Lupton had a greater number of tillers on each plant but of these a higher proportion contribute to yield and thus there is no indication of a larger proportion of carbohydrate being used in unproductive tillers. (Lupton et al.,1972). Yields of the varieties grown by Lupton, which were the same varieties as those grown in the experiment reported in 3B were greater than those of the conventional varieties with which they were compared.

Yield improvement in Australian semi-dwarf wheat varieties was attributed to a larger sink for the carbohydrate being provided relative to the leaf area after anthesis (Syme,1969). A similar result was found by Cock (1969) in U.K. using imported North American semi-dwarf material. The highest yielding semi-dwarf variety had the largest number of grains per ear while differences in ear population or grain size could not be related to the differences in the final yield. Efficiency of utilisation of tillers in the semi-dwarf varieties was again reported in this work (Cock,1969).

Physiological studies in Mexico have been carried out in the last two seasons (Fischer, Personnal comm.). These studies have been conducted at two levels. Agronomic studies have been made to establish whether there is a need for changes in farming practice to make the best use of the dwarf character and physiological studies have been conducted from the standpoint that some character of the growth of wheat is limiting the yield of crops i.e. the source of carbohydrate is limiting yield or the sink is too small to accommodate the carbohydrate produced. Preliminary studies of the influence of the sink appeared to support the view that the sink was inadequate as the yield increased markedly when the number of grains was artificially increased on a given area but the grain size remained the same. The effect was not so marked in the second year but temperatures were higher at the grain filling period in this year. Thorne (1972) found temperatures above 20°C increased the rate of senescence and also increased the contribution from the stem storage of the early part of the season, suggesting that the sink size is not limiting under these conditions. In the Mexican experiment of 1971-2 (Fischer, Personnal communication) temperatures were within the range where these conditions apply and the increased radiation accompanying the increased temperature seems to be insufficient to overcome the effect of the temperature. Under certain conditions it is probable that sink capacity can limit yields.

In the agronomic studies the semi-dwarf varieties appear to be able to utilise a wider range of conditions of fertiliser usage and seed rate than conventional varieties though there is a wide range within the semi-dwarf type in terms of response. The two gene dwarfs have a much greater harvest index than the conventional varieties but tripple gene dwarfs show no further improvement in this parameter suggesting a limit in the shortness of the straw may have been reached (Fischer, Personnal comm.).

Yield of wheat grown under ideal husbandry conditions seems to have reached a plateau especially in those countries where extensive breeding work has been undertaken over a prolonged period (Fischer 1972). Even the introduction of dwarf wheats in Mexico while lifting the yield from a low point to a much higher one now seems to have reached a limit as yields are levelling off. Further understanding of the limits which are now being imposed by the plants in a crop by way of insufficient grain capacity or a shortage of photosynthetic tissue would help to break down the next barrier to further increases in yield.

3:B Experimental Methods

(i) Wheat experiments 1970-71 and 1971-72. An experiment was made in each of the two years 1970-71 and 1971-72 in which five varieties of wheat were compared under five rates of nitrogen. The experimental design was the same in both years and was a 5 x 5 randomised block design in which the third order and some of the second order interactions were confounded to constrain the block size to five plots per block. The design was balanced by having four replicates (Nair, 1940).

Five varieties were sown at approximately 235kg/ha., account being taken of the thousand grain weights in an attempt to sow the same number of grains of each variety. The varieties sown were TL363/30, TL365a/34, TL365a/37, all semi-dwarf varieties from the Plant Breeding Institute at Cambridge, Maris Nimrod, a medium height variety in commercial use and N59, a tall variety grown only for its extreme straw length. The experiments were sown on the farms of the Edinburgh School of Agriculture on a Macmerry series (Soil Survey of Scotland) sandy clay loam in 1970-71 and on an alluvial fan in 1971-72. The 1970 crop was the first after a two year ley and that of 1971 the first crop after potatoes.

Plots were 1.54 m wide by 6.15 m and were eight rows wide with 15.4 cm between the rows. The experiments were sown with a plot seed drill designed and manufactured at the Scottish Society for Research in Plant Breeding (Cameron et al, 1967).

The experiment was sown on 7th December 1970 after ploughing and two runs of the disc harrows in fine dry weather and on the 3rd and 4th November 1971, except for one replicate which was sown on 9th November.

In 1971 the land was ploughed and cultivated with a spring-time harrow.

The five nitrogen rates which were applied on 1 May 1971 and 17 April 1972 were as follows:

1971 N_0 - 0kg/ha
N_1 - 31 "
N_2 - 63 "
N_3 - 94 "
N_4 -125 "

1972 N_0 - 0kg/ha
N_1 - 40 "
N_2 - 80 "
N_3 -120 "
N_4 -160 "

Weed control was affected by spraying with Actril C (Ioxynil with Mecoprop) on 14 May 1971 and on 19 May 1972, spraying at 7 Litre/ha.

The crop was harvested with a Hegge 125 plot harvester on 16 September 1971 and on 27 September 1972. Grain was dried on a bag drier and cleaned before weighing. When the grain was weighed a sample was removed for dry matter determination. 3.1 m of plot were combined each year and all 8 rows of the plot were taken.

(ii) Sampling procedure. One half of each plot was used for sampling and half preserved for the final harvest. Samples were taken from one half metre length of two adjacent rows and each sample 'site' was protected by at least on intact row. In 1971 the plots were sampled approximately fortnightly, the sample site from each plot being chosen at random. All the tillers from two sites in each plot were harvested and taken to the laboratory for leaf area measurement and dry weight determination as described in the next section. The time involved in the measurement of leaf area meant that only part of the experiment could be sampled on each day, so sampling was spread over 3, 4 or 5 days, depending on the work force available. The sampling dates in 1971 were 20-26 May, 7-9 June, 28 June - 2 July, 19-21 July and 9-11 August.

In 1972 the method of leaf area measurement was changed and this enabled all the plots to be sampled in two days. 10 whole plants, 5 from each of two separate drills were taken from each plot in 1972. All the plots were sampled from the same position in the plot at each sample date to speed the sampling process. These plants were taken to the laboratory for leaf area measurement by the second method described in the next section (3:B iii). The first sample from each plot was taken at anthesis when 50% of the ears on the plot had one half of the anthers visible on the outside of the ear. This sample differed from those subsequent to it in that all the shoots were taken from 4 x $\frac{1}{2}$ m length of row from two pairs of adjacent rows. Tiller number, leaf area and dry weight were determined from this first sample. Sample two was taken on the 12-14 July from those plots which had reached anthesis and had therefore been sampled previously. Samples were taken weekly from all plots subsequent to this, until both flag leaf and ears on the plot were deemed to be greater than 85% senesced, after which only one more sample was taken to determine the extent of the senescence of the flag leaf sheath and the peduncle. Field senescence estimation was made on each plot one week after the last sample to establish the date of final senescence.

In addition to these samples for leaf area measurement, non-destructive measurement of emergence of plants was made on 4 February 1971 and 30

December 1971. Tiller counts were taken on 10 May 1971 and just before harvest in 1972 on 12-13 September. These counts were made on two separate metre lengths of row. Height measurement was made on all plots on 28 July 1971 and 11 September 1972. The degree of lodging was measured when it first occurred and on subsequent dates.

(iii) Leaf area measurement. A different method was used in each year. In 1971 a modified version of that used by Thorne (Thorne and Watson, 1955) was used which was dependent on rating the individual shoots. The sample was collected in the field as described in the previous section. The total number of shoots in the sample was determined. Of these, 20 were laid aside for rating. A number of standards representing the range of shoots in the field were selected to represent the range of leaf area. These were arrayed near the operator. The operator looked at each shoot of the sample of 20 shoots and rated it according to the scale of standards, taking care to look only at leaf area without confusion with length, colour or any other distraction. The rating awarded to each shoot was noted. Of these 20 rated shoots, 5 were measured for leaf area on a light interception meter. The leaves were stripped off the shoot and placed as flat as possible on the glass plate of the meter and the reading on the associated galvanometer was noted. At the end of each sample the regression of the log of leaf area, calculated from the galvanometer reading for each shoot, on the rating for each shoot was calculated. It was found that the leaf area did not give a straight line when plotted against rating but that the log of the leaf area did and therefore the log of leaf area was used to calculate the regression. The regression coefficient and intercept on the axis were calculated for each variety and nitrogen rate and these were compared by analysis of variance to test whether the assessment of leaf area was influenced by treatment. No significant differences were found between varieties or nitrogen rates in the regression coefficient and therefore the combined coefficient was used to calculate plot leaf area for all plots, on the one sampling date. This was calculated by using the mean rating of the 20 plants and converting this to an area by the regression coefficient of the log of the leaf area on rating taken from the 5 plants on which rating and measurement were made. This area was multiplied by the number of shoots in the sample to give the leaf area over the sample area. In this method the areas of the ear, the stem and the peduncle were not considered but the areas of all the leaves were.

In 1972 a more direct measurement was made which only took account of the leaf area above the flag leaf node. A sample of ten plants was taken from the field as described in 3:B (ii). These plants were divided into main and auxilliary shoots. The linear dimensions of the various parts of the shoots were measured with a ruler. The length of the ear from the collar to the tip of the glume of the terminal spikelet was measured and the breadth both ways at the middle of the ear. The length of the stem from the top of the flag leaf node to the collar and the breadth at the node and the collar were measured to determine the area of the flag leaf sheath and peduncle. The flag leaf itself was removed from each shoot and all these were collected from the main and auxilliary shoots separately and were measured on the leaf area meter described in the previous method. In 1972 the leaves were held flat with transparent adhesive tape.

The photosynthetic area above flag leaf node of the sample of ten plants was thus established and with reference to the tiller counts taken in the first sample, the leaf area per unit ground area could be calculated.

The surface areas were calculated as follows:

Surface area of the ear (Se)

$Se = 2(LxB_1) + (LxB_2))$ L - Length of ear

B_1 and B_2 - Breadth of ear both ways.

Surface area of sheath and peduncle (Sp)

$$Sp = \frac{2\pi D \times L}{4}$$

i.e. one half the area of a cylinder where L is the length from the collar to the top of the flag node and D is the mean diameter of the diameter at the collar and at the top of the flag leaf node. Half the area was taken as the peduncle and sheath were found by Stoy (1965) to be half as efficient as the leaves in photosynthesising.

3:C Results of wheat experiments. There was a large difference between years in both the weather (Appendix 1) and the yield. The mean yields were 5015 kg/ha in 1970-71 and 6797 kg/ha in 1971-72. The yield response to nitrogen was similar in both years, with yield showing a sharp rise with the first two rates of nitrogen and then a slight reduction in the response to nitrogen (Table 3:1). Yield results of both experiments are presented in Table 3:1.

The interaction of variety and linear nitrogen on yield was significant in 1971. The maximum yield of TL363/30 was achieved with 63 kgN/ha and that of N59 with 94 KgN/ha. The other three varieties gave a response to all rates of nitrogen (Table 3:1).

CHAPTER 3

Table 3:1 Yield of Wheat (kg/ha)

1970/71

	kgN/ha		TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
Nitrogen	N_0	0	4880	4802	3376	4372	3751	4236
Rate	N_1	31.4	5220	5162	4218	5419	4258	4855
	N_2	62.8	5786	5692	5000	5738	4312	5306
	N_3	94.2	5592	5719	4863	5908	4328	5282
	N_4	125.6	5597	6152	5215	6180	3865	5402
	Mean		5415	5505	4534	5523	4103	5015
	SE		208.65		93.31			

Significant Effects NL** NQ** Cv** Cv x NL**

1971/72

			TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
	N_0	0	5150	5456	5168	5055	4306	5027
	N_1	40	6399	6852	6541	6511	5423	6345
	N_2	80	7557	8503	7089	7208	6406	7352
	N_3	120	8252	8033	7828	7632	6587	7667
	N_4	160	7990	8269	7451	7826	6428	7593
	Mean		7070	7423	6815	6847	5830	6797
	SE		583.0		231.6			

Significant Effects NL** NQ** Cv**

i) Response of yield components to nitrogen and variety.

The pattern of response of the yield components to nitrogen was similar in both years of the experiment (Table 3:2).

Table 3:2 Effect of Nitrogen on the Yield Components

1970/71	N_0	N_1	N_2	N_3	N_4	Signif. Level
Kg nitrogen/ha	0	31	63	94	126	
Yield (kg/ha)	4236	4855	5306	5282	5402	
Height (cm)	87.8	95.5	90.2	94.4	93.1	4th*
1000 grain weight (g)	43.5	44.1	41.6	39.8	38.3	lin ** quad*cub*
Ear number/.305 m	137	134	144	151	154	lin**
Grains/ear	20.5	21.8	26.1	27.9	28.4	lin**cub*
Grains/sq m	9208	9591	12318	13823	14325	lin**
Straw weight (g)	221.5	238.1	269.2	296.6	308.1	lin**
Grain/straw ratio	.5594	.5532	.5790	.5681	.5487	NS
1971-72						
Kg nitrogen/ha	0	40	80	120	160	
Yield (kg/ha)	5027	6345	7352	7667	7593	
Height (cm)	92.7	99.4	100.5	99.9	98.7	lin**quad**cub**
1000 grain weight (g)	46.4	46.7	46.1	46.3	43.4	lin**quad**
Ear number/.305 sq m	145	158	170	190	196	lin**
Grains/ear	30.0	34.6	38.2	39.0	39.5	lin**
Grains/sq m	10834	13587	15948	16599	17495	lin**

The only variation in the response between the years was in thousand grain weight where the decline with increased nitrogen did not occur in 1972 until 160 kgN/ha was applied but in 1971 this decline occurred with only 63 kgN/ha. For the other parameters, the response was similar between years but the extent of the response was greater in 1972 than in 1971.

Straw weight was measured in 1971 which allowed the calculation of grain to straw ratios. The response of this parameter to nitrogen was non-significant however.

The behaviour of the five varieties in the two years is shown in Table 3:3.

Table 3:3 Effect of Variety on the Yield Components

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Signif
Yield (kg/ha)	5415	5505	5523	5523	4103	
Height (cm)	88.0	81.2	85.0	91.2	115.5	
1000 grain weight (g)	41.81	40.42	44.28	44.38	36.33	**
Ear no./.305 sq m	144	155	137	134	150	*
Grains/ear	27.25	26.27	21.69	26.96	22.54	**
Grains/sq m	12866	13350	9743	11845	11085	**
Grain/straw ratio	.641	.634	.544	.591	.398	**
Straw weight	252.2	256.4	241.5	271.9	311.7	**

1971/72

Yield (kg/ha)	7070	7423	6815	6847	5830	
Height (cm	94.5	83.9	96.6	95.4	120.8	
1000 grain weight (g)	47.57	42.87	45.29	52.08	41.12	**
Ear no./.305 sq m	176	176	168	174	167	NS
Grains/ear	36.50	41.79	37.44	34.51	30.99	**
Grains/sq m	14862	17315	15047	13147	14178	**

All varieties showed an increase in yield over the previous year in 1972, which, the yield components showed, was largely due to an increase in the number of grains per unit area. TL365a/37, which showed the largest increase in yield between the years of the experiment, also gave the greatest increase in grains per unit area. Both numbers of grains and the size of grains increased in the second season. Varieties differed in the response of grain to straw ratio to nitrogen in 1971 (Appendix table 3:1). N59 had much lower ratios throughout the range of nitrogen applied but also showed a decline in the ratio as nitrogen usage increased. All the other varieties had a peak of this ratio at 63 kgN/ha or above.

The interaction of linear nitrogen and cultivar on 1000 grain weight was significant in both years. All the semi-dwarf varieties and N59 showed a decline in 1000 grain weight in 1971, with increase in nitrogen above 32 kgN/ha. Only Maris Nimrod showed an increase in 1000 grain weight up to 63 kgN/ha in 1971. A similar response occurred in 1972 where all varieties of semi-dwarf habit had the highest 1000 grain weight with no nitrogen but N59 and Maris Nimrod had their peak of 1000 grain weight at 120 kgN/ha (See Appendix table 3:2).

The 1971 response of the cultivars, in grain number per ear with nitrogen, differed significantly also (Appendix table 3:3). TL365a/34 and TL365a/37 responded with an increase in grain number to all rates of nitrogen but N59 and Maris Nimrod responded up to 63 kgN/ha and TL363/30 to 95 kgN/ha. In 1972 the interaction was non-significant but N59 and Maris Nimrod again showed a response up to a lower rate of nitrogen than the other varieties (Appendix table 3:3).

Leaf areas were measured in both years but in 1971 the area of all the leaves on each shoot was measured and the area of the stem and ear was ignored. In 1972 the area of all the photosynthetic tissue above the flag leaf node was measured. Thus a comparison, of the leaf area, between the years, is not possible. The 1971 measurements show the growth of the whole plant in dry weight and leaf area, while those of the 1972 experiment, concentrate on the production of grain. (Figs. 3:1A, 3;2A)

Values of Net assimilation rate (NAR) were calculated between the various samples in 1971. The calculation of NAR is dependent on the constancy of the relationships, Leaf area: time and Dry weight: time over the intervals between samples (Watson, 1952; Radford, 1967). For periods of a week or less, the assumption of a constant relation is feasible, but for the 3 week periods between samples in this experiment, the assumption of constancy of the relationships becomes doubtful. The values of NAR presented in table 3:4 should therefore be treated with caution.

Figure 3:1 A Leaf Area Index vs Time (1970/71)

Variety Means

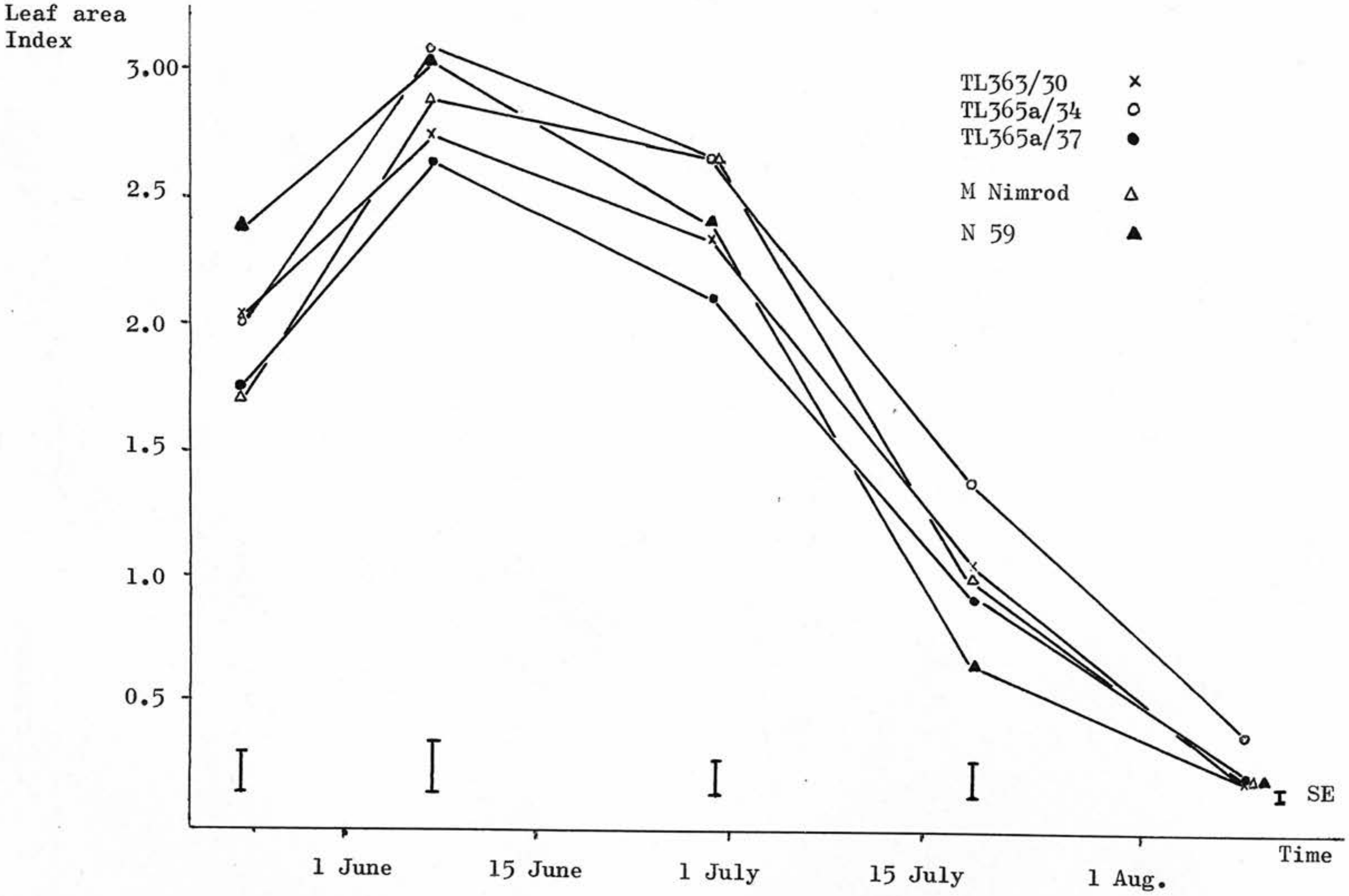


Figure 3:1 B Dry Weight Accumulation with Time (1970/71)

Variety Means

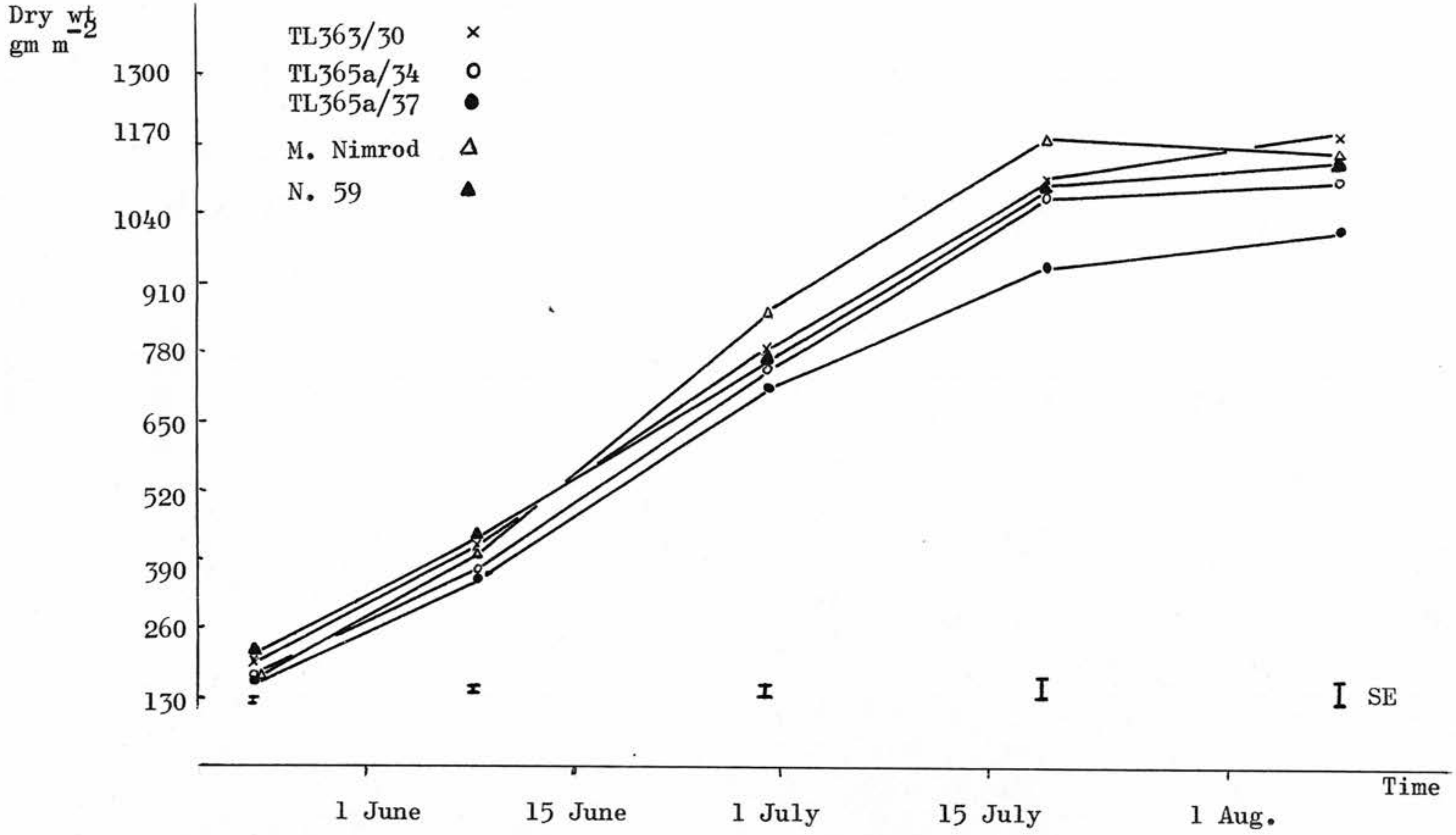


Figure 3:2 A Leaf Area Index vs Time (1970/71)
Nitrogen Means

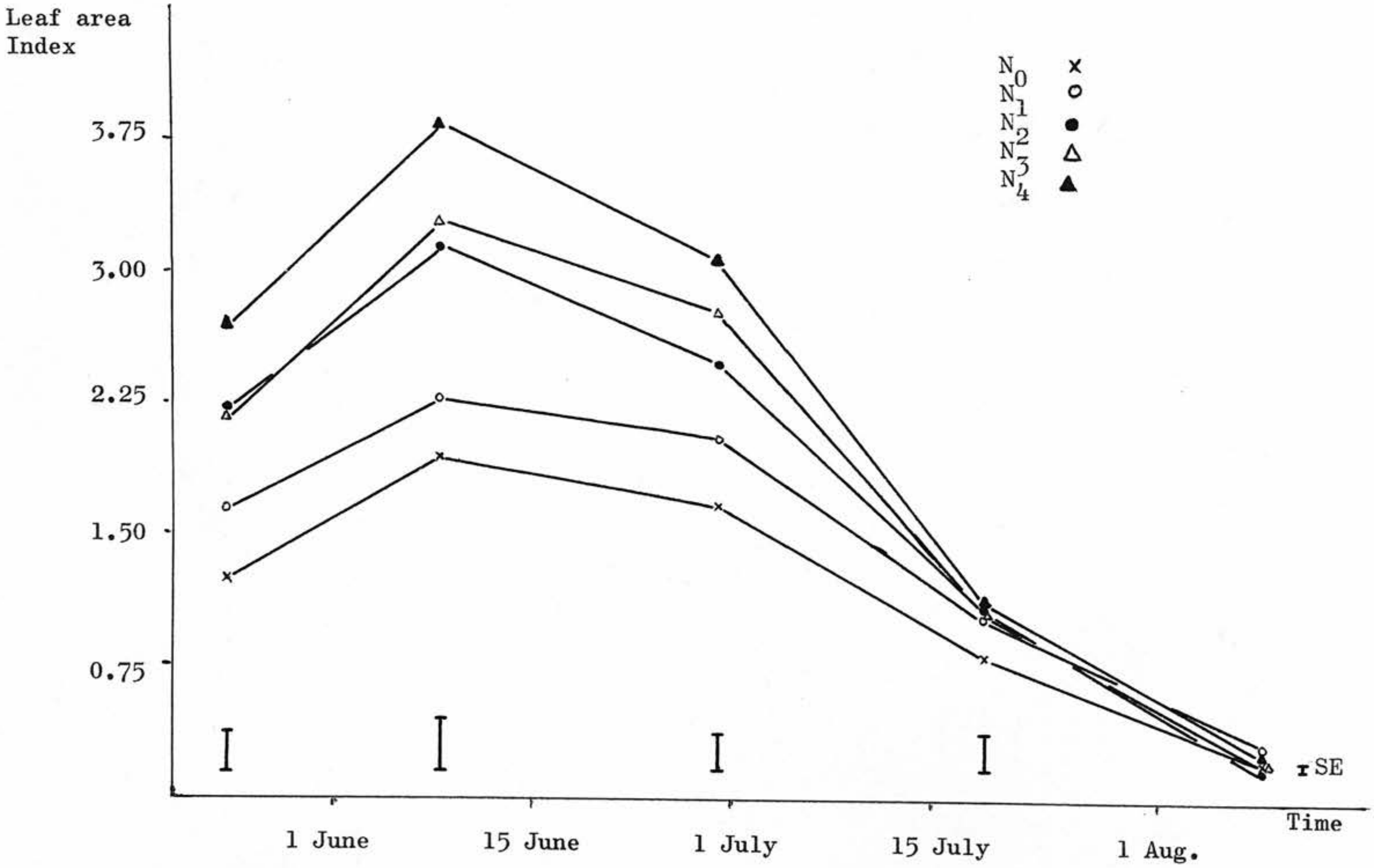


Figure 3:2 B Dry Weight Accumulation with Time

Nitrogen Means (1970/71)

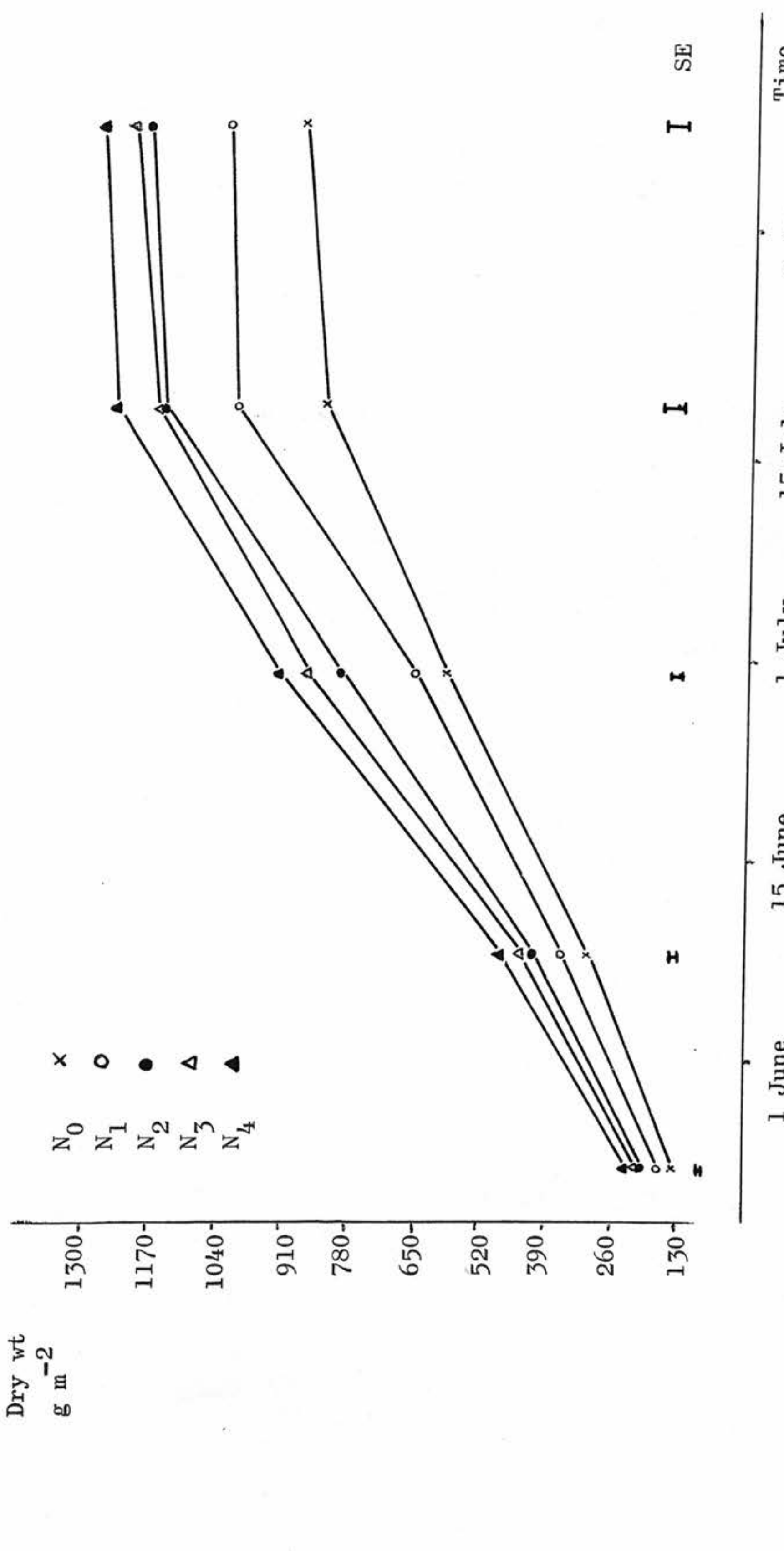


Figure 3:3 Effect of Time and Variety on Tiller Number (1970/71)

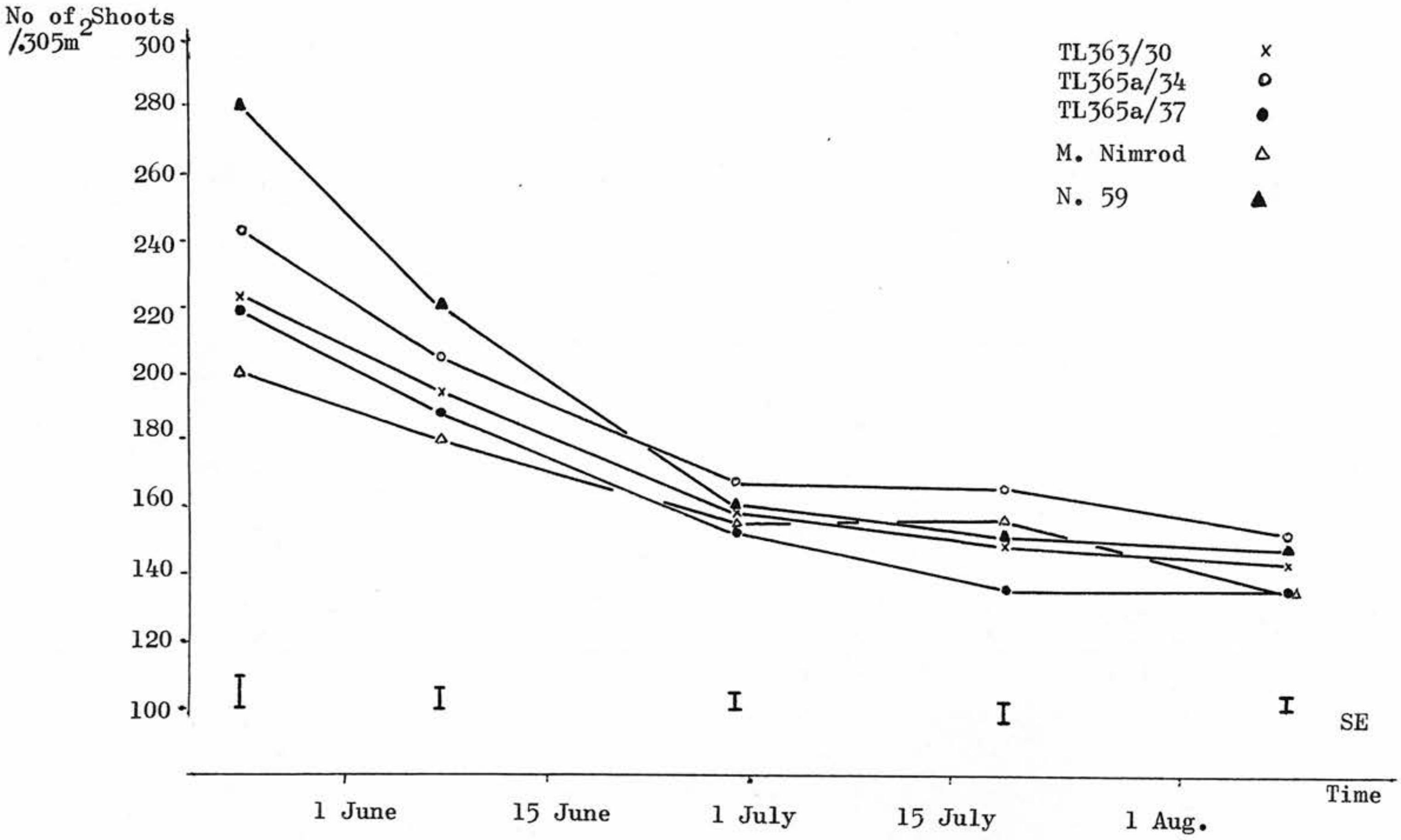


Figure 3:4 Effect of time and Nitrogen on Shoot Number (1970/71)

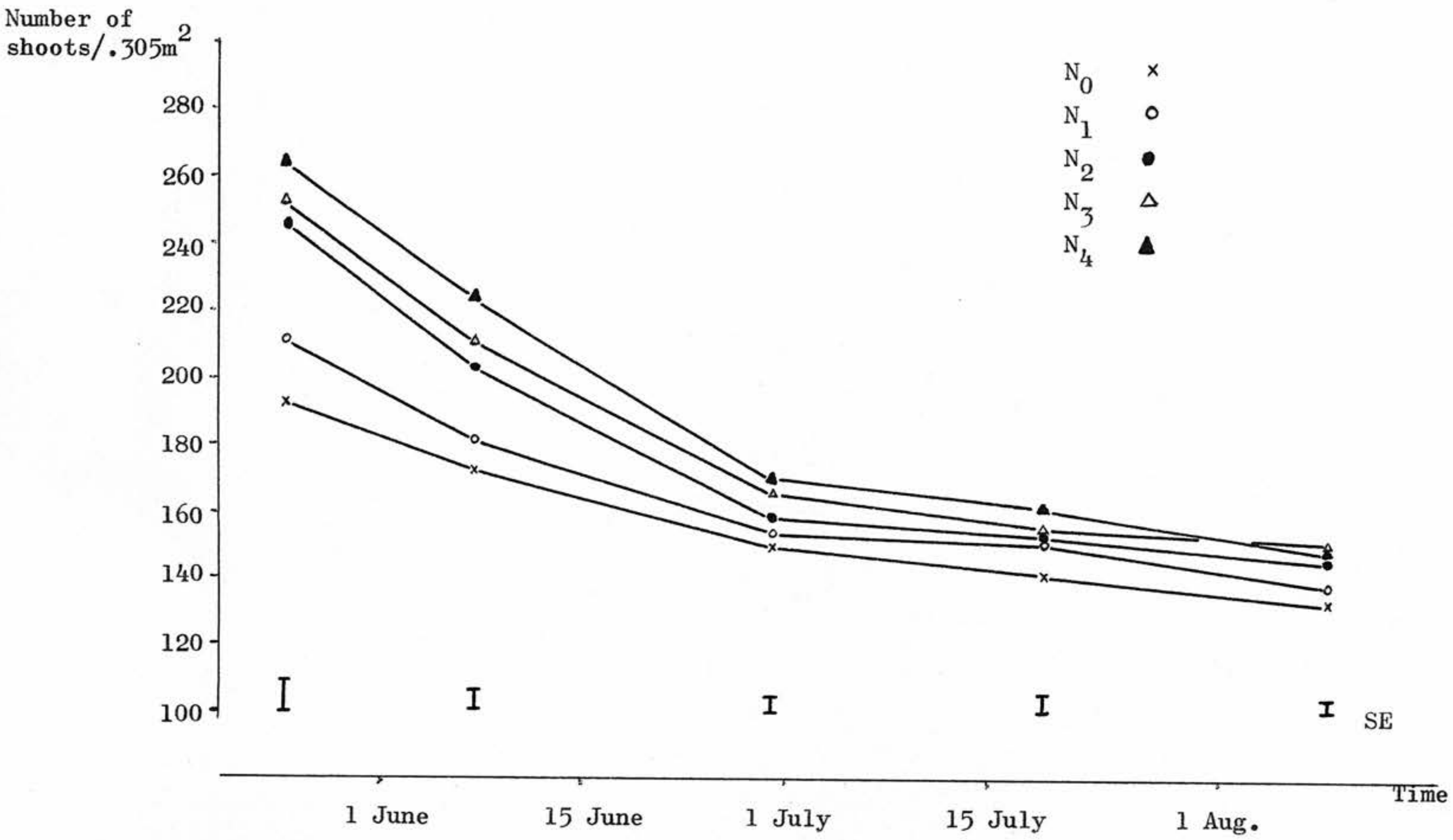
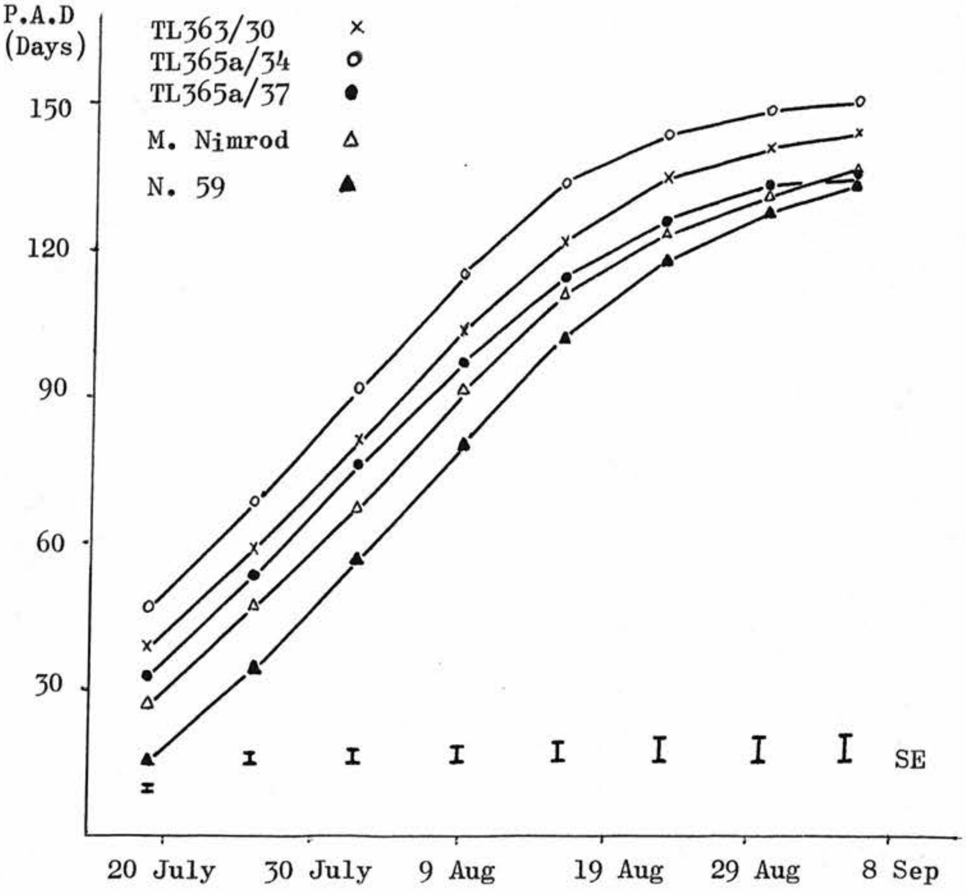


Figure 3:5 P.A.D. on Sample Date

A. Variety Means



B. Nitrogen Means

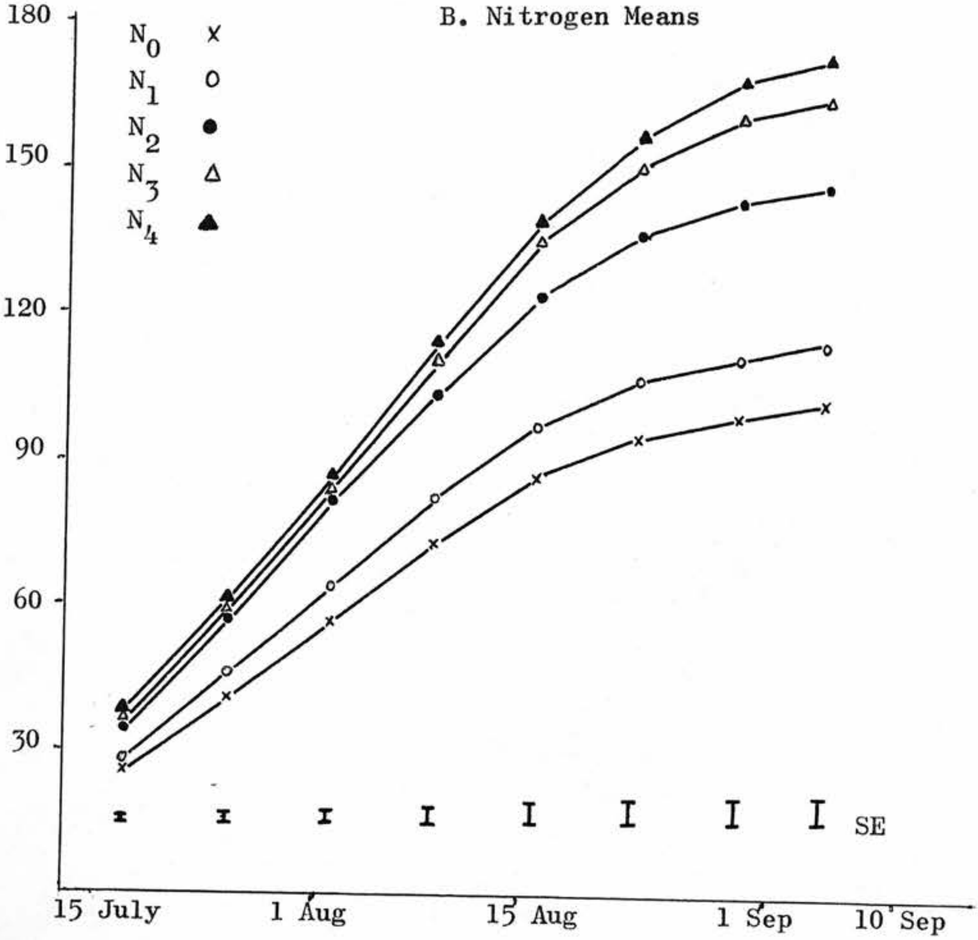
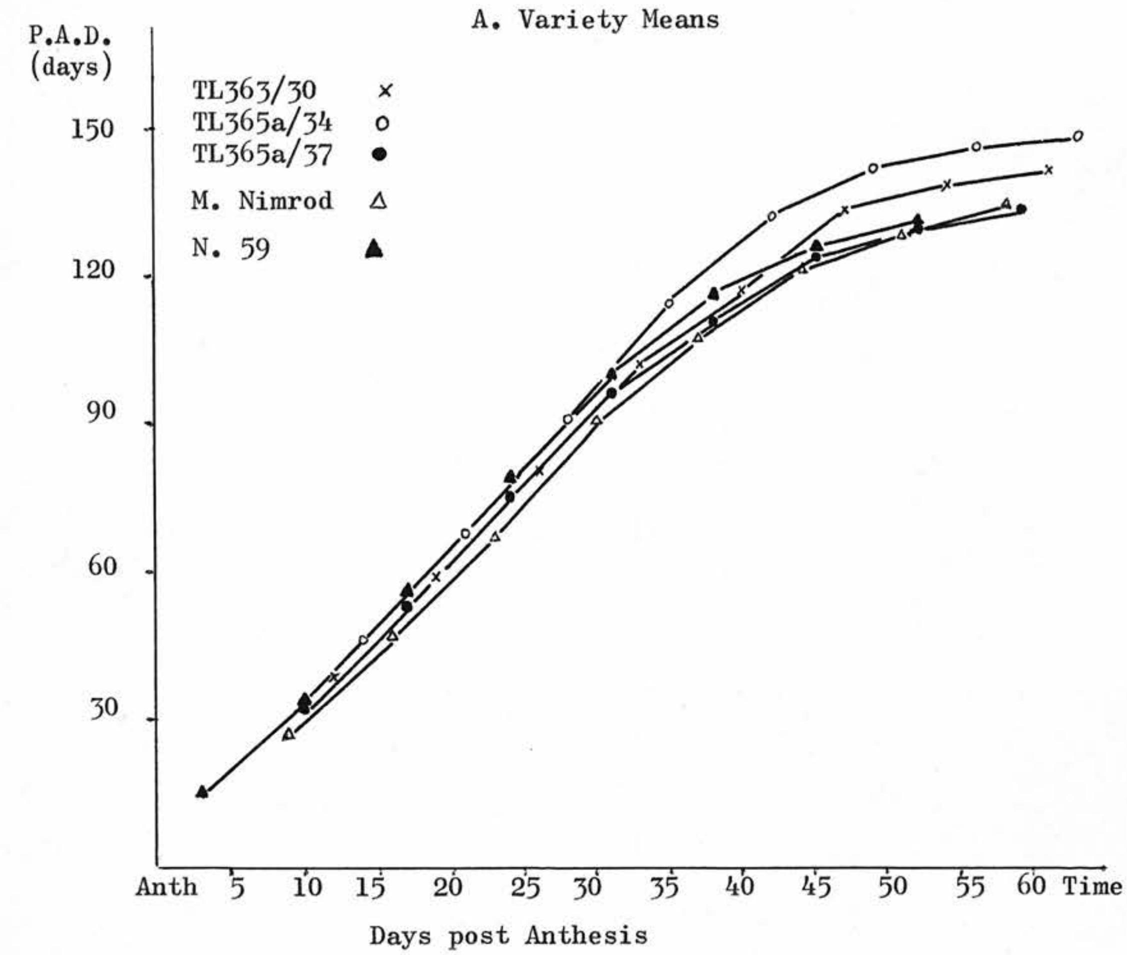
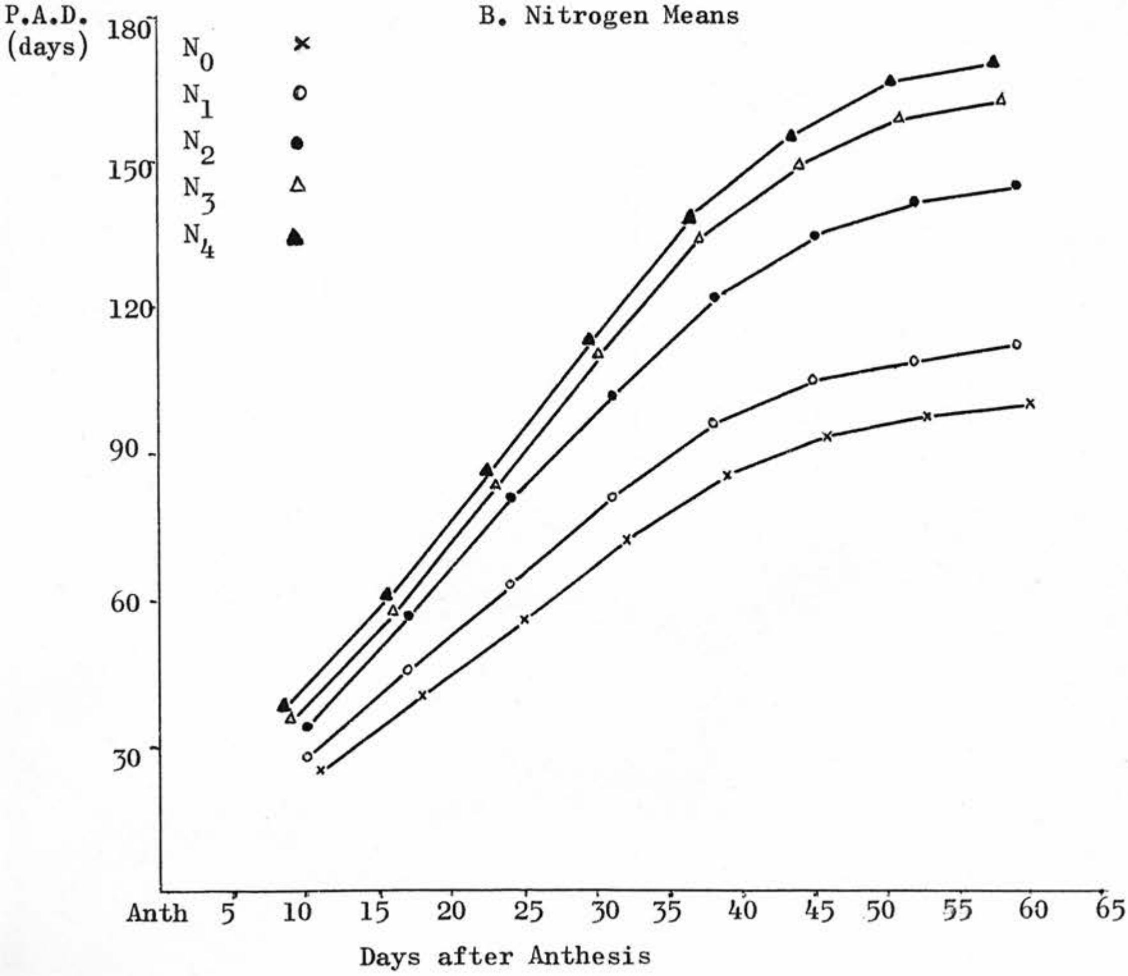


Figure 3:6 P.A.D. on No of days post Anthesis (1971/72)



A. Variety Means



B. Nitrogen Means

table 3:4 The Effect of Varieties and Nitrogen Rates on NAR

NAR gm dm^{-2} wk^{-1}	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59
24/5 - 8/6	.4605	.3682	.4241	.4749	.3981
8/6 - 30/6	.4741	.4670	.5560	.5457	.4284
1/7 - 20/7	.8070	.6363	.5504	.7168	.9585
21/7 - 10/8	1.4348	.3823	.3957	-.4006	-.2343

	N_0	N_1	N_2	N_3	N_4
24/5 - 8/6	.5013	.4617	.3827	.4081	.3720
8/6 -30/6	.5343	.5538	.4694	.4685	.4452
1/7 - 20/7	.7405	.7305	.7911	.7046	.7023
21/7 - 10/8	.3045	-.2484	-.0204	1.0370	.5052

Coefficients of variation were very high in these derived variates, particularly in the last (21/7 - 10/8), where the points lay on either side of zero. The interaction of nitrogen and variety, in the third NAR (1/7 - 20/7), was significant, as TL365a/34 and N59 both had increasing NAR with increase in nitrogen (Appendix table 3:4).

Tables of leaf area and dry weight at the five sample dates are presented in Appendix tables 3:5 to 3:9. Variety and nitrogen means are plotted in figs 3:1 and 3:2. Leaf area values were very skew and the analysis of variance was therefore calculated on the square root transformation of the data.

Significant effects quoted in the tables are from this transformed data analysis. The area of leaf on each shoot was assessed in the course of calculating total leaf area. Log values of these areas are presented in Appendix table 3:19 and 3:20. Only main effects are given as no interactions were significant.

In the measurement of the leaf area, the number of shoots on the sample area of .305 sq m were counted, at each sampling date. The response of this parameter, to variety and nitrogen rate and the decline in number with time, are clearly shown in figures 3:3 and 3:4.

The measurement of leaf area in 1972 was carried out from the day the plot reached anthesis and was measured thereafter, at weekly intervals, on the Tuesday and Wednesday of each week, half the plots on each day. The total photosynthetic area above the flag leaf node was measured. Measurements were recorded in such a way that the proportion of the total photosynthetic area comprised of flag leaf lamina area, flag leaf sheath and peduncle area and ear area could be determined at each date, as well as the total photosynthetic area.

Total photosynthetic area index (PAI) at three sample dates and the proportion of the lamina, stem and ear at these dates are presented in table 3:5. Leaf area index (LAI) has been the term most commonly used to describe this parameter by Thorne and her co-workers at Rothamsted and many others. Here PAI and PAD (photosynthetic area duration, the integral of PAI with time after anthesis) will be used, to emphasise the contribution made by all the photosynthetic tissue above the flag leaf node, including the flag leaf lamina.

Table 3:5 Photosynthetic Area Index of Constituent Parts of Plant above Flag Leaf Node and Percentage of Total PAI

Sample 3	19 July	PAI Flag Leaf	% of total PAI	PAI of Stem & Ped.	% of total	PAI of ear	% of total	total PAI
Cv	TL363/30	.5326	18.78	.7518	26.51	1.5514	54.71	2.8358
	TL365a/34	.6284	21.04	.7610	25.47	1.5980	53.49	2.9874
	TL365a/37	.5740	19.72	.7346	25.24	1.6022	55.04	2.9110
	Maris Nimrod	.5650	19.70	.7628	26.60	1.5396	53.69	2.8674
	N59	.4842	16.65	.8716	29.97	1.5520	53.37	2.9078
N rate	N_0	.3120	14.64	.6400	30.03	1.1792	55.33	2.1312
	N_1	.4380	17.00	.7466	28.98	1.3916	54.02	2.5762
	N_2	.5666	18.64	.8138	26.78	1.6590	54.58	3.0394
	N_3	.6968	21.22	.8338	25.39	1.7530	53.39	3.2836
	N_4	.7710	22.16	.8476	24.36	1.8604	53.48	3.4790
Sample 6	9 August							
Cv	TL363/30	.4238	13.61	.8140	26.16	1.8738	60.23	3.1112
	TL365a/34	.4342	13.45	.8458	26.20	1.9480	60.35	3.2280
	TL365a/37	.3530	11.72	.7692	25.53	1.8910	62.76	3.0132
	Maris Nimrod	.4998	15.26	.7834	23.92	1.9912	60.81	3.2744
	N59	.4358	12.59	.9456	27.33	2.0790	60.08	3.4604
N rate	N_0	.2336	9.79	.6526	27.36	1.4992	62.85	2.3854
	N_1	.2854	10.88	.7396	28.20	1.5980	60.92	2.6230
	N_2	.4462	13.18	.8720	25.99	2.0414	60.84	3.3556
	N_3	.5612	14.89	.9414	24.98	2.2666	60.13	3.7692
	N_4	.6238	15.77	.9524	24.09	2.3778	60.14	3.9540

Table 3:5 Cont.

Sample 9	30 August	PAI of Flag Leaf	% total PAI	PAI of sheath & Ped.	% of total PAI	PAI of ear	% of total PAI	Total
Cv	TL363/30	.0302	4,24	.3368	47.28	.3454	48.48	.7124
	TL365a/34	.0276	5.08	.3078	56.67	.2078	38.25	.5432
	TL365a/37	.0310	4.42	.3386	48.23	.3323	47.35	.7020
	Maris Nimrod	.0316	3.65	.4348	50.24	.3990	46.11	.8654
	N59	.0142	1.24	.5992	52.87	.5200	45.88	1.1334
N rate	N_0	.0144	3.07	.2468	52.69	.2072	44.24	.4684
	N_1	.0152	3.29	.2122	45.97	.2342	50.74	.4616
	N_2	.0238	3.21	.3846	51.90	.3326	44.89	.7410
	N_3	.0270	2.50	.5654	52.33	.4880	45.17	1.0804
	N_4	.0542	4.50	.6082	50.47	.5426	45.03	1.2050

The duration of the photosynthetic area (PAD) was calculated from anthesis up to each sample date. The variety and nitrogen means were plotted against time in figs 3:5 and 3:6. In fig 3:5 the PAD is plotted against sample date i.e. calendar time, and in fig 3:6 the time is measured in numbers of days post anthesis. The mean anthesis dates are given in table 3:6 for each variety and nitrogen rate. The numbers are dates in the month of July.

Table 3:6 Anthesis Dates

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59
Anthesis date	7	5	9	10	16
	N_0	N_1	N_2	N_3	N_4
Anthesis date	8	9	9	10	10.5

Plotting the increase in PAD versus sample date (~~table~~ Fig 3:5) shows the effect of the duration of the leaf area after anthesis at each sampling date. That is, the variety which reached anthesis at the earliest date, TL365a/34, has the greatest PAD at the earliest sample. The alternative presentation (~~table~~ Fig 3:6) shows the effect of increased PAI more clearly. Among the varieties there is very little difference in PAI as the curves almost merge in the earlypart. After 35 days, however, the varieties which maintain a greater PAI for a longer period e.g. TL365a/34 stand out from the rest as PAD maintains a steep gradient for a longer period. The effect of nitrogen, on PAD, is thus largely through its effect on PAI as in fig 3:6 the curves are distinct. At high nitrogen levels (N_2 and above), increased maintenance of PAI also has an effect, as the curves separate more rapidly after 25 days post anthesis.

Total PAD at maturity for all varieties is given in table 3:7.

Table 3:7 Total Photosynthetic Area Duration at Maturity

PAD (days)	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N_0	97.8	104.6	100.2	88.3	113.4	100.8
N_1	98.3	116.2	114.2	114.9	118.7	112.5
N_2	146.0	175.8	134.3	144.2	126.7	145.4
N_3	176.0	169.2	160.1	157.7	155.6	163.7
N_4	197.3	180.8	162.0	167.9	149.5	171.5
Mean	143.1	149.3	134.2	134.6	132.8	

N lin** N cub** Cv** N lin x Cv**

The interaction of linear nitrogen and cultivar in this parameter is probably the result of the smaller response of N59, to nitrogen, than that of the other varieties. At the earlier sample dates this interaction was more markedly significant and the explanation holds good on each occasion. The lower response of N59 to nitrogen, than the other varieties, was noticeable in the PAD of main shoots alone, though the interaction was non-significant. This variety thus seems to be less well fitted to respond to nitrogen, by increasing photosynthetic area, as a smaller proportion of the leaf area is composed of flag leaf lamina which was part of the area most responsive to nitrogen (table 3:5). The tables of PAD, of total shoots, at all sample dates after 18 July are presented in Appendix tables 3:10 to 3:17 and that of PAD, of main shoots at maturity, in Appendix table 3:18.

Grains from separate parts of the main shoot ears were weighed for the study of grain filling and development in Chapter 5. From these results the total grain weight per ear at each sample date after anthesis was calculated. The variety and nitrogen means of these values are graphed against the number of days post anthesis on which the sample was taken (figs 3:7 A and B respectively). From these weights, an approximation to the accumulation of grain dry matter per unit area was calculated by calculation of the product of the grain weight per main shoot ear and the total number of ears per unit area. The variety and nitrogen means of this parameter are plotted in figs 3:8 A and B.

The efficiency of the photosynthetic area in producing grain carbohydrate can be measured by the grain leaf ratio (G). This parameter is the ratio of final grain weight per unit area per unit of PAD, post anthesis. This ratio was calculated from the 1972 results and is presented in table 3:8.

Table 3:8 G. (Grain/Leaf Ratios) $g\ m^{-2}\ day^{-1}$

	KgN/ha	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N_0	0	5.32	5.31	5.31	5.82	3.83	5.12
N_1	40	6.52	5.87	5.76	5.71	4.72	5.72
N_2	80	5.28	4.85	5.23	5.08	5.15	5.12
N_3	120	4.74	4.84	4.93	4.94	4.08	4.70
N_4	160	4.04	4.53	4.68	4.66	4.40	4.46
Mean		5.18	5.72	5.18	5.24	4.48	

N lin** N quad* N cub* Cv*

Figure 3:7 Total Grain Weight per Ear vs time

A. Variety Means

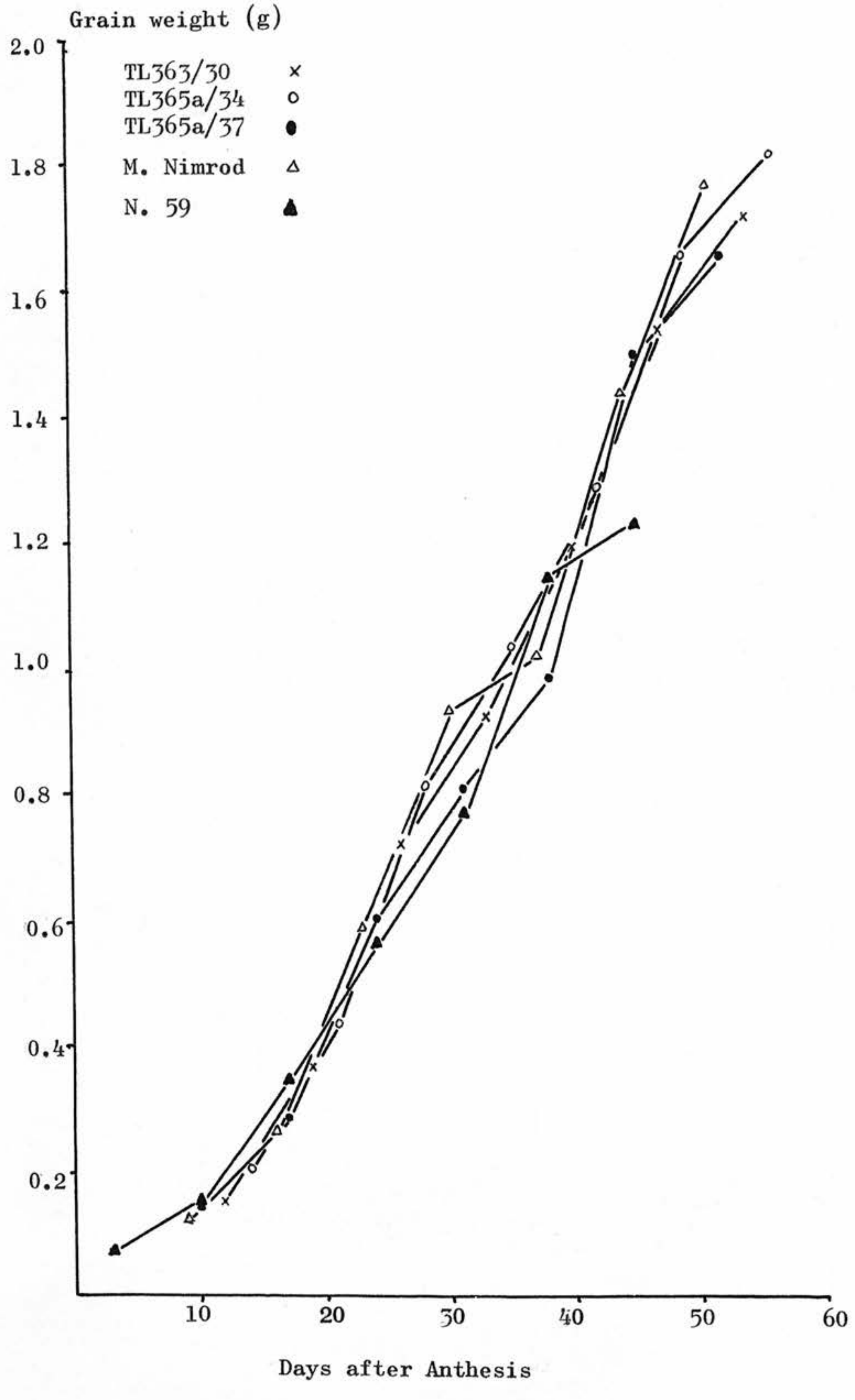


Figure 3:7 Total Grain Weight per ear vs Time.

B. Nitrogen Means

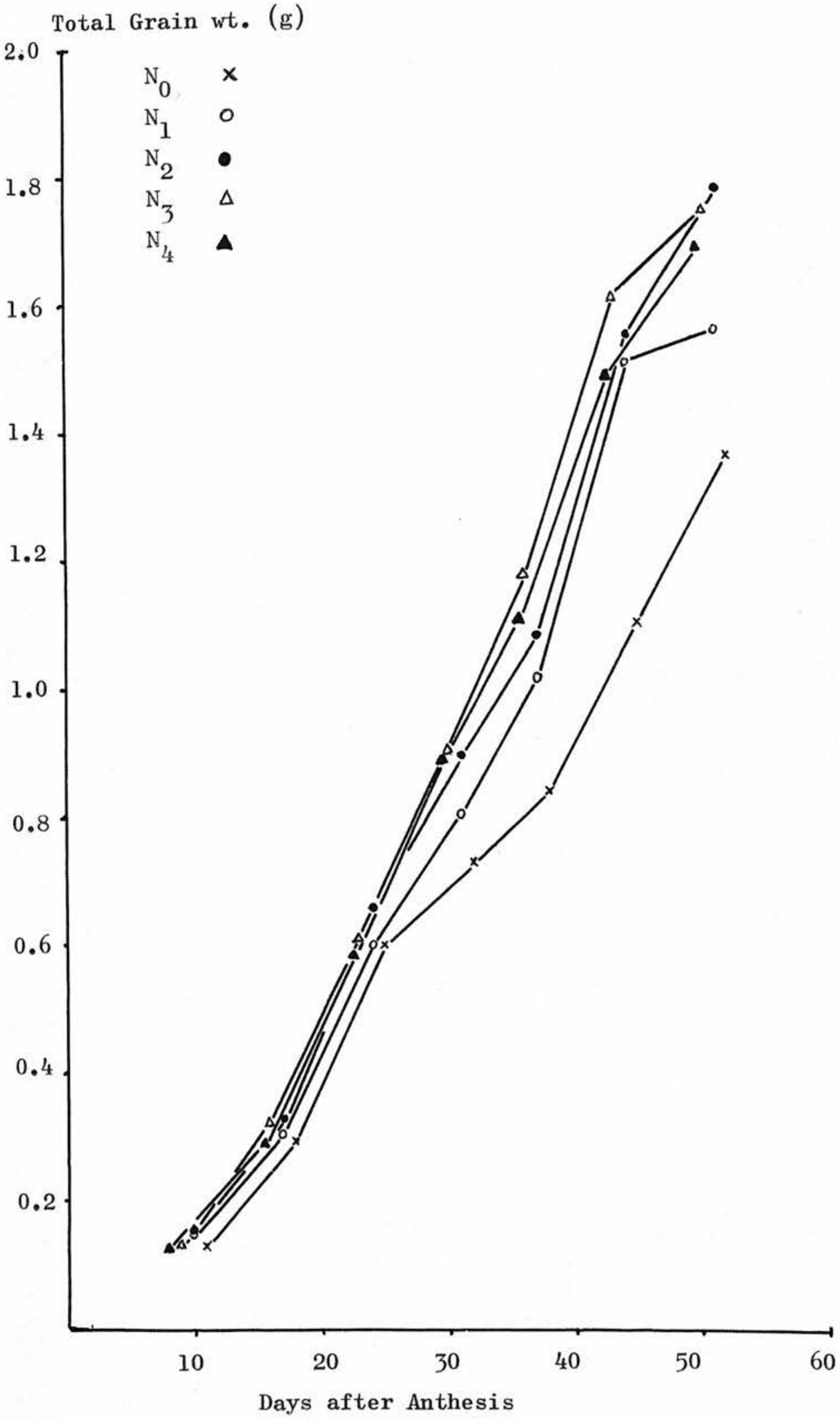


Figure 3:8 Total Grain Weight per unit area vs Time

A. Variety Means

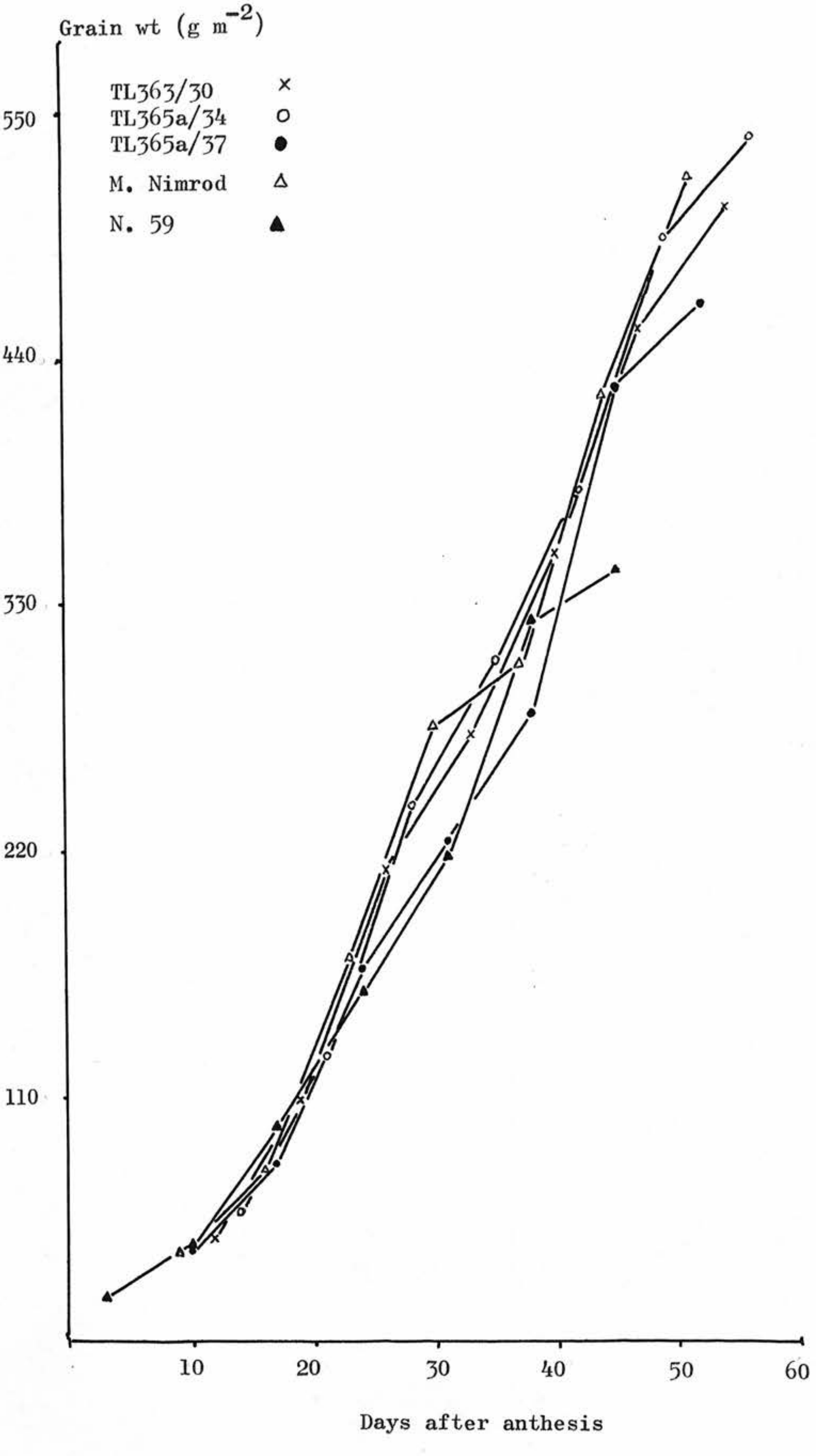
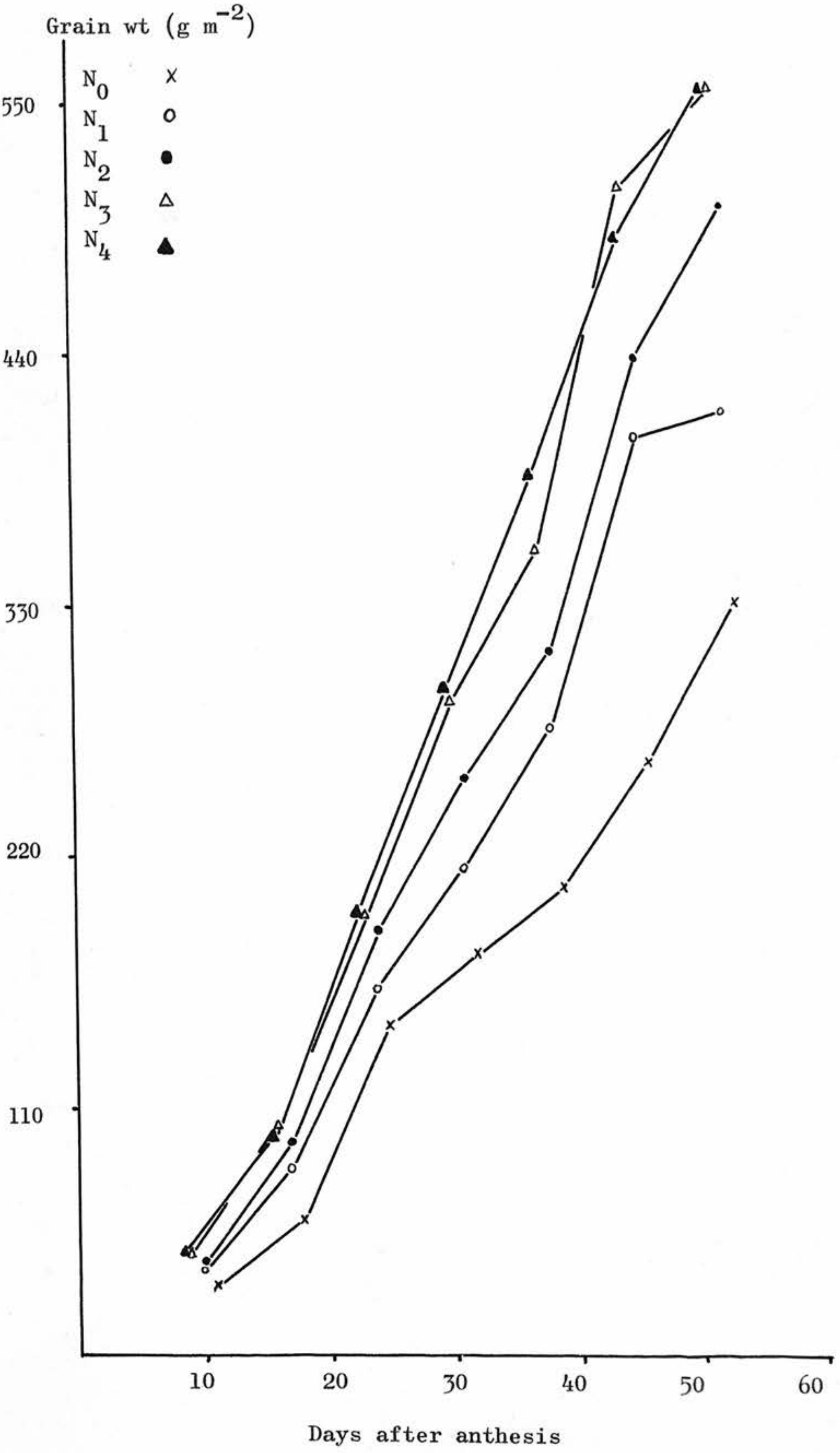


Figure 3:8 Total Grain wt per unit area vs Time

B. Nitrogen Mean



This parameter is comparable to the NAR calculated in 1971 which measured the efficiency of the leaves in producing dry matter. Lodging occurred in very few plots in either year. In 1972, TL363/30 showed the most lodging with 3 out of 4 plots of the highest nitrogen rate lodged by over 50%. No other treatment combination showed a tendency to lodge however.

3:D Discussion of Wheat Results. The higher yield of 1971/72 over that of the previous year was due to an increase in all the yield components which were measured. The amount by which these increased is shown in table 3:9.

Table 3:9 Percentage Increase in the Yield Components Between Years (% of 1971/72 Results)

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59
Yield	23.4	25.8	33.5	19.3	29.6
1000 gr wt	12.1	5.7	2.2	14.8	11.7
Ear no/.305 m^2	18.2	11.9	18.5	23.0	10.2
Grains/sq m	13.2	22.9	35.2	9.9	21.8

	N_0	N_1	N_2	N_3	N_4
Yield	15.7	23.5	27.9	31.1	28.9
1000 gr wt	6.3	5.4	9.7	14.2	11.9
Ear no/.305 m^2	5.5	15.2	15.3	20.5	21.4
Grains/sq m	15.0	29.4	22.8	16.7	18.1

In the comparison of the varieties between years it must be noted that the nitrogen applied was increased in the second year by 17% in all varieties. Similarly the nitrogen applied at all rates, except the nil rate, increased by 21.5% in the second year.

In 1971/72 the yield response to nitrogen was sustained to 120 kg/ha before a slight decline. In the previous year the maximum yield was reached with 126 kgN/ha but the response after 63 kgN/ha was very slight. The largest difference, between years, in yield, is thus found at N3 and N4. The change in the yield components between years is dependent on the rate of nitrogen applied. At the three lower rates the largest change between the years of the experiment is found in grain number per unit area but at the two higher rates the change in 1000 grain weight becomes more important in explaining the change in the yield and the changes, in both number of grains and the size of each grain, have an almost equal effect on the change in yield between the two years.

In both years the number of grains per square metre increased with increase in nitrogen but in 1000 grain weight the increase in nitrogen caused a decline from 31 kg/ha in 1971 but had no effect until 120 kg/ha in 1972. Thus in 1972, the size of the grains was maintained throughout a much wider range of grain population per unit area which indicates that the grain filling period, in 1972, must have been more suitable than the previous year. The increase in grain population per unit area between years was less at the highest nitrogen rates, which implies that the ceiling for this parameter was being approached in the second year. At high nitrogen rates a larger part of the change in grain number per unit area was due to an increase in the number of ears per unit area than to changes in grain number per ear. The conditions, in 1972, must, therefore, have been adequate to support a large tiller population but not to increase the number of grains on these ears after a high ear population was reached, when competition between tillers became more intense.

In this second year the decline in yield at the highest nitrogen rate, (table 3:2) was due to a reduction in the 1000 grain weight. As greater grain weights were achieved at lower nitrogen rates and the grain number per unit area did not decline, it is unlikely that the cause of the yield reduction could have been a shortage of sink capacity for the available photosynthetic area, but must have been due to a reduction in the efficiency of the photosynthetic organs. This source/ sink discussion will be opened again when the leaf growth and grain filling pattern are discussed.

The order in which the varieties were placed differed between the two years of the experiment. TL363/30 and TL365a/34 both had a higher yield than Maris Nimrod in 1972 though they were lower yielding in 1971. The yield change in Maris Nimrod, between years, followed a different pattern to that of the other varieties. The greatest increase in the yield components of Maris Nimrod, between years, was in 1000 grain weight while the other varieties either had a very slight change in this component, and a large change in grain numbers, or, had equally large changes in both the number and the size of grains. As well as showing the differences between seasons in a different way, Maris Nimrod and N59, both had a different pattern of response to nitrogen from the semi-dwarf varieties, in terms of the yield components. In 1000 grain weight, Maris Nimrod and N59 showed a positive response to nitrogen in the lower part of the range of nitrogen rate, but the semi-dwarfs showed a decline throughout the range of nitrogen rates. In grain number per ear the semi-dwarf varieties gave a response to a wider range of nitrogen rates than the other two varieties. The semi-dwarf varieties thus seem to have a greater flexibility of grain population than the conventional varieties but, as the population of the grains increases, the leaf area provided, seems to be inadequate to maintain the grain size found at lower populations.

Although Maris Nimrod showed a smaller increase, in yield, in the better season for grain filling and had the smallest grain number per unit area of all the varieties in the second year, the smaller sink capacity does not seem to be the principal reason for the poorer relative performance of this variety as, at the highest nitrogen rate, the grain size of this variety is not as large as it is at lower rates (Appendix table 3:2) and thus, the sink capacity is not used to the full. The smaller increase in performance in 1972, than the semi-dwarfs, must therefore be due to poorer utilisation of the leaf area, by Maris Nimrod, at the high ear density which it achieved in the second year. The other parameters measured in these experiments help to clarify the differences between varieties.

The relationship between leaf area and dry weight of the different varieties and nitrogen rates in 1971 is shown in figures 3:1 and 3:2. TL365a/34 has the greatest LAI after the first sample but the second lowest yield of dry weight. In the light of the high performance of this variety in grain yield and in biological yield (tables 3:1 and appendix table 3:23), inefficiency of the photosynthetic area, of the variety itself, is unlikely i.e. reduced photosynthetic rate. The only explanation, therefore, is, that the short stature and the high leaf area expressed by this variety, lead to an increase in the mutual shading of the leaves over this phase of growth, which reduces the performance more than that of the other varieties.

At the opposite end of the height spectrum, N59, shows the highest dry weight of all cultivars when its leaf area is at its peak and is higher than any other variety. LAI, in N59, is reduced more rapidly in 1971 than in 1972 (figures 3:1 and 3:6) but, as the LAI in 1971 was measured in leaf lamina area only and a large proportion of N59's PAI, in 1972, was made up of stem area (table 3:5) this difference is readily understood.

The linear increase in dry weight, with nitrogen (fig. 3:2), at each sample date is not reflected in the grain yield (table 3:1) as the grain to straw ratio (Appendix table 3:1) is reduced at high nitrogen rates. Biological yield however increased almost linearly with nitrogen rate (table 3:23).

Differences between varieties in NAR were not significant at any of the sampling dates in 1971. The variation in this parameter was very great and the sampling period, over which the calculation of NAR was made, was too long for any firm conclusions to be drawn from the values computed. The reasons for this were pointed out in the previous section (3:C). No single variety had consistently better or worse values in NAR, though TL365a/34 and N59 had the lowest values over the first two sample intervals. By the third interval however, they had comparable values to the other varieties.

The different behaviour of TL365a/34 and N59 in response to nitrogen in the third NAR (Appendix table 3:4 and section 3:C), from that of the other varieties, could be the result of the dry weight, at high nitrogen rates, increasing more rapidly between harvests 3 and 4 in these two varieties than in the other three varieties. At low nitrogen rates, a lesser increase in dry weight between harvests 3 and 4 in TL365a/34 and N59, than the other varieties, was also apparent (Appendix table 3:7 and 3:8). Leaf area senescence was less rapid at the high nitrogen rates in TL365a/34 and N59. This would have the opposite effect to the change in dry weight noted, but the combined result of these two differences in response to nitrogen, gave the observed reversal of the response of NAR to nitrogen, of these two varieties, from the response of the other three.

Anthesis dates were not accurately recorded in 1971 so accurate determination of the leaf area duration after anthesis of the lamina area of all the leaves was not possible. From the graphs of the variety and nitrogen means of LAI (fig. 3:1 and 3:2), an approximation of LAD can be made by calculating the area under the curves. These approximate values of LAD are given in table 3:10.

Table 3:10 Approximate LAD of Leaf Laminae Area

Variety and Nitrogen Means (1970-71)

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59
LAD (days)	34.9	49.6	30.8	35.74	25.3
	N_0	N_1	N_2	N_3	N_4
	27.38	35.74	37.3	38.7	40.99

The order in which the varieties are placed in leaf area duration is the same as the order in the total yield excepting that, the position of TL365a/34 and Maris Nimrod are reversed. The response to nitrogen is similar, in LAD to the response of total yield to nitrogen though, at the higher rates of nitrogen, the reduction in response noted in final yield, is not as noticeable in leaf area duration. This could be the result of the leaf area being inefficiently utilised due to increased mutual shading at high leaf areas.

In 1972 the order of the varieties in final PAD is again the same as that of final yield. The relative differences between the varieties were also the same as in final yield, with the exception of N59, which had a lower yield than would be expected from the PAD recorded (cf. table 3:1 and 3:7). TL365a/34 had the highest PAD at the final harvest due to greater duration of leaf area, rather than through an increase in PAI.

The accumulation of dry matter in each ear and of the grain dry matter per unit ares (figures 3:7 and 3:8), follow a broadly similar pattern to the PAD curves with time (fig. 3:6), particularly in the nitrogen means. The PAD and grain weight at each sample date increase with increase in nitrogen. At the top two nitrogen rates, the curves of the grain weight per unit area converge slightly more than the curves of PAD at the same rates of nitrogen. The convergence could be an indication that the sink is unable to accommodate the increased carbohydrate contribution from the larger leaf area, or that the leaf area was less efficient at the highest nitrogen rates due to mutual shading becoming more intense. The effect is however very slight and is not sufficiently strong evidence to suggest that the sink size imposed a limit on either the rate or the duration of the grain dry matter accumulation.

The rate of dry matter accumulation per unit area differed little between the varieties. N59, which had the shortest post-anthesis period had, by far the smallest grain weight per unit area. The rate of grain filling showed a decline after only 38 days in N59 which was much sooner than the other varieties. Most of this reduction in the photosynthetic area of N59 was due to the loss of flag leaf lamina area and at the last sample (sample 9, table 3:5) the lamina area of N59 was considerably less than that of the other varieties. As the variety with the largest lamina area at the final sample, was also the one to show the least reduction in grain filling rate, i.e. Maris Nimrod, it appears that at this stage the photosynthate of the ear and the leaf sheath is less fully utilised than has been thought and that senescence of the flag leaf leads to a rapid reduction in the rate of grain filling.

The increased duration of the leaf area of TL365a/34 (fig. 3:6) did not lead to an increase in grain weight per unit area (fig. 3:8A) but the lamina area of this variety was reduced to a greater extent than in any other except N59. This is further support for the suggestion that lamina senescence results in a rapid fall in the rate of grain filling.

The nitrogen results support this view except at the lowest rate. As the flag leaf area at the last sample (sample 9, table 3:5) declines with nitrogen rate, so that the rate of grain filling reduces more rapidly over the last sample interval (fig. 3:8).

Another reason for the low grain weight per unit area achieved by N59, compared to the other varieties, could be that N59 had fewer tillers per plant than the other varieties. This would mean that the overestimate of the grain weight, caused by using the weight of the heavier, main shoot ears alone, to calculate the grain weight per unit area, would be smaller in N59 than in the other varieties where the lighter tiller ears made up a larger proportion of the total ears in the crop. The difference between N59 and the other varieties in grain weight per ear (fig. 3:7A) is not as great as it is in grain weight per unit area (fig. 3:8A) which would support this conclusion.

The nitrogen means of PAD at each date (fig. 3:5 and 3:6) increase throughout the range of nitrogen usage but the total yield showed a decline in response after 80 kgN/ha and a drop in yield between 120 and 160 kgN/ha. Thus in both years of the experiment, the efficiency with which the leaf area was utilised was reduced at high nitrogen rates, and in the second year, when all the photosynthetic tissue above the flag leaf node was measured, the efficiency of N59 in producing grain was lower than the other varieties. This efficiency of utilisation of the leaf area is conveniently measured by G, the grain leaf ratio, values of which are presented in table 3:8. These values were only calculated in 1971-72 due to the unreliability of the LAD data in 1970-71. The difference between the varieties, other than N59, are very slight, both in response to nitrogen and in their numerical values. N59 had considerably lower values of G than the other varieties, and in response to nitrogen, the decline in G with increased nitrogen, which occurred after 40 kgN/ha in all the other varieties, did not occur until 80 kgN/ha in N59. In 1970-71 the grain to straw ratio was calculated, which is also a measure of the efficiency of the crop in partitioning the assimilates between the grain and the straw. In this parameter TL365a/34, TL363/30 and Maris Nimrod all behaved similarly (Appendix table 3:1), having the greatest efficiency of utilisation of the assimilates at 63-94 kgN/ha. TL365a/37 was at its most efficient with the maximum supply of nitrogen though the efficiency was always lower in this variety than in the afore-mentioned varieties.

N59 had reducing efficiency of utilisation throughout the nitrogen range and also had considerably lower values in this ratio than all the other varieties.

In total biological yield in 1970-71 all the varieties gave similar yields (Appendix table 3:23) and the smaller proportion of the biological yield made up of grain yield, in N59 and to a lesser extent in TL365a/37, must have been due to poorer distribution of assimilates rather than to a poorer assimilation of photosynthate.

Both in 1971 and in 1972, the efficiency of all the varieties in utilising the increased leaf area, which was furnished by increased nitrogen usage, is reduced after 40-60 kgN/ha have been applied. This reduction in efficiency could be due to increased mutual shading of higher leaf areas or it could be that the capacity of the grains for carbohydrate could be insufficient to utilise the abundant supply from the increased PAD. The latter explanation is unlikely as the size of the grains as measured by 1000 grain weight is reduced with increase in nitrogen, indicating that the sink capacity is not used to the full. This reduction in 1000 grain weight is least in Maris Nimrod and N59 but at the highest rates of nitrogen a reduction in the 1000 grain weight is still apparent (Appendix table 3:2).

The improved sink capacity of the semi-dwarf varieties with increase in nitrogen, described earlier, does not manifest itself in any increase in the efficiency of carbohydrate utilisation, which would be apparent as a smaller reduction in G with increased nitrogen, than in the other varieties. This suggests that the efficiency reduction is probably due to the increase in mutual shading.

In N59, the reduction in G occurs after 80 kgN/ha has been applied, while in the other varieties this reduction in efficiency occurs after only 40 kgN/ha. N59 has a higher proportion of the photosynthetic tissue made up of stem and peduncle surface (table 3:5), which, in itself, is less efficient (Stoy, 1965), which could account for the lower efficiency at all nitrogen rates, but mutual shading by the stems will not occur until a higher photosynthetic area is reached which could account for the greater response in G (table 3:8), by this variety with nitrogen. That is, a greater photosynthetic area must be produced in response to nitrogen before any reduction in the efficiency of the area is noticed in N59 as this form of photosynthetic tissue, stems and ears, is less susceptible to mutual shading than the tissue of the other varieties which is made up of a greater proportion of flag leaf lamina area (table 3:5).

The reported yield improvement in upright leaf type grains (Pearce et al, 1967: Tanner et al, 1966) could be the result of a greater proportion of the photosynthetic area being made up of stem area and thus, a reduction in mutual shading of the photosynthetic tissue at high populations would result. The photosynthetic efficiency of this type of tissue is however, not as great as that of leaf laminae (Stoy, 1965). If the difference in the proportion of lamina to stem was not so great as in N59 in this experiment, or the stem was more efficient in cultivars with a small lamina area, this could be the reason for the reported findings. A greater drop in yield with reduction in the population would be the result of greater efficiency derived from such a reduction in mutual shading. This result was reported by Pearce et al (1967) who found that the upright leaf type only showed increased rates of photosynthesis when the leaf area index was greater than 2 in the early stages of growth. No results are reported for differences at a later stage of growth when grain production would be affected.

The proportion of the total PAI made up of the constituent parts at the several dates of sampling in 1972 (table 3:5) is surprising in some respects. Ear area, at the first sample (19 July) i.e. 14 days after anthesis of the earliest variety and 4 days after in the latest, accounts for over 50% of the total PAI. At 9 August it makes up over 60% of PAI and thus, the contribution of the ear, to the measured PAD, would be over 50% of the total in this experiment. Of this, a greater proportion would be in the later stages of the development of the crop, as the flag leaf senesced before the ear (table 3:5).

Earlier estimates of the contribution of the ear to the yield of grain in wheat give values for this contribution of nil or even negative (more respiration than photosynthesis) (Thorne, 1966), up to 37%, though the latter figure was quoted as the photosynthetic contribution of the peduncle and ear together, (Stoy, 1965) (Sect. 3:A).

Values of the gross photosynthetic rates of the ear and the flag leaf have been found to be similar (Stoy, 1965), though the respiration of the ear is very much larger than that of the flag leaf (Stoy, 1965). Of the assimilates produced by the ear some will be respired so that the actual contribution of the ear will be less than the total photosynthetic contribution but there is no reason to suppose that the ear assimilates are any more readily respired than those from the other contributing parts of the plant. On this basis, as the ear is the sink for the assimilates from the whole surface area above the flag leaf node, the respiration of the ear should be debited from the whole PAI contribution and not from that of the ear alone. Thus the ear contribution to the total net photosynthesis of the area above the flag leaf would be in proportion to its surface area, as the flag leaf and ear photosynthesise at the same rate. That is, the contribution to yield of the constituent parts would depend on their gross photosynthesis and area. The contribution of the stem (flag leaf sheath and peduncle) is smaller, as the rate of photosynthesis of this part has been shown to be about half that of the flag leaf lamina (Stoy, 1965). This was taken into account when the area of the stem was measured in the present study, as it was calculated as half the area of a cylinder. This way of assessing the contribution of the parts of the plant contributing to the final ear weight, by measuring photosynthetic area and rate of photosynthesis of each part and crediting this positive contribution to the separate parts while debiting the total respiration of the whole area from all parts equally, allows a simpler interpretation of the complex processes involved.

If the nil contribution suggested by Thorne (1966) is accepted, and the area of the ear is removed from the calculation of the PAD in this experiment, the effect would be to reduce the numerical values of the PAI and PAD by approximately 50% in each case. No differences due to variety or nitrogen rate from those already discussed, would be evident, as the ear's proportion of PAI was unaffected by treatment.

The values of G computed using the PAD, inclusive of ear area, are comparable to those of Thorne (1966). Thorne's results place the value of the ratio at around 12 g m^{-2} wk^{-1} for winter wheat but in her experiments the PAD used, was calculated from ear emergence and, G values are thus, about 50% smaller than those of table 3:8. Any reduction in the leaf area used to calculate G, by the removal of the ear area in the present study, would raise its value to an impossibly high figure suggesting a photosynthetic rate in excess of any suggested to date. Such a situation is improbable and thus the contribution of the ear to photosynthesis and to the growth of the crop must be similar to the values measured, i.e. up to 50%.

The proportion of the gross photosynthetic product provided by the ear, which contributed to the ear weight has been variously quoted at values from 17-59% (Langer, 1967), with the larger proportion of the values at around 20%. The generally accepted value for the gross photosynthesis of the ear is the value of Thorne (1965) of 17% of the total photosynthetic contribution. The respiration losses by the ear in this experiment (Thorne, 1965) were greater than the ear photosynthesis with the result that the net contribution of the ear was negative. Kriedman (1966), however, using a gas exchange technique similar to that of Thorne (1965), found net photosynthesis of the ear to contribute 29% of the total yield. This was in part due to the re-utilisation of respired CO2 by the ear. The value for this net contribution of the ear, in one of Kriedeman's experiments (the only one with summer radiation input), was as high as 46%. Spikelet removal techniques (Buttrose and May, 1959) have frequently given values of the net contribution by the ear of between 21 and 50% of the grain weight (Thorne, 1966; Kriedeman, 1966) and shading techniques have given values of net ear contribution of 41% (Thorne, 1966). The value of the assimilates of the component parts, of the area above the flag leaf node, is thus not clear. Higher values, of the net contribution of the ear, than would be expected from the 17% gross contribution of Thorne (1965), have been found regularly. If the gross values of Thorne (1966) were treated in the way suggested i.e. the total respiration of the upper parts of the plant be shared among the photosynthetic tissues, the contribution of the ear would be similar to the net values found and to the 50% contribution suggested in the earlier discussion. As there are differences in respiration rate between varieties (Stoy, 1965), this method would give a more realistic picture of the contribution of the various parts without penalising the ear photosynthetic tissues in high respiration varieties with the total respiration of the tissues derived from all the contributing photosynthetic area.

The recorded shoot numbers in 1971 show an interesting difference between the varieties (fig. 3:3 and 3:4). At the earliest sample, N59 has considerably more tillers on the sample area than the other varieties but, by the final sample the tiller numbers in all the varieties are similar, though the differences are still significant. N59 is thus wasteful in tiller production in the early stages of growth. The other varieties are all similar in the efficiency with which they utilise the tiller production (see table 3:1).

Table 3:1 Percentage of Tiller Number at 24 May lost by 9 August (1970-71)

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59
% lost shoots	35.8	37.4	38.6	33.2	47.1
	N_0	N_1	N_2	N_3	N_4
% lost shoots	31.4	35.2	40.8	40.5	43.6

The proportion of shoots utilised increases with increase in nitrogen usage. The effect of these wasted shoots on plant growth is the subject debate as some consider this production of non-productive shoots is detrimental to the plant (Lupton, 1966; Wardlaw and Porter, 1967), others consider it beneficial to the plant as it enhances the root formation (Stoy, 1965), while others consider that neither benefit is gained nor harm is done by the non-productive shoots (Thorne, 1966; Bremner, 1969) (Sect. 3:A). The generally agreed fact is, that the variety which utilises the largest proportion of the tillers it produces, is generally the highest yielding (Thorne, 1966; Stoy, 1965; Lupton, 1966). This was the observed response in the 1971 experiment as Maris Nimrod with the highest proportion of surviving tillers, was the highest yielding variety, while N59, with the lowest proportion, was the lowest yielding.

The steepest fall in the number of tillers, with time, occurs when the leaf area is increasing rapidly. This is the period of stem extension, which appears to be a critical phase in the life of a tiller. After this initial rapid drop in tiller number, the number decreases at a similar rate to leaf area (fig. 3:1; 3:2 and 3:3). This suggests that the reduction in leaf area was due to the reduction in the tiller population. During this period just prior to anthesis, the production of leaf area on each tiller closely matches the reduction due to senescence of the lower leaves and the leaf area of each shoot stays more or less constant (Appendix table 3:19, 3:20). After ear emergence, which almost coincided with sample 3 (30 June), there is little further change in the number of tillers up until harvest. In 1972 the measurement of leaf area depended on this finding, as the tiller number was counted at anthesis, and this number was used throughout the post anthesis period to calculate the PAI and PAD. Leaf area declined throughout this phase in 1971 but this was largely due to the senescence of the lower leaves followed by complete senescence (Appendix table 3:19-20) and not to a reduction in the number of tillers.

In 1972, after anthesis, the area of the photosynthetic tissues above the flag leaf node increased for a short time with the extension of the peduncle and the ear and then senescence reduced the area of the flag leaf lamina followed by the sheath and the ear (table 3:5). At high nitrogen rates, the flag leaf lamina formed a larger proportion of the total photosynthetic tissue than at low rates. This would have a tendency to increase the degree of mutual shading which, in turn, would counteract the greater photosynthetic efficiency of the lamina tissue over that of the stem and the ear.

From the evidence available, the reduced response of yield at high nitrogen rates would appear to be due to a reduced response in the supply of photosynthates to the grain at higher PAI due to increased mutual shading or, due to assimilates being wasted in the production and maintenance of the higher PAI at high nitrogen rates.

The slight differences in the behaviour of the different varieties in sink size, in response to increased nitrogen, would be unlikely to have a great enough effect on the yield to cause the observed yield response of the varieties, to nitrogen, There is, however, a slight indication that the higher yielding dwarf varieties in this experiment, TL363/30 and TL365a/34, may have the potential of a greater sink capacity which could lead to a higher yield in years in which the supply of photosynthetic assimilates was too great for a variety with a smaller sink to utilise. The sink capacity and the rate at which the parts of it are filled, will be examined more closely in Chapter 5.

In all the other aspects of the behaviour of the plant which have been discussed here, there are no clear cut distinctions to be drawn between the dwarf varieties and Maris Nimrod though the outdated variety N59 differed in a number of respects from the behaviour of the more modern varieties. The dwarf varieties did not behave in an identical fashion but showed as great a degree of variation among themselves as would be expected when comparing several conventional varieties of similar performance. Dramatic yield increases, of the size achieved in India and the Middle East (CIMMYT, 1970 and 1972), are thus not to be expected with the introduction of semi-dwarf varieties to this country, but these varieties, TL363/30 and TL365a/34 in particular, have performed well in these experiments as, Maris Nimrod is one of the highest yielding varieties at present on the market, and they have compared favourably with Maris Nimrod, in their performance throughout.

These varieties of semi-dwarf stature are now undergoing statutory performance trials for future release as commercial varieties. TL365a/34 and TL365a/37 are now in their second year of trials, while TL363/30, has just entered these trials this year. The results of the first year's Statutory Performance trials including these varieties were recently published (P.V.S.G., 1973) and these were:

% of Yield Control (mean of Maris Ranger and Cappelle)

TL365a/34	119%
TL365a/37	114%
Maris Nimrod	119%
Control Yield	5.89 tonnes/ha

These are the mean results of trials at six sites throughout Britain. In similar trials conducted by the Plant Breeding Institute, Cambridge, at several sites in Britain these varieties performed thus (Lupton et al, 1972):

% Yield of Control (Maris Huntsman)

TL363/30	110%
TL365a/34	109%
TL365a/37	102%
Maris Nimrod	105%

These results indicate that these varieties are likely to be used on a large acreage in Britain in years to come and that the varieties have no serious shortcomings.

CHAPTER 4

ROOT GROWTH

4i Introduction. The aspects of root growth which were studied experimentally were, the root growth of tall and semi-dwarf varieties of wheat and barley, and the growth of both species through the season with samples being taken on several occasions. To enable a fuller understanding of the complexities of the growth of roots a brief review of the endogenous and external factors affecting the growth of roots is included together with a review of root studies already carried out in the comparison of semi-dwarf and tall varieties of wheat.

4ii The Growth of Roots. In the cereal plant the roots are the first organs to emerge from the seed after germination. After the imbibition of water by the seed the coleorhiza containing the primary root emerges and very shortly afterwards the primary root and two pairs of seminal roots emerge from the coleorhiza. These five roots make up the primary or seminal root system in the cereal plant (Wellington, 1966). These roots arise from below the insertion of the coleoptilar node which distinguishes them from the subsequently formed adventitious or nodal roots which form the bulk of the root system of cereal plants. The relative importance of these two types of root in terms of activity and contribution to the growth of the plant is a subject of some doubt. The activity per gram of root is greater in the seminal than the adventitious roots but the longevity of the seminal roots has been doubted (Brouwer, 1966). Bonnett (1961) showed that the seminal roots were present even at a late stage of the growth of cereal plants however. More recently, relative uptake of nutrients by seminal and nodal roots were suggested (Russell and Newbould, 1969) which showed nodal roots to be more important, though lateral roots of both types were responsible for the greatest activity.

The seminal roots have more branch roots than adventitious roots have (Brouwer, 1966). The branching of seminal roots has been studied by Hackett (1969) in barley and was found to be sensitive to potash deficiency which prevented branching in two cultivars of barley while phosphate deficiency only stopped branching in one of the varieties while promoting it in the other. This highlights two of the important aspects controlling the growth of roots. Firstly the nutrition of the root is of prime importance both from internal sources i.e. the provision of carbohydrate from the shoot and from external sources for the provision of minerals and water. The second feature demonstrated is the degree of control exercised by the genotype on the growth of the roots even within a species.

The overriding control of root growth appears to be the nutrition of the root from the shoot (Brouwer, 1966) especially nutrition with carbohydrate. A number of experiments have also established that the control of various root developments i.e. extension and branching is by chemical control mechanisms (Hess, 1969; Street, 1969). The nature of this control of the root is complex and in addition to the provision of carbohydrate, the stem also provides nitrogen compounds, auxins and phenolic compounds which all seem to have a part to play in the efficient functioning of the root (Hess, 1969).

The other principal requirements for adequate, healthy root growth can be considered as

1. An adequate pore space
2. An adequate air and water supply

3. A supply of nutrients in the soil solution
4. An adequate temperature (Russell, 1966).

The importance of pore space lies in the requirement of the root for space to grow in the soil medium. A root is unable to pass through a space smaller than the unstressed width of the meristem as cell size does not fall below a certain minimum and cell arrangement is strictly adhered to in a root (Greacen et al, 1969). In addition, the pore space is vital to the second requirement, in that, a soil with an adequate pore space allows roots to ramify through the soil and provides a large interface between the root, the soil atmosphere and the soil water supply (Eavis and Payne, 1969).

The importance of the air supply to the roots is difficult to demonstrate except by the total removal of air. The growth of roots of a mesophytic species, in oxygen free agar ceased after penetrating the agar to a depth of 2 centimetres (Greenwood, 1969). This demonstrated that oxygen transportation was possible in such species.

There is also evidence that oxygen can be transported through the barley plant to the roots, though the quantities are unlikely to be sufficient to support the growth of the root system (Greenwood, 1969). Waterlogging of the soil for even a few days can reduce the yield of a barley crop by at least a third as a result of the formation of toxins in anaerobic conditions (Greenwood, 1969). Although the quantity of air in a soil can be measured with considerable accuracy none of these measures relate to performance of the plant or the crop (Grable, 1966). This is probably the result of a number of interactions in the soil of the various root requirements.

For example the provision of an adequate air supply may reduce the available water to a level where it starts to inhibit the growth of the roots or the temperature in the soil may be too high or low for root growth to be sustained.

Thus the water and air requirements of a soil are in conflict as they share the pore spaces in the soil and a balance must be sought. In a freely drained soil the most readily available water for the roots is lost by gravity but a large quantity of water is held in the pore spaces. A considerable amount of energy is required to remove this water from the soil particles but the structure of the soil, and in particular the provision of pore spaces in which water can be held has a considerable bearing on the ease with which the soil water can be utilised by the roots (Eavis and Payne, 1969). The energy required by the roots to utilise the water in the soil can be measured by the suction tension of the water in the soil which can be related to the reduction of the growth of the roots as the tension increases (Brouwer, 1966).

The air-water relations in the soil are thus complex when measured in plant growth terms and the true effects of changes in either are difficult to measure.

The provision of nutrients to the roots is bound up with the water supply to the roots and is thus in part affected by the restraints described in the previous paragraph. Nutrient uptake is not however, directly proportional to the amount of water taken up by the roots particularly in periods of rapid root growth (Eavis and Payne, 1969). In the agricultural context the principal nutrients are provided to the plant in the form of granulated mineral compounds. The ease with which such minerals are utilised and the efficiency of the utilisation have been examined by Russell and Newbould (1969) who concluded that provided the water status of the soil was adequate, provision of nutrients in this form was satisfactory as the root has the ability to transfer nutrients within the plant. The activity of the roots is the most important aspect of the root growth for plant productivity but the relative activity of old and young roots and seminal and nodal roots has not been determined. Russell and Newbould (1969) presented figures for the percentage uptake by nodal axis, seminal axis and lateral roots but these were calculated from small sections of root which may not have been representative of the remainder of the root system. The thickening of the wall of the older roots interferes with uptake though it has been shown recently (Clarkson and Sanderson, 1971) that the suberised tertiary wall of roots is not a complete barrier to the passage of ions into the root as the ions pass through the plasmodesmata in the tertiary wall. The best parameter of root growth i.e. the one most closely related to the activity of the root seems to be the volume of the root (Clarkson and Sanderson, 1971) though the volume of the lateral roots must be included. Care must be exercised therefore in removing the roots from the soil to avoid loosing the finer lateral roots.

The final prerequisite for root growth to be maintained is a temperature within the range in which the processes of growth and active absorbtion can continue. Roots tend to be more sensitive to temperature than shoots (Nielsen and Humphries, 1966). At low temperatures absorbtion of water and nutrients is slowed as the viscosity of the water increases and the permeability of the protoplasm of the cells of the root is reduced. Ion uptake is also affected by low temperature as this is an energy requiring process and is thus dependent on the oxidation of carbohydrate for the release of energy, but, as this reaction is slowed by low temperature, the uptake of ions is also slowed. Roots grown at low temperatures are thicker and less branched than when temperature is adequate. The reduction in branching is probably the result of a reduction in the supply of carbohydrate or one of the other requirements for branching described earlier, either through reduced shoot growth at the low temperature or, through a reduction in translocation to the root of these substances. The increase in the thickness of the roots will also reduce the amount of ramification of the roots through the soil and increased mechanical impedance has been shown to further retard root growth (Russell, 1966).

The effects of low temperature are thus considerable, and these effects become apparent at higher temperatures than those which reduce shoot growth (Neilsen and Humphries, 1966).

4iii Provision of a Root Environment. In cultivating the soil for crop sowing an attempt is being made to provide an environment in which all the requirements of root growth are being met. The effect of tillage on the soil was studied by deRoo (1969) in the tobacco crop through the effect on the root growth of the crop. He concluded that primary tillage, ploughing, was desirable in that it removed the effects of compaction of the previous year's crop but that secondary tillage, harrowing and other cultivations caused compaction and should be kept to a minimum. Compaction was as great at each successive harvest after the normal round of traffic over the soil after ploughing. Pans in the soil form an impermeable barrier to root growth and should be broken (deRoo, 1969). The most common shortage to arise in the world, of the requirements of the previous section (4ii), is a shortage of moisture. The effect of water shortage on the plant growth has been extensively studied and the effect most commonly noted is a reduction in the shoot/root weight ratio. This is a result of the root, being closest to a scarce resource, having first call on that resource and undergoing extension growth seeking new supplies of the scarce resource in this case, moisture. Thus the root weight increases relative to the shoot weight and the ratio is reduced. In a similar way when the carbohydrate supply to the root is limiting as the shoot is receiving too little sunshine the scarce resource becomes carbohydrate which is utilised preferentially at the source of the supply, namely in the shoot which increases in weight. Under the same environmental conditions and at the same stage of growth the shoot/root ratio of a cultivar has been found to be constant (Brouwer, 1966). Any influence which upsets the growth by altering the ratio will, when the stress is removed, result in an acceleration of the growth of one part of the plant which will bring the ratio to a similar equilibrium to that found in plants which did not undergo the stress (Brouwer, 1966). In a field situation where two treatments have differing effects on the shoot/root ratio, for example mulching versus no mulching, the resultant effect on the plant and crop growth can be considerable. When drought becomes a limiting factor in the non-mulched soil the shoot growth is slowed sooner than in the mulched crop where the water retention characteristics of the soil are improved. With the return of moist conditions equilibrium of shoot growth to the different sized root systems is sought by the crop and consequently the mulched crop reaches a greater size. This greater shoot growth is capable of supporting root growth for a longer period in the next period when moisture is limiting with the result that crop growth is considerably improved by mulching in dry conditions (Eavis and Payne, 1969).

The other major control of the soil contribution to plant growth exercised by the farmer is the provision of nutrients. This is achieved by the addition of granular, mineral fertilisers. This has been shown to be a suitable means of achieving an efficient utilisation of the fertiliser (Russell and Newbould, 1969).

4iv The Root Systems of Different Varieties. Between species large differences in root growth have been recognised for many years but recently it has been realised that differences can exist between similar strains of one species (Troughton and Whittington, 1969; Monyo and Whittington, 1970; Russell and Newbould, 1969; Hackett, 1969). These are not only differences in the structure of the root system which can result in changes in apparent uptake due to differences in ramification through the soil but there appear also to be differences in real uptake by the roots (Hackett, 1969). The extent of such differences is such that consideration should be given to the distribution of the roots in breeding though the difficulty of measurement makes this unlikely.

The introduction of semi-dwarf varieties of wheat and barley (Chapter 1) prompted the question of whether the dwarfness of the stem was reflected in the root growth. Experiments to examine whether this was the case have been reported from India (Subbiah et al, 1968; IARI, 1968) and the United Kingdom (Newbould et al, 1969, 1971; Cannell et al, 1972; Welbank and Taylor, 1971).

In India two semi-dwarf Mexican varieties, Sonora 64 (2 gene dwarf) and Lerma Rojo (single gene) were compared with four indigenous tall varieties under identical field conditions with a P32 injection technique.

Differences in the rooting pattern were observed. Sonora had a vertical penetrating root system about 4 inches in diameter to a depth of 15 inches with a dense pattern in the top 6 inches. Lerma Rojo however had almost all its roots in a shallow laterally spread pattern. The indigenous varieties had a deep, spreading pattern with greater spread than Sonora. The pattern of the indigenous varieties was considered to be the best but those of the imported varieties were considered to be adequate though in years of drought with no irrigation Lerma Rojo could suffer the effects of drought (Subbiah et al, 1968).

In the United Kingdom, home bred semi-dwarf varieties were compared with other commercial conventional varieties over a number of years. The semi-dwarf varieties included the ones used in the experiment reported in the next section. One of the semi-dwarfs differed significantly in its early root growth in that growth was slower in TL365a/37 though one of the conventional varieties had the same slow growth (Welbank, 1972). These experiments were carried out using Rubidium 86 injection (Ellis and Barnes, 1968; Russell and Ellis, 1968) and measuring the uptake of P32 from the soil. Later in the season no difference could be found between the varieties and it was concluded that no harmful effect on root growth was associated with the dwarf character in these varieties (Cannell et al, 1972).

4v Materials and Methods. Root study was undertaken on two varieties of barley in 1971 and on four varieties of wheat in 1972. In both years root sampling plots were laid out adjoining the main barley or wheat experiment described in Chapter 2 and Chapter 3.

(a) Barley Root Study 1971. Two varieties were compared, namely Golden Promise (short strawed) and Zephyr (tall) in the absence of any applied nitrogen. No other treatment was included but six replicates of the two plot block were sown and sampled. Samples were taken at approximately fortnightly intervals on the 17 and 31 May, 14 and 28 June, 12 and 28 July and on the 9 and 24 August. The sampling technique and measurement method are described later (sect. 4vc). The stages of growth of the crop with which these sampling dates coincide most closely are complete braird May 6, 4 leaf stage June 3 (Sample 2), in boot (G.S.10) June 28 (Sample 4), anthesis 15 July (Sample 5), maturity September 7 onward. These dates are approximate due to the variation between varieties.

(b) Wheat Root Study 1972. Four varieties of wheat were compared in the early part of the spring with the last sample being taken on 5 June. The varieties grown in the experiment were TL365a/34, TL363/30, Maris Nimrod and N59. The growth characters of these varieties have been described in chapter 3. In this study no other treatment was applied but four replicates of the four varieties were sown specifically for root study. Sample dates were 24 January, 31 March and 5 June which coincided with the early tillering stage, the early ear initiation stage and the late ear initiation stage respectively.

(c) Sampling and Measurement Techniques. The method of sampling was essentially the same as that used by Lockhart (1971). Soil cores of 6.5 cm diameter and 36 cm or 50 cm length were taken from each plot. At each sampling date four cores were taken from each plot. The 36 cm cores were taken first and divided into three equal, 12 cm, divisions which were bulked, weighed, crumbled and subsampled. When a deep

(50 cm) sample was taken the 50 cm core was inserted in the hole left by the 36 cm core. Again four samples were taken from each plot which were bulked, weighed, crumbled and subsampled as before. 1000 g or 300 g subsamples were taken from the upper three divisions i.e. divisions of the first 36 cm cores and 300, 500 or 1000 g samples from the "deep" cores. The subsample was mixed with water, stirred with a variable speed stirrer to break up aggregates and washed onto an 8" 30 guage sieve. The sieve was placed under a sprinkler to remove the fine soil fraction before washing the remainder of the sample into a sedimentation tank from which the roots were decanted off into a beaker. The water was then removed by suction filtration and the sample was stored on its filter paper at -5^{o}C until the measurements of length and diameter were to be carried out.

The root length per unit volume of soil was measured using Newman's method (Newman, 1966). This method estimates the length of an unknown quantity of root by the number of intersections between the root and a known length of fixed line within a known area. The intersections were counted by scanning a black tray with white lines and arcs etched on it with a binocular microscope (magnification 5 x 1.25) mounted on a swinging racked arm. The roots from the filter paper were washed onto the black tray with a little water which did not need to be removed. By using regular fixed fields quick counting of the intersections on a long length (450 cm) of line was possible.

The diameter of the roots was measured by counting the divisions on a linear scale in the eye piece of a higher power lens (x 14). For this measurement the roots were washed onto a red perspex tray with black lines etched on it and diameter of the roots was measured where the root crossed one of the lines. Greater magnification (14 x 1.25) was used for this measurement.

Knowing the length and mean diameter of the roots the volume and surface area of the roots in a volume of soil could be calculated. The method was tested by Lockhart (1971) who found that the least significant difference at the 5% level was 15% for root length and 9% for diameter when means of 8 replicates of 4 treatments were compared. The coefficient of variation was in the range of 30-40% on the basis of 4 cores per sample for lengths between 200 cm and 600 cm but at lengths less than 100 cm and greater than 1000 cm the errors became considerably larger. 1000 and 500 g samples were taken from some of the cores to avoid root lengths falling into the range where the measurement became less accurate. At lengths greater than 1000 cm the clumping of the roots became a serious problem and the number of intersections was difficult to determine accurately. For consistent measurement of the viable root in a sample the measurement had to be carried out by one operator.

The layers of the soil from which the samples were taken will be described as

Top layer	0 cm - 12 cm depth
Middle layer	12 cm - 24 cm depth
Bottom layer	24 cm - 36 cm depth
Deep layer	36 cm - 50 cm depth

4vi Results of Root Study in Barley. The length, surface area and volume of barley root in the two varieties at the eight sampling dates through the season are shown in tables 4:1, 4:2 and 4:3 respectively. Few of the differences between the varieties are significant in any of the parameters but slight, fairly consistent differences in the results from the first four sampling dates are noticeable.

In the top layer Golden Promise, the 'semi-dwarf' variety, had a slightly greater root length up to anthesis. This greater length was also evident in the middle layer but in the bottom layer Zephyr seemed to have a slightly greater length of root in the early stages of growth. After anthesis the differences between the varieties were inconsistent and it is doubtful if any real differences exist. The greatest increase in root length occurred before the 4 leaf stage in both varieties and at all depths in the soil. After this, growth proceeded at a slower rate and the root length reached a peak at, or just before anthesis. No rapid decline in root length after anthesis was apparent in any of the layers though this could have been a failure to recognise senesced root in the later samples. The length of root in the bottom layer at the first sampling in the tall variety was very much less than that of the dwarf variety suggesting that the growth of the tall variety at this depth was slower in the earliest stages though, by the 4 leaf stage, the length of root of the tall variety had overtaken that of the dwarf, as described earlier.

The differences noted in the length of root of the varieties were also apparent in the surface area measurement (table 4:2). The dwarf variety again had a slightly greater surface area of root in the top two layers up to anthesis while the tall variety had the greater surface area in the bottom layer except at the first sampling date. In the top layer a slight increase in the surface area after anthesis was noted which may have been a real effect in that the roots thickened without any

TABLE 4:1

Length of Root BARLEY 1971 cm/cm^3 of Soil

SAMPLE	1	2	3	4	5	6	7	8
Date	17/5	31/5	14/6	28/6	12/7	28/7	9/8	24/8
Top Layer	**	NS	NS	*	NS	NS	NS	NS
tall	2.44	5.44	6.39	6.09	5.26	7.76	6.04	6.65
dwarf	2.90	5.81	7.01	7.39	5.54	7.38	6.44	6.37
cv%	5.89%	19.6%	40.64%	9.81%	37.15%	19.3%	21.7%	21.9%
Middle Layer	NS	NS	NS	NS	*	NS	NS	NS
tall	2.54	4.44	4.18	4.96	2.17	3.61	3.86	3.67
dwarf	3.32	5.17	5.84	5.52	2.74	3.93	3.53	2.90
cv%	21.8%	49.3%	16.96%	16.7%	15.4%	9.8%	11.2%	29.6%
Bottom Layer	NS	NS	**	NS	NS	**	NS	NS
tall	0.80	2.15	2.05	2.31	0.99	1.20	1.55	1.42
dwarf	1.29	1.46	0.96	2.38	1.00	1.75	1.55	1.52
cv%	38.0%	34.7%	16.75%	17.3%	18.1%	13.9%	39.0%	35.0%
Deep Layer			NS		NS			
tall			1.82		1.58			
dwarf			1.98		1.38			
cv%			25.77%		42.4%			

cv% = coefficient of variation

TABLE 4:2

Surface Area of BARLEY Root 1971 $cm^2\ cm^{-3}$ of Root in Soil

SAMPLE	1	2	3	4	5	6	7	8
Date	17/5	31/5	14/6	28/6	12/7	28/7	9/8	24/8
<u>Top Layer</u>	*	NS	NS	*	NS	NS	NS	NS
tall	0.103	0.271	0.365	0.355	0.350	0.416	0.302	0.325
dwarf	0.129	0.281	0.395	0.427	0.346	0.408	0.335	0.303
cv%	11.9%	25.8%	39.3%	11.6%	41.4%	20.6%	19.4%	19.2%
<u>Middle Layer</u>	NS	NS	NS	NS	NS	NS	NS	NS
tall	0.104	0.238	0.233	0.269	0.147	0.193	0.214	0.201
dwarf	0.141	0.254	0.268	0.299	0.194	0.212	0.176	0.142
cv%	21.6%	44.7%	23.0%	21.1%	18.5%	17.1%	15.7%	27.5%
<u>Bottom Layer</u>	NS	NS	**	NS	NS	*	NS	NS
tall	0.032	0.121	0.128	0.153	0.071	0.073	0.095	0.092
dwarf	0.052	0.079	0.058	0.143	0.081	0.106	0.090	0.083
cv%	33.7%	35.9%	13.6%	11.7%	16.5%	18.0%	37.3%	36.6%
<u>Deep Layer</u>			NS		NS			
tall			0.090		0.111			
dwarf			0.101		0.104			
cv%			16.0%		55.6%			

TABLE 4:3

Volume of BARLEY Roots 1971 $cm^3\ cm^{-3} \times 10^{-3}$ of Root in Soil

SAMPLE	1	2	3	4	5	6	7	8
Date	17/5	31/5	14/6	28/6	12/7	28/7	9/8	24/8
Top Layer	NS	NS	NS	NS	NS	NS	NS	NS
tall	0.351	1.111	1.674	1.663	1.888	1.820	1.209	1.293
dwarf	0.459	1.089	1.784	1.981	1.730	1.815	1.400	1.154
cv%	21.8%	36.4%	38.2%	14.1%	46.6%	29.0%	28.4%	22.9%
Middle Layer	NS	NS	NS	NS	NS	NS	NS	*
tall	0.341	1.019	1.043	1.175	0.814	0.835	0.962	0.879
dwarf	0.477	1.009	1.188	1.309	1.118	0.919	0.715	0.561
cv%	27.4%	41.6%	29.9%	31.1%	30.8%	26.9%	26.9%	26.2%
Bottom Layer	NS	NS	**	NS	NS	NS	NS	NS
tall	0.110	0.559	0.652	0.819	0.441	0.357	0.468	0.478
dwarf	0.167	0.328	0.280	0.699	0.539	0.522	0.415	0.360
cv%	41.2%	37.3%	27.1%	18.1%	32.9%	30.3%	36.9%	43.8%
Deep Layer			NS		NS			
tall			0.357		0.653			
dwarf			0.413		0.668			
cv%			14.6%		74.6%			

further length extension at this stage.

Fewer significant differences were noted in root volume as the coefficients of variation were higher in this derived variate (table 4:3). In the top two layers the supremacy of the dwarf variety in terms of length and surface area is not evident in root volume. In the bottom layer however the greater length and surface area of the tall variety is also apparent in the volume measurement where the difference is, if anything, more obvious up to anthesis. A decline in volume after anthesis is noticeable in the dwarf variety in particular, though it is also evident in the top division of the tall variety. This could suggest an earlier reduction in the activity of the dwarf variety's roots than in the tall variety. Rapid volume growth in the top layer was sustained beyond the 4 leaf stage in both varieties before the growth slowed. Length and surface area both showed an earlier reduction in rate of growth.

The differences between the varieties in the deep layers in all three parameters are unlikely to be real differences as they are very slight. It is interesting to note however that the difference between the two sampling dates is very small in both length and surface area but that this difference is considerable in volume thus the roots at this depth become thicker around anthesis. In all other layers the increase in volume and surface area occurs most rapidly in the earliest stage of growth measured i.e. between samples 1 and 2 after which the rate of increase is reduced.

4vii Results of Root Study in Wheat. The results of the root measurements on the three sample dates are shown in table 4:4 for length,

TABLE 4:4

Roots WHEAT 1972

Length of Root

	SAMPLE		1			2			3			
	Date		24 January			31 March			5 June			
	Layer		Top	Middle	Bottom	Top	Middle	Bottom	Top	Middle	Bottom	Deep
	VARIETY											
L												
E		* M	1.24	0.93	0.51	10.00	7.43	3.90	8.80	7.53	4.36	6.47
N		N	2.64	0.81	0.60	11.40	9.27	4.52	8.03	7.54	3.62	3.48
G		A	1.40	0.99	0.60	9.84	6.35	2.48	8.52	6.79	4.81	7.95
T	cm cm^{-3}	B	2.35	0.65	0.43	10.92	5.56	2.62	9.38	8.64	4.03	6.36
H	cv%		52	44	60	17	14	32	19	15	19	51
	signif.								NS	NS	NS	NS

* M = Maris Nimrod   N = N59   A = TL363/30   B = TL365a/34

TABLE 4:4

Roots WHEAT 1972

Surface Area and Volume as at 5 June

S	Layer		Top	Middle	Bottom	Deep				Top	Middle	Bottom	Deep
U	VARIETY												
R													
F		* M	0.48	0.40	0.25	0.09	V		* M	2.12	1.68	1.11	0.46
A		N	0.45	0.41	0.19	0.05	O		N	2.02	1.81	0.82	0.23
C	$cm^2\ cm^{-3}$	A	0.46	0.34	0.25	0.12	L		A	2.05	1.41	1.01	0.62
E		B	0.54	0.49	0.22	0.10	U	$cm^3\ cm^{-3} x10^{-3}$	B	2.47	2.27	0.96	0.53
	cv%		19	18	1	54	M	cu%		24	22	24	59
A	signif.		NS	NS	NS	NS	E	signif.		NS	NS	NS	NS
R													
E													
A													

* M = Maris Nimrod N = N59 A = TL363/30 B = TL365a/34

surface area and volume measurements. The earliest sample (24 January) was very variable as the root lengths were very short and the intersection counts fell within the range (<100) where the method becomes unreliable (sect. 4vc). 1000 gram samples were used in the second sample to avoid this danger.

The samples were too widely spaced to enable conclusions regarding growth patterns to be drawn but comparison of the varieties at the separate dates will give an indication of the extent of the root development of the different varieties.

At the first two sample dates varieties N59 and TL365a/34 had by far the greatest root growth in the top layer and N59 also in the middle and bottom layers. At the final sample however, N59 had the least root in all the layers except the middle where it was intermediate in root length between the other varieties. TL365a/34 had the least root of all the varieties in the middle and bottom divisions at the first two dates which suggests a more extensive growth at a shallow depth at the expense of the deeper roots. The results of the third sample do not bear out this conclusion as this variety has the largest amount of root at the middle layer as well as the top and an intermediate amount at greater depth.

Values of all the parameters are higher at the second sampling date than at the third. This could arise through one of two causes. Firstly there may have been more roots at the second sample or the disparity of the results could be due to a different operator making the measurements at the third sample from the operator at the other two dates. The first two samples in the wheat study were measured by a B.Sc. student (A.G. Courtice, 1972) for his honours thesis while all the other measurements were made by the author. If the first cause is the real one all varieties have less root at the end of the ear emergence phase than at the start and the reduction in the amount of root is greatest in N59.

The variability of the results both within and between sampling dates makes it difficult to draw any firm conclusions regarding the growth of roots of the four varieties under examination. It can however be stated that there does not appear to be any large difference between the growth of roots in the dwarf varieties to that of the taller ones.

4viii Discussion of Root Study Findings. The relevance of the measures made on the roots in this study to the activity of the roots in the soil is doubtful. Of the three parameters measured, length, surface area and volume, the volume appears to be the one most closely relating to the activity of the roots in the soil (Clarkson and Sanderson, 1971) though this close relationship only exists where the fine lateral roots are measured as well as the larger axis roots. With the technique of root extraction used in this study the only point at which lateral roots could be lost is on the 30 mesh sieve where the fine soil fraction is removed. Here losses could only occur if roots were washed through the sieve which is unlikely as the force of water used on the soil at this stage was slight. It can therefore be assumed that the volume measurements made in this study relate most closely to the activity of the roots in the soil. The discussion will not however be restricted to discussion of the volume of root as the evidence to support the conclusions of Clarkson and Sanderson (1971) has not been extensively verified to date.

The pattern of growth of the two barley varieties was essentially similar. Growth of roots in length and surface area was rapid up to the four leaf stage at all depths though the dwarf variety had greater growth in the middle and bottom layers before the first sample was taken. After the four leaf stage the roots grew more slowly with a cessation of growth at or around anthesis. A slight decline in the amount of root after anthesis was noticed particularly in the volume of root and this decline was more rapid in the dwarf variety than in the tall one. Volume growth maintained the early rapid growth up to the sample after the four leaf stage was reached i.e. for a fortnight after the length and surface area growth had slowed. In barley therefore the root system is developed early in the life of the plant with only a little new growth occurring after the four leaf stage and most of this being thickening of the existing roots. The technique of measurement measured the total root in a volume of soil and thus no conclusion can be drawn regarding the amount of new growth which occurs to replace dead roots in this slow growth phase between four leaves and the flowering of the plant. Such regeneration of tissue occurs in the shoots of the plant with lower leaves dying and being replaced by younger leaves with little overall effect on the total leaf area and it is therefore probable that some thing similar occurs in the root system but escapes unnoticed.

The main differences between the barley varieties were, the more extensive early length growth of the dwarf and its earlier reduction in volume, in particular, though length was also reduced. The early growth of Golden Promise roots is similar to the tiller growth observed in this variety (Table 2:6, Chapter 2Dix). More tillers are produced by Golden Promise than by Zephyr and as each tiller produces some roots the root growth of the greater tillering variety would be expected to be more extensive. In the discussion of the shoot growth (Chapter 2E) it was concluded that Zephyr produced a large number of infertile tillers. These would be produced near anthesis and would thus be instrumental in reducing the difference between the root growth of the two varieties at this stage. The early reduction in the volume and length of Golden Promise roots observed would result in a reduction in the activity of the root system during the grain filling period which could result in a reduction in the supply of some essential elements for the grain filling process or the reduction could be a result of the earlier ripening of Golden Promise. Earlier, (Chapter 2Dix) it was shown that Golden Promise had smaller grains and, in 1971, a smaller yield than Zephyr which could have been in part due to the reduction in the root activity during the grain filling stage.

The only other difference between the barley varieties which was noticed was the earlier depth penetration of the dwarf variety. Only in a very dry spring would such a difference in root growth manifest itself in shoot growth differences. Although the dwarf variety established extensive roots in the bottom layer early in the growth of the plant, the tall variety developed a more extensive system in this layer by the four leaf stage and had a greater quantity of root, particularly in volume up to anthesis. Lack of such deep roots could be detrimental in a dry year when the roots in the upper soil layers would be in dry soil and the plant might be in danger of suffering lost production through drought. Similar amounts of root were found in the deep layer however which would alleviate this danger.

Thus the slight differences in the growth of the roots of the two barley varieties could have an effect on the growth of the plants and on the crop performance particularly in drought conditions though the reduction in root volume of the dwarf could have detrimental results even in the absence of drought.

The wheat findings point to no obvious differences between tall and dwarf varieties in the growth of their roots though the outmoded variety, N59, may in fact, behave differently to the other varieties, in that, it has a greater length of roots than the other varieties at the first two sample dates and less at the final sample. This could be the result of a greater tiller loss by this variety by the end of the ear initiation phase resulting in a greater loss of roots associated with these tillers. Unfortunately no tiller counts were made in association with these root measurements. Should this be the true position it tends to refute the argument put forward by Stoy (1965) (Chapter 3i) in favour of tillers helping the plant by enhancing the root system as the roots appear to die with their associated tillers and contribute little to benefit the plant as a whole. All varieties showed a reduction in roots at this stage but as the measurements were made by different operators they must be treated with caution especially as no such reduction in rooting before anthesis was noticed in the more comprehensive barley root study (Chapter 4vi). The varietal differences at individual sampling dates would not be affected by the change in operator and the change in the position of N59, from having the greatest amount of root, to having the least is, in all probability, a real difference.

Of the other three varieties, Maris Nimrod was intermediate in length of root between the two dwarf varieties. The difference between the two dwarfs was always present in all parameters with TL365a/34 having slightly greater amounts of root than TL363/30. Differences between the varieties were small however and it is concluded that any differences between the varieties in this experiment were too small for the experimental method to detect. Variation within the dwarf varieties seems to be as great as that within conventional varieties.

These same varieties with the exception of N59 were studied elsewhere (Newbould et al, 1969, 1971 and Cannell et al, 1972) in terms of root growth and activity and the same conclusion was reached.

Comparison of the growth of barley and wheat roots is unfortunately not possible due to the doubtful between-sample comparisons in the wheat study. At the start of June however wheat had a greater length and a comparable volume of root to that of barley (same operator (the author) for barley and final wheat sample) showing that the barley roots were thicker than those of wheat at this stage.

The root growth of dwarf varieties of wheat seems to have no serious shortcomings over the growth of conventional varieties and the fears that short stem growth would be associated with a reduction in root growth appear to be groundless. In barley there was weak evidence to support the farmers' view that Golden Promise is unsuitable for soils susceptible to drought as it had poorer root growth. In the bottom layer this is probably true but the difference between the varieties in the deep layer is very slight so poorer performance by Golden Promise would be unlikely.

CHAPTER 5

Study of the ear formation and filling in wheat (Triticum aestivum L).

5i Introduction. The production of grain in cereals can be considered to be the result of two separate operations by the plant:

1. the production of the carbohydrate in the leaves, stems and other photosynthetic organs in the plant and
2. the assimilation of these photosynthetic products in the utilisable form of the grains in the ear.

In Chapters 2 and 3 the contribution of the photosynthetic organs has been discussed.

The second operation requires firstly, that a suitable sink in the form of an ear of adequate size to cope with the assimilates produced be formed, and, after the necessary processes of fertilisation have been performed, that this sink be filled. In this section therefore there are three critical periods in which knowledge is required. These periods are (1) the period of initiation and development of the spikelets and florets of the ear, (2) the period influencing grain set, and (3) the period after anthesis when the ear becomes active as a competitive sink.

5ii The Initiation of the Ear. Bonnett (1936) and Friend (1965) described in detail the morphological development of the wheat ear from the initiation of double ridges which developed into spikelets, the upper ridge developing greatly while the lower of the two ridges represents the leaf subtending a branch and shows little development. Bonnett (1936) further described the order of development within the spike. The earliest part to develop is the middle section of the spike after which growth and development proceed in both directions at the same time. Within each spikelet of the ear development proceeds from the outside of the spikelet to the centre with the glumes being the first part to develop followed by the florets which develop from the basal floret to the top floret. Within each floret development proceeds from the outer parts inward. The lemma is the first to develop followed by the anthers, palea, and pistil and within the pistil the ovary, styles and stigmas develop, in that order. This development of the ear is under the influence of environmental factors which impinge on the rate of development and the length of time during which the ear development can take place.

Calder (1966) describes three stages prior to the start of the flowering cycle; (1) the juvenile stage, (2) the inductive stage and (3) the stage of realisation (i.e. initiation). All gramineae do not exhibit all three stages. Spring cereals are considered to have no juvenile or inductive stage but are considered to be capable of responding to a photoperiodic stimulus to flower without any preparation. Winter cereals however, are deemed to require an induction which brings them to a state where they are ready to respond to a photoperiodic stimulus. This induction is in the form of vernalisation. The juvenile stage is a feature of some grasses which require more than one stimulus, be it in the form of a temperature, photoperiodic or growth period stimulus. The physiological mechanisms by which these stimuli are effective are not understood (Calder, 1966). Once the stimulus to flower has been received the environment plays a large part in controlling the rate of development during, and the extent of, the initiation phase in cereals. This phase is the period from the appearance of the first spikelet initial in the form of a double ridge to the initiation of the last floret to be initiated on a particular ear. In barley the end of the initiation period coincides with the start of internode elongation (Nichols and May, 1963). The start of the initiation period in these experiments (Nichols and May, 1963) occurred when the apex of the barley plants was a particular length. Lucas (1972), however, found that with wheat, the length of the apex had no apparent bearing on the time of the appearance of the first double ridge. Friend et al, (1963) found that the appearance of the first double ridge was influenced by the environmental conditions prevailing. Higher temperatures advanced initiation as did an increase in light intensity. Once the double ridge stage is reached, the size of the sink is dependent on two separate aspects in the control of grain number i.e. the number of spikelets and the number of florets which develop. Lucas (1972) examined the effect of day-length on the number of spikelet primordia produced and at the same time looked at the effect under two levels of light intensity in wheat. The effect of keeping plants under short days for varying lengths of time before moving them to long day conditions on the primordia number was examined. Plants kept under short days continuously produced the largest number of spikelet primordia. The plants kept under short days for the longest period before moving to long days gave the next largest number of primordia and the number of primordia reduced with the length of the short day period thereafter. The light intensity had varying effects on the production of primordia. In this experiment only the number of spikelet primordia was noted, except on the terminal spikelets, where the floret primordia were counted. Therefore the effect on total grain number was not wholly examined. By analysis of the data it was deduced that the potential spikelet number was determined at the double ridge stage and that the most important factors controlling the number were the timing of floral initiation and the spike length at floral initiation.

Thorne and Ford (1967) and Rawson (1970, 1971) both found that short days increased the spikelet number. Rawson deduced that any factor which prolonged the period of spikelet initiation increased the number of spikelets. This view is supported by the findings of Friend (1965), who found that low temperatures, while retarding the morphological development of the ear to a greater extent than the rate of growth of the whole plant thus prolonged the duration of ear development resulting in larger ears with more spikelets. The increase in spikelet number does not necessitate a greater number of grains per ear and Thorne and Ford (1967) found a reduction in the number of grains per ear when the plants were subjected to short days between initiation and anthesis.

The effect of temperature reported by Thorne and Ford (1967) was the same as that found by Friend (1965) i.e. that low temperatures gave a larger number of spikelets per ear. Friend (1965) found a consistent effect of light intensity on spikelet number in that high light intensities increased the number, the same conclusion reached in a review of this effect (Friend, 1965).

Thus any factor which tends to increase the time span of the intiation period to a greater extent than its effect on the growth of the whole plant would appear to increase the number of spikelets. The environmental factors which have this effect are a low temperature, a high light intensity and a short day length.

Defoliation of tillers before the stage of initiation of the spikelets was found to delay the onset of floral and spikelet initiation and to reduce the length of the apex at the stage of initiation. The capacity of the ear was thus reduced (Bremner and Ingham, 1960).

In only two of the experiments where the environmental effects were studied was more than one variety compared (Rawson, 1970, 1971). In the first of these experiments the varieties studied were divided into those which needed a vernalisation treatment to flower and those which did not. Those varieties which had a pronounced vernalisation response were found to require a long period prior to the start of floral initiation as this period was when the spikelet primordia were differentiated. Those varieties where vernalisation was not required were found to produce most of their spikelet primordia in the period between the start of floral initiation and the formation of the terminal spikelet. Where the reaction to vernalisation was only mild both periods were important in determining spikelet number. In the first experiments the influence of a varying number of short periods of long days (inductive cycles) was studied (Rawson, 1970). As the number of cycles increased from 2 to 9 the number of spikelets was reduced. The rate of development was accelerated by the exposure of the plants to inductive cycles. The second series of experiments (Rawson, 1971) further explored the variety reaction to photoperiod. Varieties from a range of sources were subjected to different photoperiodic treatments. Differences in final spikelet number were related to three factors i.e. the number of double ridges at floral initiation, the rate of production of spikelet primordia and in duration of production of primordia. The varieties could be divided into two types, those which were early and those which were late, by their response to changes in photoperiod. The late varieties had an increased spikelet number with decreasing photoperiod down to a 10 hour period after which there was no response while early varieties responded to an 8 hour period with a further increase in the number of spikelets which were formed.

The rates of production of the two types were also different. Thus the number of spikelets per ear and, therefore, one part of the control of the number of grains per ear is dependent on variety and several of the environmental factors which impinge on it. The response of the number of grains per ear to the environmental influences discussed is not clear. Thorne and Ford (1967) found that the grain number per ear dropped with increase in the number of spikelets in one experiment but found that grain number per ear was increased by the same treatments in the following year. Rawson (1970) however found a very close relation between the spikelet number and the grain number but not with grain yield as the grains were very variable in weight between varieties. Kirby (1969) also described photoperiodic response as an increase in both spikelets per ear and grains per ear with short days suggesting a close relation between spikelets per ear and grains per ear.

From this review of the influence of the various factors on the number of spikelets, the number of grains and thus the resultant capacity of the ears of the wheat crop it appears that any factor which is likely to slow development will increase the capacity of the resultant ears. The evidence of Bremner and Ingham (1960) is the only evidence to refute this statement.

In this work (Bremner and Ingham, 1960) the leaf area was artificially reduced which had the effect of slowing the rate of development but, unlike the findings of the other workers mentioned, the ear size was reduced instead of increased when the rate of development was slowed. This suggests that the leaves may have a greater influence than that of mere suppliers of photosynthate and that they may also be suppliers of some growth substance which stimulates and encourages development by the apex. Friend et al (1963) suggested that certain wavelengths of light were responsible for the stimuli required by the ear for development. The photochrome system of the leaves was implicated as being responsible for the provision of a stimulus to the ear. From this suggestion, and that of Bremner and Ingham (1960) it would seem that the leaves are responsible in part for the development of the ear in its early stages both as suppliers of photosynthetic products and as the source of a stimulus to the apex to differentiate.

The environmental influences on the plant at this stage of development are thus considerable. Variety also has an influence especially when varieties of different daylength response or different response to vernalisation are compared. Cultural effects on the plant at this stage are unknown but it would appear that a compromise should be sought between practices which will delay the onset of initiation and reduce the rate of development and those which will accelerate this development. This would ensure a satisfactory number of grain sites in the ear without slowing development to the detriment of the plant in the later stages of growth.

5iii Factors Affecting Grain Set. At this period in the growth of the plant there are two ways in which the fertility of the flowers can affect the number of grains set after anthesis;

1. the flowers themselves may not be fertile;
2. having flowered the development may be halted and the flower may abort.

These two effects are not easily examined in isolation but the resultant absence of grains in certain sites in the ear can be attributed to one or other of these two factors. The picture is further confused by the fact that the plant is able to compensate, by the development of more distal florets, for any grain sites lost in this way. Thus records of numbers of grains per ear do not give a complete picture of the effect on the plant of conditions at the period around anthesis.

Evans et al (1972) studied the effect on the distal grains in the ear of emasculation of the basal florets in the central spikelets of the ear. The effect noted was an increase in the number of the distal florets which set grains. In intact ears the florets which set grains were the ones which reached anthesis within two days of the first floret regardless of the position in the ear. When pollination of the earliest florets was delayed, this resulted in an increase in the total number of grains set over the number in control plants. This evidence suggests, that there is some form of growth substance control of the flowering process which tends to inhibit the later flowering florets from setting grain and thus imposes a limit of the sink size at this stage. The distal florets would thus appear to be fertile but, unless the need for them to flower is very great e.g. as a result of lower florets aborting, they merely abort. Thus the effect on the number of grains is controlled within the plant in a complex way which makes study of the environmental effects on the processes within the plant even more difficult to establish. Bingham (1966) tried to compare three varieties in the field in their grain setting response to water stress. The field trial was unsuccessful in that effects noted were not consistent. In an associated glasshouse experiment however plants which were subjected to water stress at a few days before pollen meosis showed male sterility in the basal florets of the spikelets but a marked increase in the number of more distal florets which set grain was noted. This finding would agree with those of Evans et al (1972). Bingham concludes however that the field experiment results show that the yield was reduced by a lack of sink capacity which he suggests could be overcome by the breeding of plants with more florets per spikelet. Evans' evidence would tend to disagree with this suggestion and rather suggest that some means of overcoming the inhibition of the distal florets flowering should be found before attempting to increase the number of florets.

The effects of day length and temperature on the numbers of grains set in different varieties was studied by Kolderup (1970). The varieties studied were two local Norwegian varieties and Sonora 64. The local varieties had an altogether different response to temperature in that they had highest seed set at 12-15°C (95%) which fell with higher temperatures while Sonora had its lowest seed set at 12°C and about 80% at higher temperatures up to 24°C. The number of flowers in Sonora was not dependent on temperature but in the local varieties a peak was reached between 18-21°C. Owen (1971) also studied the effect of temperature on the development of spikelets. In this work the higher end of the temperature scale was studied and it was found that the high temperatures (greater than 32°C) adversely affected the development of florets and prevented the filling of fertile grains. These results agreed with Wardlaw (1970) who found highest grain set at low temperature (15/10°C) and with full sunlight. At the high temperature (27/22°C) treatment grain set was reduced.

5iv Grain Filling. Early work on the study of the yield of cereals concentrated on the supply of photosynthate from the photosynthetic organs of the plant and has been reported earlier in this publication. More recently the importance of the sink for this photosynthate has attracted attention. It has been suggested that the requirements of the photosynthetic system for storage space need not always be met by the ear (Evans and Rawson, 1970; Bremner, 1972) i.e. that the ear is too small to accommodate all the photosynthate produced. Bremner (1972) altered the supply of photosynthate by shading and defoliating the shoots and found that, with reduced supply of photosynthate the reduction in grain weight was smaller than in the total dry weight as the shortage in the supply of photosynthate became more acute. From this he deduced that the control plants produced dry matter surplus to the needs of the ear. Evans and Rawson (1970) found the supply of photosynthate of the ear and flag leaf to be adequate at all times in supplying the needs of the ear as a sink. Similarly Asana et al (1969) came to the conclusion that the way to improve yield still further was to produce a more efficient sink for the storage of photosynthate.

From the above workers' findings it becomes clear that we must know more about the mechanisms which control the physiology of the ear, in particular what controls its capacity and the partitioning of assimilates to the various grain sites in the ear. Asana and Bagga (1966) were the first to look at the growth of individual grains within the ear of wheat. They compared two varieties of wheat in terms of grain weight, volume, linear dimensions, water content and chemical composition. The two varieties differed in the relationship of grain weight between the two basal and the upper grains of the central spikelets. In one variety the basal grains were heavier and the upper grains lighter than those of the other variety after four weeks post-anthesis. In the next two weeks the first variety increased the dry weight of all its grains but the other variety did not although they were both senescing at the same rate. The difference was attributed to the difference in the moisture content of the grains of the two varieties, in that, the variety with the higher moisture content continued to increase in dry weight at a greater rate than the other variety. Thus there is at least one further control on the filling of the grains beyond that of the supply of photosynthate. The control mechanisms were further investigated by Rawson and Evans (1970). In their experiment they looked at both intact ears and ears in which some of the florets were sterilised. In intact ears the grains of the second floret of the central spikelet maintained the highest growth rate and the first floret of the basal spikelet the lowest growth rate. When the basal one or two florets of the central spikelets were sterilised the other spikelets made compensating increases in weight and in the number of grains set. In one variety this even led to an increase in the weight of grain per ear by up to 20%. This last finding has not been backed up by subsequent experiments (Evans et al, 1972). The distribution of labelled carbon has also been studied in this work from both the ear and from the flag leaf. Ear assimilated carbon was found to be evenly distributed but that of the flag leaf was found to be partitioned preferentially to the grains which grew fastest. When these were sterilised the $_{14}C$ was found in an increased proportion in the distal and basal florets. From these findings it appears that the greater growth rate of the second grains of the middle spikelets inhibits the development of later flowering and slower growing florets in the ear resulting in a reduction in grain yield. Walpole and Morgan (1972) did not find the uneven distribution of photosynthate from the flag leaf in barley but found that the flag leaf contribution was evenly distributed and that the grain weight of an individual grain was in part proportional to the length of the awn subtending that grain. Such a difference between species would be quite feasible when the different ear structure is considered as the differences in morphology are certain to result in differences in the vascular connections of the ear. That such a difference does exist,is implied from the results of Walpole and Morgan's two previous papers

(1970, 1971) which looked at the growth of different grains of wheat and barley. In barley, grains in the centre of the ear were found to grow more quickly in the early stages of grain filling, while the basal grains grew quicker after the first week post-anthesis. In wheat, these workers detected no difference in the growth rate of grains from different parts of the ear. This latter finding has been disputed by Bremner (1972) who found that grains in middle spikelets were larger at anthesis and remained larger throughout the growth period of the ear while those of the bottom spikelets while starting smaller grew to be larger than those of the top spikelets. Within spikelets the basal grain was largest immediately after anthesis but was outgrown by the second grain. These findings of Bremner (1972) corroborate those of Rawson and Evans (1970). If these later findings are accepted the spikelets of wheat would appear to behave in a similar fashion to those of barley but the partitioning within the spikelet of wheat has no counterpart in barley.

Within spikelets the effect of the absence of a grain from a site within the spikelet has provoked some debate. Rawson and Evans (1970) found that if the third grain from the base of the spikelet was missing the other two grains were larger. This effect was noted on the growth during the period immediately after anthesis. Bremner (1972) however found that the effect of the absence of the third grain on the other two was apparently non-existent instead of the expected weight gain. This effect could have been due to a difference in the vigour of the spikelets examined. When further testing of the results was carried out the absence of the third grain did not seem to affect the growth of the other grains in the spikelet or those of neighbouring spikelets. The test employed to examine the effect of the presence or absence of the third grain of the fifth spikelet (5_3) was as follows.

The ratio $(5_1+5_2)/(7_1+7_2+9_1+9_2+11_1+11_2)$was studied in both the presence and absence of 5_3 and no difference was found in the value of the ratio. This test takes into account the degree of vigour of the ear and the spikelet from which the spikelets under test are derived. Bremner (1972) suggested that at the stage of Rawson and Evans'(1970) plants i.e. just after anthesis the florets could be competing for some limiting factor while at the later stage of grain filling the supply of carbohydrate is rarely limiting.

The preceeding discussion has been wholly centred on the growth of the ear under one set of environmental conditions. The effect of the environment on this stage of the plant's development has not been examined very extensively to date. Wardlaw (1970) examined the effect of light and temperature on the early grain filling period of wheat. High temperature (27°day/22°night C) led to more rapid grain development and to greater dry matter accumulation in the grain. Lower temperature ($21^{\circ}/16^{\circ}$C) led to an increase in the dry weight of the stem. A reduction in the light intensity led to a reduction in the dry matter accumulation of both the stem and the ear and with tracer studies it was concluded that the stem and ear competed for assimilates when the light was limiting. The effect of light reduction on the two stages of grain growth i.e. from anthesis to 10 days and the starch deposition stage thereafter was similar in that it caused a reduction in the weight of grain per ear at both stages. The effect of temperature, however, when varied over the same stages, differed. High temperature in either stage reduced grain yield but this effect was greatest at the later stage. The low yield at the early stage was partly due to a reduction in grain set which was in part compensated for by larger grains. High temperature in the later stage reduced the size of grains though the development was more rapid. These findings are backed up in part by those of Marcellos and Single (1972) who looked at the duration of the post flowering phase under different conditions of temperature and photoperiod and found that the phase of growth was shortened by high temperature. The effect of variety and photoperiod on the rate of development was not significant.

The rate of development appears to affect the yield in this phase in a similar way to the way in which the rate of development in the ear initiation phase affected the number of spikelets differentiated and thus indirectly affecting the yield. Any factor which accelerates the development of the ear to a greater extent than it affects the growth of the ear will reduce the yield.

The influence of variety on the development of the ear hos not been studied to any great extent in wheat. Marcellos and Single (1972) found no difference in the length of the post flowering phase with variety. Walpole and Morgan (1970) found with one cultivar that there was no difference in the rate of growth between grains within the ear but the results of Bremner (1972) and Rawson and Evans (1970) contradict this finding. There is thus a case for examining the growth and development of the ear and the grains within the ear in different cultivars to examine whether there are differences in the degree of competition between grains within the ear in different cultivars or differences in the ear development. Such an examination would allow selection for the more efficient sink which has been shown to be necessary (Asana et al, 1969) to utilise more of the photosynthate produced by the photosynthetic system of the plant.

In addition the effect of cultural practice such as fertiliser application on the growth and development of the ear have not been studied. The compound effects of the nutrition of the plant on leaf area have been studied (Chapter 3) but how these changes are manifest in the development of the ear will be examined in the experimental section of this chapter (5B and C).

5B Experimental Method

i Study of grain filling in wheat 1971 and 1972. In 1971 a pilot study was carried out to examine methods of determining the extent of differences between varieties and treatments in terms of the weight of grains from different parts of the spikelet in wheat. Ears of wheat at a similar growth stage in the experiment described in Chapter 3 B and C were marked in the field just after anthesis with pieces of red wool tied around the peduncle. The growth stage was determined by the number of dehisced anthers which were visible on the outside of the ear. Nine ears from each plot were marked in this way for sampling at a later date. Samples of these ears were harvested on 19-21 July and 9-11 August three ears being taken from each plot at each sampling. These ears were dried in a forced draught oven at 100°C and stored. Three ears per plot were harvested at random at harvest and were dried and stored as before. The final sample of marked ears could not be made as the wool was blown off the ears of the tallest variety.

When removed from storage the samples were dried again before being weighed intact. The number of spikelets on each ear was determined and the four spikelets nearest to the middle of the ear were separated out from each ear. The twelve spikelets now making up the sample were broken up and the grains from the top, middle and bottom florets were separated out of each and the grains making up each group were counted and weighed. The division into top, middle and bottom grains was effected by reference to the following table

Number of florets	No. of Basal grains	No. of Middle grains	No. of Top grains
1	1	0	0
2	1	0	1
3	1	1	1
4	1	2	1
5	1	3	1
etc			

The mean weight of each grain from each position in the spikelet was calculated and the results analysed.

In 1972 the method was modified and expanded to give information on the grain weights from nine different positions in the ear. These positions were; Grains from the top floret of the bottom third of the ear; Grains from the middle florets of the bottom third of the ear; Grains from the bottom floret of the bottom third of the ear and grains from the same florets in the middle third and top third of the ear.

A sample of ten ears was taken weekly from each plot after anthesis. These ears were the ones measured in the determination of photosynthetic area. The sample was dried and stored for further examination in the winter. After storage the ears were again dried. The number of spikelets on each ear was counted and the ear was broken into its component spikelets. The spikelets were placed in three separate piles one for each of the top, middle and bottom thirds of the ear. The division into thirds was carried out according to the following table.

No of Spikelets	No. of Bottom spikelets	No. of Middle spikelets	No. of Top spikelets
6	2	2	2
7	3	2	2
8	3	2	3
9	3	3	3
10	4	3	3
11	4	3	4
12	4	4	4
13	5	4	4
14	5	4	5
15	5	5	5
16	6	5	5
17	6	5	6
18	6	6	6
19	7	6	6
20	7	6	7

20 spikelets were taken from each pile of spikelets and each spikelet was further divided into top, middle and bottom grains. This division was done according to the table used in 1971. The grains in each category were then counted and weighed. From these figures themean weight of each grain in each category could be determined. The total number of fertile spikelets was also recorded and from these results the weight of grain in each ear was established as well as the weight of grain in the three divisions of the ear. Growth rates of grains between sampling dates were also calculated and the varieties and treatments were compared. This method of examination of different grain sites in the ear overcomes the problem of vacant grain sites encountered in earlier studies (Walpole and Morgan, 1970; Rawson and Evans, 1970; Bremner, 1972). These vacant sites are the result of the failure of the grains to develop in certain positions in the ear. In the earlier studies (Walpole and Morgan, 1970; Rawson and Evans, 1970 and Bremner, 1972) the grains in each spikelet position were weighed. As many of these were absent, either a large standard error was accepted or some means of accounting for the lack of the grains was found. Walpole and Morgan (1970) examined only ears which conformed to a particular pattern of grain set within the ear. Bremner

(1972) however calculated values for the missing grains on the basis of missing values. In the present study only grains which were present contributed to the calculation of mean weight for a particular site. Only in one division, (Top spikelet, middle floret) did this lead to a wide range of values for grain weight and thus a high standard error due to, a high proportion of vacant sites as there were a large number of two grain spikelets in this division.

5B ii Ear development study methods. A pilot study of the early stages of development of the ear was undertaken. Samples of three main shoots per variety were taken from discard plots beside the main 1971-2 wheat experiment on various dates after the beginning of April. The growing points were dissected under a microscope and were examined. A number of observations of the size and development of the parts of the ear was made. No measurement criteria were fixed in the early stages i.e. before the start of floret differentiation but, after floret initiation had commenced, the number of florets of the terminal spikelet which had reached the stages of development described and illustrated by Williams (1966), were counted and a comparison between varieties in the development of the ear was obtained. The technique of Friend (1963) of numbering stages in the development lacked clarity of definition of the stages described as no one spikelet was selected for timing the development and, as the spikelets in the various parts of the ear display a wide range of development stages, one key spikelet must be used for development study. In this pilot study the terminal spikelet was the one selected for study. Recent work by Kirby (personal communication) has concentrated on the early stages of ear development and the measure used in his study is to count the spikelet primordia which have started to differentiate at each sample date and plot the number against time. Some degree of success is being achieved with this approach

5C i Results and discussion of ear development study.

The measurements of size and development of the ears of the five varieties on the various sampling dates are shown in Table 5:1. The first double ridges were noted on 10 April. By 14 April spikelets were discernible as extensions of the upper of the two ridges of the double ridge. The number of such "developing spikelets" was determined (Table 5:1). At the next sample on the 8 May the terminal spikelet had been differentiated and its development was followed closely from this stage until the last sample on 6 June, 2 weeks prior to ear emergence when development was almost complete. The number of developing florets on the terminal spikelet were counted on 8 May and their development noted. Similar samples were made on 16 and 23 May and on 6 June which included, in addition to the measurement of floret number and development, the length of the spike from the collar to the tip of the terminal spikelet.

The flexibility of the wheat plant in the production of grain sites is clear from the results in Table 5:1. Although spikelet number per ear reaches a maximum before 16 May the number of florets per spikelet increases into June that is up to two weeks before ear emergence. Dates of ear emergence were not recorded but anthesis dates from the main experiment are included in Table 5:1 for the no nitrogen treatment (NO) as the plots from which these samples were taken were grown without applied nitrogen. N59 and Maris Nimrod were later in reaching anthesis than the three semi-dwarf varieties and their later development is noticeable throughout ear development. The rate of development of the varieties differs but when the lengths of the

Table 5:1A Length and Spikelet development of wheat ear pre-anthesis.

Length of ear	Date	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59
Primordiun (mm)	16 May	5.02	6.94	7.01	6.61	3.71
	23 May	11.45	15.68	12.30	6.36	6.61
	6 June	42.96	45.36	30.00	32.04	23.04
Spikelet development						
Number of spikelets	10 April	4	6	4	3 -	3+ (D.R.*)
	14 April	5.33	6.33	5.67	4.83	4.17
Mean of	16 May	15.33	15.50	17.33	16.00	15.67
3 ears	23 May	15.67	16.50	16.33	15.00	16.33
	6 June	15.67	16.33	15.69	15.67	16.33
No. of Florets in Terminal Spikelet						
	8 May	2.30	2.00	2.00	1.00	0
MEAN of	16 May	3.67	5.50	4.00	3.00	2.67
3 ears	23 May	5.00	6.25	5.33	4.00	4.33
	6 June	5.33	6.67	5.00	5.33	5.00
Anthesis date. (Days after 1st July)						
		6.50	3.50	7.00	10.00	13.75

* DR Double ridges

Table 5:1B Development of florets within terminal spikelet at 23 May.

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59
Basal Floret (No. at each stage. 3 florets at each cultivar examined)					
Stamen development 1st visible (34 days *)	0	0	0	1	1.5
Stamen development well progressed (36 days *)	2	0	1.5	2	1.5
Carpels and stamens developed (40 days*)	1	3	1.5	0	0
Top Floret (No. at each stage, 3 florets of each cultivar except TL365a/34 where 4 florets)					
Stage 1 *	0	2	2	3	2
Stage 2 *	1	1	0	0	1
Stage 3 *	0	0	0	0	0
Stage 4 (32 days) *	2	1	1	1	0

* stages 1, 2, 3 and 4 refer to the number of protuberances visible in the developing floret, i.e. stage 1 - one protuberance earliest stage; stage 2-2 protuberances differentiation of stage 1
stage 3-3 protuberances differentiation of stage 2
stage 4-4 protuberances differentiation of stage 3
32, 34, 36 and 40 days refer to Williams (1966) as days after sowing. Double ridge at 22 days. Stage of development of each is described above.

Table 5:1C Development of florets within terminal spikelet at 6 June.

Total No. of florets at stage	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59
(a) Completely developed	5	11	7	7	6
(b) 40 day *	2	0	1	0	2
36 day *	2	2	2	3	2
34 day *	0	1	0	0	0
32 day *	3	1	1	1	1
Stage 3 *	1	1	2	2	0
Stage 2 *	1	2	2	1	2
Stage 1 *	1	2	0	2	2

* see note at Table 5:1B

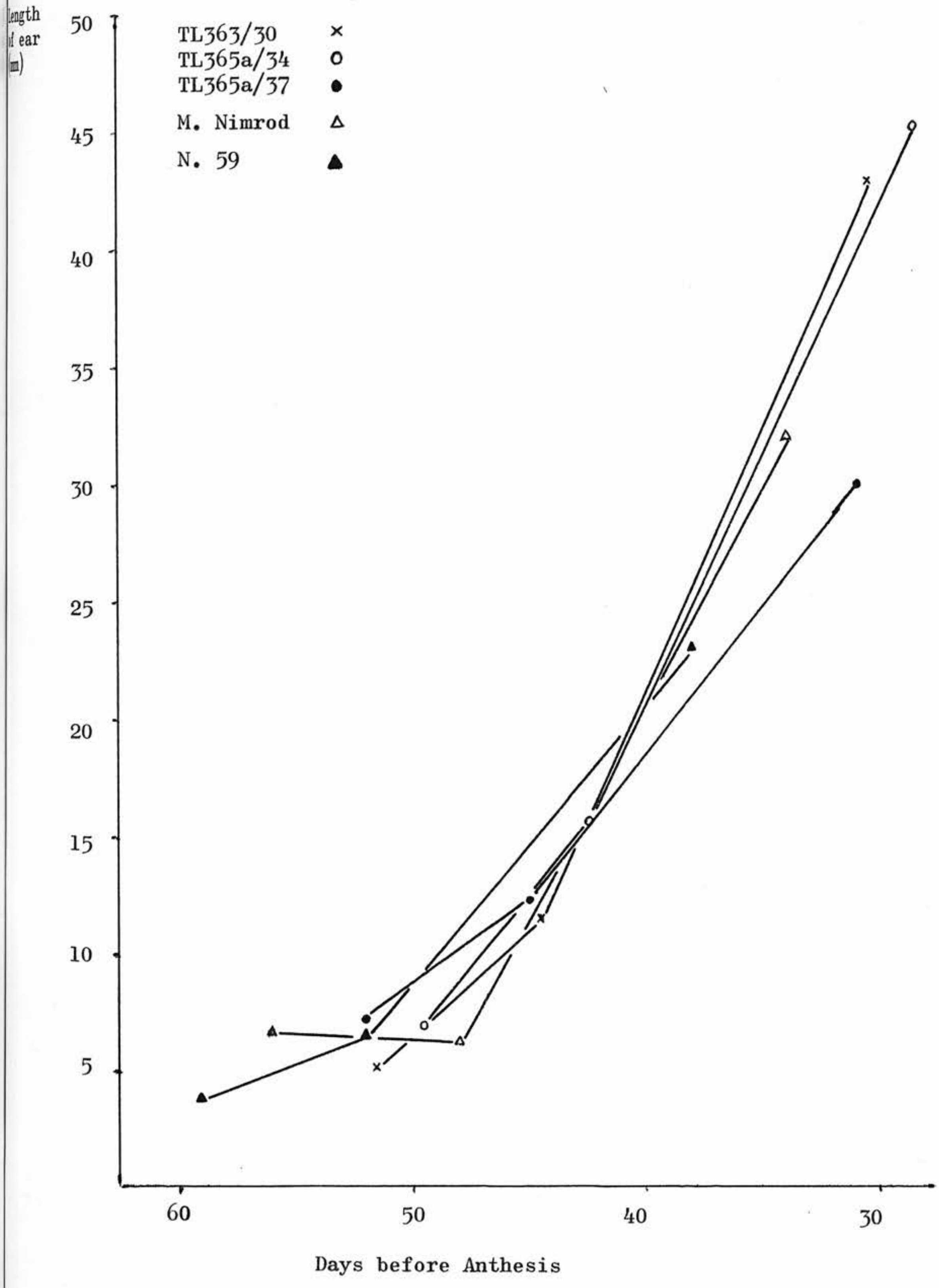
developing ear are plotted against the number of days prior to anthesis some of the differences are removed (Fig 5:A). In all varieties the rate of length of the ear increase is greater after 50 days prior to anthesis. The rate of growth of TL365a/37 is less than the other two dwarf varieties and less than Maris Nimrod. The relationship between rates of growth of TL365a/37 and N59 is uncertain as another sample taken nearer to anthesis would be required to show the rate of growth of N59 with greater accuracy.

The rates of development are less readily compared as varieties differed in anthesis date. The differences in stage of development reached at a particular sample date may thus be indicative of no more than the difference between the early-flowering and a late-flowering variety.

At each sample date N59 is the least developed variety but this variety is also the latest in flowering, of those studied. At 23 May N59 is 52 days short of anthesis which is the same number of days pre-anthesis as TL365a/37 is at 16 May sample. Comparison of development of these two varieties at the two separate sample dates shows that N59 has reached a comparable stage of development by 52 days before anthesis. Similarly by comparison of N59 at 6 June sample with TL365a/34 at 23 May the rate of development of N59 was comparable to the other varieties at the same number of days pre-anthesis.

Taking these constraints on the interpretation of the results in Table 5:1 into account, TL365a/34, TL363/30 and Maris Nimrod all appear to have faster rates of development than TL365a/37. The rate of development of N59 is again difficult to ascertain as it is later in developing. Rawson and Evans (1970) proposed that the rate of development and final grain number per ear were inversely related, i.e.

Figure 5:A Growth of Wheat ear pre-anthesis



that the fastest developing variety had the lowest number of grains per ear. The present study tends to contradict this finding as the three varieties with the faster development rate also have a higher number of grains on each ear in the absence of nitrogen fertiliser (Appendix Table 3:3) while TL365a/37 which had the lowest development rate also has the lowest number of grains on each ear if N59 is ignored for the present discussion. The uncertainty regarding the rates of development, in the present study, however casts doubt on any relationships with the other, accurately determined parameters.

This pilot study failed in its objective of assessing the rate of growth and development of the ears in the pre-anthesis period principally through the lack of constancy of the parameters measured and the unsuitability of these parameters for numerical presentation and comparison.

The method of Friend (1963) of relating stages of development to the development of a plant grown in standard conditions on a numerical basis has much to commend it in the period after floral initiation but spikelets in fixed positions in the ear must be selected on which the observations are to be made. The technique of Kirby (personnal communication) where the primordia are counted as they appear is very suitable for the stages before floret differentiation commences. The use of these methods would make possible a graphical presentation of the results of each day's measurements against the number of days before anthesis on which the sample was taken. This would be the most suitable method of examining the rate of development of the different varieties.

5C ii Results of grain filling study. The results of the weighings of the grains from the nine sample positions in each ear at the several sample dates are presented graphically in Figures 5:1 and 5:8. Varietal and nitrogen means of the average weight of the grains from each position in the ear are plotted against the number of days after anthesis on which each sample was taken. This form of presentation shows the treatment effects in terms of absolute rate of growth more clearly than by graphing the weights against chronological time as it removes the effect of the differences in the duration of the grain filling prior to the first sample being taken.

The graphs of the nitrogen means (Figs. 5:5;-5:8), where the effect of treatment on grain growth is very slight, show the absolute rate of growth of the individual grain positions very clearly against the days after anthesis. Only near maturity do the effects of nitrogen become marked on the growthof each grain.

A Growth within the ear. The absolute rate of growth of the grains in the different positions in the ear at one nitrogen rate, N_1 (40 kgN/ha), are presented in Table 5:2 and the values of the relative growth rate at the same rate of nitrogen are presented in Table 5:3.

Differences between spikelets in the absolute growth rate and the duration of growth are shown most clearly in Fig 5:8. The middle spikelet has the largest grains in the earliest samples with the top spikelet grains only very slightly smaller. At this stage the grains of the bottom spikelet are the smallest. The absolute growth rates of the middle and bottom spikelets are similar and are greater than that of the top spikelet (Table 5:2, Fig. 5:8) which results in the weight of the bottom spikelet becoming greater than that of the top

Figure 5:1 Wt of Grain within Bottom Spikelet

Effect of Variety

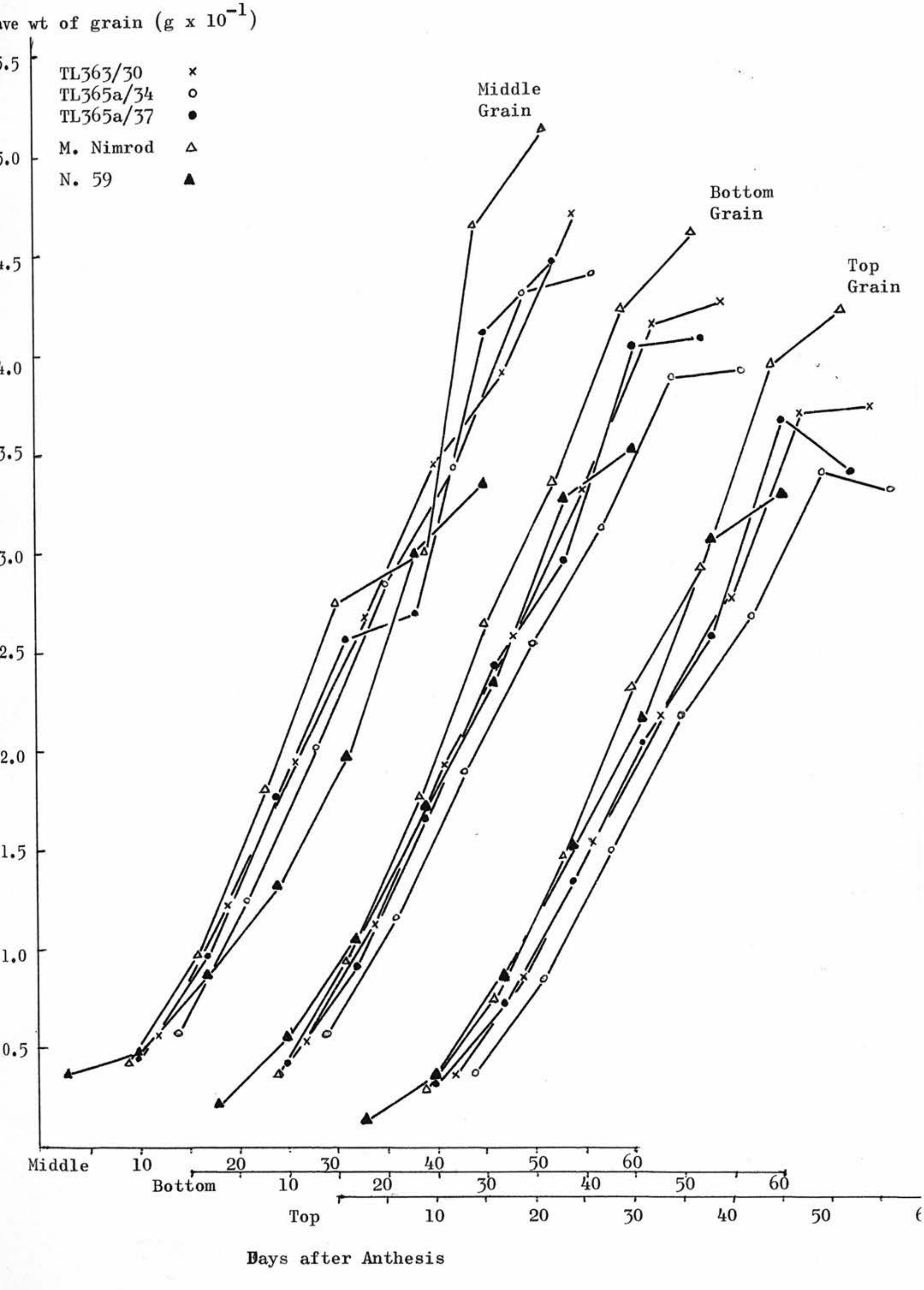
Days after Anthesis

Figure: 5:2 Weight of grain within Middle Spikelet

Effect of Variety

Figure 5:3 Weight of Grain within Top Spikelet

Effect of Variety



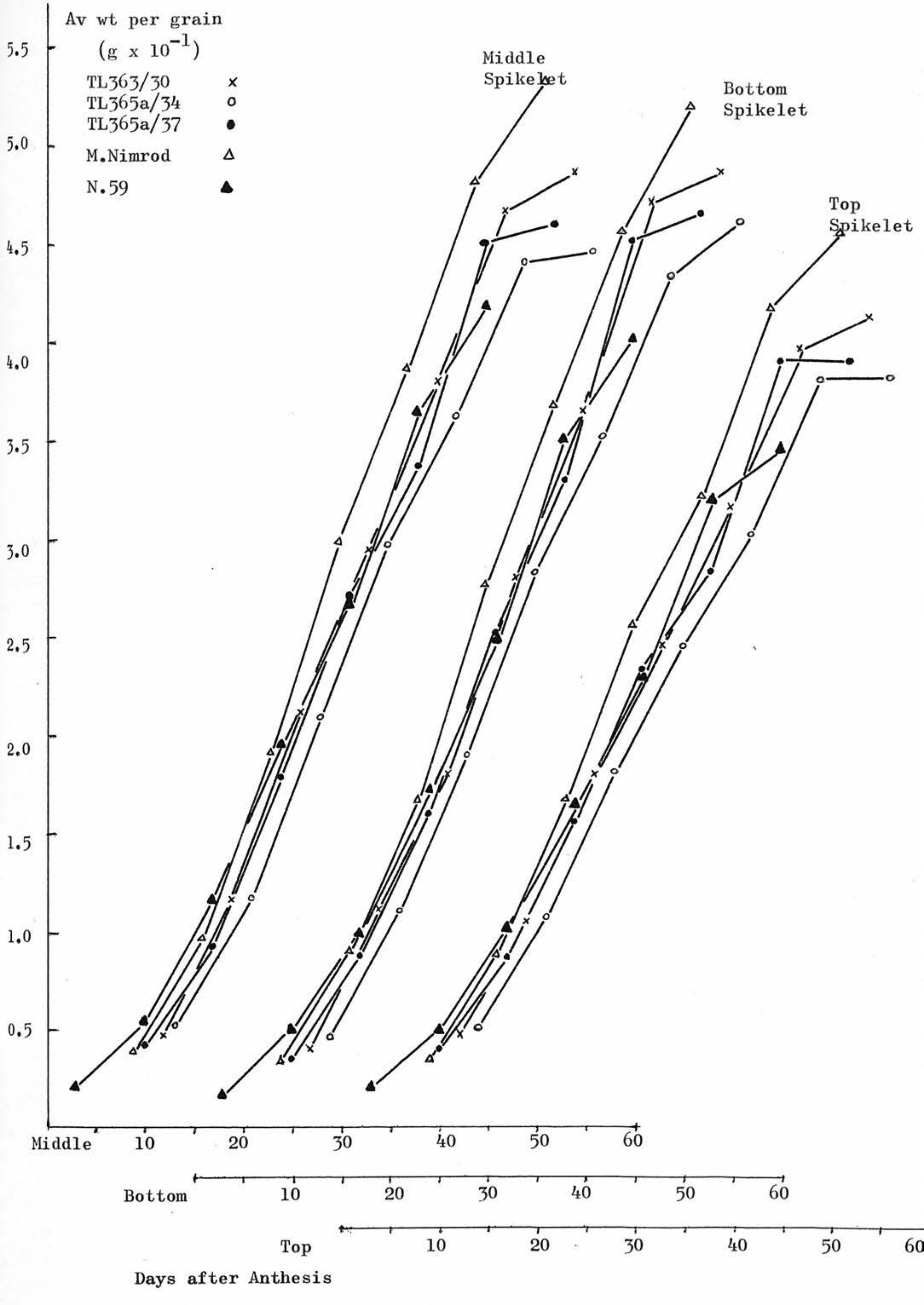


Figure 5:4 Growth of Grains within Spikelets with time

Effect of Variety.

Figure 5:5 Weight of Grain within the Bottom Spikelet - Effect of Nitrogen

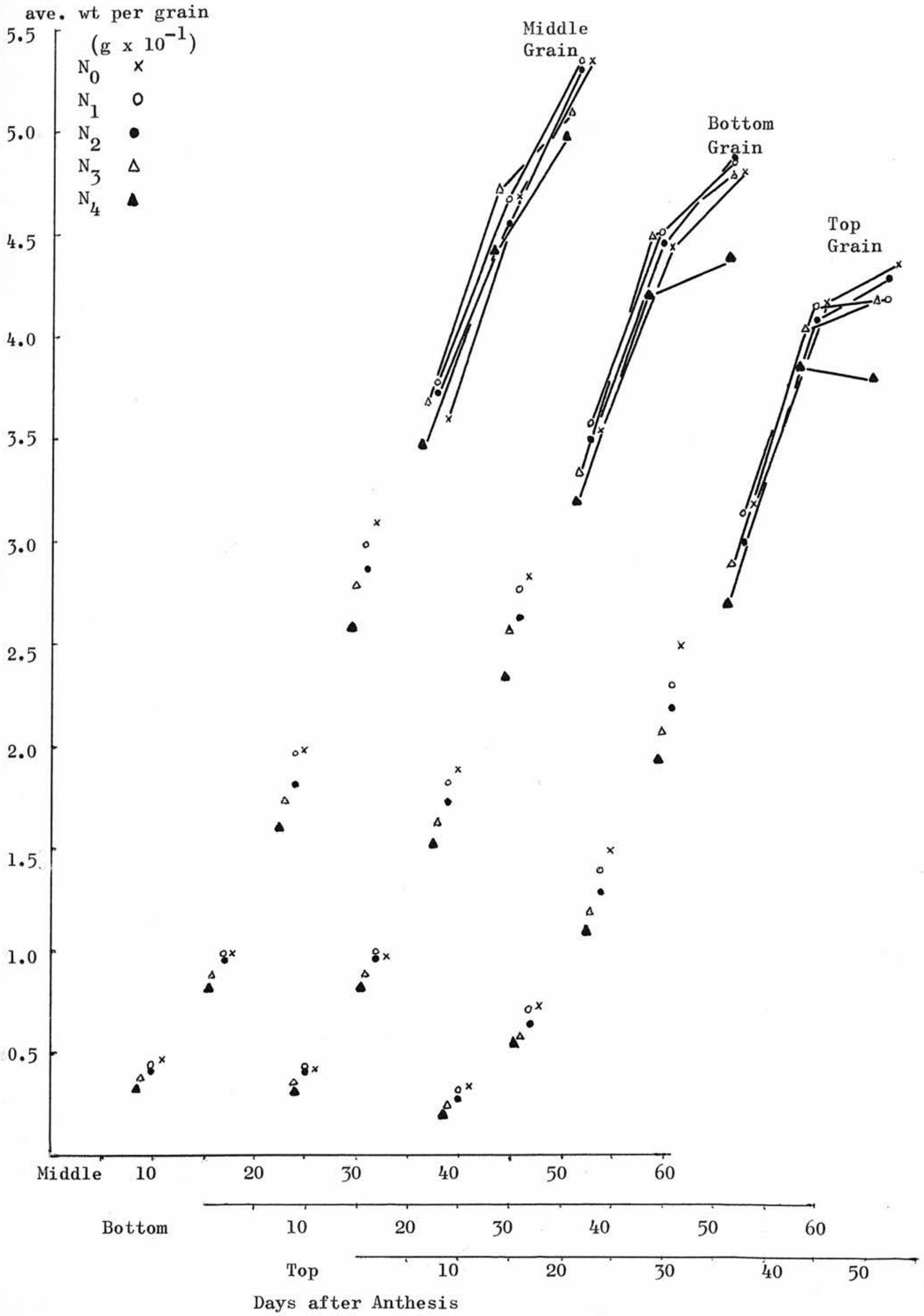


Figure 5:6 Weight of Grain within the Middle Spikelet
Effect of Nitrogen

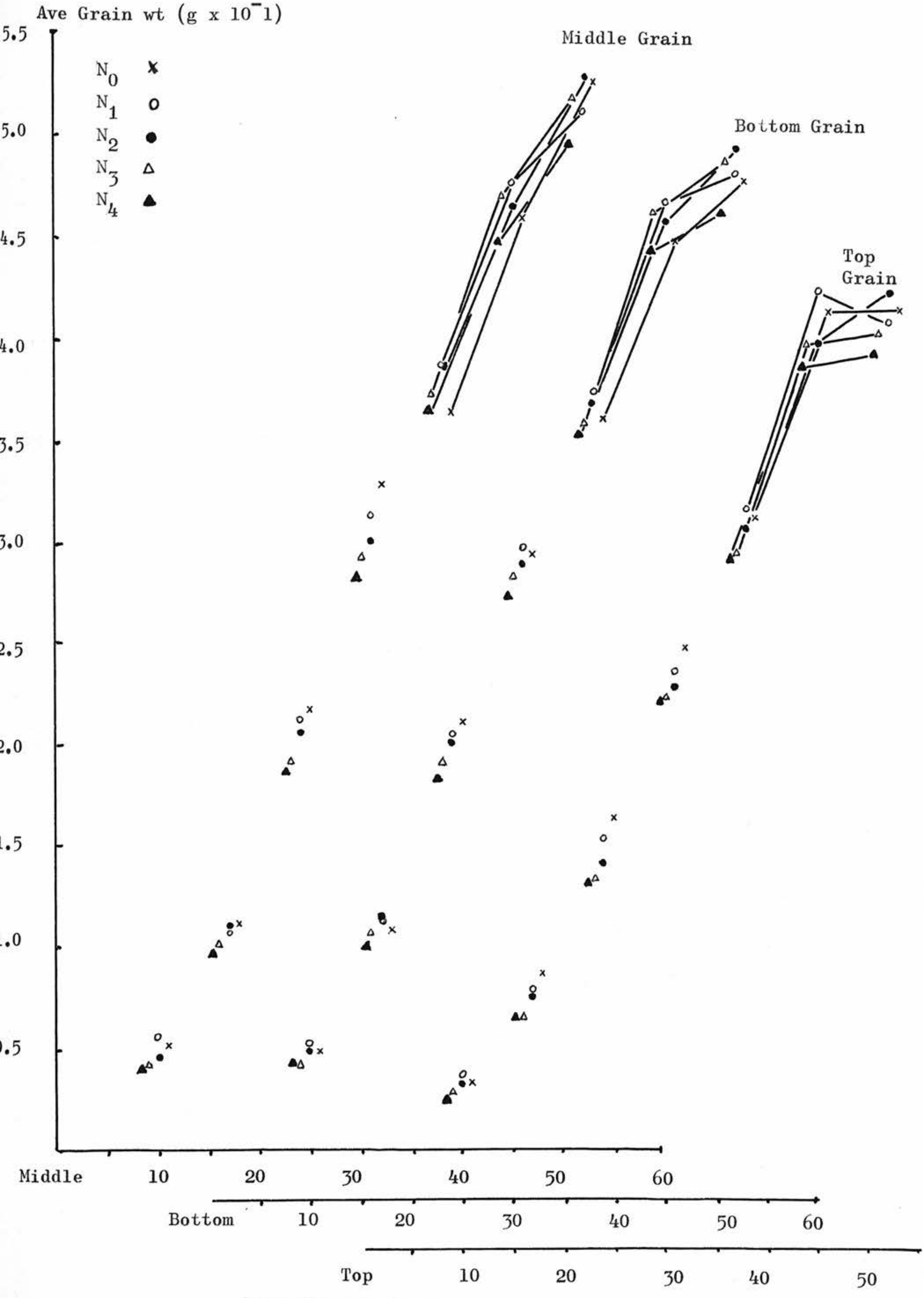
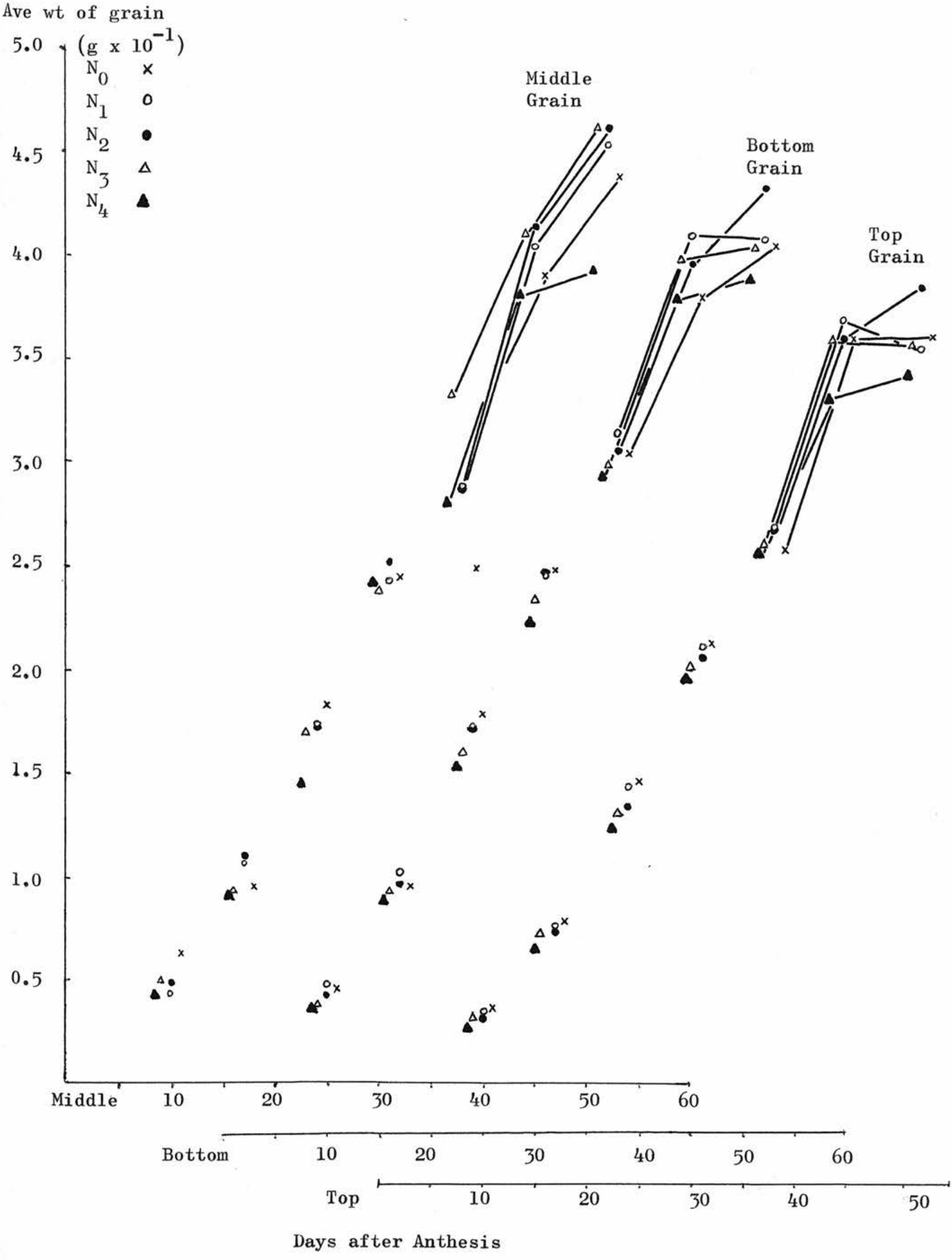


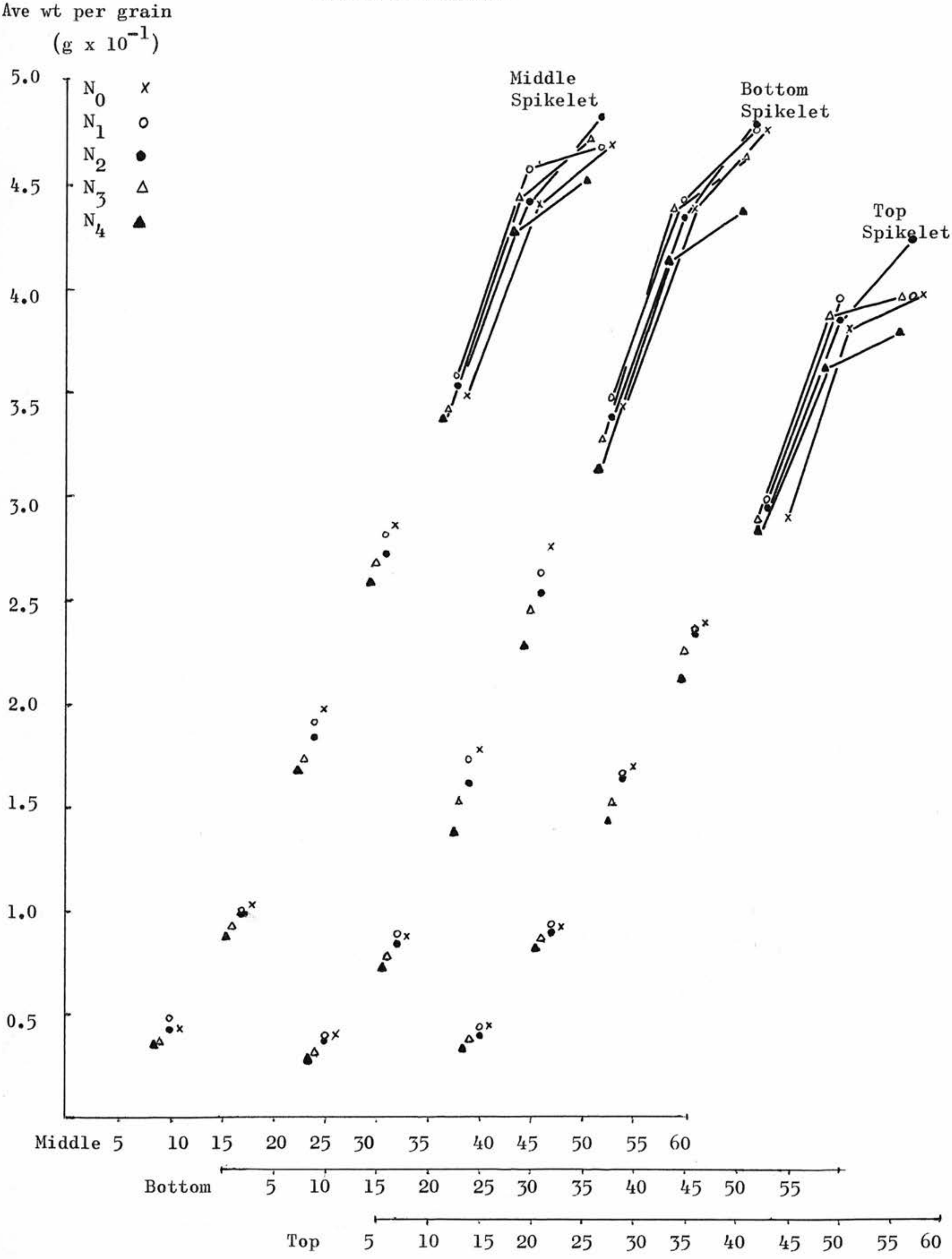
Figure 5:7 Weight of Grain within the Top Spikelet
Effect of Nitrogen



Days after Anthesis

Figure 5:8 Growth of Grains Within Spikelets with Time

Effect of Nitrogen



Days after anthesis.

Table 5:2 Absolute growth rate of grains in different positions in ear of wheat.

Mean of all varieties at N_1 (40 kgN/ha) g x 10^{-2} (1971-72)

$$AGR = W_2 - W_1 \quad (t_2 - t_1)$$

SPIKELET POSITION Grain Position	$H_3 - H_4$	$H_4 - H_5$	$H_5 - H_6$	$H_6 - H_7$	$H_7 - H_8$	$H_8 - H_9$
Harvest Dates	19-26 July	27 July - 2 Aug	3-9 Aug	10-16 Aug	17-23 Aug	24-30 Aug
BASAL						
Bottom	.0805	.1193	.1326	.1157	.1323	.0469
Middle	.0780	.1384	.1456	.1101	.1286	.0951
Top	.0570	.0980	.1297	.1196	.1423	.0039
MIDDLE						
Bottom	.0864	.1327	.1287	.1114	.1331	.0201
Middle	.0747	.1489	.1434	.1051	.1283	.0481
Top	.0617	.1056	.1173	.1144	.1541	- .0203
TOP						
Bottom	.0752	.1017	.1040	.0969	.1373	- .0023
Middle	.0879	.0971	.0984	.0664	.1629	.0733
Top	.0574	.0980	.0967	.0820	.1436	- .0057

Table 5:3 Relative growth rate of grains in different positions in ear of wheat

Mean of all varieties at N_1 (40 kgN/ha) $g \times 10^{-2}/g \times 10^{-2}/day$

(1971-72)

SPIKELET POSITION Grain Position	$H_3 - H_4$	$H_4 - H_5$	$H_5 - H_6$	$H_6 - H_7$	$H_7 - H_8$	$H_8 - H_9$
Harvest Dates	19-26 July	27 July - 2 Aug.	3-9 Aug	10-16 Aug	17-23 Aug	24-30 Aug
BASAL						
Bottom	.1133	.0846	.0578	.0366	.0330	.0100
Middle	.1083	.0937	.0589	.0327	.0306	.0190
Top	.1136	.0939	.0704	.0441	.0392	.0009
MIDDLE						
Bottom	.1049	.0834	.0514	.0333	.0307	.0043
Middle	.0908	.0927	.0546	.0301	.0297	.0098
Top	.1064	.0906	.0603	.0415	.0417	- .0049
TOP						
Bottom	.1002	.0742	.0498	.0347	.0380	- .0006
Middle	.1168	.0694	.0472	.0250	.0470	.0171
Top	.1046	.0897	.0545	.0342	.0450	- .0206

$$R.G.R. = \frac{(W_2 - W_1)}{(t_2 - t_1)} \quad \frac{1}{\bar{W}}$$

Table 5:4 Absolute Growth Rate $g \times 10^{-2} \times days^{-1}$ 1970-71
of grains in different positions in the ear.

Basal Grain

	TL363/30	TL365a/34	TL365a/37	M. Nimrod
$H_1 - H_2$	.1105	.1155	.1300	.1420
$H_2 - H_3$	.0168	.0091	.0203	.0112

	N_0	N_1	N_2	N_3	N_4
$H_1 - H_2$	.1415	.1380	.1270	.1165	.1165
$H_2 - H_3$	.0035	.0068	.0091	.0097	.0132

Middle Grain

	TL363/30	TL365a/34	TL365a/37	M. Nimrod
$H_1 - H_2$	.1180	.1210	.1310	.1455
$H_2 - H_3$	.0091	- .0059	.0009	.0091

	N_0	N_1	N_2	N_3	N_4
$H_1 - H_2$	.1375	.1355	.1265	.1130	.1245
$H_2 - H_3$	- .0182	.0065	.0047	.0076	.0068

Top Grains

	TL363/30	TL365a/34	TL365a/37	M. Nimrod
$H_1 - H_2$	.0890	.0255	.1105	.122
$H_2 - H_3$	.0179	.0215	.0200	.0141

	N_0	N_1	N_2	N_3	N_4
$H_1 - H_2$	.1200	.1025	.0870	.1005	.0975
$H_3 - H_4$	.0126	.0162	.0221	.0056	.0185

Table 5:5 Relative Growth Rate $g \times 10^{-2}/g \times 10^{-2}/dy$ 1970-71

Basal Grain

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod
$H_1 - H_2$	.0421	.0450	.0480	.0513
$H_2 - H_3$	.0038	.0022	.0043	.0023

	N_0	N_1	N_2	N_3	N_4
$H_1 - H_2$	.0535	.0496	.0474	.0449	.0471
$H_2 - H_3$	.0008	.0015	.0020	.0023	.0032

Middle Grain

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod
$H_1 - H_2$	.0461	.0490	.0520	.0540
$H_2 - H_3$	.0022	- .0015	.0002	.0019

	N_0	N_1	N_2	N_3	N_4
$H_1 - H_2$	.0556	.0492	.0463	.0436	.0536
$H_2 - H_3$	- .0047	- .0015	.0011	.0018	.0017

Top Grain

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod
$H_1 - H_2$	.0500	.0493	.0551	.0592
$H_2 - H_3$	.0055	.0067	.0053	.0037

	N_0	N_1	N_2	N_3	N_4
$H_1 - H_2$	.0594	.0504	.0470	.0525	.0582
$H_2 - H_3$	.0034	.0045	.0066	.0017	.0057

spikelet. This superiority of the bottom and middle spikelets, in absolute growth rate, is clear from harvest 4 to harvest 7 but, between the first two samples the rates of growth are similar for all spikelets. (Table 5:2) At the last sample, the growth rate of the top spikelet was reduced more rapidly than that of the other two spikelets, with the least reduction being shown by the bottom spikelet.

Within the spikelets the three grain positions showed differences in the absolute rate and duration of growth which are seen, most clearly, in Figs 5:5–5:7. In the two lower spikelets, the middle grain showed slightly faster growth than the bottom grain but, in the distal spikelet, after the second harvest, the bottom grains grew very slightly faster than the middle grains until the last two intervals, when the middle grains grew at a faster rate. The lowest absolute growth rate was shown by the top grains in all the spikelets particularly in the early part of the growth period. Near the end of the sample period (between sample harvest 6 and 8) the growth rate of the top grain equalled that of the other two grain positions or even exceeded it. The greatest decline in growth rate was found in the top grain in all spikelets between the last two harvests (harvests 8 and 9) while the middle grain showed the least reduction in absolute growth rate in this period.

Differences in relative growth rate were slight within spikelets, between spikelets however there were discernible differences. After harvest 4 the relative growth rate of the top spikelets was less than that of the others up to harvest 7 when all spikelets were similar in this parameter. (Table 5:3) No clear trend was obvious in the comparison of relative growth rates within spikelets though the top grain may in fact have a greater relative growth rate after harvest 4 as the values, of the R G R of the top grain, in all the spikelets, were slightly higher throughout the sampling period.

B Effect of nitrogen. The effect of nitrogen on the rate of growth of the grains is very slight (Figs. 5:5,-5:8) excepting at the end of the growth period. At the highest nitrogen rate the growth of the top and bottom grains of each spikelet showed the earliest reduction in absolute growth rate. This early decline in growth with high nitrogen is also clear in the mean of all the grains in the bottom and top spikelets (Fig. 5:8). All the other nitrogen rates behaved similarly having a more prolonged growth period than N_4 with the exception of N_2 (80 kgN/ha) which seemed to show an even more prolonged growth period than the other nitrogen rates. This is clear in Figure 5:8 in the top spikelet where the growth of the other nitrogen rates has shown a decline at the last sampling date. Within the spikelets the smaller decline in N_2 is also apparent in the top and bottom grains of the top spikelet and the top grain of the middle spikelet (Figs 5:6 and 5:7).

C Effect of variety. Differences between varieties were much more easily discernible than differences between nitrogen rates in both the rate and duration of the growth of the grains in the different positions in the ear. (Fig 5:1 to 5:4) All the differences found were apparent in each of the nine grain positions examined and were almost entirely consistent throughout. Figure 5:4 shows the differences between varieties in the growth of each spikelet while Figures 5:1 - 5:3 show the differences between grains within each of the three spikelets. Three of the varieties were outstanding while TL365a/37 and TL363/30 exhibited the standard pattern against which the other varieties were compared.

Over the first period of 10-15 days after anthesis, N59, had the most rapid growth of all the varieties in all the grain positions but after this period the growth rate of N59 equalled that of the other varieties and near the end of the grain filling period the growth rate of N59 grains declined sooner and more rapidly than those of the other varieties.

The final weight of N59 grains was invariably less than that of the other varieties but N59 reached anthesis between 6 and 10 days later than the other varieties. The first example, in N59, was thus taken between 6 and 10 days sooner after anthesis than in the other varieties. Senescence of the photosynthetic tissues of the plants did not occur as early as N59 as in the other varieties but grain weights were still less at final harvest as was seen in 1000 grain weight (Appendix Table 3:2) in chapter 3. The slight reduction in growth rate evident in the last sample of N59 is thus probably the start of the rapid decline in the growth rate seen in the other varieties.

TL365a/34 had a slower growth rate in the first two weeks after anthesis which resulted in the grains being smaller after this early period. The growth never subsequently exceeded that of the other varieties and thus this variety had the smallest grain weight throughout excepting N59.

Maris Nimrod was the other variety which stood out from the standard pattern in both rate of grain growth and the final grain size. Over the first week after anthesis the growth of this variety was similar to the standard and grain weight was thus also similar to the standard at the first sample. After this initial period of growth the growth rate accelerated over that of the standard and the grain size in all positions in the ear in this variety was greater after 20-25 days post-anthesis. This greater size was maintained throughout and, at the final sample harvest, the decline in growth rate in Maris Nimrod was less than the other varieties, which resulted in the differences in the grain size, increasing at the last sample. The increased rate of growth lasted for approximately two weeks from 16 to 30 days post-anthesis. This acceleration in the growth rate of Maris Nimrod could not be associated with any increase in the radiation received during this time period. Likewise when the growth of the grains was plotted against chronological time no differences, which could be related to differences in radiation input were recognised.

The order of the varieties in the final sample weight was the same as that observed in 1000 grain weight (Table 3:3 and Appendix Table 3:2). The order of the varieties in grain weight is most easily seen in Figure 5:4 where the mean weight of all the grains in each spikelet are compared. The total weight of grain on each ear was calculated, presented and discussed in Chapter 3 (Fig. 3:7).

The results of the pilot study carried out on the 1970-71 experiment are presented in Tables 5:4 and 5:5 in which the absolute growth rate and the relative growth rates are shown between the three sample dates on which the grains from the middle spikelets were weighed. The interval between samples was very long in the pilot study with 20 days between the first two harvests and 34 days from harvest two to the final harvest. The values of the absolute growth rate between the first two harvests, at nitrogen rates N_1 and N_2 are similar to those of table 5:2 which shows that the rate of growth of the grains was similar in both years. The values of relative growth rate are not comparable with any in the second year as they cover a much longer time interval during which the relative growth rate is constantly declining. The values of RGR in the pilot study did remain more or less constant throughout the three positions in the spikelet. Nitrogen had very slightly more effect on the absolute growth rate, in the pilot study, than was found in the second year as increased nitrogen caused a slight reduction in growth rate. The differences between the varieties were similar to those found in the second year and were constant in each position in the spikelet. Variety differences were again much larger than differences due to nitrogen.

The results for N59 were lost in the pilot study as the second sample was lost in this variety when the markers used to identify the ears which had been at the same stage of growth at anthesis were blown off the taller N59 ears. No accurate dates of anthesis were recorded in the pilot study so the growth of the different treatments could not be related to the duration of grain filling as it was in second year.

As these results do not differ in any major respect from those of the more comprehensive second year study no specific mention of them will be made in the succeeding discussion.

5D Discussion of the grain filling. The principal features of the comparison of the growth of the grain in the different positions in the ear are the differences in the absolute growth rate within and between spikelets (Table 5:2) differences in the time of cessation of growth in the different positions of the ear and differences in the relative growth rate between grains.

Between spikelets the differences in absolute growth rate observed were similar to those reported by Bremner (1972) and Rawson and Evans (1970). Grains in the middle spikelets were larger than those of the top and bottom spikelets at the first sample date and maintained the advantage by maintaining a similar growth rate to that of the bottom spikelets and a greater growth rate than the top spikelets. Grain size in the bottom spikelets overtook the top in most treatments by the third sample (H5) and in all treatments by the fourth (H6) i.e. by six weeks after anthesis and before growth had slowed. In Bremner's (1972) study growth had slowed in all the spikelets by the sixth week after anthesis and it was only by greater duration of growth that the bottom spikelet grains became heavier than those of the top spikelet.

Within spikelets the absolute growth rate of the bottom and middle grains were almost identical and only in the top spikelets was there slightly faster growth of the bottom grain over the middle grain. This finding differs slighly from that of Bremner (1972) who found the bottom grain to be faster growing in all the spikelets of the ear. In no treatment in the present study was the final weight of the bottom grain greater than that of the middle grain though this frequently occurred in Bremner's study (1972). This is surprising as in the present study the middle grain was made up of the average weight of the grains within the spikelet other than the top and bottom grain and would thus have been expected to be lighter, relative to a bottom grain than a single middle grain in a three grain spikelet as in Bremner (1972) study.

The relative size of the top grain within all spikelets was the same in the present study as in Bremner's. A different order of size was found within spikelets by Walpole and Morgan (1970) where the bottom grain was always larger than the middle grain. This is a complete reversal of the size relation found in the present experiment within spikelets and is not readily understood.

Growth continued for a longer period in the present study than in the previous work (Walpole and Morgan, 1970 and Bremner, 1972). The experiment of Bremner (1972) was carried out in a glasshouse while in Walpole and Morgan's (1970) study the reduction in the growth rate observed coincided with lodging in the crop under study. The lodging caused rapid curtailing of the growth which masked the differences which could have occurred with more gradual senescence. In the present study the growth continued unabated until the last interval between samples when sudden reduction in the growth rate of certain grains was noticed. The reduction in the growth rate in Bremner's study was more gradual. In the present study the bottom spikelets were least affected by the slowing of growth and the top spikelets showed the greatest reduction. Within spikelets the top grain showed the greatest reduction in growth rate and the middle grain the least, i.e. the middle grain continued growth for the longest period. These differences were not observed in the earlier work (Walpole and Morgan, 1970; Bremner, 1972).

The grains which showed the earliest reduction in grain growth i.e. the grains of the top spikelets and the distal and bottom grains of the other spikelets were the same grains which Rawson and Evans (1970) found to be least dependent on the supply of assimilates from the flag leaf. As theflag leaf was the first to senesce (Table 3:5) of the photosynthetic tissues supporting the ear, the grains which were most dependent on it as a source of supply would have been expected to be the first to show signs of a slower growth rate, i.e. the opposite of what was observed. It is therefore proposed that what Rawson and Evans (1970) observed was, that the middle grains and, the lower and middle spikelets had the greatest demand for assimilate from any source and their greatest demand for assimilates coincided with the period when the flag leaf was most active as a source. These grains thus received a greater proportion of flag leaf assimilate than the more distal grains and spikelets but not due to their being more dependent on the flag leaf. The flag leaf is most important as a source of assimilate in the earliest part of the post anthesis period which is the period when the most rapid grain growth occurs in the lower grains in each spikelet and in all grains of the middle and bottom spikelets.

Finally only small differences were found in the relative growth rate (RGR) of grains, which showed the growth to be largely related to the size of the grains in the various positions though there was one exception to this theory. Grains in bottom spikelets were always smaller than grains in the top spikelet at the first sample and by faster growth these grains overtook the top spikelet grains and their RGR must therefore have been greater. The RGR of the top spikelets was thus slightly less than that of the lower spikelets (Table 5:3). Walpole and Morgan (1970) showed no differences between the relative growth rates of the grains in different positions in the ear in the first 31 days post anthesis, i.e. in the period before the reduction in grain weight growth occurred in their experiment. Bremner (1972) disagreed with this finding as he also found grains of the bottom spikelets overtook those of the top spikelet in weight.

This could arise from one of two causes. Either the supply of assimilates was insufficient to maintain the growth of the grains in the top spikelets at a rate of growth proportional to their grain size, in the same way as the growth of the other spikelets, or the grains were inherently less able to utilise the assimilates which were available. A shortage of assimilates is unlikely. With increased nitrogen the

the increased photosynthetic area produced more than matched the increase in the number of grains as grain number only increased with the first increase in nitrogen while the PAD increased throughout the range of nitrogen used. The amount of assimilate moving to the top grain was unaffected by this increase in the supply and it therefore seems likely that the top grains are less able to utilise the supply through some other cause. This could be that there is a poorer vascular supply to the slower growing grains or, as the grains are smaller they may possess a smaller pool of enzymes with which to effect the biochemical changes necessary to incorporate assimilates as starch storage. The vascular supply to a spikelet has been examined by Zee and O'Brien (1971) but no comparison was made of the vascular connections to spikelets in different positions in the ear. The size of the vascular connections may not be the most important character in determining their activity. The distance of the slower growing grains from the source of supply may in fact be the principal factor in causing their slow growth rate but it seems that the growth rate of these grains is inherently less than that of the bottom grains in the spikelets.

Differences in the pattern of growth of grains within the ear due to either changes in the supply of nitrogen to the crop or due to different varieties were not found. From this finding it can be concluded that within the range of genotypes examined there are no differences in the pattern of assimilate distribution within the ear. Bremner (1972) also examined different varieties but as the results within one variety were very inconsistent he could not draw any firm conclusions regarding the difference between genotypes in the pattern of grain filling within the ear of wheat.

In Chapter 3 it was indicated that TL363/30 and TL365a/34 had a greater potential sink capacity, in that they had higher grain populations per unit area and gave a greater response to nitrogen in this character. The individual grains of these varieties filled at a slighly slower rate than those of the varieties where grain numbers were not so great, with the result that grain weight per ear and per unit area (Figures 3:7 and 3:8) increased at the same rate in all varieties with time. All the varieties had a similar development of PAD with time (Figure 3:6) though TL363/30 and TL365a/34 had a slightly greater maintenance of PAI than the other varieties. Although these varieties had a greater grain capacity, they did not show any increase in the rate of individual grain growth nor in the rate of grain growth per unit area. This must be due to a reduction in the efficiency of the increased photosynthetic area as sink size could not be limiting.

The rate of individual grain filling may be a restriction on the capacity of the grains. The varieties showed different rates of grain filling from each other but these were consistent throughout the several sites within the ear. The effect of nitrogen on the rate of grain filling was negligible though the increase in the PAD with increased nitrogen (Fig. 3:6) far exceeded the increase in the grain number per unit area (Table 3:2) but no increase in the rate of individual grain filling was observed. It is suggested that the rate of individual grain filling of a variety is a measurable trait and increased yields could result from the selection of a variety with a large grain population and a rapid rate of individual grain filling

CHAPTER 6

General discussion and conclusions. In the preceeding chapters the effects of several husbandry treatments on the new semi-dwarf and taller, more conventional varieties of wheat and barley have been examined. The semi-dwarf varieties chosen for these studies were bred in the United Kingdom and therefore had adequate resistance to the disease spectrum in this country as well as possessing a suitable response to natural constraints such as daylength and temperature.

This choice allowed the effects of the treatments applied to the varieties to be examined without other major factors interfering with their interpretation. The implications of the findings of both agronomic and the physiological studies for farmers and plant breeders will be discussed here.

On a world wide basis, the introduction of varieties which possess the semi-dwarf character, has had an enormous impact on agriculture. When the semi-dwarf varieties were introduced to the underdeveloped countries, they were backed up with large scale training programmes to teach the farmers the benefits of the use of irrigation and fertilisers in conjunction with the short statured varieties. In the United Kingdom, such a training programme is not necessary, but any changes in the husbandry requirements for the semi-dwarf varieties would need to be passed to the farmer.

The semi-dwarf barley varieties examined in the present study, responded to the husbandry treatments applied, in a similar fashion to the conventional varieties with which they were compared. In response to increases in seed rate it was found that the barley varieties reached a ceiling of yield after which further increases in seed rate resulted in neither increase nor decrease in yield until lodging occurred.

No greater response to nitrogen was found in the dwarf barley varieties which would have led to an increase in the fertiliser recommendations for such varieties. A greater tolerance of high nitrogen was evident however, as no lodging occurred in the dwarf varieties. The peak yield was reached before lodging imposed a limit and increase in nitrogen application beyond this peak level resulted in a slight reduction in yield before lodging occurred.

In the wheat study, yield reductions were evident, in all varieties, at the highest rates of nitrogen, which were seldom due to lodging. Thus, some further limit to yield must be responsible for this ceiling to further increase in yield.

In the seasons in which high average yields of grain were harvested the tolerance of greater nitrogen application and seed rate usage was increased and the ceiling yield was maintained over a greater range of nitrogen rates before yield reduction occurred. This effect was most noticeable in the semi-dwarf barley varieties.

The introduction of the dwarf varieties in Europe has not led to such a large increase in yield as their introduction in underdeveloped countries, largely due to the different lodging resistance of the indigenous varieties of European and underdeveloped countries. European varieties have been developed for lodging resistance in the past and possess this character in such a degree that lodging does not seem to be the yield limiting factor with modern varieties. Semi-dwarf varieties do not extend the yield limits any further than the lodging resistant varieties but merely postpone lodging to more extreme rates of sowing and nitrogen usage, thus providing a wider safety margin between the maximum yield and the point at which lodging occurs and causes large reductions in yield. In underdeveloped countries the introduction of semi-dwarf varieties gave the farmers lodging resistance for the first time and the slow progression towards adequate, varietal lodging resistance, experienced by European breeders was avoided by breeders in underdeveloped countries.

Semi-dwarfism in a variety is not a guarantee that the variety will not lodge but lodging resistance varies within the semi-dwarf varieties in much the same way as it does in conventional varieties. In other characters also, the variation among the semi-dwarf varieties is considerable and depends to some extent on the indigenous parent which was chosen to confer disease resistance and tolerance of United Kingdom conditions, to the semi-dwarf selections.

Although semi-dwarf varieties do not improve yield dramatically, as they did in the underdeveloped countries, they can still make a considerable contribution to the breeding of improved varieties. This can be done by incorporating dwarf plasma into lodging susceptible, but otherwise suitable, varieties as a quick method of conferring lodging resistance. Such breeding programmes can be embarked on since it has been shown, in this thesis and elsewhere, that the dwarf varieties have very few traits which could reduce their performance in crosses with indigenous varieties. Those few traits which may affect the performance of the semi-dwarfs are the shortening of the coleoptile which reduces emergence, and possibly poorer root development in some cultivars, though this could already be found within the indigenous cultivars, as large differences have recently been found within species in root growth. In shoot growth, there do not appear to be any dileterious characters associated with the semi-dwarf character.

The problem of further extending the upper limit of yield still remains, The factors implicated in preventing further yield increase are, too small a sink capacity to accommodate the supply from the photosynthetic organs or too small a supply from these organs to fill the sinks provided.

From the study of the leaf area production and activity in wheat in Chapter 3 it was concluded that the total sink capacity of the varieties under examination was adequate to utilise more assimilate than the photosynthetic area produced. With large photosynthetic areas the efficiency was reduced, in terms of grain production. The reduced efficiency was believed to be caused by an increase in mutual shading.

On closer examination of the sink capacity, and the rate and duration of the grain filling process, an additional factor in the control of grain production was found. The rate of grain filling appeared to be limited by some constraint which was characteristic of each variety. Those varieties which had faster rates of individual grain growth showed this consistently in all the grain positions within the ear. Nitrogen had no effect on the rate of individual grain growth. The rate of grain dry matter accumulation per ear or per unit area was the same in all the varieties although some had greater numbers of grains and a greater leaf area. It was concluded that varieties had a characteristic maximum rate of individual grain growth which could not be exceeded.

The implications of these findings in terms of increasing the yield ceiling are twofold. To produce more dry matter per unit area it is necessary to have a greater amount of photosynthetic tissue but the efficiency of this increase photosynthetic area must not be reduced by increased shading. An improvement in the efficiency of large photosynthetic areas must be sought by improvement in the distribution of the canopy and by an increase in duration of the canopy's active life. The increase in the duration of the photosynthetic area should be sought by extending the post-anthesis period by earlier anthesis rather than by delayed senescence. The reason for this is that, by delaying senescence, harvesting difficulties will be increased and the crop will be growing in a period of shortening days and reduced radiation input, whereas, by advancing anthesis, the post-anthesis period will coincide more closely with the period of maximum incident radiation. Acceleration of the early development of the plant may cause conflict with the other requirement to arise from the findings of the present study. This requirement is for an increase in the population of the grains per unit area coupled with an increase in the rate of individual grain filling. From the conclusions reached in Chapter 5, this would appear to be the best combination to produce a further increase in the yield of grain.

Neither of these conditions for improved yield may be easy to achieve but the yields of present day varieties fall far short of the world record wheat yield of 14 tons/ha achieved in Washington State in 1965 (Fischer, 1971), but similar yields must be attainable.

BIBLIOGRAPHY

ALLAN, R.E.; VOGEL, O.A.; RUSSELL, T.S. and PETERSON, C.J. (1965). Relation of seed and seedling characteristics to stand establishment of semi-dwarf wheat selections. Crop Sci., 5, 5-8.

ANGUS, J.F.; JONES, R. and WILSON, J.H. (1972). A comparison of barley varieties with different leaf inclinations. Aust. J. agric. Res. 23, 945-57.

ASANA, R.D. and BAGGA, A.K. (1966). Studies in the physiological analysis of yield (VIII). Comparison of the development of upper and basal grains of spikelets of two varieties of wheat. Ind. J. Pl. Physiol., 9, 1-21.

ASANA, R.D.; PARVATKAR, S.R. and SAXENA, N.P. (1969). Studies in the physiological analysis of yield (IX). Effect of light intensity on the development of the wheat grain. Physiol. Plantarum, 22, 915-924.

ASANA, R.D. and CHATTOPADHYAY, N.C. (1970). Relation of some growth attributes of tall and dwarf wheat varieties to their productivity. Ind. J. agric. Sci., 40, 309-17.

ASPINALL, D. (1961). The control of tillering in the barley plant. (i) The pattern of tillering and its relation to nutrient supply. Aust. J. biol. Sci., 14, 493-505.

ASPINALL, D. (1963). Control of tillering in the barley plant. (ii) Control of tiller bud growth during ear development. Aust. J. biol. Sci., 16, 285-304.

BEECH, D.F. and NORMAN, M.J.T. (1968). A preliminary assessment of the adaptation of semi-dwarf wheat varieties to the Ord River Valley. Aust. J. Exp. agric. and Anim. Husb., 8, 349-57.

BENGTSSON, A. (1972). Radavstand och utsadesmangd fur varvete och kom. Lanstsbrukshogslolans neddelanden. Reports of the agric. College of Sweden. Summary. Row space and seed rate in spring wheat and barley. Seric A. NR 160 Uppsala.

BERBIGIER, A. (1968). The creation of semi-dwarf barley varieties. Euphytica supplement no. 1, 177-184.

BINGHAM, J. (1966). Varietal response in wheat to water supply in the field and male sterility caused by a period of drought in a glasshouse experiment. Ann. Appl. biol., 57, 365-377.

BLACK, J.N. and WATSON, D.J. (1960). Photosynthesis and the theory of obtaining high crop yields by A.A. Niciporovic. Field Crop Abstr., 13, 169-175.

BONNETT, O.T. (1935). Development of the barley spike. J. agric. Res., 51, 451-57.

BONNETT, O.T. (1936). Development of wheat spike. J. agric. Res., 53, 445-451.

BONNETT, O.T. (1961). Morphology and development in Oats and oat improvement, ed. Coffman, F.A., 41-75. Am. Soc. Agron., Madison, Wisconsin.

BOROJEVIC, S. (1968). Characteristics of some new dwarf and semi-dwarf wheat lines. Euphytica Supp. no. 1, 143-151.

BREMNER, P.M. and INGHAM, A.P. (1960). Some aspects of ear development in winter wheat. Univ. of Nottingham Rep. 1960.

BREMNER, P.M. (1969). Growth and yield of 3 varieties of wheat with particular reference to the influence of unproductive tillers. J. agric. Sci. Camb., 72, 281-87.

BREMNER, P.M. (1972). Accumulation of dry matter and nitrogen by grains in different positions of the ear of wheat as influenced by shading and defoliation. Aust. J. biol. Sci., 25, 657-68.

BRIGGLE, L.W. and VOGEL, O.A. (1968). Breeding short statured, disease resistant wheats in the United States. Euphytica Supp. no. 1, 107-130.

BROUWER, R. (1966). Root growth of grasses and cereals, in The growth of cereals and grasses ed. Milthorpe, F.L. and Ivins, J.D., 153-164, Butterworths, London.

BUNTING, A.H. and DRENNAN, D.S.H. (1966). Some aspects of the morphology and physiology of cereals in vegetative phase. ibid., 20-39.

BURLEIGH, J.R.; ALLAN, R.E. and VOGEL, O.A. (1965). Varietal differences in seedling emergence of winter wheat as influenced by temperature and depth of planting. Agron. J., 57, 195-8.

BUTTROSE, M.S. and MAY, L.H. (1959). Physiology of cereal grain. The source of carbon for the developing barley kernel. Aust. J. biol. Sci., 12, 40-52.

CALDER, D.M. (1966). Inflorescence induction and initiation in the gramineae in The growth of cereals and grasses. ed. Milthorpe, F.L. and Ivins, J.D., 59-73, Butterworths, London.

CAMERON, D.; MILNER, J.B. and CARRUTHERS, J. (1967). An automatic self-propelled seed drill for cereal plots. J. agric. Engng. Res., 12, 142-146.

CAMPBELL, C.A. and READ, D.W.L. (1968). Influence of air temperature, light intensity and soil moisture content on growth, yields and some growth analysis characteristics of chinnook wheat in growth chambers. Can. J. Pl. Sci., 48, 299-311.

CANNELL, R.Q.; ELLIS, F.B.; WHORWOOD, K.B.; LUPTON, F.G.H.; SAGE, G. and WELBANK, P.J. (1972). Intervarietal comparisons of the root system of wheat. A.R.C. Letcombe Laboratory ann. Rep. for 1971.

CIMMYT (1970). 1968-69 Report of International Maize and Wheat improvement centre, Mexico.

CIMMYT (1972). 1970-71 Report of International Maize and Wheat improvement centre, Mexico.

CLARKSON, D.T. and SANDERSON, J. (1971). Relationship between the structure of root systems and abrorption of nutrients and water. A.R.C. Letcombe Lab. ann. Rep. for 1970.

COCK, J.H. (1969). The physiology of yield of semi-dwarf and standard winter wheats. Ph.D. Thesis, Univ. of Reading.

DOBBEN, W.H. van. (1966). Systems of management of cereals for improving yield and quality, in The growth of cereals and grasses. ed. Milthorpe, F.L. and Ivins, J.D. 320-334, Butterworth, London.

DONALD, C.M. (1963). Competition among crop and pasture species. Adv. Agron., 15, 1-114.

DOODSON, J.K.; MANNERS, J.G. and MYERS, A. (1964). The distribution pattern of 14C assimilated by the third leaf of wheat. J. exp. Bot., 15, 95-103.

DRENNAN, D.S.H. and KRISHNAMURTHY, K. (1964). Dry matter production by detached ears of wheat. Nature, Lond., 203, 1194-5.

EAVIS, B.W. and PAYNE, D. (1969). Soil physical conditions and root growth, in Root growth. ed. Whittington, W.J., 315-36, Butterworth, London.

ELLIS, F.B. and BARNES, B.T. (1968). Estimation of distribution of plant roots in soil under field conditions. A.R.C. Letcombe Lab. ann. Rep., 24-6.

EVANS, L.T. and RAWSON, H.M. (1970). Photosynthesis and respiration by the flag leaf and components of the ear during grain development in wheat. Aust. J. biol. Sci., 23, 245-54.

EVANS, L.T.; BINGHAM, J. and ROSKAMS, M.A. (1972). The pattern of grain set within ears of wheat. Aust. J. biol. Sci., 25, 1-8.

FEATHER, J.T.; QUALSET, C.O. and VOGT, H.E. (1968). Planting depth critical for short statured wheat varieties. Calif. agric., 22 (9), 12-14.

FISCHER, R.A. (1971). Factors limiting the yield of wheat. 12th Pacific Science Congress. Canberra.

FRIEND, D.J.C.; FISHER, J.E. and HELSON, V.A. (1963). The effect of light intensity and temperature on floral initiation and inflorescence development in Marquis Wheat. Can. J. Bot., 41, 1663.

FRIEND, D.J.C. (1965). Ear length and spikelet number of wheat grown at different temperatures and light intensities. Can. J. Bot., 43, 345-53.

FRIEND, D.J.C. (1966). The effects of light and temperature on the growth of cereals, in The growth of cereals and grasses. ed. Milthorpe, F.L. and Ivins, J.D., 181-97, Butterworth, London.

GABRIELSEN, E.K. (1942). Carbon dioxide assimilation and dry matter production in ears of wheat. Yearbook. Roy. Vet. agr. Coll., 28-54.

GRABLE, A.R. (1966). Soil aeration and plant growth. Adv. in Agron., 18, 57-106.

GREACEN, E.L.; BARLEY, K.P. and FARRELL, D.A. (1969). The mechanics of root growth in soils with particular reference to the implications for root distribution, in Root growth. ed. Whittington, W.J., 256-68, Butterworth, London.

GREENWOOD, D.J. (1969). Effect of oxygen distribution in the soil on plant growth. ibid., 202-220, Butterworth, London.

GUPTA, K.P.; KURCHANIA, S.P. and SINGH, S.P. (1968). A note on the effects of different depths and methods of sowing on the yield of dwarf wheats. Ind. J. Agron., 13, 197-99.

HACKETT, C. (1969). Quantitative aspects of the growth of cereal root systems, in Root growth. ed. Whittington, W.J., 134-45, Butterworth, London.

HAFIZ, A. (1972). Summary report of country visits. Inf. bull. Near East Cereal impr. and Prod. Proj., 9, 64.

HARVEY, P.N. (1964). Method of applying fertiliser for spring cereals. Expl. Husb., 11, 14-21.

HESS, C.E. (1969). Internal and external factors regulating root initiation, in Root growth. ed. Whittington, W.J., 42, Butterworth, London.

HOLLIDAY, R. (1960). Plant population and crop yield. Field Crop Abstr., 13, 159-67 and 247-54.

HOLLIDAY, R. (1963). Effect of row width on yield of cereals. Field Crop Abstr., 16, 71-81.

HOLLIDAY, R. and WILLEY, R.W. (1969). Variety potential in cereals and its improvement. Agric. Progress, 44, 56-77.

HOLMES, J.C.; LANG, R.W.; GILL, W.D. and RODGER, J.B.A. (1971). A comparison of two row widths for spring barley and winter wheat at varying seed and nitrogen rates. Expl. Husb., 21, 93-103.

I.A.R.I. (1968). Five years of research in dwarf wheat. Indian Agricultural Research Institute, Delhi.

JOHNSON, V.A. (1953). Environmental factors affecting plant height in winter wheat. Agron. J., 45, 505-8.

JOHNSON, V.A.; SCHMIDT, J.W. and MEKASHA, W. (1966). Comparison of yield components on agronomic characters of four winter wheat varieties differing in height. Agron. J., 58, 438.

KIRBY, E.J.M. (1968). Plant density and yield in cereals. N.A.A.S. q. Rev., 80, 139-145.

KIRBY, E.J.M. (1969). The effects of day length upon the development and growth of wheat, barley and oats. Field Crop Abstr., 22, 1-7.

KOLDERUP, F. (1970). Effect of temperature and day length on seed setting in some varieties of common spring wheat. Meldinger Gra Norges Landsbrakshogskole 49; also Field Crop Abstr., 25, (1972), 420, abstr. no. 3039.

KONSAK, C.F.; RAMIREZ, I.A.; WOO, S.C. and SADAM, M. (1969). New semi-dwarfing genes in wheat. Inf. bull. Near East wheat and barley Impr. and Prod. Proj. Rome, 6, 38.

KRIEDEMANN, P. (1966). Photosynthetic activity of the wheat ear. Ann. Bot. N.S., 30, 349-63.

KRISHNAMURTHY, K. (1963). Ph.D. Thesis. Univ. of Reading.

LANGER, R.H.M. (1966). Mineral nutrition of grasses and cereals, in The growth of cereals and grasses. ed. Milthorpe, F.L. and Ivins, J.D., 213-226, Butterworth, London.

LANGER, R.H.M. (1967). Physiological approaches to yield determination in wheat and barley. Field Crop Abstr., 20, 101-6.

LESSELS, W.J. and WEBBER, J. (1965). The effect of nitrogen on spring cereals. Expl. Husb., 12, 62-73.

LOCKHART, D.A.S. (1971). A study of plant/soil relationship in barley grown in soil cultivated in different ways. Ph.D. Thesis, Univ. of Edinburgh.

LUCAS, D. (1972). The effect of day length on primordia production of wheat apex. Aust. J. biol. Sci., 25, 649-56.

LUEBS, R.F. and LANG, A.E. (1969). Evapotranspiration and water stress of barley with increased nitrogen. Agron. J. 61, 921-24.

LUPTON, F.G.H. (1966). Translocation of photosynthetic assimilates in wheat. Ann. Appl. biol., 57, 355-64.

LUPTON, F.G.H. (1968). Analysis of grain yields of wheat in terms of photosynthetic ability and efficiency of translocation. Ann. Appl. biol., 61, 109-19.

LUPTON, F.G.H. and BINGHAM, J. (1970). Semi dwarf wheats. Rep. Pl. Breed. Inst., 1969, 60-62.

LUPTON, F.G.H. and BINGHAM, J. (1971). Semi dwarf wheats. ibid., 1970.

LUPTON, F.G.H.; BINGHAM, J.; OLIVER, R.H. and SUTHERLAND, J.A. (1972). Physiological basis of yields of semi dwarf wheats. ibid., 1971, 70-72.

MARCELLOS, H. and SINGLE, W.V. (1972). Influence of cultivar, temperature and photoperiod on post flowering development in wheat. Aust. J. agric. Res., 23, 533-40.

MARSHALL, C. and WARDLAW, I.F. (1973). A comparative study of the distribution and speed of movement of 14C assimilates and foliar applied 32P labelled phosphate in wheat. Aust. J. biol. Sci., 26, 1-13.

MILTHORPE, F.L. (1955). Plant growth and the weather. Univ. of Nott. inaug. lect.

MISRA, N.M. and RAM, D.N. (1968). Yield behaviour of Sonora 64 versus Indian wheat varieties under rates and methods of urea application. Ind. J. Agron., 13, 13-16.

MOFFATT, J.R. and WIDDOWSON, F.V. (1967). Methods of sowing and manuring winter wheat and spring barley. Rep. Rothamsted exp. sta. for 1966, 236-40.

MONTEITH, J.L. (1966, i). Physical limitations to crop growth. Agric. Prog., 41, 9-23.

MONTEITH, J.L. (1966 ii). Analysis of the microclimate in cereals and grasses, in The growth of cereals and grasses. ed. Milthorpe, F.L. and Ivins, J.D., 123-137, Butterworth, London.

MONYO, J.H. and WHITTINGTON, W.J. (1970). Genetic analysis of root growth in wheat. J. agric. Sci. Camb., 74, 329-38.

McNEAL, F.H.; BERG, M.A. and KLAGES, M.G. (1960). Evaluation of semi dwarf selections from a spring wheat breeding programme. Agron. J., 52, 710-2.

NAIR, K.R. (1940). Balanced confounded arrangements for the 5^n type of experiments. Sankhya, 5, 57-70.

NEILSEN, K.F. and HUMPHRIES, E.C. (1966). Effects of root temperature on plant growth. Soils and Fertilisers, 29, 1-7.

NEWBOULD, P.; ELLIS, F.B.; BARNES, B.T.; HOWSE, K.R. and LUPTON, F.G.H. (1969). Intervarietal comparison of root systems of winter wheat. A.R.C. Letcombe Lab. ann. Rep., 38-40.

NEWBOULD, P.; ELLIS, F.B.; BARNES, B.T.; HOWSE, K.R.; LUPTON, F.G.H. and WELBANK, P.J. (1971). Intervarietal comparison of the root system of winter wheat. ibid. for 1970.

NEWMAN, E.J. (1966). A method of estimating the total length of root in a sample. J. appl. Ecol. 3, 139-45.

NICHOLLS,P.B. and MAY,L. (1963). Studies on the growth of the barley apex. (i) Inter-relationships between primordium formation, apex length and spikelet development. Aust. J. biol. Sci., 16, 561-71.

OSWALD, J. (1970). A study of some factors affecting the yield of cereals. B.Sc. Thesis, Univ. of Edinburgh.

OWEN, P.C. (1971). Wheat (semi dwarf) response to temperatures representing a tropical dry season. 1 and 2. Non extreme and extreme temperatures. Expl. agric., 7, 33-47.

PAQUET, J. (1968). Effects of selection for semi dwarfness on the other characters of bread wheat (autumn sown). Euphytica Supp. no. 1, 131-142.

PAQUET, J. (1969). Dwarf wheats. Bull. tech. Inf. Paris, 244, 779-89, and Field Crop Abstr.

PATRICK, J.W. (1972). Distribution of assimilate during the stem elongation in wheat. Aust. J. biol. Sci., 25, 455-67.

PEARCE, R.B.; BROWN, R.H. and BLASER, R.E. (1967). Photosynthesis in plant communities as influenced by leaf angle. Crop Sci., 7, 321-24.

PORTER, K.B.; ATKINS, I.M.; GILMORE, E.C.; LAHR, K.A. and SCOTTINO, P. (1964). Evaluation of short statured winter wheats for production under Texas conditions. Agron. J., 56, 393-6.

PUCKRIDGE, D.W. (1971). Photosynthesis of wheat under field conditions (3) Seasonal trends in CO_2 uptake of crop communities. Aust. J. agric. Res., 22, 1-9.

PUCKRIDGE, D.W. and RATHOWSKY, D.A. (1971). Photosynthesis of wheat under field conditions (4) The influence of density and leaf area index on response to radiation. Aust. J. agric. Res., 22, 11-20.

P.V.S.G. (1973). Plant variety and seeds Gazette, 99, April, 1973.

QUINLAN, J.D. and SAGAR, G.R. (1962). An autoradiograph. study of the movement of 14C-labelled assimilates in the developing wheat plant. Weed Res., 2, 264-73.

RADFORD, P.J. (1967). Growth analysis formulae - their use and abuse. Crop Sci., 7, 171-175.

RAWSON, H.M. and HOFSTRA, G. (1969). Translocation and remobilisation of 14C assimilated at different stages by each leaf of the wheat plant. Aust. J. biol. Sci., 22, 321-31.

RAWSON, H.M. and EVANS, L.T. (1970). Pattern of grain growth within the ear of wheat. Aust. J. biol. Sci., 23, 753-64.

RAWSON, H.M. (1970). Spikelet number, its control and relation to yield per ear in wheat. Aust. J. biol. Sci., 23, 1-15.

RAWSON, H.M. (1971). An upper limit for spikelet number per ear in wheat as controlled by photoperiod. Aust. J. agric. Res., 22, 537-46.

REITZ, L.P. and SALMON, S.C. (1968). Origin, history and use of Norin 10 wheat. Crop Sci., 8, 686-9.

ROO, H.C. de (1969). Tillage and root growth, in Root growth. ed. Whittington, W.J., 339-55, Butterworth, London.

ROY, R.K.; SINHA, R.N. and PRASAD, R. (1969). Relationship of the plant characters attributing to the yield of dwarf wheat varieties. Ind. J. agron., 14, 233-5.

RUSSELL, E.W. (1966). The soil environment of gramineous crops, in The growth of cereals and grasses. ed. Milthorpe, F.L. and Ivins, J.D., 138-151, Butterworth, London.

RUSSELL, R.S. and ELLIS, F.B. (1968). Estimation of the distribution of plant roots in the soil. Nature, Lond., 217, 582-3.

RUSSELL, R.S. and NEWBOULD, P. (1969). Pattern of nutrient uptake in root systems, in Root growth. ed. Whittington, W.J., 296-313, Butterworth, London.

SMITH, L.P. (1967). The effect of weather on the growth of barley. Field Crop Abstr., 20, 273-8.

STOY, V. (1965). Photosynthesis, respiration and carbohydrate accumulation in spring wheat in relation to yield. Physiologia Plantarum Supplementum (IV) 1-125.

STREET, H.E. (1969). Factors influencing the initiation and activity of meristems in roots, in Root growth. ed. Whittington, W.J., 20, Butterworth, London.

SUBBIAH, B.V.; KATVAL, J.C.; NARISMHAM, R.L. and DAITSHINAMUTRI, C. (1968). Preliminary investigations on root distribution of high yielding wheat varieties. Int. J. appl. Radiat. and Isotopes, 19, 385-90.

SYME, J.R. (1967). Growth and yield of irrigated wheat cultivars at several rates of nitrogen fertiliser. Aust. J. Expl. agric. and Animl. Husb., 7, 337-43.

SYME, J.R. (1969). A comparison of semi dwarf and standard height wheat varieties at two levels of water supply. ibid., 9, 528-31.

TANNER, J.W.; GARDNER, C.J.; STOSKOPF, N.P. and REINBERGS, E. (1966). Some observations on upright leaf type small grains. Can. J. Pl. Sci., 46, 690.

TEARE, I.D. and PETERSON, C.J. (1971). Surface area of chlorophyll-containing tissue on the inflorescence of Triticum aestivum L. Crop Sci., 11, 627-8.

THORNE, G.N. and WATSON, D.J. (1955). The effect on yield and leaf area of applying nitrogen as a top dressing in April or in sprays at ear emergence. J. agric. Sci., Camb., 46, 449-56.

THORNE, G.N. (1965). Photosynthesis of ears and flag leaves of wheat and barley. Ann. Bot. N.S., 29, 317-29.

THORNE, G.N. (1966). Physiological aspects of grain yield in cereals, in The growth of cereals and grasses. ed. Milthorpe, F.L. and Ivins, J.D., 88-105, Butterworth, London.

THORNE, G.N. and FORD, M.A. (1967). Ear size and grain yield in wheat. Rep. Rothamsted Expl. Sta. for 1966, 87.

THORNE, G.N.; FORD, M.A. and WATSON, D.J. (1967). Effect of temperature variation at different times on the growth and yield of sugar beet and barley. Ann. Bot. N.S., 31, 71-101.

THORNE, G.N.; WELBANK, P.J. and BLACKWOOD, G.C. (1968). Grain yield of semi-dwarf wheats. Rep. Rothamsted Expl. Sta. for 1967, 93.

THORNE, G.N.; WELBANK, P.J. and BLACKWOOD, G.C. (1969). Growth and yield of 6 short spring wheat varieties derived from Norin 10 and of 2 European varieties. Ann. appl. biol., 63, 241-51.

THORNE, G.N. (1970). Grain yield of semi-dwarf wheats. ann. Rep. Rothamsted Expl. Sta. for 1969, 108-9.

THORNE, G.N. and BLACKLOCK, J.C. (1971). Effect of plant density and nitrogen fertiliser on the growth and yield of short varieties of wheat derived from Norin 10. Ann. appl. biol., 78, 93-111.

THORNE, G.N. (1972). Growth of short and tall spring wheat varieties. ann. Rep. Rothamsted Expl. Sta. for 1971.

TROUGHTON, A. and WHITTINGTON, W.J. (1969). The significance of genetics variation in root systems, in Root growth. ed. Whittington, W.J., 296-313, Butterworth, London.

VOGEL, O.E.; CRADDOCK, J.C.; MUIR, C.E.; EVERSON, E.A. and ROHDE, C.R. (1956). Semi-dwarf growth habit in winter wheat improvement for the pacific North-West. Agron. J., 48, 76-8.

VOGEL, O.E.; ALLAN, R.E. and PETERSON, C.J. (1963). Plant and performance characteristics of semi-dwarf winter wheats producing most efficiently in Eastern Washington. J. Am. Soc. Agron., 55, 397-8.

WALPOLE, P.R. and MORGAN, D.G. (1970). A quantitative study of grain filling in Triticum aestivum L. Cultivar Maris Widgeon. Ann. Bot. N.S., 34, 309-18.

WALPOLE, P.R. and MORGAN, D.G., (1971). A quantitative study of grain filling in 3 cultivars of Hordeum Vulgare L. Ann. Bot. N.S., 35, 301-10.

WALPOLE. P.R. and MORGAN, D.G. (1972). Physiology of grain filling in barley. Nature, London, 240, 416.

WARDLAW, I.F. (1967). The effect of water stress on translocation in relation to photosynthesis and growth. (1) Effect during grain development in wheat. Aust. J. biol. Sci., 20, 25-39.

WARDLAW, I.F. and PORTER, H.K. (1967). The redistribution of stem sugars in wheat during grain development. Aust. J. biol. Sci., 20, 309-18.

WARDLAW, I.F. (1968). The control and pattern of movement of carbohydrates in plants. Bot. Rev., 34, 79-105.

WARDLAW, I.F. (1970). The early stages of grain development in wheat: Response to light and temperature in a single variety. Aust. J. biol. Sci., 23, 765-74.

WATSON, D.J. (1952). Physiological basis of variation in yield. Adv. Agron., 4, 101-45.

WATSON, D.J.; THORNE, G.N. and FRENCH, S.A.W. (1958). Physiological causes of differences in grain yield, between varieties of barley. Ann. Bot. N.S., 22, 321-52.

WATSON, D.J. (1968). A prospect of crop physiology. Ann. appl. biol., 62, 1-9.

WELBANK, P.J. and WITTS, K.J. (1965). Dependence of grain:leaf ratio on radiation. Rep. Rothamsted Expl. Sta. for 1964, 100.

WELBANK, P.J.; FRENCH, S.A.W. and WITTS, K.J. (1966). Dependence of yield of wheat varieties on their leaf area durations. Ann. Bot. N.S., 30, 291-300.

WELBANK, P.J. and TAYLOR, P.J. (1971). Report on growth of roots in length and dry weight. Rep. Rothamsted Expl. Sta. for 1970.

WELBANK, P.J. (1972). Root growth of wheat varieties. Rep. Rothamsted Expl. Sta. for 1971, 104-6.

WELLINGTON, P.S. (1966). Germination and seedling emergence, in The growth of cereals and grasses. ed. Milthorpe, F.L. and Ivins, J.D., 3-19, Butterworth, London.

WIDDOWSON, F.V. and PENNY, A. (1968). Results of an experiment at Rothamsted testing F.Y.M. and N.P.K. fertilisers on 5 arable crops and permanent grass. J. agric. Sci. Camb, 70, 53-8.

WIDDOWSON, F.V. and PENNY, A. (1969). The effects in barley and kale of N.P.K. fertiliser containing different proportions of urea and ammonium nitrate and either triple superphosphate or mono-urea phosphate. J. agric. Sci. Camb., 73, 125-32.

WILLEY, R.W. and HOLLIDAY, R. (1971). Plant population, shading and thinning studies in wheat. J. agric. Sci. Camb., 77, 453-61.

WILSON, J.W. (1960). Influence of spatial arrangement of foliage area on light interception and pasture growth. Proc. 8th Int. Grassland Congress, Reading, 275-79.

ZEE, S.Y. and O'BRIEN, T.P. (1971). Vascular transfer cells in the wheat spikelet. Aust. J. biol. Sci., 24, 35-49.

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APPENDIX I

Weather Records for Bush and Dunbar 1970-72

1970 BUSH

Month	Mar	A	M	J	J	A	S	O	N	D
Dry bulb °C	2.9	5.2	9.9	13.2	12.8	13.9	12.4	8.9	4.8	3.5
Screen max °C	6.6	8.4	13.6	17.0	15.8	17.6	15.3	12.2	7.7	5.7
Screen min °C	-0.3	1.4	6.3	7.9	9.2	10.6	8.7	5.4	2.1	1.1
Rainfall mm	36.83	52.3	24.1	46.7	87.4	65.3	75.7	75.2	109.5	54.1
Sunshine hrs	3.97	3.70	3.61	5.70	3.39	4.50	3.81	3.21	1.91	1.13

APPENDIX I

Weather Records for Bush and Dunbar 1970–72

1971 BUSH

Month	J	F	M	A	M	J	J	A	S	0	N	D
Dry bulb °C	3.4	3.7	4.2	6.9	10.9	10.9	14.8	13.6	13.0	9.6	4.9	5.7
Screen max °C	5.7	6.5	7.2	10.2	14.3	13.4	18.8	16.6	16.4	13.2	7.6	8.6
Screen min °C	0.6	1.2	0.8	2.3	4.6	3.6	9.8	9.7	8.4	5.3	2.0	4.1
Rainfall mm	49.4	56.0	123.7	30.6	57.0	50.3	92.3	112.2	25.4	67.1	64.8	50.1
Sunshine hrs	0.75	2.15	2.71	4.58	7.10	4.01	6.45	3.42	4.70	3.06	1.71	0.55

Mean of 10 Yrs – 1962–71 BUSH

Dry bulb °C	2.3	1.9	3.9	6.9	9.5	13.4	14.5	13.8	12.9	9.4	4.2	3.1
Screen max °C	4.0	4.8	6.8	9.7	12.8	16.2	16.7	16.7	15.1	12.5	7.2	5.7
Screen min °C	-0.3	- 1.1	0.6	2.2	4.9	8.1	9.2	9.3	8.1	5.7	1.4	0.3
Rainfall mm	66.9	56.7	61.5	51.9	79.5	58.4	80.2	101.7	83.9	77.8	95.5	60.7
Sunshine hrs	1.20	2.41	3.18	4.45	4.73	5.32	4.77	4.39	3.54	2.88	1.67	0.95

Mean of 10 Yrs
1962–71

APPENDIX I

Weather Records for Bush and Dunbar 1970–72

1972 BUSH

Month	J	F	M	A	M	J	J	A	S	O	N
Dry bulb °C	2.66	2.64	4.08	7.15	9.53	10.91	14.19	12.85	10.69	9.69	4.54
Screen max °C	5.19	5.27	7.96	10.70	12.80	14.16	17.75	16.75	14.35	13.16	7.44
Screen min °C	0.14	0.32	1.24	3.75	5.60	6.25	9.11	8.55	5.89	4.88	1.73
Rainfall mm	57.2	59.5	54.7	78.6	71.8	64.0	30.6	31.6	10.3	23.0	64.3
Sunshine hrs	1.04	1.56	3.37	4.60	3.61	5.37	6.04	4.83	3.99	3.37	1.56

1972 DUNBAR

Dry bulb °C											
Screen max °C		6.3	8.5	11.4	12.9	15.5	17.1	17.5			
Screen min °C		1.5	2.7	5.2	6.9	8.2	10.4	10.3			
Rainfall mm		53	29	29	47	31	24	31			
Sunshine hrs		1.78	4.38	5.88	4.76	6.72	6.71	5.9			

APPENDIX 2

Yield Components Barley

Table 2:1 Grain Number per Ear

1970 CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
N0	21.20	17.90	20.78	18.88	33.96	22.55
N1	21.37	19.94	18.76	18.48	37.57	23.22
N2	19.97	17.62	19.01	18.69	38.43	22.74
N3	22.59	19.85	19.63	19.43	37.52	23.80
N4	22.11	19.53	21.04	19.54	38.36	24.12
Mean	21.45	18.97	19.85	19.00	37.17	23.29

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
S1	24.15	22.12	23.09	21.80	48.50	27.93
S2	23.00	21.16	19.88	20.26	39.14	24.69
S3	22.23	19.21	20.16	18.83	36.99	23.48
S4	19.31	16.49	19.10	17.34	35.48	21.55
S5	18.55	15.88	16.99	16.78	25.73	18.79
Mean	21.45	18.97	19.85	19.00	37.17	23.29

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	28.58	24.08	23.71	19.11	17.26	22.55
N1	27.49	23.67	23.37	22.43	19.16	23.22
N2	27.46	25.49	21.57	21.11	18.09	22.74
N3	27.00	26.22	23.69	21.97	20.15	23.80
N4	29.13	24.00	25.07	23.11	19.27	24.12
Mean	27.93	24.69	23.48	21.55	18.79	23.29

SE 1.027 0.459

Significant Effects NL * CV ** SL **

CV x S **

Table 2:2 Ear Number per 3715 sq cm.

1970

CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
N0	247	263	213	250	110	217
N1	270	332	251	276	119	250
N2	289	367	262	329	124	274
N3	289	326	327	291	124	271
N4	291	313	263	292	140	260
Mean	277	320	263	288	123	254

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
S1	204	215	198	171	73	172
S2	241	264	258	278	101	228
S3	291	314	254	277	123	252
S4	318	378	306	362	150	303
S5	334	430	301	350	170	317
Mean	277	320	263	288	123	254

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	147	185	228	259	264	217
N1	193	223	235	281	318	250
N2	180	243	273	321	354	274
N3	190	249	256	342	320	271
N4	152	242	267	312	328	260
Mean	172	228	252	303	317	254

SE 20.47 9.15

Significant Effects NL ** NQ ** SL ** CV **

Table 2:3 Straw Dry Weight (g)

<u>1970</u>

CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
N0	161.0	135.9	172.4	143.7	122.2	147.0
N1	184.3	180.9	181.9	145.7	136.6	166.0
N2	162.4	184.1	187.3	159.2	154.2	169.4
N3	195.2	187.4	223.4	155.6	158.4	184.0
N4	195.2	180.4	204.1	154.4	162.9	179.0
Mean	180.0	174.0	193.0	152.0	147.0	169.1

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
S1	191.0	186.1	222.6	140.3	154.3	179.0
S2	200.8	174.8	185.6	160.4	129.6	170.2
S3	176.3	165.6	181.9	153.4	136.8	163.0
S4	168.4	161.4	202.6	154.1	168.5	171.0
S5	161.6	180.8	176.4	150.4	145.1	163.0
Mean	180.0	174.0	194.0	152.0	147.0	169.1

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	149.8	142.0	152.9	148.8	141.7	147.0
N1	179.2	159.5	164.0	175.3	151.4	166.0
N2	181.3	177.2	165.4	166.8	156.5	169.4
N3	209.4	180.9	165.5	177.8	186.4	184.0
N4	174.6	191.6	166.2	186.3	178.3	179.4
Mean	179.0	170.2	163.0	171.0	163.0	169.1

SE 12.00 5.37

Significant Effects NL ** CV **

Table 2:4 200 Grain Weight (g)

1970 CV X N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
N0	6.64	6.66	7.62	6.70	7.18	6.96
N1	6.25	6.12	6.88	6.34	6.84	6.49
N2	5.96	6.04	7.08	6.22	7.00	6.46
N3	5.40	5.18	6.76	6.32	6.78	6.09
N4	5.20	5.30	7.26	5.70	6.66	6.02
Mean	5.89	5.86	7.12	6.26	6.89	6.40

CV X SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
S1	5.64	5.56	7.04	5.60	6.48	6.06
S2	5.65	5.76	6.76	6.52	7.02	6.34
S3	6.04	6.24	7.44	6.40	6.98	6.62
S4	6.18	5.90	7.28	6.58	6.88	6.56
S5	5.94	5.84	7.08	6.18	7.10	6.43
Mean	5.89	5.86	7.12	6.26	6.89	6.40

SR X N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	6.66	6.86	7.02	7.20	7.06	6.96
N1	6.14	6.47	6.74	6.84	6.24	6.49
N2	6.20	6.26	6.82	6.68	6.34	6.46
N3	5.98	6.02	6.48	6.00	5.96	6.09
N4	5.34	6.10	6.04	6.10	6.54	6.02
Mean	6.06	6.34	6.62	6.56	6.43	6.40

SE 0.237 0.106

Significant Effects NL ** SL ** SQ ** CV **

Table 2:5 Grain Sample Dry Weight (g)

1970 CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
N0	152.3	156.7	145.7	133.8	98.4	137.4
N1	138.9	174.0	148.5	147.2	124.3	146.6
N2	147.9	157.4	151.9	163.1	127.8	149.6
N3	143.7	138.7	177.0	157.4	129.2	149.2
N4	151.1	129.1	175.7	142.0	131.9	145.9
Mean	147.0	151.1	160.0	149.0	122.3	145.7

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
S1	114.6	123.5	139.3	103.6	90.8	114.4
S2	127.0	130.7	154.6	152.6	118.6	136.7
S3	163.1	160.8	161.3	159.1	122.6	153.4
S4	165.6	166.8	189.6	169.4	151.6	168.6
S5	163.6	174.1	154.0	158.8	128.0	155.7
Mean	146.8	151.2	159.8	148.7	122.3	145.8

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	130.9	119.5	149.1	151.5	135.9	137.4
N1	120.5	116.9	160.0	176.3	159.2	146.6
N2	116.4	143.7	159.2	173.4	155.4	149.6
N3	112.6	152.2	159.3	160.7	161.2	149.2
N4	91.4	151.2	139.3	181.1	166.8	146.0
Mean	114.4	136.7	153.4	168.6	155.7	145.8

SE 11.27 5.04

Significant Effects SL ** SQ ** CV **

Table 2:6 Grain to Straw Ratio

<u>1970</u> CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
N0	0.967	1.215	0.860	0.959	0.821	0.964
NL	0.842	0.969	0.812	1.012	0.941	0.915
N2	0.931	0.913	0.816	1.022	0.822	0.901
N3	0.755	0.744	0.826	0.983	0.830	0.828
N4	0.778	0.732	0.863	0.913	0.820	0.821
Mean	0.855	0.915	0.835	0.978	0.847	0.886

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
S1	0.621	0.816	0.632	0.729	0.604	0.680
S2	0.711	0.757	0.836	0.951	0.937	0.838
S3	0.934	0.968	0.892	1.043	0.905	0.948
S4	0.989	1.042	0.933	1.106	0.897	0.993
S5	1.019	0.990	0.883	1.059	0.891	0.969
Mean	0.855	0.915	0.835	0.978	0.847	0.886

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	0.981	0.854	0.980	1.037	0.970	0.964
N1	0.670	0.876	0.975	0.999	1.057	0.915
N2	0.673	0.819	0.964	1.049	0.999	0.901
N3	0.542	0.848	0.967	0.910	0.870	0.828
N4	0.536	0.796	0.855	0.972	0.947	0.821
Mean	0.680	0.838	0.948	0.993	0.969	0.886

SE 0.0740 0.0331

Significant Effects NL ** SL ** SQ ** CV *

Table 2:7 Grain Number Per Ear

1971

CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
N0	21.26	18.60	19.03	18.87	20.88	19.73
N1	20.21	18.92	19.02	21.13	20.62	19.98
N2	19.28	18.13	19.32	19.78	20.33	19.36
N3	20.41	20.33	18.48	18.99	19.91	19.62
N4	20.82	20.42	19.17	17.09	18.53	19.20
Mean	20.39	19.28	19.00	19.10	20.05	19.58

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
S1	23.39	24.01	21.67	22.33	23.33	22.94
S2	20.95	19.35	20.47	21.48	21.82	20.81
S3	20.52	18.45	18.60	18.45	19.45	19.09
S4	19.50	18.23	17.33	17.70	17.36	18.02
S5	17.62	16.36	16.95	15.89	18.30	17.02
Mean	20.39	19.28	19.00	19.17	20.05	19.58

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	25.30	20.36	18.82	17.66	16.50	19.73
N1	22.75	21.48	19.52	19.12	17.02	19.98
N2	22.79	20.10	19.29	17.09	17.56	19.36
N3	21.87	20.56	19.49	18.68	17.51	19.62
N4	22.02	21.57	18.35	17.57	16.53	19.20
Mean	22.94	20.81	19.09	18.02	17.02	19.58

SE	1.038	0.464

Significant Effects SL **

Table 2:8 Ear Number per 3715 sq cm.

1971 CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
N0	191	232	137	157	198	183
N1	244	238	177	199	197	211
N2	257	243	151	209	165	205
N3	236	235	172	217	183	209
N4	226	221	173	231	164	203
Mean	231	234	162	203	181	202

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
S1	161	181	117	169	119	149
S2	204	208	143	176	147	176
S3	241	254	182	211	200	218
S4	265	248	186	231	222	230
S5	283	278	182	227	219	238
Mean	231	234	162	203	181	202

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	149	162	195	175	233	183
N1	157	185	209	247	257	211
N2	160	166	231	262	206	205
N3	134	170	240	254	246	209
N4	146	194	214	215	246	203
Mean	149	176	218	230	238	202

SE 14.1 6.3

Significant Effects. NQ ** SL ** SQ ** CV **

CV x NL **

NQ x SQ *

Table 2:9 Straw Dry Weight (g)

1971

CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
N0	163.5	178.0	158.2	137.4	228.5	173.1
N1	206.5	189.1	180.7	184.5	211.0	194.4
N2	237.9	215.6	179.4	200.5	195.2	205.7
N3	225.3	212.2	200.6	167.5	228.2	206.8
N4	218.0	210.2	208.2	189.1	226.7	210.4
Mean	210.2	210.0	185.4	175.8	217.9	198.1

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
S1	213.0	188.2	187.1	180.1	202.3	194.1
S2	197.9	209.4	173.5	164.7	200.4	189.2
S3	215.6	206.6	192.3	175.5	249.3	207.9
S4	206.3	196.9	213.7	172.5	222.3	202.3
S5	218.4	204.0	160.5	186.2	215.3	196.9
Mean	210.2	201.0	185.4	175.8	217.9	198.1

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	199.5	173.3	166.4	152.0	174.4	173.1
N1	199.1	182.8	188.1	209.1	192.7	194.4
N2	208.3	180.9	241.2	215.8	182.4	205.7
N3	182.6	185.7	217.9	236.7	210.9	206.8
N4	181.2	223.2	225.7	198.1	224.0	210.4
Mean	194.1	189.2	207.9	202.3	196.9	198.1

SE 13.09 5.85

Significant Effects NL ** NQ * CV **
CV x NQ *
NL x SL ** NL x SQ *

Table 2:10 200 Grain Weight (g)

<u>1971</u> CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
N0	6.24	5.55	6.93	6.16	6.76	6.33
N1	5.70	5.41	6.41	5.78	6.11	5.88
N2	5.34	5.08	6.18	5.44	6.26	5.66
N3	5.66	5.13	6.37	5.16	6.03	5.67
N4	4.96	4.97	5.94	5.15	5.35	5.27
Mean	5.58	5.23	6.37	5.54	6.10	5.76

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
S1	5.91	5.04	6.70	5.80	6.71	6.03
S2	5.35	5.46	6.69	5.56	5.99	5.81
S3	5.60	5.29	6.43	5.55	6.38	5.85
S4	5.57	5.31	6.17	5.23	5.81	5.62
S5	5.46	5.04	5.85	5.55	5.63	5.51
Mean	5.58	5.23	6.37	5.54	6.10	5.76

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	6.79	6.66	6.25	6.01	5.94	6.33
N1	5.91	6.05	6.00	6.16	5.27	5.88
N2	6.05	5.37	5.79	5.47	5.63	5.66
N3	6.13	5.84	5.81	5.32	5.25	5.67
N4	5.27	5.13	5.40	5.14	5.43	5.27
Mean	6.03	5.81	5.85	5.62	5.51	5.76

SE 0.188 0.084

Significant Effects NL ** NC * SL ** CV **

CV x SL *

NL x SL *

Table 2:11 Grain Sample Dry Weight (g)

1971

CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
N0	107.3	103.8	87.6	80.6	118.9	99.6
N1	114.3	105.1	89.9	94.1	107.2	102.1
N2	102.7	94.2	72.8	89.5	84.7	88.8
N3	107.3	102.0	79.2	83.5	93.6	93.1
N4	89.2	77.6	75.0	88.7	69.5	80.0
Mean	104.2	96.5	80.9	87.3	94.8	92.7

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
S1	95.4	81.8	73.1	87.9	82.9	84.2
S2	90.7	96.4	81.5	82.9	81.3	86.6
S3	105.6	103.0	91.3	93.3	111.5	100.9
S4	116.1	105.3	87.9	86.3	100.7	99.3
S5	113.0	96.2	70.7	86.0	97.5	92.7
Mean	104.2	96.5	80.9	87.3	94.8	92.7

SR X N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	107.5	97.5	102.0	89.6	101.6	99.6
N1	85.9	99.2	101.9	125.7	97.9	102.1
N2	95.7	68.6	107.2	93.4	79.0	88.8
N3	68.8	84.3	109.1	110.5	92.9	93.1
N4	63.2	83.2	84.5	77.1	92.0	80.0
Mean	84.2	86.6	100.9	99.3	92.7	92.7

SE 8.75 3.91

Significant Effects NL ** SL * SQ * CV **

Table 2:12 Grain to Straw Ratio

1971

CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
N0	0.663	0.602	0.561	0.603	0.522	0.590
N1	0.554	0.561	0.498	0.512	0.511	0.527
N2	0.429	0.438	0.409	0.443	0.442	0.432
N3	0.475	0.486	0.396	0.495	0.412	0.453
N4	0.401	0.379	0.357	0.462	0.308	0.381
Mean	0.505	0.493	0.444	0.503	0.439	0.477

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
S1	0.439	0.451	0.386	0.492	0.410	0.436
S2	0.481	0.468	0.498	0.516	0.413	0.475
S3	0.505	0.516	0.483	0.542	0.449	0.499
S4	0.574	0.548	0.417	0.511	0.455	0.501
S5	0.524	0.481	0.437	0.454	0.466	0.473
Mean	0.505	0.493	0.444	0.503	0.439	0.477

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	0.552	0.592	0.620	0.611	0.575	0.590
N1	0.435	0.553	0.545	0.599	0.504	0.527
N2	0.459	0.396	0.448	0.435	0.423	0.432
N3	0.380	0.459	0.503	0.470	0.452	0.453
N4	0.352	0.377	0.380	0.390	0.408	0.381
Mean	0.436	0.475	0.499	0.501	0.473	0.477

SE 0.0390 .0175

Significant Effects NL ** N4 * SQ * CV *

Table 2:13 Establishment (plants/m of row)

1971

CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
N0	30.50	33.85	23.90	27.05	23.10	27.68
N1	25.40	33.70	22.55	30.75	22.35	26.95
N2	27.85	32.80	25.90	28.90	22.75	27.64
N3	26.50	35.20	23.45	27.75	21.95	26.97
N4	28.95	29.00	25.05	25.65	26.95	27.12
Mean	27.84	32.91	24.17	28.02	23.42	27.27

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
S1	9.20	9.25	6.45	8.05	6.70	7.93
S2	18.65	21.05	13.95	17.10	15.00	17.15
S3	26.70	30.30	24.70	27.75	24.70	26.83
S4	38.50	45.30	33.45	37.90	31.80	37.39
S5	46.15	58.65	42.30	49.30	38.90	47.06
Mean	27.84	32.91	24.17	28.02	23.42	27.27

SR x N

	S_1	S_2	S_3	S_4	S_5	Mean
N0	8.00	16.75	26.35	41.55	45.75	27.68
N1	8.75	16.85	26.85	35.40	46.90	26.95
N2	7.90	18.15	27.10	36.65	48.40	27.64
N3	7.80	17.00	28.40	35.50	46.15	26.97
N4	7.20	17.00	25.45	37.85	48.10	27.12
Mean	7.93	17.15	26.83	37.39	47.06	27.27

SE 1.976 0.884

Significant Effects SL ** CV **

CV x SL **

Table 2:14 % Nitrogen in Barley Grain Dry Matter

1970

CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
N0	1.81	1.73	1.74	1.84	1.75	1.77
N1	1.76	1.89	1.93	1.93	2.00	1.90
N2	2.03	1.96	2.01	2.02	2.02	2.01
N3	2.07	2.09	2.11	2.22	2.42	2.18
N4	2.34	2.31	2.04	2.22	2.37	2.26
Mean	2.00	2.00	1.97	2.05	2.11	2.02

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
S1	2.12	2.24	2.04	2.19	2.30	2.18
S2	2.19	1.91	1.99	2.09	2.02	2.04
S3	1.87	1.95	2.02	1.96	2.16	1.99
S4	1.91	1.87	1.86	2.02	2.01	1.93
S5	1.91	2.02	1.93	1.97	2.07	1.98
Mean	2.00	2.00	1.97	2.05	2.11	2.02

N x SR

	S_1	S_2	S_3	S_4	S_5	Mean
N0	1.95	1.77	1.77	1.69	1.69	1.77
N1	2.02	1.92	1.86	1.78	1.94	1.90
N2	2.08	2.15	2.00	1.81	2.00	2.01
N3	2.44	2.02	2.13	2.17	2.15	2.18
N4	2.40	2.35	2.20	2.20	2.13	2.26
Mean	2.18	2.04	1.99	1.93	1.98	2.02

SE 0.089 0.040

Significant Effects NL ** S **

Table 2:15 % Nitrogen in Barley Straw Dry Matter

1970 CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
N0	0.83	0.62	0.65	0.75	0.56	0.68
N1	0.91	0.88	0.76	0.87	0.66	0.82
N2	1.07	0.99	0.92	0.98	0.77	0.95
N3	1.25	1.15	1.17	1.18	0.92	1.13
N4	1.48	1.33	1.10	1.33	1.04	1.26
Mean	1.11	0.99	0.92	1.02	0.79	0.97

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Clermont	Mean
S1	1.31	1.27	1.12	1.26	1.06	1.20
S2	1.53	0.99	0.92	1.06	0.73	1.05
S3	0.95	0.91	0.84	1.01	0.73	0.89
S4	0.87	0.89	0.86	0.97	0.62	0.84
S5	0.88	0.91	0.86	0.82	0.81	0.86
Mean	1.11	0.99	0.92	1.02	0.79	0.97

N x SR

	S_1	S_2	S_3	S_4	S_5	Mean
N0	0.75	0.81	0.69	0.60	0.57	0.68
N1	1.02	0.93	0.70	0.67	0.77	0.82
N2	1.08	1.11	0.89	0.76	0.89	0.95
N3	1.51	1.17	0.95	1.03	1.01	1.13
N4	1.65	1.21	1.22	1.16	1.04	1.26
Mean	1.20	1.05	0.89	0.84	0.86	0.97

SE 0.090 0.040

Significant Effects NL ** SL ** CV *

Table 2:16 % Nitrogen in Grain dry Matter

1971 CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
N0	1.85	1.79	1.72	1.85	1.97	1.84
N1	1.82	1.99	1.94	1.90	1.98	1.93
N2	1.96	1.99	1.99	2.08	2.00	2.01
N3	1.97	2.06	1.99	2.16	2.06	2.05
N4	2.15	2.12	2.18	2.17	2.29	2.18
Mean	1.95	1.99	1.96	2.03	2.06	2.00

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
S1	1.88	1.98	2.02	2.16	2.18	2.05
S2	2.05	2.05	1.98	2.01	2.02	2.02
S3	1.85	1.89	1.91	2.05	2.18	1.98
S4	1.98	2.05	2.00	2.04	2.01	2.02
S5	2.00	1.99	1.91	1.91	1.92	1.95
Mean	1.95	1.99	1.96	2.03	2.06	2.00

N x SR

	S_1	S_2	S_3	S_4	S_5	Mean
N0	1.98	1.78	1.82	1.82	1.79	1.84
N1	1.96	1.92	1.96	1.96	1.83	1.93
N2	2.12	2.01	1.88	1.99	2.02	2.01
N3	1.97	2.15	2.09	2.03	2.00	2.05
N4	2.20	2.23	2.12	2.28	2.09	2.18
Mean	2.05	2.02	1.98	2.02	1.95	2.00

SE 0.070 0.031

Significant Effects NL **

Table 2:17 % Nitrogen in Barley Straw Dry Matter

1971 CV x N

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
N0	0.70	0.70	0.61	0.64	0.57	0.64
N1	0.90	0.80	0.82	0.82	0.75	0.82
N2	1.24	1.30	0.94	1.08	0.91	1.08
N3	1.03	1.23	1.05	1.08	1.14	1.08
N4	1.45	1.48	1.31	1.30	1.20	1.30
Mean	1.06	1.10	0.95	0.90	0.91	

CV x SR

	Dwarf A	Dwarf B	Zephyr	Golden Promise	Julia	Mean
S1	1.15	1.23	1.12	1.01	0.88	1.08
S2	1.21	1.18	0.89	0.88	1.12	1.05
S3	1.08	1.08	0.90	0.88	0.89	0.96
S4	0.83	1.05	0.93	0.98	0.75	0.91
S5	1.04	0.99	0.89	0.73	0.94	0.92
Mean	1.06	1.10	0.95	0.90	0.91	0.98

N x SR

	S_1	S_2	S_3	S_4	S_5	Mean
N0	0.71	0.65	0.66	0.61	0.60	0.64
N1	0.99	0.78	0.79	0.73	0.82	0.82
N2	1.14	1.28	1.06	0.97	0.93	1.08
N3	1.17	1.11	0.99	1.15	1.00	1.08
N4	1.38	1.46	1.33	1.08	1.25	1.30
Mean	1.08	1.05	0.96	0.91	0.92	0.98

SE 0.095 0.042

Significant Effects NL ** S * CV **

Table 2:18 200 Grain Weight (g)

<u>1972</u> CV x Nitrogen

	Dwarf A	Zephyr	Golden Promise	Mean
N1	7.32	7.29	6.91	7.17
N2	7.16	7.14	6.64	6.98
N3	7.25	7.19	6.13	6.86
Mean	7.24	7.20	6.56	7.00

Significant Effects CV ** N ** CV x N *

Table 2:19 % Nitrogen in Grain Dry Matter

<u>1972</u>

	Dwarf A	Zephyr	Golden Promise	Mean
N1	1.435	1.508	1.481	1.475
N2	1.606	1.793	1.648	1.683
N3	1.826	2.05	1.936	1.938
Mean	1.62	1.78	1.68	1.693

APPENDIX 3

Results 1970/71 1971/72

(Throughout this appendix standard errors of comparisons within the table will be placed first and the standard errors for the comparisons of means second)

Table 3:1 Grain to Straw Ratio 1970/71

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	0.6325	0.5989	0.5057	0.6009	0.4591	0.5594
N1	0.6300	0.6385	0.5035	0.5925	0.4013	0.5532
N2	0.6494	0.6877	0.5526	0.6048	0.4004	0.5790
N3	0.7086	0.6118	0.5604	0.5970	0.3627	0.5681
N4	0.5855	0.6332	0.5972	0.5590	0.3686	0.5487
Mean	0.6412	0.6340	0.5439	0.5908	0.3984	0.5617

SE within table comparison 0.0223 Cv & N means 0.00997

Significant Effects Cv** Cv x NL**

Table 3:2 1000 Grain Weight 1970/71 1971/72 (g)

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	45.37	43.66	46.06	45.43	36.88	43.48
N1	45.63	44.50	45.77	45.08	39.71	44.14
N2	41.21	40.55	44.79	46.05	35.33	41.59
N3	40.88	36.79	42.56	43.55	35.00	39.75
N4	35.97	36.63	42.24	41.79	34.66	38.26
Mean	41.81	40.42	44.28	44.38	38.26	41.44

SE within table comparison 1.050 Cv & N means 0.469

Significant Effects Cv** NL** NQ* Nc* Cv x NL*

200 Grain Weight 1971/72 (g)

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	9.767	9.209	9.695	9.749	7.987	9.281
N1	9.609	8.830	9.621	10.208	8.414	9.336
N2	9.622	8.818	9.140	10.185	8.316	9.216
N3	9.517	8.369	8.731	11.176	8.537	9.266
N4	9.055	7.643	8.106	10.759	7.864	8.685
Mean	9.514	8.574	9.058	10.415	8.223	9.157

SE within table comparison 0.2829 Cv &N means 0.1124

Significant Effects NL** NQ** Cv** NL x Cv**

Table 3:3 Number of Grains/Ear 1970/71 1971/72

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	21.93	18.92	16.63	21.59	23.42	20.50
N1	22.13	21.05	18.82	27.44	19.71	21.83
N2	27.17	29.96	20.82	28.34	24.16	26.09
N3	33.30	30.39	25.99	27.73	22.17	27.92
N4	31.73	31.01	26.19	29.71	23.23	28.37
Mean	27.25	26.27	21.69	26.96	22.54	24.94
SE	1.534		0.686			

Significant Effects Cv** NL** Nc* Cv x NL**

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	26.40	29.60	24.92	21.23	23.53	25.13
N1	32.11	35.68	25.33	29.66	26.37	29.83
N2	37.32	41.28	27.17	25.25	31.69	32.54
N3	31.46	38.33	37.09	30.29	36.52	34.74
N4	38.87	43.85	39.16	33.00	32.35	37.45
Mean	33.23	37.75	30.73	27.89	30.09	31.94
SE	4.939		1.963			

Significant Effects Cv** NL**

Table 3:4 Net Assimilation Rate 1/7 - 20/7 (g dm^{-2} wk^{-1})

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	1.289	0.488	0.427	0.854	0.645	0.741
N1	1.184	0.209	0.624	0.708	0.929	0.731
N2	0.585	0.794	0.356	1.089	1.133	0.791
N3	0.578	0.781	0.451	0.702	1.012	0.705
N4	0.399	0.911	0.895	0.232	1.074	0.702
Mean	0.807	0.636	0.550	0.717	0.959	0.734
SE	0.2335		0.1045			

Significant Effects Cv x NL*

Table 3:5 (A) Leaf Area (sq cm) 24 May 1971

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	42.65	45.17	33.32	32.01	37.96	38.22
N1	52.76	55.04	42.63	34.96	65.69	50.22
N2	76.72	63.66	58.83	63.43	77.72	68.07
N3	58.30	63.52	62.67	71.70	81.98	67.63
N4	77.34	79.04	76.52	66.78	101.46	80.23
Mean	61.55	61.29	54.79	53.78	80.23	60.88
SE	10.098		4.516			

Significant Effects Cv* NL** Calculated from square root transformation of skew data

Table 3:5 (B) Dry Wt of Sample (g) 24 May 1971

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	48.90	42.20	42.70	38.00	49.70	44.30
N1	57.80	51.50	45.60	49.40	62.90	53.40
N2	66.60	60.60	56.80	62.40	68.80	63.00
N3	69.60	64.60	61.00	64.00	71.00	66.00
N4	68.50	65.90	67.70	67.60	79.30	69.80
Mean	62.30	56.90	54.80	56.30	66.30	59.30
SE	4.89		2.19			

Significant Effects Cv** NL** NQ*

Table 3:6 (A) Leaf Area (sq cm) 8 June 1971

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	73.44	77.61	37.26	50.46	57.92	59.34
N1	58.40	74.92	68.69	67.72	79.46	69.84
N2	92.13	82.23	101.94	90.66	114.98	96.39
N3	97.22	106.82	102.95	96.81	99.85	100.73
N4	97.12	135.30	93.99	137.72	121.94	117.20
Mean	83.66	95.37	80.95	88.67	94.83	88.70
SE	14.194		6.348			

Significant Effects NL**

Table 3:6 (B) Dry Wt of Sample (g) 8 June 1971

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	122.0	102.6	81.7	78.9	103.8	97.8
N1	107.3	97.6	95.1	121.0	135.0	111.2
N2	131.2	124.6	125.4	136.2	133.9	130.2
N3	152.2	115.6	128.0	152.3	146.3	138.9
N4	144.4	142.6	130.8	154.2	163.8	147.1
Mean	131.4	116.4	112.2	128.5	136.5	125.0
SE	9.67		4.32			

Significant Effects Cv** NL**

Table 3:7 (A) Leaf Area (sq cm) 30 June 1971

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	45.07	60.32	47.50	46.36	54.99	50.85
N1	61.48	69.96	48.59	74.81	58.49	62.66
N2	75.45	79.54	64.75	71.49	86.18	75.48
N3	94.19	84.18	71.43	90.11	84.38	84.86
N4	82.93	108.73	79.10	118.28	82.75	94.36
Mean	71.82	80.55	62.27	80.21	73.36	73.64

SE 8.923 3.991

Significant Effects Cv** NL**

Table 3:7 (B) Dry Wt of Sample (g) 30 June 1971

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	172.0	184.8	181.8	186.2	192.7	183.5
N1	206.5	234.1	188.0	246.4	231.1	221.2
N2	268.2	235.4	244.0	260.4	237.0	249.0
N3	265.1	246.6	267.4	284.2	281.5	269.0
N4	299.1	267.1	248.2	351.2	259.7	285.0
Mean	242.2	233.6	225.9	265.7	240.4	241.5

SE 14.81 6.62

Significant Effects Cv** NL** NQ*

Table 3:8 (A) Leaf Area (sq cm) 20 July 1971

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	27.23	32.42	20.93	29.57	15.38	25.11
N1	36.50	36.17	32.36	37.95	15.91	31.78
N2	40.86	39.33	26.10	27.06	30.03	32.68
N3	34.23	49.49	26.82	22.72	23.73	31.40
N4	25.39	53.39	35.60	35.00	18.06	33.49
Mean	32.84	42.16	28.36	30.46	20.62	30.89
SE	9.429		4.217			

Significant Effects Cv**

Table 3:8 (B) Dry Wt of Sample 20 July 1971 (g)

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	296.1	247.1	214.9	272.4	261.2	258.3
N1	354.4	281.7	258.8	336.9	327.3	311.8
N2	361.3	366.9	305.0	390.7	352.5	355.3
N3	348.5	360.8	302.5	382.6	404.7	359.8
N4	354.6	406.0	368.0	431.8	358.3	383.7
Mean	342.9	332.5	289.8	362.9	340.8	333.8
SE	28.41		12.71			

Significant Effects Cv** NL** NQ*

Table 3:9 (A) Leaf Area (sq cm) 10 August 1971

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	7.47	10.20	7.19	3.93	5.48	6.85
N1	7.80	15.92	4.41	8.25	9.52	9.18
N2	7.32	8.33	1.78	5.62	7.49	6.11
N3	3.36	11.99	5.31	6.94	6.04	6.73
N4	3.52	9.60	14.50	7.23	5.38	8.05
Mean	5.90	11.21	6.64	6.39	6.78	7.38
SE	2.54		1.14			

Significant Effects Cv** Cv x NL*

Table 3:9 (B) Dry Wt of Sample (g) 10 August 1971

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	362.5	268.4	222.1	243.6	260.5	271.4
N1	305.4	287.6	260.6	328.7	371.7	310.8
N2	376.5	372.4	331.4	374.5	377.6	366.5
N3	367.6	350.6	362.6	403.2	403.7	377.5
N4	401.1	418.8	374.7	418.1	351.9	392.9
Mean	362.6	339.5	310.3	353.6	353.1	343.8
SE	27.45		12.28			

Significant Effects Cv* NL** NQ*

Table 3:10 PAD (3) 19 July 1972 (days)

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	27.53	34.47	29.55	20.40	19.80	26.35
N1	30.22	41.26	28.83	28.22	13.53	28.41
N2	44.04	54.39	35.08	29.22	13.87	35.32
N3	47.70	49.79	36.38	32.17	14.74	36.15
N4	46.97	55.42	35.25	32.52	14.14	36.86
Mean	39.29	47.07	33.02	28.50	15.22	32.62
SE	3.334		1.325			

Significant Effects NL** NQ* N_4* Cv** NL x Cv**

Table 3:11 PAD (4) 26 July 1972 (days)

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	42.09	50.66	43.39	33.33	35.51	40.99
N1	46.39	59.04	45.91	46.94	31.97	46.05
N2	64.71	79.28	56.26	50.96	34.49	57.14
N3	72.14	74.01	62.76	51.92	37.52	59.67
N4	72.41	81.17	60.23	55.86	37.56	61.45
Mean	59.55	68.83	53.71	47.80	35.41	53.06
SE	4.683		1.861			

Significant Effects NL** NQ** N_4* Cv** NL x Cv**

Table 3:12 PAD (5) 2 August 1972 (days)

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	57.57	67.43	59.04	47.04	52.12	56.64
N1	62.43	76.52	64.01	65.89	50.67	63.90
N2	86.17	106.38	77.27	74.36	57.15	80.27
N3	98.28	101.33	88.55	73.35	62.04	84.71
N4	100.32	107.96	86.91	76.69	61.76	87.33
Mean	80.95	91.92	75.16	68.07	56.75	74.57

SE 5.962 2.369

Significant Effects NL** NQ** Nc* N_4* Cv** NL x Cv**

Table 3:13 PAD (6) 9 August 1972 (days)

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	73.99	82.79	76.49	62.60	71.69	73.51
N1	77.34	94.09	82.10	85.08	72.47	82.22
N2	109.10	133.55	98.04	98.04	80.17	103.78
N3	125.56	128.54	112.14	103.21	88.71	111.63
N4	129.44	134.76	113.87	107.73	87.43	114.65
Mean	103.09	114.74	96.53	91.33	80.09	97.16

SE 7.697 3.058

Significant Effects NL** NQ** Nc* Cv** NL x Cv**

Table 3:14 PAD (7) 16 August 1972 (days)

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	86.9	94.4	88.4	74.6	88.6	86.6
N1	86.7	106.4	98.3	101.2	93.3	97.2
N2	129.2	155.5	115.3	118.5	99.4	123.6
N3	148.5	151.3	133.3	127.5	114.2	135.0
N4	157.5	157.7	135.0	134.0	111.8	139.2
Mean	121.8	133.1	114.0	111.2	101.5	116.3
SE	9.66		3.84			

Significant Effects NL** NQ** Nc* Cv** NL x Cv**

Table 3:15 PAD (8) 23 August 1972 (days)

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	93.7	101.3	95.7	81.8	98.9	94.3
N1	93.1	111.9	108.1	110.1	107.2	106.1
N2	141.4	167.3	125.4	132.8	113.6	136.1
N3	162.8	160.2	147.5	143.9	135.0	149.9
N4	178.7	171.7	149.8	149.6	131.1	156.2
Mean	133.9	142.5	125.3	123.6	117.2	128.5
SE	11.24		4.47			

Significant Effects NL** NQ* Nc* Cv** NL x Cv**

Table 3:16 PAD (9) 30 August 1972 (days)

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	96.7	104.1	99.7	86.4	107.4	98.9
N1	97.3	115.9	112.7	113.7	114.5	110.8
N2	143.8	173.9	132.3	140.4	122.3	142.5
N3	171.7	166.5	155.9	152.3	149.5	159.2
N4	191.2	178.7	159.3	160.6	143.2	166.6
Mean	140.1	147.8	132.0	130.7	127.4	135.6

SE	12.00		4.77			

Significant Effects NL** Nc** Cv** NL x Cv**

Table 3:17 PAD TOTAL ALL SHOOTS to HARVEST (days)

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	97.8	104.6	100.2	88.3	113.4	100.8
N1	98.3	116.2	114.2	114.9	118.7	112.5
N2	146.0	175.8	134.3	144.2	126.7	145.4
N3	176.0	169.2	160.1	157.7	155.6	163.7
N4	197.3	180.8	162.0	167.9	149.5	171.5
Mean	143.1	149.3	134.2	134.6	132.8	138.8

SE	12.95		5.15			

Significant Effects NL** Nc** Cv** NL x Cv**

Table 3:18 PAD TOTAL MAIN SHOOTS ONLY to HARVEST (days)

1971/72	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	91.6	95.1	95.2	85.0	102.8	93.9
N1	86.6	107.5	102.8	110.7	110.1	103.5
N2	118.9	150.9	117.7	134.9	114.0	127.3
N3	142.4	137.3	135.4	145.5	136.0	139.3
N4	152.6	143.5	127.6	153.7	133.2	142.1
Mean	118.4	126.9	115.7	126.0	119.2	121.2

SE 11.38 4.52

Significant Effects NL** NQ* Nc * NL x Cv*

Table 3:19 Logarithm to Base 10 of Leaf Area/Shoot VARIETY MAIN EFFECTS

1970/71	Cv Signif	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
24 May	NS	1.4062	1.3649	1.3612	1.4128	1.3785	1.3847
8 June	NS	1.6129	1.6378	1.5911	1.6592	1.6015	1.6205
30 June	**	1.6275	1.6540	1.5761	1.6825	1.6521	1.6385
20 July	**	1.3022	1.2886	1.2751	1.1892	1.0272	1,2165
10 August	**	0.1736	0.7371	0.4994	0.4905	0.4766	0.4754

Table 3:20 Logarithm to Base 10 of Leaf Area/Shoot Nitrogen Means

1970/71	NL Signif	N0	N1	N2	N3	N4	SE
24 May	**	1.2769	1.3471	1.4263	1.4134	1.4599	0.0218
8 June	**	1.5170	1.5650	1.6548	1.6612	1.7045	0.0221
30 June	**	1.5210	1.5865	1.6636	1.6996	1.7216	0.0181
20 July	*	1.2178	1.2918	1.2566	1.1968	1.1193	0.0448
10 August	*	0.6380	0.6173	0.3316	0.3550	0.4354	0.0971

Table 3:21 (A) Grain No/sq m 1970/71

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	9563	9057	7252	8848	11441	9208
N1	9360	10629	7837	11966	8336	9591
N2	14520	14243	9420	10778	12674	12318
N3	16159	17138	12015	13547	11267	13823
N4	14981	17488	12108	13053	11425	14325
Mean	12866	13350	9743	11845	11085	

Table 3:21 (B) Grain No/sq m 1971/72

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	10545	11849	10661	10370	10783	10834
N1	13319	15520	13597	12757	12890	13593
N2	15708	19286	15512	14154	15406	15948
N3	17342	19197	17932	13658	15432	16599
N4	17648	21638	18384	14548	16348	17495
Mean	14862	17315	15047	13148	14180	

Table 3:22 Ear Number per 2m of Drill

1970/71	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	133	146	133	125	149	137
N1	129	154	127	133	129	134
N2	163	145	138	116	160	144
N3	148	159	146	149	155	151
N4	148	172	141	150	158	154
Mean	144	155	137	134	150	144

SE 10.7 4.8

Significant Effects NL** Cv*

1971/72						
N0	158.4	154.4	132.4	143.8	134.8	144.8
N1	161.0	179.2	153.0	154.2	147.4	159.0
N2	159.6	173.8	159.0	169.2	187.0	169.6
N3	198.8	186.4	183.4	205.8	183.4	190.4
N4	208.4	185.8	210.4	195.4	180.6	196.0
Mean	176.0	175.8	167.6	173.6	166.6	172.0

SE 18.98 7.54

Significant Effects NL**

Table 3:23 Biological Yield 1970-71

	TL363/30	TL365a/34	TL365a/37	Maris Nimrod	N59	Mean
N0	341.6	318.9	303.5	324.9	426.2	343.0
N1	331.9	376.1	321.9	457.1	351.4	367.7
N2	459.4	422.3	377.6	393.3	466.4	423.8
N3	473.6	464.2	449.8	478.5	454.8	464.1
N4	464.8	511.1	418.1	506.7	472.7	474.6
N5	414.3	418.5	374.2	432.1	434.3	414.6

APPENDIX 4

Sample Analyses of Variance Calculations

Table 1 Barley grain yield (1971)

Source	df	SSq	MSq	VR Ratio	
Replicates	1	86.8997	86.8997		
Blocks	8	772.4108	96.5518		
Nitrogen Linear	1	28.4708	28.4708		
quad.	1	689.4220	689.4220	75.73	**
Cubic	1	207.9509	207.9509	22.84	**
Rem.	1	35.9312	35.3912	3.89	*
Seed Rate Linear	1	1056.5254	1056.5254	116.06	**
quad.	1	266.4814	265.4814	29.27	**
Cubic	1	4.9379	4.9379		
Rem.	1	7.3022	7.3022		
Cultivar	4	248.4277	62.1069	6.82	**
Cv x NL	4	208.4325	52.1081	5.72	**
Cv x NQ	4	96.1091	24.0273	2.64	*
Cv x N	8	148.8864	18.6108	2.04	*
Cv x SL	4	56.2552	14.0638		
Cv x SQ	4	33.8726	8.4682		
Cv x S	8	43.3531	5.4191		
NL x SL	1	2.1791	2.1791		
NL x SQ	1	18.6165	18.6165		
NQ x SL	1	86.4587	86.4587	9.50	**
NQ x SQ	1	4.6875	4.6875		
N x S	12	121.4951	10.1246		
N x S x Cv	64	478.7430	7.4804		
Error	112	1019.5297	9.1029		

Design. Randomised Block design 5 Nitrogen Rates x 5 seed rates x 5 cultivars
Block size 25 plots 2 replicates of 5 blocks
1970 Experiment same design.

Table 2 Analysis of Variance, Total yield (1972)

Source	df	SSq	MSq	V.R.	
Blocks/reps	5	1121.4762	224.2952		
N level	2	1918.7300	959.3658	20.187	**
Cultivar	2	76.9968	38.4984		
N x Cv	4	122.4106	30.6026		
Error	40	1900.9585	47.5239		
Total	53	5140.5721			

Design: Completely randomised design of 3 nitrogen rates x 3 cultivars
6 Replicates.

Table 3 Yield of Wheat 1971-72

Source	df	SSq	MSq	V.R.	
Reps	3	5543287	1847762	3.443	
Blocks	16	8877867	554867	1.034	
N lin	1	83287392	83297392	155.213	**
quad	1	17274576	17274576	32.193	**
cub	1	11888	11888	0.022	
quot	1	134710	134710	0.251	
Cultivar	4	28073936	7018484	13.079	**
NL x Cv	4	836019	209005	0.389	
Nq x Cv	4	308752	77188	0.144	
N6 x Cv	4	399650	99912	0.186	
N4 x Cv	4	1353028	338257	0.630	
Error	56	30049728	536602		
Total	99	176150992			

Design Randomised block design of 5 nitrogen rates x 5 cultivars
Block size 5 plots 4 replicates 5 blocks per replicate.
1970-71 same design

Same analysis used in all yield components and in grain filling study (Chapter 5) for analysis of measurements at each sample date.

Table 4 Root length in Barley (1971) on 14/6/71 bottom layer

Bottom layer

Source	df	SSq	MSq	V.R.
Blocks	5	0.8671	0.1734	
Varieties	1	3.5305	3.5305	55.598 **
Error	5	0.3174	0.06348	
Total	11	4.715		

Design Completely randomised 2 plots per replicate; 2 varieties
6 replicates. Other layers calculated similarly.
Surface area and volume calculated similarly.

Table 5 Root length in wheat on 5 June 1972 top layer

Top layer

Source	Df	SSq	MSq	V.R.
Blocks	3	0.0248	.00829	
Varieties	3	0.0170	.00507	
Error	9	0.0788	.00875	
Total	15	0.1206		

Design Completely randomised 4 varieties per replicate
4 plots per replicate
4 replicates Other layers calculated similarly
Surface area and volume calculated similarly.

Table 6 Analysis of variance calculation for comparison of regression coefficient of log of leaf area on rating in leaf area measurement 1970-71 wheat
Day 3 sample 2 comparison of effect of nitrogen treatments

Source	Df	SSq	MSq		
Combined b	1	4.1059	4.1059		
Deviation	4	0.0528	0.0132	1.7143	NS
Difference in Mean	4	1.3680	0.3420	44.4123	**
Error	115	0.8904	0.0077		
Total	124	6.3270			