THE INFLUENCE OF COMPETITION FOR LIGHT ON THE DRY MATTER PRODUCTION AND EAR FORMATION OF WHEAT PLANTS.

by

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C O N T E N T S

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FIGURES

PLATES

SUMMARY

Wheat plants were grown in a glasshouse without artificial illumination to study the effect of plant density on yield. By growing the plants in narrow individual containers the effects of root competition were controlled and this allowed a closer study of competition for light and its effects on tillering, dry matter production and head formation. The spacing could be altered at any stage with little effect on growth, thus providing information on the effects of treatments of different duration. All plants commenced growth with the containers packed closely together at a high density of 1150 plants/m^2 and at intervals plants were removed and spaced out widely, thus having the effect of transferring from conditions of intense competition for light to conditions of low density with negligible competition.

The plants at high density were limited in their growth by intense competition, apparently for light. Transfer to low density removed this limitation and the plants produced a greater amount of dry matter, particularly with the plants that produced tillers. Plants remaining at high density did not produce tillers as a result of the intense competition, but did produce tillers if removed to low density by day 38. Low nitrogen level was an additional factor in the reduced tillering of the widely spaced plants.

The total number of spikelet primordia per ear increased with increasing nitrogen level, but was not affected by time of transfer to low density. However, the number of these primordia which developed to give fertile spikelets was affected by both nitrogen level and time of transfer. It is suggested that competition for light at high density resulted in a reduced supply of assimilates to the developing apex and competition for this assimilate between spikelets. There was also an interaction with nitrogen. The critical period for the effect of this competition on the development of the spikelets was from immediately prior to elongation of the rachis to ear emergence. Intense competition at this stage could reduce the grain yield per ear to less than half of that which would be obtained if all spikelets developed fully.

SOURCE OF INFORMATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in the University and to the best of the candidate's knowledge and belief, the thesis contains no material previously published or written except where due reference to the author is made in the text of the thesis.

(D. W. Puckridge).

A C K N O W L E D G M E N T S

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I N T R O D U C T I O N

In recent years there has been renewed interest in the study of plant spacing, on density of sowing, in relation to competition for light energy. This interest has developed particularly since the production of suitable instruments for measuring changes in light intensity within a crop or pasture canopy and the development of the concept of leaf area index by Watson (1947).

Several useful methods have been used to study the effects of light intensity on plant growth but difficulties have arisen in interpretation of results, particularly in isolating the effects of light intensity from other factors. Shading experiments have been used to give changes in light intensity within crops, but shading reduces the light intensity over the whole crop surface, whereas in a field community the uppermost leaves are in full daylight with light intensity diminishing towards the ground surface. The materials used for shading also affect temperature, air movement and transpiration. Artificial environments can be used to control the level and duration of light intensity, but in this case there are differences in light quality and intensity compared with natural light, and the pots normally used restrict the range of densities which can be employed. The effects of light intensity on plant growth have also been studied by the correlation of measured seasonal changes in natural daylight with plant growth and

development, or by the correlation of penetration of light into a plant association with growth and development. While these types of experiment do not directly affect light quality or quantity, growth is dependant on other factors of the environment at the same time, for example, temperature, soil moisture and soil nutrients, with resultant interactions between factors.

Density of sowing is of particular interest in the study of competition for light, as changes in density can be used to alter the light environment. However, any variation in spacing between plants immediately alters the volume of soil available to plants of different density treatments, unless the plants are in individual containers, so that differences occur in the availability of soil moisture, nutrients and soil air. These differences could be great enough to mask entirely the effects of competition for light, or may at least prevent identification of the primary effects.

The present experiment was designed to study the effect of plant density on the yield of wheat, particularly the yield of grain, using a glasshouse without artificial illumination and controlling the effects of root competition. This was accomplished by growing the plants in narrow individual containers which were spaced at two extreme densities. They were either packed closely together (high density) or spaced out widely (low density) without any change in soil volume per

plant. The spacing could be altered at any stage with little effect on growth, thus providing information on the effects of treatments of different duration.

REVIEW OF LITERATURE

(a) Competition in general.

Competition usually occurs when plants make similar demands on the same environment. Clements, quoted by Clements, Weaver and Hanson (1929), states that "Competition arises from the reaction of one plant upon the physical factors about it and the effect of these modified factors upon its competitors. In the exact sense, two plants, no matter how close, do not compete with each other as long as the water-content, the nutrient material, the light and the heat are in excess of the needs of both. When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins".

Many of the concepts developed by Clements *et al.* on the nature of competition are still generally accepted, although the emphasis on particular facets has tended to alter. The evidence obtained by them as to the relative importance of the three primary factors of the environment suggested that water is first, light next and nutrients last in native communities, with the order changed to water, nutrients and then light in the case of intensive field crops. Hudson (1941) suggested that competition will only become operative when the spheres of absorption of the roots overlap. He ruled out light and proposed that competition is primarily underground for water, soil

nutrients and soil air, and that of these competition for water is the most important in determining yield.

(b) Competition for light.

Although the above relationships may often be of the orders given, the "orders" are based on empirical studies in particular environments and any one of the factors may assume the dominant role in competition dpeending on local circumstance. In many areas water is non-limiting owing to adequate rainfall or the use of irrigation, and with increased development and use of artificial fertilizers more interest has been taken in the study of competition for light. Donald (1951) points out that light is the factor which determines the ultimate yield of a plant community, and when light only has become the factor limiting the growth per unit area, then the maximum production of which the genotype is capable has been obtained.

The subject of competition for light in relation to light intensity, leaf area and density of sowing, as well as these effects on net assimilation rates and relative growth rates, has been extensively reviewed in the literature (Black 1957, Donald and Black 1958, Blackman and Black 1959, Stern 1960, and Donald 1961). Donald (1961) points out that even where water or nutrients impose some limitation on the rate of growth, competition for light is still almost certainly important. Thus if light energy is to be most effectively used in the process of photosynthesis, then the arrangement of the plant

foliage must be such that all the light per unit area is intercepted, with the majority of the leaves receiving sufficient light energy for a positive balance of photosynthesis over respiration. The number of leaves of a particular plant receiving sufficient light in turn depends on the degree of competition from its neighbours.

It is extremely difficult to isolate the effect of a single factor, especially light, in the analysis of competition effects. For example, Khalil (1956) found that the dry matter production of wheat was much greater at high nitrogen level than with low nitrogen, but the difference corresponded with the absolute amount of light energy, i.e., the higher the light intensity the larger the difference between the two nitrogen treatments. Khalil suggests in this study that the role of nitrogen is entirely dependent on the prevailing light conditions. Blackman and Black (1959) in their study of light limitation of growth indicate that in tropical conditions, apart from greater radiation leading to increased assimilation, higher temperatures positively influence the leaf-area ratio and hence the relative growth rate. However, Blackman, Black and Kemp (1955) found that the net assimilation rate of Helianthus annuis was not affected by temperature. Friend, Helson and Fisher (1962 a) also found an interaction between light intensity and temperature on the relative growth rate of wheat. The relative growth rate increased with increasing

light intensity, but the rate of its fall with time increased with temperature within the range from 10 to 30°C. At the same time increasing temperature in the same range increased the rate of development of the plants. These examples show that interactions between factors make the interpretation of results very difficult, and the effects are still important even in the study of a single factor. Donald (1958) in a study of the interaction of competition for light and nutrients found that competition for even a single factor involves interaction between direct and indirect effects, but when competition occurs for two factors it leads to multiple interactions between two groups of effects and thus greatly intensifies the effects of competition for the two operating independently.

In spite of the difficulties in isolating the absolute effects of competition for a single factor, there is ample evidence that the amount of light received by the plant will determine the rate of increase in dry weight (Stoughton 1955, Khalil 1956, and the reviews mentioned previously). In addition, Moss, Musgrave and Lemon (1961) measured assimilation of a corn crop in field enclosures and found that the intensity of solar radiation was the predominant factor of the environment which affected the rate of photosynthesis. There was no appreciable flattening of the photosynthetic curve during midday on clear days as would be the case if the plants were light saturated at midday sunlight intensities. However,

the efficiency curve had a distinct midday depression, indicating that the upper leaves may have been light saturated and some other factor of the environment, possibly diffusion of CO_2, was then having an effect. Gaastra (1962) suggests that under field conditions light intensities and CO_2-concentrations are such that for a wide range of temperatures the photochemical and/or diffusion processes are limiting photosynthesis. He states that efficiencies of closed crop surfaces are mostly at least 50% lower than the optimum efficiency of the photochemical process. Therefore, photosynthesis is probably limited by the capacity of the diffusion process. On the other hand, Hesketh and Musgrave (1962) in a study of net assimilation of corn found that most individual leaves were not saturated with light at 10,000 f.c. This could be the reason for the non-flattening of the midday photosynthetic curve described above for corn.

(c) The effect of competition on the components of yield.

Many crop studies, particularly on rates of seeding, can be regarded as competition studies, although, as observed by Donald (1951), since the criterion of yield has usually been a part of the plant, they give an incomplete picture of the competitive relations of plants. The effect of density of sowing on the development of plants has been studied by a number of workers (Clements et al. 1929, Engledow and Wadham 1930, Donald 1951, 1954, Hodgson and Blackman 1956, Iwaki 1958, and Kamel 1959 and many others). The general picture which emerges from

these studies is a decrease in dry weight, branching and seed production with increasing density. For wheat, increasing seeding rate gives a moderate curvilinear decrease in the number of kernels per head, and a smaller, linear decrease in 1,000 grain weight (Guitard, Newman and Hoyt 1961). Associated with these effects in cereals is a decrease in tiller numbers per plant, but relatively little change in yield of dry matter or grain per unit area. Puckridge (1962) in a study of competition among spaced wheat plants sown at a wide range of densities obtained similar yields of dry matter and grain over a range of sowing of from 35 to 875 plants per square metre, with decreased yield at higher and lower densities. The response to decreased competition was shown in increased tiller numbers and tiller size per plant. However, the optimum plant population may be influenced by the nutrient level with subsequent effects on the components of yield as was shown by the results of Lang, Pendleton and Dungan (1956). At low nitrogen level the maximum yield of corn (75 bushels/acre) was given by a population of 12,000 plants/acre. At moderate nitrogen a maximum yield of 92 bushels/acre was obtained with 16,000 plants, while at high nitrogen the peak yield was only obtained when the population was raised to 20,000 plants per acre. Examination of the components of yield, namely, ears per hundred plants, weight per ear, and weight per kernel, revealed that ears per 100 plants was

influenced most by varying populations and fertility levels. This stalk barrenness was affected more by plant population than by type of hybrid or by nitrogen level.

With crop plants, interest lies not in the total dry matter, or biological yield, but in the economic yield (Michiporovich 1954). In the case of wheat, with which this study is concerned, the economic yield is the grain. Competition, in addition to its effects on total yield of the plants, may have differing effects on the yield of various organs and therefore may affect the ratio of the economic yield to biological yield. (This ratio has been termed the "Coefficient of Efficiency" by Michiporovich (1954), but Donald (1960) suggests that a more explicit term is "Harvest Index"). For instance, Kamel (1959) in a shading experiment with barley found that the plants at 50% daylight produced more ears than those at 80% daylight, but owing to the smaller number of seeds per ear and the failure of late ears to form seeds, produced less grain. The number of seeds per ear increased with light intensity. The response of the various plant organs to changes in fertility may also differ with variety, as was shown by Langfield (1961). With an *indica* variety of rice addition of up to 40 lb./acre of nitrogen fertilizer gave a slight increase in grain yield, but further additions of nitrogen, over forty pounds per acre, had little effect on grain yield although greatly increasing the yield of straw. On the other hand, with a *japonica* variety, grain yield

increased almost linearly with increased nitrogen, while straw yield did not change. Thus with increased fertiliser there was a large increase in the harvest index of the japonica variety, whereas the harvest index of the indica variety actually declined at high nitrogen levels.

There is some agreement that to increase the yield of grain per unit area an increase of harvest index is desirable, but there is no general agreement as to the components of yield which are most important in this respect. Donald (1962) quotes varying emphasis on each of the components, ears per plant, weight per grain, grains per ear by different workers. These factors in turn are influenced by the degree of competition as affected by the density of sowing.

(d) Factors affecting tillering.

While there are many studies in which the degree of tillering has been observed, there is little information available on the principles involved, mainly because of the number of factors contributing to variation. Working with barley in pot culture, Aspinall (1961) found that tillering is largely dependent on nutrition. When nutrients were repeatedly renewed throughout growth, tillering was almost continuous. However, when nutrients were supplied only before germination, tiller emergence was restricted to two periods in the development of the plants, while the extent and duration of tillering in the first phase was governed by the level of nutrient supply. The period of non-

tillering was not due to the absence of tiller buds and tillering could be induced at any time by the application of nutrients. On the other hand, Khalil (1956) found a positive relationship between tillering and light intensity, with the extent of the response to light dependent on the level of nitrogen supplied. Kamel (1959) found a similar response to light intensity.

In the field tillering is largely dependent on the density of sowing, although there is no definite evidence of the degree of influence exerted by light, water, or nutrient supply. The effect of these factors may also vary with the type of cereal, and therefore the responses of wheat, barley and oats may not be the same. Engledow (1928) found that the rate of tiller survival at harvest was higher among thinly spaced plants of wheat than in aggregates of denser populations, but counteracting this was a diminution of ear size among successive tillers of a single plant. The length of the tillering period could also be of importance to the eventual population of tillers. For instance, Forster and Vasey (1931) found that the Australian wheat varieties they investigated normally produced shoots or tillers from the axils of the first three leaves of the main shoot in about six weeks from seeding. The rosette stage comparable to that of the English wheats was reduced to a minimum. However, Puckridge (1962) found that when the Australian wheat Insignia was sown at a very wide spacing (1.4 plants per square metre), tillering continued for 17 weeks after sowing to give a mean of 40 tillers per plant.

With increased density tiller numbers per plant decreased and production of tillers ceased at an earlier date until with an initial plant density of 1080 plants/m^2 only 1.5 tillers per plant were formed. An even further reduced period of tillering at normal planting rates, compared with that obtained with wheat by Forster and Vasey, was observed by Frey and Wiggans (1957) with oats. Here maximum tillering appeared to be determined within the two weeks immediately after emergence. This is in direct contrast to the shading experiments of Kamel (1959) where barley sown at 250 plants per square metre continued tillering until 66 days after planting, with an average of seven tillers per plant under high light intensity and 4 to 5 under low light intensity. However, these responses are for different species and thus not directly comparable.

Nitrogen appears to be the major nutrient involved in tillering. (Russell and Watson 1940, Holmes and Tahir 1956, Khalil 1956, Frey and Wiggans 1957, Langer 1959 and Thorne 1962). The effect over a wide range of application is mainly to increase the number and weight of tillers, with little change in the form of development.

(e) Differences in field and pot responses to nitrogen.

Comparison of field studies with pot cultures show that the effect of nitrogen in the field is modified by other factors. Watson (1936) found with pot cultures that shoot number is closely related to the nitrogen supply and the effect of the

added nitrogen depended on when it was applied. Nitrogen applied to pots between germination and early March increased the number of ears per plant, but depressed both the number of grains per ear and the 1,000 grain weight. All applications between germination and May produced the same increase in yield, the early application by producing more ears with smaller grain, and the later applications by producing fewer ears but with more grains per ear. Thorne (1962) obtained similar results with March and April applications in pots, but found the response in total dry weight and grain yield to be much less with late applications at ear emergence.

However, under field conditions applications in March or at ear emergence gave similar increases in yield, presumably because there were no late unproductive tillers with late nitrogen application, and hence the nitrogen was used more effectively by existing shoots so that more of them attained maturity. It appears that tillering of the field plants was suppressed by low light intensity at the base of the plants at the time of application. This condition would not develop in pots.

The differences in response to field and pot application of nitrogen may also be associated with differences in uptake. Thorne (1962) found nitrogen uptake in the field to continue to maturity; at ear emergence barley had absorbed only 75% of the final content of nitrogen. Similar proportions were recovered by wheat in the field; whereas with both species

in pot culture no nitrogen was absorbed after ear emergence from early applications. She observed that recoveries of less than 60% are common in pots; the remainder apparently being incorporated in soil organic matter or lost by denitrification (Walker, Adams and Orchiston 1956). Presumably these factors in association with the small volume of soil in pots limits uptake from the soil and small dressings of nitrogen must be applied regularly to simulate field conditions.

Although these studies have shown the importance of such factors as mineral nutrition, light and the proportion of fertile tillers, they have not given a complete picture of the mechanism involved in the production of tillers and the determination of yield. Also, tillers rapidly produce adventitious roots and become at least partially independent of vascular connections with the remainder of the plant. Thus production of more tillers results in a system of partial competition between a number of individuals (Aspinall 1961). The effect of this partial independence of tillers on the yield of grain per plant and per unit area is not clear.

(f) Photosynthesis and the grain yield of the ear.

The three possible sources for the photosynthetic products which make up the major part of the grain weight are photosynthesis in the stem, in the leaf, and in the ear itself. Archbold (1945) from a number of defoliation experiments with barley, estimated that the leaves supply not more than 10% of

the final dry weight of the ear compared with 30% by the ears themselves. The photosynthesis of the leaves before ear emergence may contribute a further 15%, mainly leading to polysaccharide and protein synthesis. There remains the 45% attributable by difference to stems and sheaths, of which more than half is contributed before ear emergence. Archbold suggests that perhaps half of the material of the ear accumulated before emergence may be attributed to the activity of the leaves and half to the stems and sheaths, of which latter half a large proportion is probably derived from the flag leaf sheath. Calculations by Asana and Mani (1950) showed that the contribution of dry matter to the grain from photosynthesis in the ear, leaf, and stem of wheat differs with varieties. At the same time it was suggested that the proportions of contribution by the stem and ear appear to determine to some extent the number of mature grains and their size. In a later study (1955) it was found that the contribution of the ear and leaf was greater than that of the stem.

Watson (1956) observed that the leaf area throughout the growing period is the main determinant of total yield of dry matter, but may not be of the yield of any particular organ or chemical constituent. From his results he suggests that only the leaf area persisting after ear emergence is directly concerned with grain production. Watson proposed that favourable conditions for high yield of grain would be a high leaf area index

at the time of ear emergence with slow senescence of surviving leaves - implying a long interval between ear emergence and maturation - which should occur at the time when conditions are favourable for maximum photosynthesis. He concludes that fulfillment of these conditions probably depends particularly on the size and longevity of the flag leaf.

Similar results as to the relative importance of the leaf, ear and stem were obtained by Buttrose and May (1959), Frey-Wyssling and Buttrose (1959), Mayer and Porter (1960) and Thorne and Watson (1962). Mayer and Porter by use of carbon-14 dioxide supported the view that assimilation by lower leaves on cereal tillers does not materially contribute to the growth of the grain even though there may be up to five green leaves on the tiller. The evidence available suggests that after ear emergence photosynthesis in the ear itself is of major importance in filling the grain, but the feature of the research in this field has been the wide range of the estimates of the contributions from several sources (Buttrose and May 1959). However, it is apparent that photosynthesis of the stem and leaf still contribute a considerable portion to the yield of grain and the evidence only partly justifies the statement of Donald (1962) that "... one can envisage a variety attaining high yields by displaying a dense population of ears unaccompanied by any functional foliage. Such a variety would have sufficient leaf before head emergence to produce a large crop of ears.

The leaf would then wither, and grain production would depend on a dense population of ears actively fixing the carbon of the grain".

Watson, Thorne and French (1958) in a study later followed up by Thorne (1962) produced some further evidence on the relative efficiency of contribution to grain production by the leaves of different varieties of barley. The varieties Proctor and Herta produced 10 - 15% more grain than Plumage-Archer without added nitrogen fertilizer, and 30% more with nitrogen, although lodging in the Plumage-Archer contributed to the difference at high nitrogen. There were no differences in L.A.I. or N.A.R. before ear emergence, so all had the same dry weight and the higher grain yield of Proctor and Herta was assumed to have come from additional photosynthesis in the ears. A large part of the difference in yield was due to Proctor and Herta having a higher number of fertile tillers per unit area, but there was also a difference in efficiency. Thorne (1962) found that the dry weight ratio of ear to shoot was smaller for Proctor than for Plumage-Archer at ear emergence and anthesis, but at maturity was greater for Proctor. The relative growth rate of ears of Proctor was greater and more dry matter was lost, presumably to the ear, from its shoots. It was suggested that leaves of Proctor were more efficient in producing for the ear. In both cases the shoot below the base of the flag leaf contributed a mean of 15% to the grain yield.

(g) <u>The determination of ear size</u>.

Despite the number of investigations on the various aspects of

yield in the cereals there is practically no information available on the determination of ear size at ear emergence and hence its potential for producing grain. It has been seen that ear size decreases on later formed tillers and with increases in density, but information on the influence of factors operating in the period between ear initiation and ear emergence on the ultimate yield of grain is meagre.

Factors acting before ear emergence and likely to be important in determining the ultimate grain yield of the ear are those influencing the number of leaves formed before the initiation of the spike, the time of initiation and the rate of growth of the spike, and the number of spikelets it carries. Differences occur in time of initiation of the spike with variety (Cooper 1956), and with density and light (Kamel 1959). Kamel found that increasing plant density induced earlier development of the spike and it was suggested that light could not be the factor in this case, as in the shading experiment the earlier development of the spike was observed at the highest light intensity.

Barnard (1955) found with the wheat varieties Victor and Yeoman that the transition from the vegetative to the reproductive stage of growth commenced when there were from five to seven expanded or externally visible leaves on the main axis. The first morphological indication of spike formation was a rapid elongation of the apical dome which became an elongated cone.

However, stages preceding spike initiation may have an influence on subsequent formation of the spike in relation to supply of energy substrates to the plant as a whole. In a study of a spring wheat variety under constant conditions Williams (1960) discussed changes in energy substrates in relation to growth rates and development. Immediately after germination the level of supply of energy substrate from seed reserves seemed to have been sufficient to supply not only the heavy demand of leaf area but also to maintain a higher relative growth rate in leaf two than in leaf three or four. With succeeding leaves the relative growth rate declined and the relative growth rate of the stem changed from being well below that of leaves to values greater. The reversal expresses a change in dominance from leaf growth to stem growth and concurrently there is a progressive increase in the rate of growth of the apex. These trends reached their conclusion, as far as the primary shoot was concerned, at the double ridge stage of inflorescence development when further development of lower ridges was suppressed and upper ridges developed as spikelets.

Friend, Nelson and Fisher (1962 b) described two stages in the growth of leaves in relation to the supply of assimilates. In the first stage the developing leaf was dependent on the supply of assimilates and other growth factors from the more mature leaves. Initiation and emergence of the lamina depended on the growth of the plant as a whole and it is likely that this would

also apply to the inflorescence. The second stage occurred when the leaf grew out of the sheath, became exposed to light and began photosynthesis. They suggested that any change in the distribution of assimilates leading to increased primordial growth is probably initiated by the emerged leaves rather than by direct effects of light intensity on the apex. The increased supply of assimilates released by the earlier cessation of leaf growth as the light intensity increased could then increase the rate of initiation, growth and expansion of developing primordia.

Cooper (1956) found that the maximum number of primordia are formed at the late spikelet-bud stage when elongation of the internodes commences and the apical meristem is transformed into the apical spikelet. This was confirmed by Nicholls (1962) who found that primordia formation ceases at initiation of cell division in the pith of the inflorescence axis, i.e. at the initiation of internode elongation. This stage also corresponds with formation of the stamen initials. Nicholls' experiments were carried out under controlled environment and he also found that dry weight and apex length increased with increase in the total number of hours of light supplied.

The studies discussed in this section give some indication of the importance of the early stages of growth on the subsequent grain yield of the plant. The number and size of the spikelet primordia, and thus the potential grain yield, are determined long before the ear emerges from the sheath. Consequently the

developing ear depends for its supply of assimilates and other growth factors on the vegetative parts of the plant. The vegetative parts, i.e. the leaves and stem, are in turn influenced in growth and development by environmental factors and in the early stages by the supply of energy substrates from the seed. This could be important in relation to the time of initiation of spikelet formation and the length of the period from initiation to cessation of spikelet formation. On the one hand earlier initiation of spikelet formation could result in a longer period with more spikelets and eventually larger ears. On the other hand, earlier initiation could be associated with earlier cessation of spikelet formation. The period would then be short, vegetative development less with a reduced supply of assimilates to the apex, resulting in fewer spikelets and smaller ears.

(h) Conclusion.

Investigations on the physiology of yield in the cereals show that tillering and head formation are influenced by competition for light, nutrients and soil moisture, and that these effects are in turn influenced by the density of sowing. However, the mode of action of these factors of the environment and their relative importance to each other need further clarification. Yield is a function of the number of ears per unit area and the grain yield per ear, and is therefore determined by the response to changes in density of tillering and head

formation. However, when the number of tillers per unit area is greatly increased both the proportion of fertile tillers and the size of the ears themselves diminish rapidly. The literature reviewed here indicates the factors involved in determination of these components of yield, but it is apparent that further investigations are warrented, particularly on the action of the mechanisms governing responses to the environment. The present study is an attempt to assess one aspect of these mechanisms, namely the influence of competition for light, induced by the presence of neighbours, on both tillering and head formation when the effects of root competition are held constant.

METHODS

I. Design of the experiment.

The aim of the experiment was to study the effects of competition between wheat plants sown at two densities, while eliminating the effects of root competition. This was done by growing the plants in plastic tubes, one inch in diameter and eighteen inches long; this enabled the plant spacing to be altered without varying the volume of soil available to each plant. The arrangement also allowed the plants to be moved from the high density treatment to low density at any stage of growth without disturbing the root system.

At planting the tubes were packed closely together so that all plants commenced growth under conditions of high density (plate 1) with 1150 plants per square metre. (This would approximate a seed rate of 360 lbs./acre). At regular intervals throughout the growing season, plants were removed from the high density population and spaced out at low density one foot apart (plate 2), thus effecting a transfer from conditions of intense competition above ground to conditions of negligible competition. There were ten occasions on which plants were removed from the high density to the low density and these are henceforth referred to as occasions of transfer (1-10) or as day of transfer (i.e. days from planting). Comparisons between these plants and those remaining at high density throughout their growth enabled a study of the response of the plants to improved light conditions after

Plate 1. View of high density treatments at day 9 showing the arrangement of tubes and early growth of the plants.

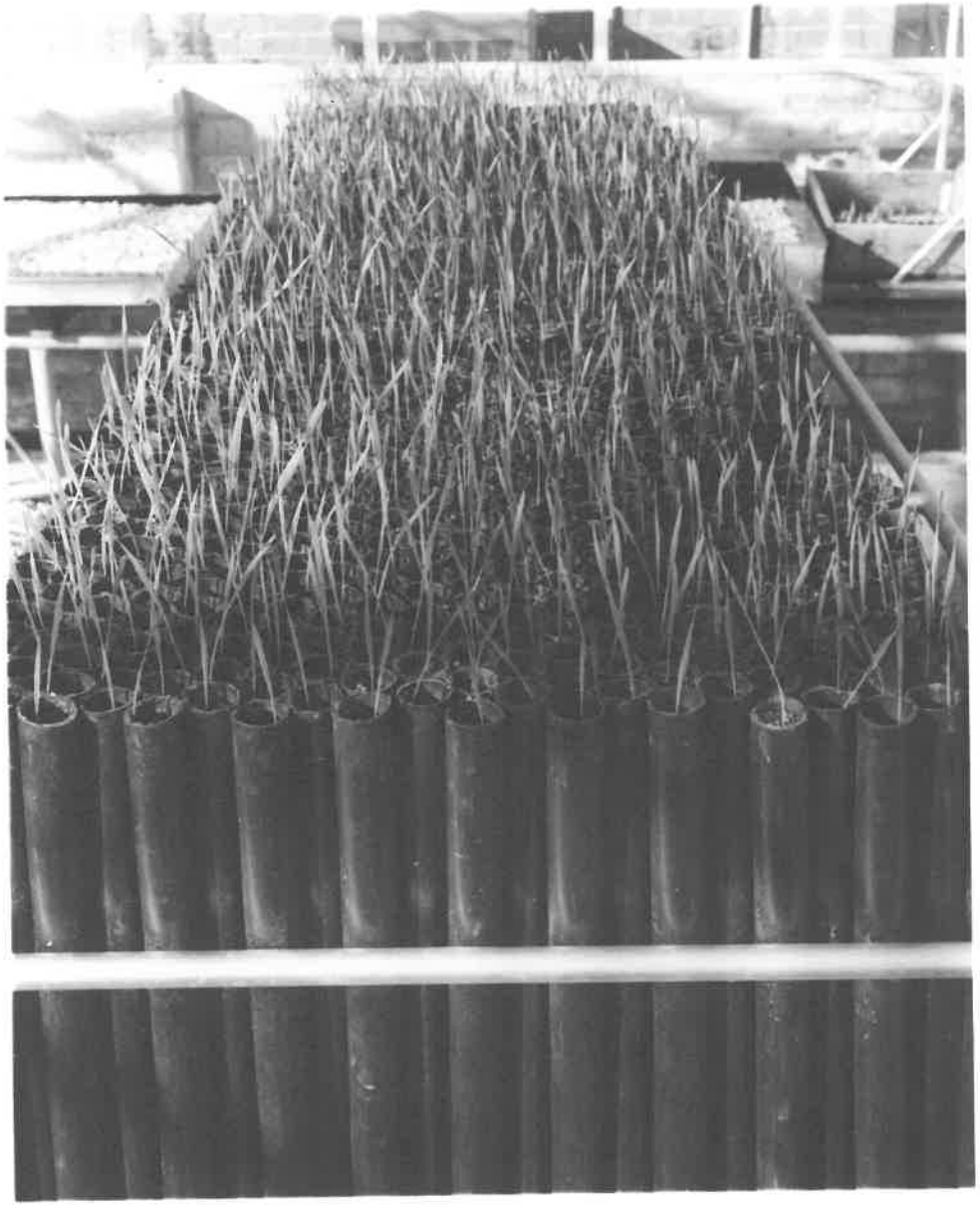


Plate 2. General view of low density plants. Positions for future occasions of transfer shown by numbered labels.

different initial periods of growth with intense competition. This procedure was repeated with low, medium and high levels of nitrogen (designated N_1, N_2, and N_3 respectively), thus giving in all: 2 densities x 3 levels of nitrogen x 10 occasions of transfer x 2 replicates.

Limitations of glasshouse space and equipment allowed only one replicate for the high density treatments and two replicates for the low density. However, the high density treatments were placed in a compact block 60 cm x 90 cm and over this small area the environment was uniform. Plants transferred from the high density to low density were divided at random between two blocks. These blocks were arranged, after measurements of light intensity in the glasshouse, to give the most uniform light environment within blocks and the greatest differences between blocks (Fig. 1).

II. Experimental technique.

(a) Preparation.

The tubes used as soil containers were made of high density black polythene water pipe of one inch internal diameter, eighteen inches long and closed at the bottom with terylene cloth. Two pilot trials had shown that wheat plants could be successfully grown in these containers.

In the main experiment the soil mixture consisted of:

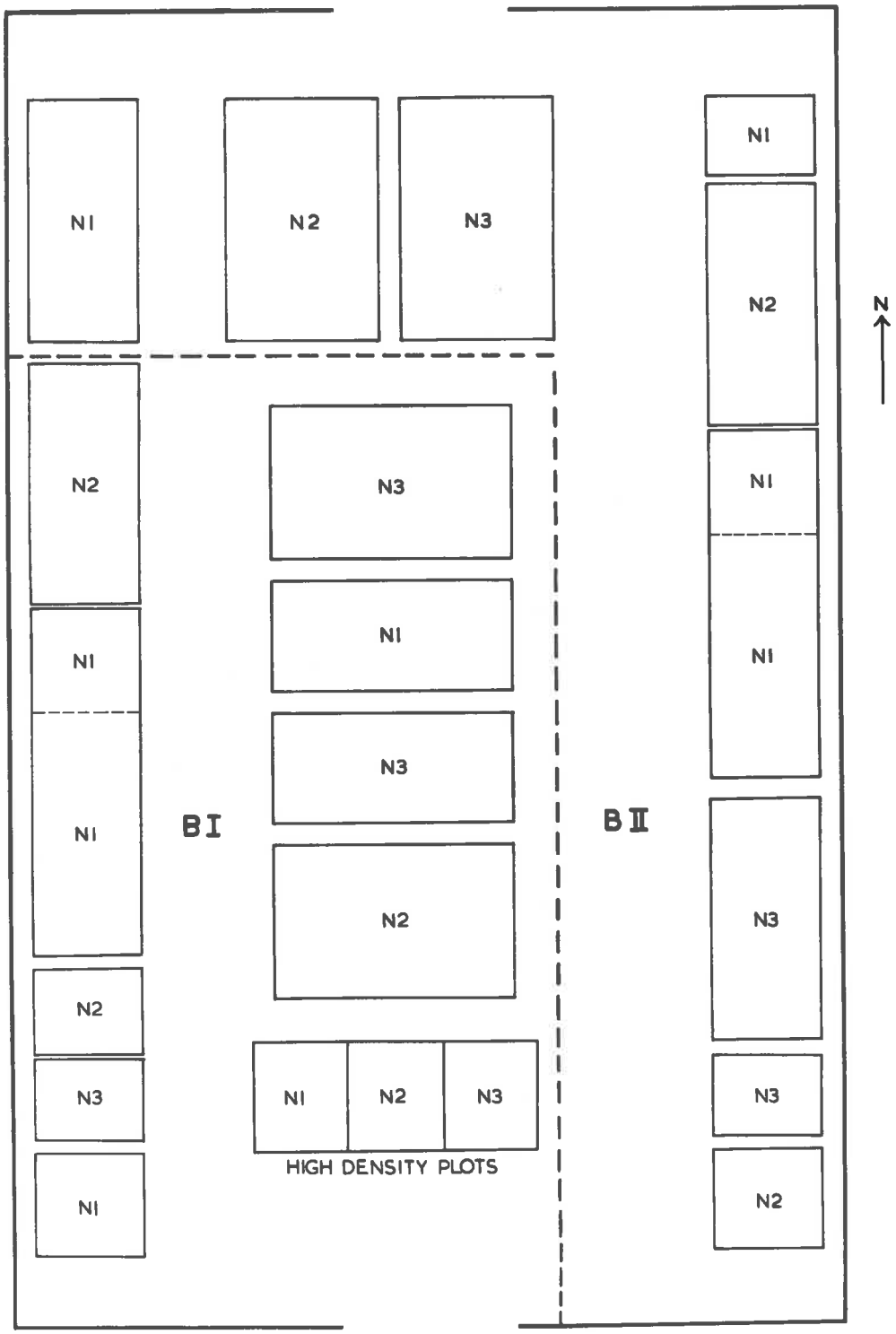
4 parts Urrbrae loam (a red-brown earth).

5 " Plympton sand (a red river sand).

2 " peat (imported from Germany).

4 " vermiculite.

Figure 1. Arrangement of blocks in the glasshouse and showing the position of the three high density plots.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HIGH DENSITY PLOTS
N1
N2
N3
N2
N

Plympton sand is very low in nitrogen and the Urrbrae loam used in this experiment showed a nitrate nitrogen content of 2-3 ppm. when tested by the brucine method of Peech and English (1944). An initially low nitrogen content was necessary in order to obtain adequate differences between nitrogen treatments. Vermiculite was added to improve aeration and water infiltration and the soil mixture thoroughly mixed by hand as well as through a mechanical sieve.

A basal fertilizer containing the elements in table 1 was dissolved in water and added to the soil during mixing. After addition of the basal fertilizer pH tests were taken and, after treating samples to determine the correct quantity, sufficient finely ground $CaCO_3$ was added to bring the soil mixture to pH 6.4. (330 g $CaCO_3$ per 75 gallons of soil mixture).

After addition of the basal fertilizer and lime the soil mixture was carefully divided into three portions for the addition of the three levels of nitrogen respectively in the form of ground hoof and horn which had been passed through a 35 mesh sieve. Owen, Winsor and Long (1953) using a wide range of samples, have shown that finely ground hoof and horn is a reasonably homogenous fertilizer and it was selected as the most suitable source of nitrogen for this experiment, where leaching and osmotic effects could have caused problems if mineral fertilizers only had been used. In addition to the hoof and horn, $Ca(NO_3)_2$ in solution was added to individual

plants of N_2 and N_3 one and four weeks after emergence. Thus the total nitrogen treatments were as shown in table 2.

Table 1.

Basal fertilizer mixture.

Element.	Equivalent of element in pounds per acre.*	Form applied	Quantity of compound as g per 75 gall. of soil mixture.
P	60	KH_2PO_4	21.0
K	73	"	-
Mg	20	$MgSO_4 \cdot 7H_2O$	17.25
S	26	"	-
S	30	$CaSO_4 \cdot 2H_2O$	10.62
Cu	1.78	$CuSO_4 \cdot 5H_2O$	0.575
Zn	1.57	$ZnSO_4 \cdot 7H_2O$	0.575
Bo	0.6	H_3BO_3	0.281
Mn	3.4	$MnSO_4 \cdot 4H_2O$	1.15
Mo	1.0	Ammonium molybdate.	0.066

* For high density.

Table 2.

Nitrogen added as fertilizer to treatments N_1, N_2 and N_3.

	mg. per tube			lbs. per acre*.		
	N_1	N_2	N_3	N_1	N_2	N_3
As hoof and horn at day 0.	Nil	3	15	Nil	30	150
As $Ca(NO_3)_2$ at day 11.	Nil	0.5	2	"	5	20
" " " " 41.	Nil	1.0	6	"	10	40
Total		4.5	21		45	210

* For high density.

Tests on the nitrate nitrogen level in the tubes were made at day 37, and the additional calcium nitrate at day 41 was provided on the results of this test which showed a very low nitrogen content in all tubes of 0 to 4 ppm. No further additions of nitrogen could be made after this time without changing the design of the experiment. Further reference to nitrogen status is made in discussion of the results.

As it was necessary to use damp soil to obtain a homogenous mixture, the soil was not weighed into the tubes but they were hand filled and shaken down systematically to give an equal volume of soil in each tube. Random weighing tests showed almost

negligible variation in weight of soil per tube. The soil in the tubes was then watered and allowed to stand overnight.

(b) Sowing.

Wheat (Triticum vulgare var. Gabo) seeds were graded for size, and after sprouting in a germination cabinet at 22°C, were sown in the tubes, one seed to a tube, and covered with a measured amount of soil. Four hundred tubes were sown for each nitrogen treatment. Measurement of the area occupied by these tubes showed an actual high density planting of 1150 plants per square metre. Six rows of plants were used as border rows on the northern side, the source of most of the direct light, with borders of three rows on the east and west and two on the southern side. Light measurements and comparison of plants at several stages throughout the growth period indicated that these borders were quite adequate.

Planting was carried out on 7 July (day 0) and the soil was kept moist until emergence. Most plants had emerged by 13 July (day 6). Extra seeds were sown in small paper tubes containing the different soil mixtures for use as transplants where necessary. Even though apparently identical to undisturbed plants, these transplants were used only for the outer border rows to prevent any growth check affecting later sampling.

(c) Procedure after planting and emergence.

The tubes were placed upright in bitumen painted galvanized trays on a two inch layer of washed gravel which was kept damp,

and were individually watered from the top of the tubes several times per week, depending on weather conditions and the needs of the plants. Excess requirements for water once the plants were well established were obtained by the roots growing through the terylene cloth into the wet gravel. The roots grew down into the gravel within three to four weeks of emergence and regular checks showed that the soil was maintained in a damp condition throughout the season. The tubes at low density were supported by wires stretched between supports as shown in Plate 2, and wrapped in aluminium foil to reduce heating of the soil within the tubes. As some of the trays were from a previous experiment there was a variation in tray size, but within each block each nitrogen treatment was allotted three trays, one large, one medium and one small, containing 24, 18 and 6 spaced plants respectively. These trays were arranged at random within the blocks and the positions for transfer were numbered systematically 1-24, 25-42 and 43-48. Using tables of random numbers (Fisher and Yates 1938), the plants were then allocated transfer and harvest positions at random.

The first occasion of transfer from high to low density was 19 July (day 12). The tubes comprising the southern border of the high density plots were set aside and then, after the required number of plants had been removed for transfer or harvesting, were moved up to the remaining tubes. The plants removed were taken at random from the rows closest to the southern border on each

occasion in order to avoid disturbing the roots of all the plants and to keep the environment as constant as possible. Table 3 gives the schedule of transfer and harvest throughout the growing period.

Table 3.

Summary of transfer and harvest data. Repeated for 2 replicates x 3 nitrogen treatments. Days are numbered from the sowing date.

Date	Day	No. of plants transferred to low density.	Days from sowing to harvests of the transferred plants.
7 Jul.	0	(sowing).	
13 "	6	(emergence).	
19 "	12	10	24, 38, 52, 66, 80, 87, 109, 135.
31 "	24	9	38, 52, 66, 80, 87, 109, 135.
14 Aug.	38	8	52, 66, 80, 87, 109, 135.
21 "	45	7	66, 80, 87, 109, 135.
28 "	52	7	80, 87, 109, 135.
4 Sep.	59	6	87, 109, 135.
11 "	66	6	87, 109, 135.
18 "	73	5	109, 135.
25 "	80	5	109, 135.
9 Oct.	94	4	135.

For the first few weeks the plants were dusted regularly with sulphur to control mildew and fans were set up near the high density plants to keep the air moving. These precautions were entirely successful in controlling mildew and no form of disease was observed.

(d) Light measurements.

Light measurements were taken at the base of the high density plants on four occasions commencing 8 August, 26 days after emergence (day 6). Readings of light intensity relative to full daylight were taken using a small selenium cell (4 cm x 1.5 cm) mounted on a probe and connected to a micro-ammeter (Barrowman 1956). Readings were taken on only four occasions as despite the small size of the probe and careful use, damage and displacement of the closely spaced plants was occurring.

(e) Air temperatures.

Measurements of air temperature were made using two maximum and minimum thermometers, one near each end of the glasshouse.

III. Collection of data.

(a) Dates of harvest.

Eight harvests were made during the period of the experiment as shown in table 4.

Table 4.

Dates of harvest and growth stages at harvests.

Date of harvest.	Days from sowing.	Stage of growth.
31 July	24	2 leaves.
14 August	38	4-5 leaves.
28 August	52	Tillering.
11 September	66	Jointing.
25 September	80	Headed; pre-anthesis.
2 October	87	Anthesis.
24 October	109	Early dough.
19 November	135	Maturity.

(b) Sampling methods.

At each of the harvests prior to anthesis, and for the harvest on day 109, one plant for each transfer occasion was taken from a preselected random position from each replicate. At the anthesis and maturity harvests two plants instead of one were taken from each replicate. For example at the second harvest (day 38) the plants harvested included plants which had been transferred from high density to low density on day 12 and day 24, to give 12 plants for the harvest (2 transfer occasions x 3 nitrogen treatments x 2 replicates). For the day 52 harvest there were three occasions of transfer and therefore 18 plants were harvested, with increases in number of harvested plants at each succeeding harvest.

On day 135 the harvest was 120 plants (10 transfer occasions x 3 x 2 x 2 reps.).

In addition to the plants harvested from the low density, six plants were harvested from each of the three high density plots at the same time.

(c) Supplementary data.

In addition to the data obtained from the harvested plants, measurements of leaf length and breadth, tiller number and stem heights were made on the intact plants for all low density plants at each of the first four harvests. This information supplemented that from the harvested plants and provided a fuller picture of the effects of the treatments while the plants were small and only a few sampled at each harvest.

(d) Harvest procedure.

The plants were cut off at ground level, placed in labelled bags and taken to the laboratory where the following measurements were made.

1. Stem height from ground level to the base of the top leaf or to the base of the ear after ear emergence.
2. Mean diameter of the stem.
3. Length and breadth of the green leaves.
4. Leaf numbers. The leaves were divided into three categories and the numbers recorded for each tiller as:-
   (i) Green; this included all leaves apparently photosynthetically active.

(ii) Senescent; consisting of leaves which were apparently degenerating, with more than half the leaf blade brown, or which were losing their green colour.

(iii) Dead; those leaves with most of the leaf blade brown and dying.

5. Leaf area. The leaf area of all plants measured, including those measured on the intact plants, was estimated from the length and breadth measurements. Regression coefficients were calculated after measuring the area of leaves from harvested plants on the airflow planimeter (Jenkins 1959) and on two occasions checking these areas with blueprints and a mechanical planimeter. The regressions obtained are listed below with the leaves numbered in order of appearence on the main stem. The data for leaves 4 and 5 were combined to reduce variability.

Owing to the small amount of leaf material available at any harvest the measurements were variable and not very reliable for leaves 1, 2 and 3. However, as the absolute leaf area was not essential in this study it is felt that the results obtained were adequate for the purpose of comparison made.

6. Development of the apex. The apices were dissected under the binocular microscope and the following observations made:

(i) Number of fully expanded leaves.

(ii) Number of expanding leaves.

(iii) Length of the shoot apex.

(iv) Number of primordia on the apex.

Table 5.

Regression analyses of leaf area on length x breadth.

Leaf No.	Sx^2.	Sy^2.	Sxy.	Reg. Coeff.	S.E.	df.
1.	17.93	22.92	11.85	0.661	0.131	50
2.	108.02	76.53	67.30	0.623	0.080	51
3.	619.86	439.73	455.50	0.735	0.061	47
4. & 5.	4602.4	2535.7	3337.6	0.725	0.017	85
6.	4538.4	2446.9	3273.1	0.721	0.018	58
7.	5940.1	3586.2	4509.9	0.759	0.018	71
8.	1993.0	1184.3	1507.4	0.756	0.026	33

These classifications were made on the basis of those by Cooper (1956). At the time of harvest only the first two observations were made and the apices then preserved in 70% alcohol, after hardening in formal-acetic-alcohol, for later investigation. The apex was also classified as to stage of development on the basis of the photographic classification of Khalil (1956).

7. Dimensions of the ear. The following measurements were made of ear size:

(i) Total length of head, excluding the awns.

(ii) Width across the widest spikelet.

(iii) Number of spikelets per ear classified as:-

a. total

b. undeveloped; referred to as sterile.

c. fully developed; referred to as fertile.

(iv) Number of grains per ear.

8. Dry weights were obtained for all material except apices after drying the samples in a forced draught oven at 90°C for 22 hours.

9. From the basic data outlined above, the derived data given in the results were calculated. The nature of the experiment and the type of measurements meant that some of the above classifications were necessarily arbitary and there is therefore the possibility of subjective bias. However, the results were reasonably consistent.

(e) Plant nitrogen determinations.

Nitrogen percentages of the plant material were determined by a modified Kjeldahl technique (A.C. Jennings 1962, pers. comm) in which ½ g of the ground plant material was digested with 4 ml of concentrated sulphuric acid and 1½ g of a mixed catalyst (20 gm potassium sulphate : 1 gm mercuric oxide) in a 100 ml flask. The digest was then transferred to a steam distillation apparatus with 20-30 ml of distilled water and 12 ml of 2.5 % sodium thiosulphate in 40 % caustic soda. The ammonia distilled over was collected in 2 % boric acid and titrated with 0.1 % HCl. This method gave consistent results and enabled the completion of 50-60 determinations per day.

(f) Total soil nitrogen.

This was determined by a modified Kjeldahl technique using 2 g samples and steam distillation. The ammonia distilled over was collected in 1 % boric acid and titrated with 0.01 N potassium bi-iodate solution (Jennings 1962, pers. comm.).

RESULTS

I. A general account of the results.

Throughout the experiment the plants transferred at the earlier occasions attained greater dry weights than those remaining at high density for longer periods. This increased production of the earlier transferred plants was also shown by increased tiller number, increased ear size and greater yield of grain per ear and per plant. However, although the growth of the high density treatments on an area basis was excellent, as shown by plate 3, the response of the individual plants to diminished competition when removed from high density to low density was slight, as shown by plates 4 and 5. Consideration of the various factors involved suggests that an inadequate nutrient supply, particularly of nitrogen, was responsible for the poor response to decreased density.

The calculation of the rates of fertilizer given in table 3 was based on the area available to the plants of the high density treatment and though satisfactory at high density, they proved inadequate at low density. That these rates of fertilizer were adequate for the high density is clearly shown by the vigorous growth and the very high dry weights obtained (3,000 gm/m^2 for N_3 = 8. 27,000 lbs./ac.). However, each plant of N_3 received only 21 mg of nitrogen as fertilizer. N_1 (with no added nitrogen) showed a maximum uptake of 27 mg of nitrogen per plant (for these plants at wide spacing throughout), whereas N_3 plants under the

Plate 3. View of the high density treatments at day 72, N_3 on left and N_1 on the right. The low hessian screen was used to reduce side-illumination at the base of the plants.

Plate 4. Plants of N_3 photographed at day 82. These plants were transferred to low density at days 12, 24, 38, 66 and 80 (left to right). Dead leaves were removed.

Plate 5. Plants photographed at day 62. N_1, N_2 and N_3 (left to right).

Above. Plants transferred at day 52.

Below. Plants transferred at day 12.

Dead leaves were removed in both cases.

same conditions yielded a maximum of 56 mg. It is thus evident that the plants at low density throughout made almost maximum utilisation of the available nitrogen and consequently the yield of dry matter per plant at low density was the most that could be expected.

At the time of application of the nitrogen fertilizer it was felt that greater application than that given would possibly result in deleterious effects on the plants and that the differences between nitrogen treatments would possibly not be clearly defined. In the pilot trial, using John Innes compost as the basic soil mixture, it was not possible to observe differences with additional nitrogen. However, although the fertilizer nitrogen added to the N_3 plots was equivalent to that in the John Innes mixture a different loam was used with a lower nitrogen status. From the results obtained it seems probable that the application of hoof and horn could have been much greater, perhaps 4 to 5 times that used. On the other hand, the second application of calcium nitrate resulted in wilting of the lower leaves and it would be unwise to increase applications of this form of nitrogen unless in regular small amounts.

The major effect of this apparent lack of nitrogen, apart from the effect on total dry weight, was on tillering which was severely reduced. However, the fact that many of the plants had only one stem enabled a closer study of the effect of density on head formation without the complication of varying number of tillers per plant.

II. The environment.

(a) Temperature.

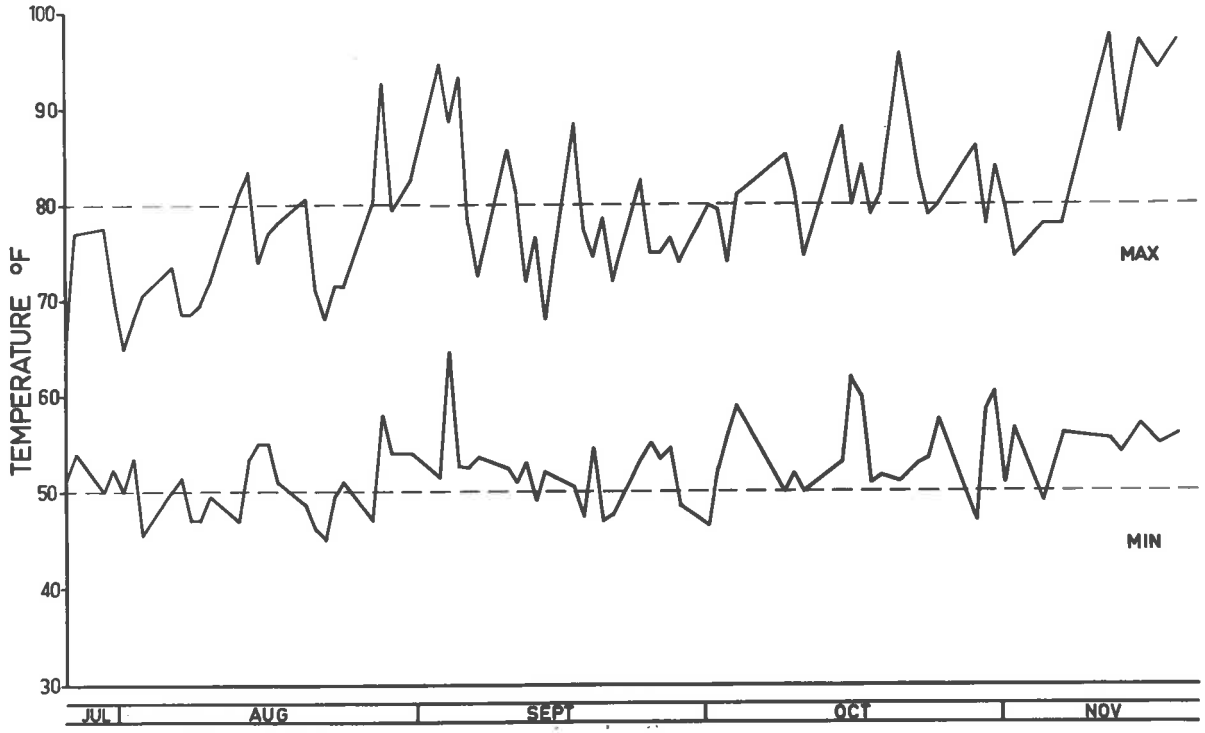
It is possible that the reduction in tiller number ascribed to low nitrogen supply was accentuated by the temperature as the rate of development of the plants was very rapid, with ear emergence occurring only ten weeks after sowing.

(1) Air temperature. Measurements of air temperature were made using two minimum and maximum thermometers. Variation between the two positions in the glasshouse was negligible and the mean of these two readings is shown in fig. 2. Readings were taken at daily interval on week days only, but the longer interval at the week ends does not affect the general picture.

The thermometers were not available until 18 days after planting, but examination of the meteorological records showed that the mean maximum air temperatures in the open were 3.1° F higher for July 7-26 than for the 18 days July 26-August 13, with the mean minimum 0.8° higher. Thus the temperatures in the glasshouse were probably slightly higher for the 18 days before temperature measurements were begun than for the initial period shown in fig. 2.

Adequate ventilation of the glasshouse was difficult until coolers were installed on 13 September, with the result that temperatures rose sharply with hot weather from 28 August to 4 September. The installation of the coolers enabled the air temperature to be maintained thereafter at a reasonable level except for a few very hot days.

Figure 2. Maximum and minimum temperatures in the glass-house from day 18 to completion of the experiment.


100
90
80
70
60
50
40
30
TEMPERATURE °F
MAX
MIN
JUL
AUG
SEPT
OCT
NOV

(2) Soil temperature. The small volume of soil in the tubes meant that they were subject to rapid fluctuations in temperature, particularly when in direct sunshine. Therefore, when the plants were transferred to low density the tubes were wrapped in tarred paper coated with aluminium foil. Measurements of soil temperature which were made with thermometers placed in the soil of plants set up for the purpose showed that the foil wrapping reduced the temperature by approximately ten degrees Centigrade in comparison with black unwrapped tubes. Mean temperatures for four periods are shown in table 6. Measurements were taken at 9 a.m. and at 2 p.m. which was usually the hottest period of the day in the glasshouse.

Table 6.

Mean soil and air temperatures at 2 p.m. ^{o} C.

Period of measurement.	Soil			Air.
	Low density		High density.	
	Foil.	Black.		
Sept. 5-16.	23.1	33.1		19.3
Sept. 17-25.	22.3	31.9		20.0
Oct. 21-31.	25.9	35.0	18.8	23.7
Nov. 7-14.	28.3	36.2	20.3	25.8

Air temperatures at 9 a.m. were 5 to 9 degrees lower than those at 2 p.m. and the temperature in the foil wrapped tubes (i.e. all low density tubes) was within half a degree of the air temperature. The soil temperature was considerably lower in the high density tubes than in those at low density as the foliage prevented direct sunshine from reaching the tubes.

As far as can be ascertained the differences in soil temperature between high and low density plants do not seem to have affected plant or root growth. Khalil (1956) found that the roots of plants grown at relatively high temperatures within the range of 10 to 30° C were proportionately weak compared with roots produced at lower temperatures, but this effect was not apparent here. With the high density plants only a few fine roots grew out through the terylene cloth at the base of the tubes and these increased in number and thickness after the plants were transferred to low density. The high temperatures shown in table 6 occurred for only a short period during the day.

(b) Light intensity.

Light measurements were taken at the base of the high density plants on four occasions commencing 8 August, 26 days after emergence. The mean values for the three nitrogen treatments are shown in table 7.

Plate 6. Root development of plants at day 88. Plants transferred to low density at day 12. N_1, N_2 and N_3 (left to right).

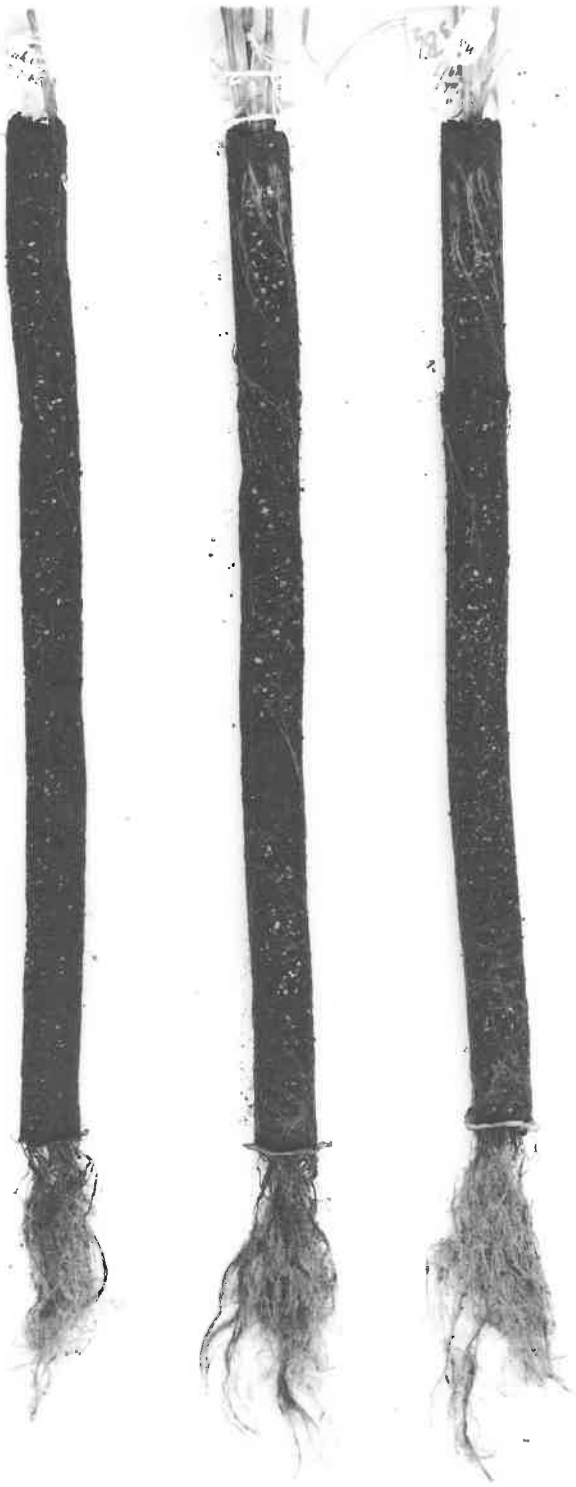


Table 7.

Light intensity (as percent full daylight) at the base of the high density plants.

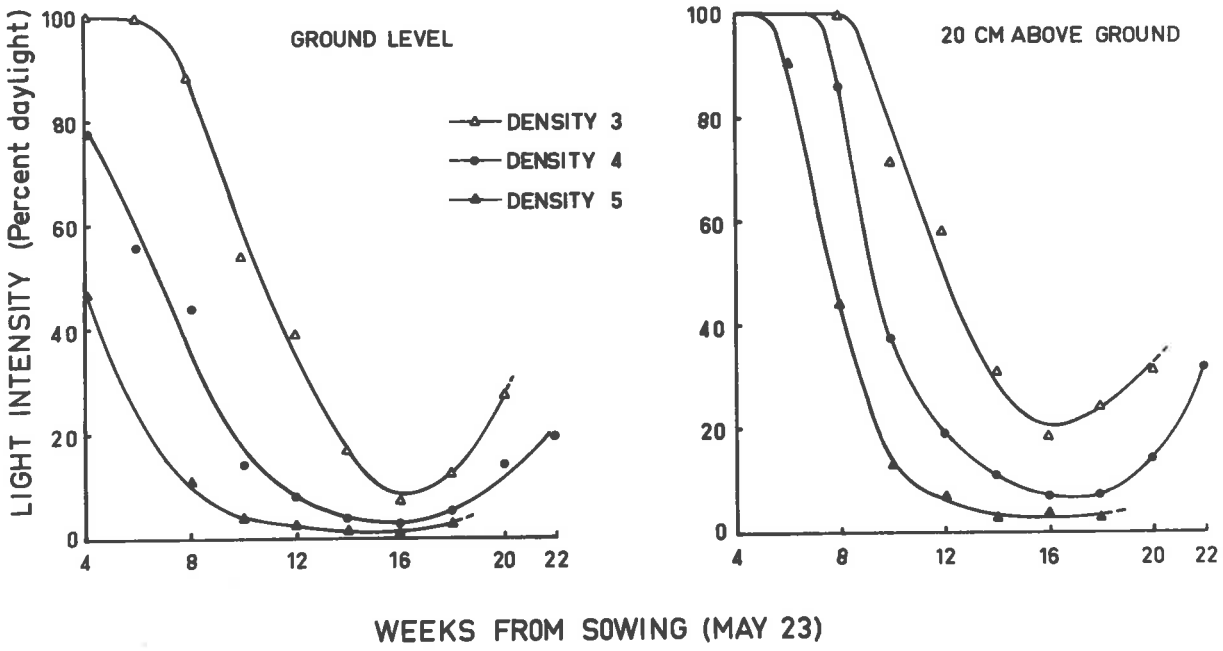
Date.	Days from sowing.	Treatment		
		N_1	N_2	N_3
Aug. 8	31	27.5	20.0	17.5
Aug. 16	39	17.4	12.3	10.3
Aug. 30	53	16.9	10.6	6.9
Sept. 19	73	19.5	15.4	7.5

The mean for each date is the mean of 16 measurements for each nitrogen treatment; the area of each plot was approximately 0.36 m^2. There was a slightly higher light intensity near the northern edge of the plots, but the variation was small in the area within the border rows. The results agree with those obtained in the field and shown in fig. 3 (reproduced from Puckridge 1962). The increased values for September 19 in table 7 resulted from the death of the lower leaves after ear emergence.

III. Plant measurements.

Abbreviated tables and/or graphs are presented in the text. The majority of the analyses were carried out by an electronic computer and the full tables of means, treatment means and analyses are given in the appendix.

Figure 3. Changes in light intensity with time at two levels within the crop for wheat plants grown in the field. Density 3 was 35, density 4 was 175 and density 5 was 875 plants/m^2 (from Puckridge 1962).


GROUND LEVEL
20 CM ABOVE GROUND
DENSITY 3
DENSITY 4
DENSITY 5
LIGHT INTENSITY (Percent daylight)
100
80
60
40
20
0
4
8
12
16
20
22
WEEKS FROM SOWING (MAY 23)

(a) Dry weight per plant.

The mean dry weight per plant is shown in fig. 4. There were no differences between treatments at day 24 when the mean weight per plant was 0.06 gm. However, by day 38 the differences between nitrogen treatments were quite marked, but not between transfer occasions. The mean dry weights for day 38 were:

N_1	N_2	N_3	
0.15	0.17	0.25	gm

From day 38 differences between treatments became more pronounced and at day 52 the mean differences between transfer occasions was significant at the 1 % level. A characteristic pattern was developed for the remaining harvests in which the plants at low density throughout their growth reached the greatest dry weight. There was then a sharp decline in dry weight at any one harvest with succeeding transfers to low density. The differences were less pronounced between plants transferred after day 66 and at the final harvest there were no significant differences in weight between plants transferred at day 66 and later. Plants transferred to low density at day 12 reached final weights of 1½ to 2 times that of those remaining at high density throughout. Mean dry weights and significant differences are given in the appendix tables.

(b) Dry weight per m^2.

The production of dry matter by plants grown continuously at high density is shown in fig. 5. The curve was exponential in

Figure 4. Mean dry weights per plant for seven harvests. The subscript L shows plants which were at low density throughout the period from day 12 to harvest and H plants which were at high density throughout the same period.

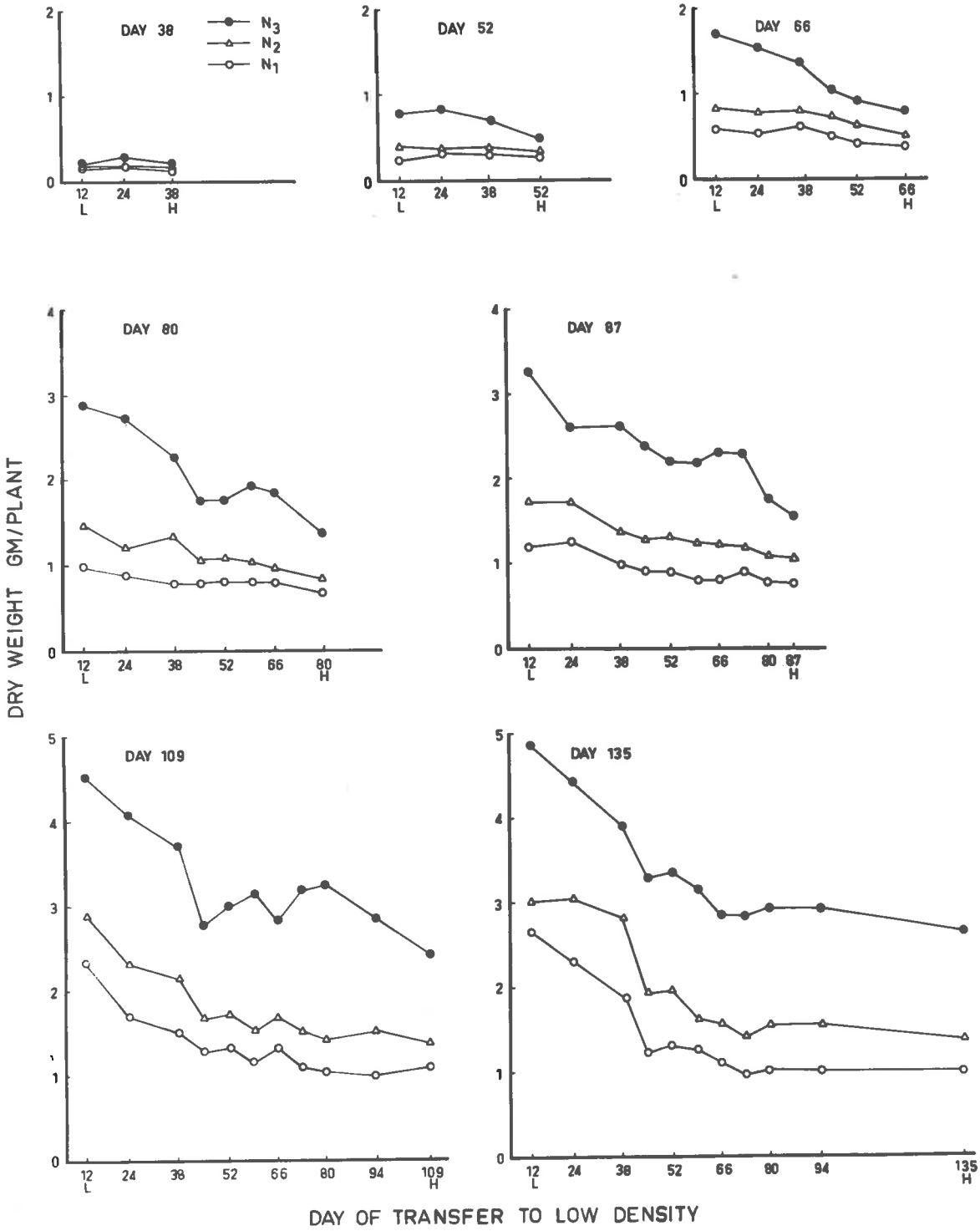
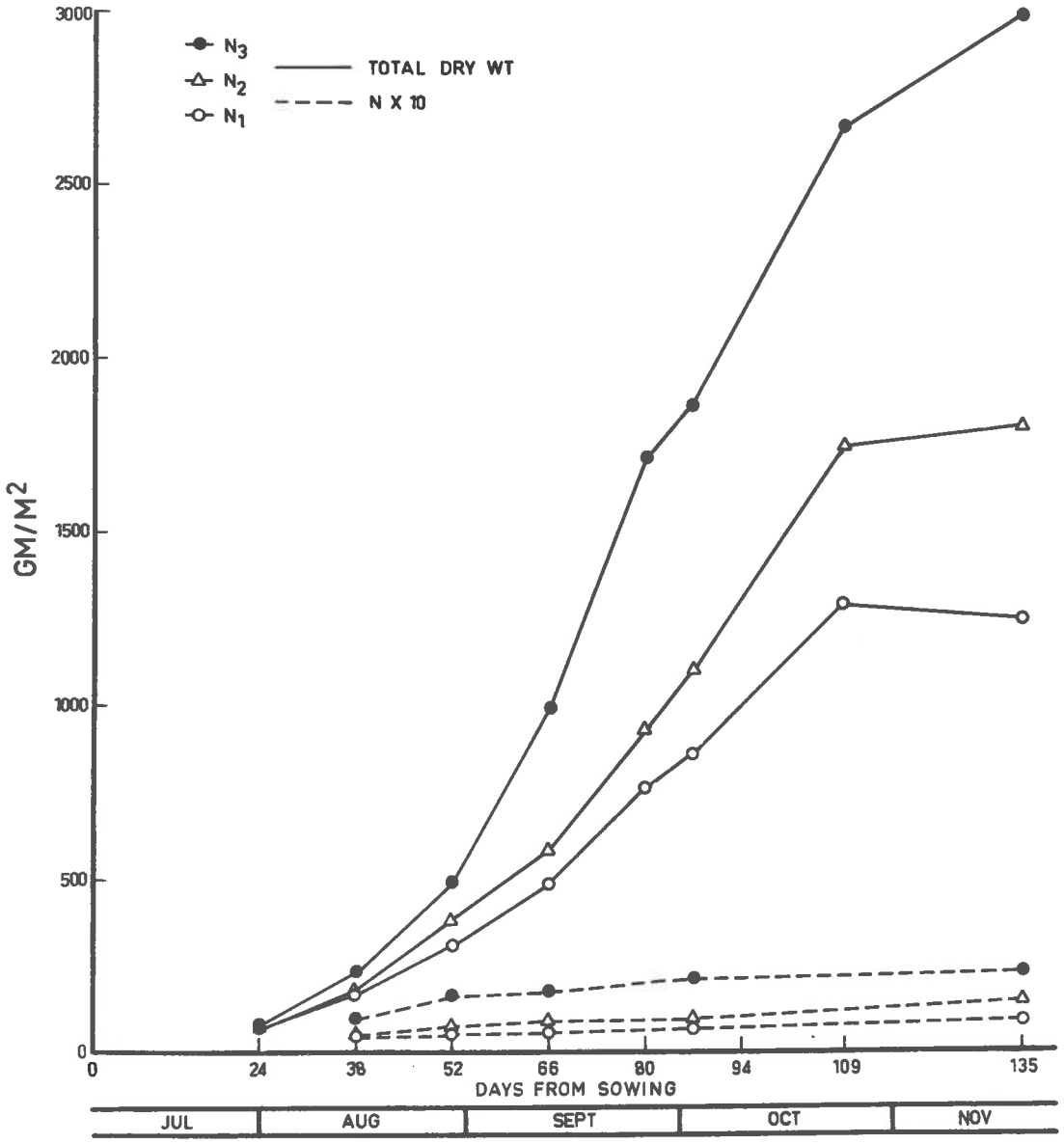

DAY 38
DAY 52
DAY 66
DAY 80
DAY 87
DAY 109
DAY 135
N_3
N_2
N_1
DRY WEIGHT GM/PLANT
DAY OF TRANSFER TO LOW DENSITY

Figure 5. Changes in total dry weight per square metre of the high density plants throughout the growing period.


3000
2500
2000
1500
1000
500
0
GM/M2
N3
N2
N1
TOTAL DRY WT
N X 10
0
24
38
52
66
80
94
109
135
DAYS FROM SOWING
JUL
AUG
SEPT
OCT
NOV

form until day 80, after which the rate of growth fell off slightly until day 109. From day 109 there was a slight fall in dry weight of N_1 and only a very slight increase by N_2. However, during the same period there was an increase of 12½ % in the dry weight of the plants of N_3.

The dry weights shown on the graph indicate the high level of production obtained. At the final harvest treatment N_3 produced 3,000 gm of dry material per square metre, which is equivalent to 11.8 tons per acre. This is a very high level of production for a wheat crop. However, because of the height and density of the foliage it was necessary to support the plants at two levels by thin wires passed between them. This mechanical support, in addition to the high nutrient level and continuous supply of water, may partially account for the high yield compared with field crops.

The production of grain by the high density plots was also high as shown by table 8.

Table 8.

Dry weight of grain produced by the high density plots with 1150 plants per square metre.

	N_1	N_2	N_3
gm/m²	400	630	1170
Equiv. as bush./ac.	59	94	174
Grain/total dry weight	0.317	0.350	0.390

(c) Tillers per plant.

As pointed out in section I the tillering of the plants was less than expected. The mean number of tillers per plant for those plants transferred from high to low density on the first two occasions is given in table 9.

Table 9.

Mean number of tillers per plant.

Day of transfer to low density.	N_1	N_2	N_3
12	1.16	2.16	2.84
24	1.25	1.75	3.00

All plants which were transferred on subsequent occasions had only one stem per plant (plate 4) with the exception of a few small tillers which died soon after appearance. The majority of these late formed tillers appeared after ear emergence on the main stem. The low tiller number prevented further analysis of the size of tillers in relation to leaf area and leaf number per tiller except for the main stem.

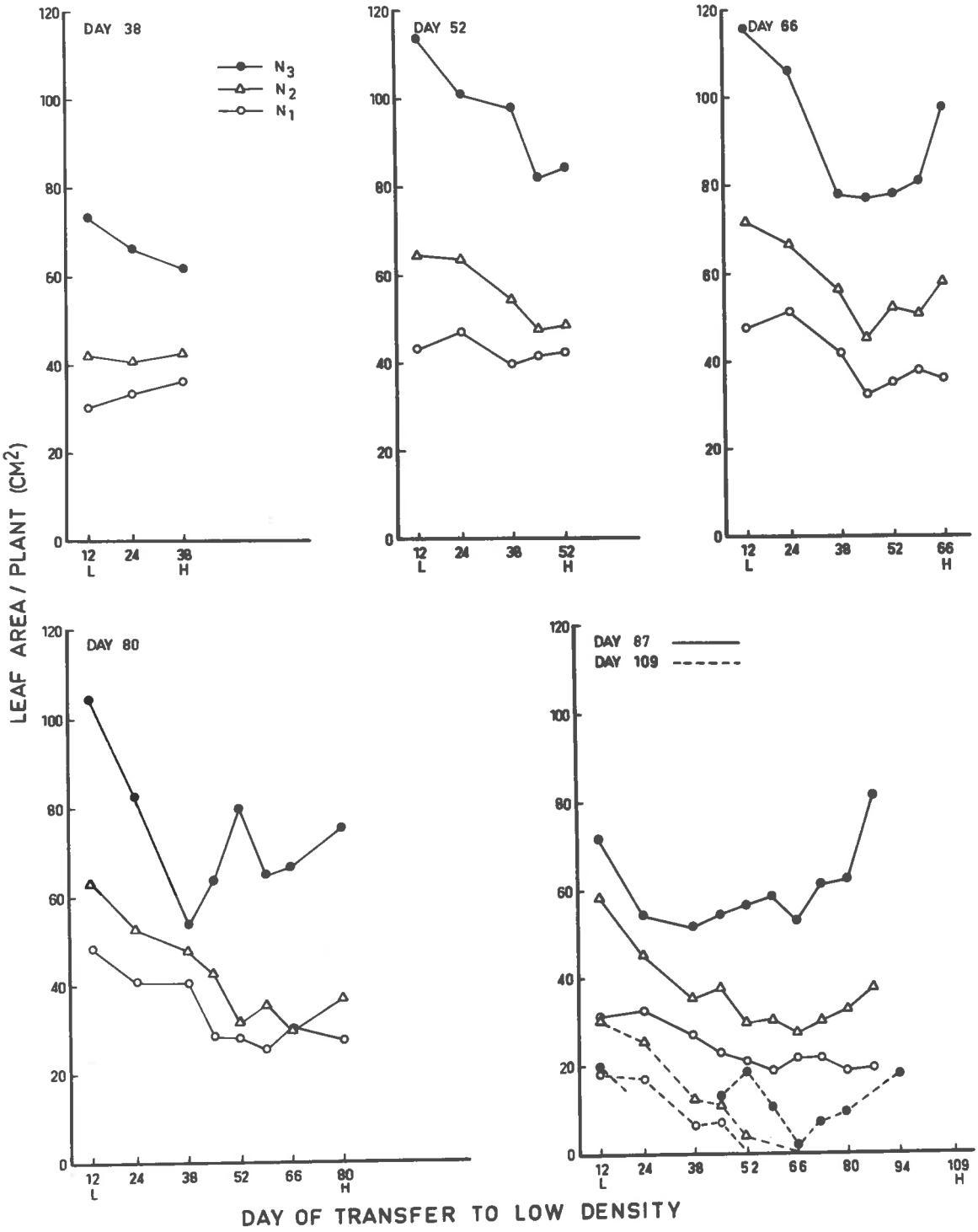
(d) Leaf area per plant.

Measurement of the leaves of 60 plants at the first occasion of transfer on day 12 showed no significant differences between nitrogen treatments at this stage, although the mean for N_3 was

slightly higher at 3.56 cm^2 per plant than N_1 and N_2 with means of 3.16 and 3.18 cm^2 respectively. By day 24 the differences were significant at the 1% level and are shown with later measurements in fig. 6.

The differences between days of transfer to low density were not significant until day 52, but it is of interest to examine the behaviour within treatments for the earlier measurements, particularly as the nitrogen x time of transfer interaction was significant at the 0.1 % level at day 38. The increase in leaf area of the earlier transferred plants of N_3 and N_2 was mainly due to increase in tiller number, but among those plants with one tiller, notably N_1 plants, there was an increase in leaf area of the plants which had remained longer under conditions of high density. This may have been the result of increased area per leaf due to the influence of low light conditions, but calculations of area per leaf did not give significant differences at this stage. At later harvests plants currently transferred from high density consistently showed higher leaf areas than those transferred in the preceding few weeks. This appears to have been due to rapid deterioration of the lower leaves when the plants were transferred to higher light intensity. As shown by Wasserman (pers. comm.) this is possibly due to accelerated growth with better light and hence more stress on N supply, drainage of N from lower leaves and death thereof. The leaf area/leaf weight ratio was much greater for the leaves of plants in high density and these

Figure 6. Leaf area per plant for six dates. Subscript L denotes plants which remained at low density from day 12 to day of measurement and H plants which remained at high density throughout the same period.


DAY 38
DAY 52
DAY 66
DAY 80
DAY 87
DAY 109
N3
N2
N1
LEAF AREA / PLANT (CM2)
DAY OF TRANSFER TO LOW DENSITY
12 L
24
38
52
66
80
94
109 H

leaves remained green longer when sheltered from the direct rays of the sun. By day 109 the leaf area was rapidly diminishing and variable as shown in fig. 6 (dashed lines of the last graph).

(e) Leaf area index.

The variation in leaf area during the growing period can be seen in fig. 7 which gives the L.A.I. of the high density treatments. The curves for these treatments show the high leaf area attained by N_3 compared with the other two treatments. As well as reaching higher maximum values of L.A.I., the values at day 109 show that senescence was delayed with the higher rates of nitrogen. Comparison with the dry weight curves of fig. 5 show that this delayed leaf senescence was associated with continued production of dry matter after day 109 by N_3 whereas with N_1 there was a slight decrease in dry weight during the same period.

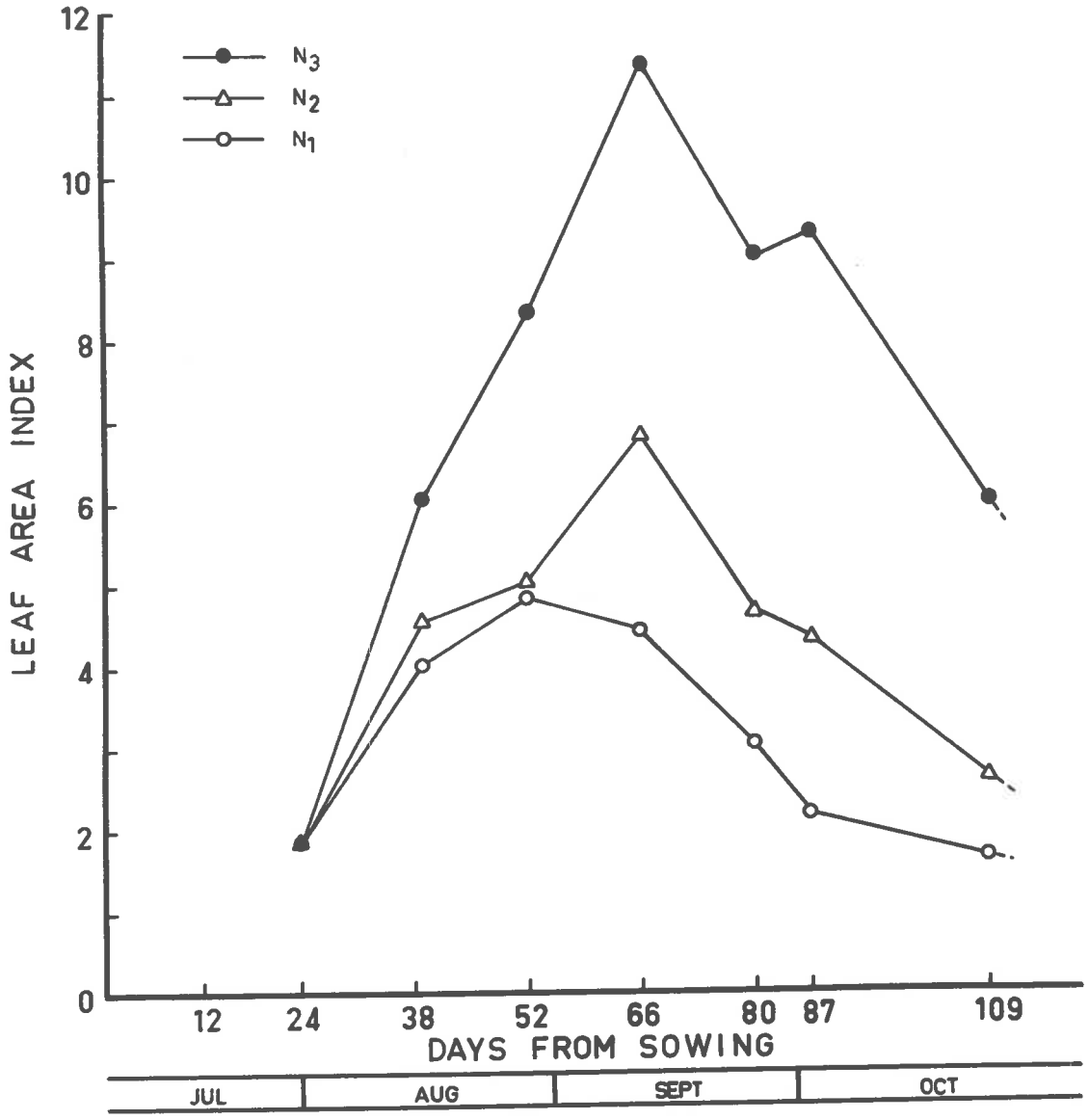
(f) Leaf numbers and leaf appearance rate.

Owing to the small amount of tillering the total number of leaves per plant is of little interest and only the mean number of leaves on the main stem is presented. There was no effect of density on the number of leaves produced by the main stem but nitrogen had some effect. The mean number of leaves for each of the three nitrogen treatments was:

N_1	N_2	N_3
7.19	7.49	7.83

Records were kept of the date of leaf appearance but it was not possible to differentiate between treatments. The mean dates

Figure 7. Changes in leaf area index of the plants at high density throughout the growing period.


12
10
8
6
4
2
0
LEAF AREA INDEX
N3
N2
N1
12
24
38
52
66
80
87
109
DAYS FROM SOWING
JUL
AUG
SEPT
OCT

at which the leaves were visible above the sheath are given in table 10 for leaves 1-7 on the main stem. Leaf 8 did not develop for all plants and is not included in the table. The variation from the mean date is also given.

Table 10.

Mean date of leaf appearance above the sheath.

Leaf No.	Date.	Days from sowing.	Variation (days).
1	Emergence	5	
2	July 16	9	
3	July 25	18	
4	Aug. 2	26	± 1
5	Aug. 11	35	± 2
6	Aug. 21	45	± 2½
7	Aug. 30	54	± 3

Dissection of the plants under the microscope showed that leaf 6 commenced growth at approximately day 20. On day 24, leaf 7 was partially or completely covering the apex; it appeared on day 54. Thus a considerable period of time elapsed between commencement of growth of the leaf and its appearance. However expansion was rapid and full size was normally attained by the next harvest after the leaf was first visible, i.e. within 14 days.

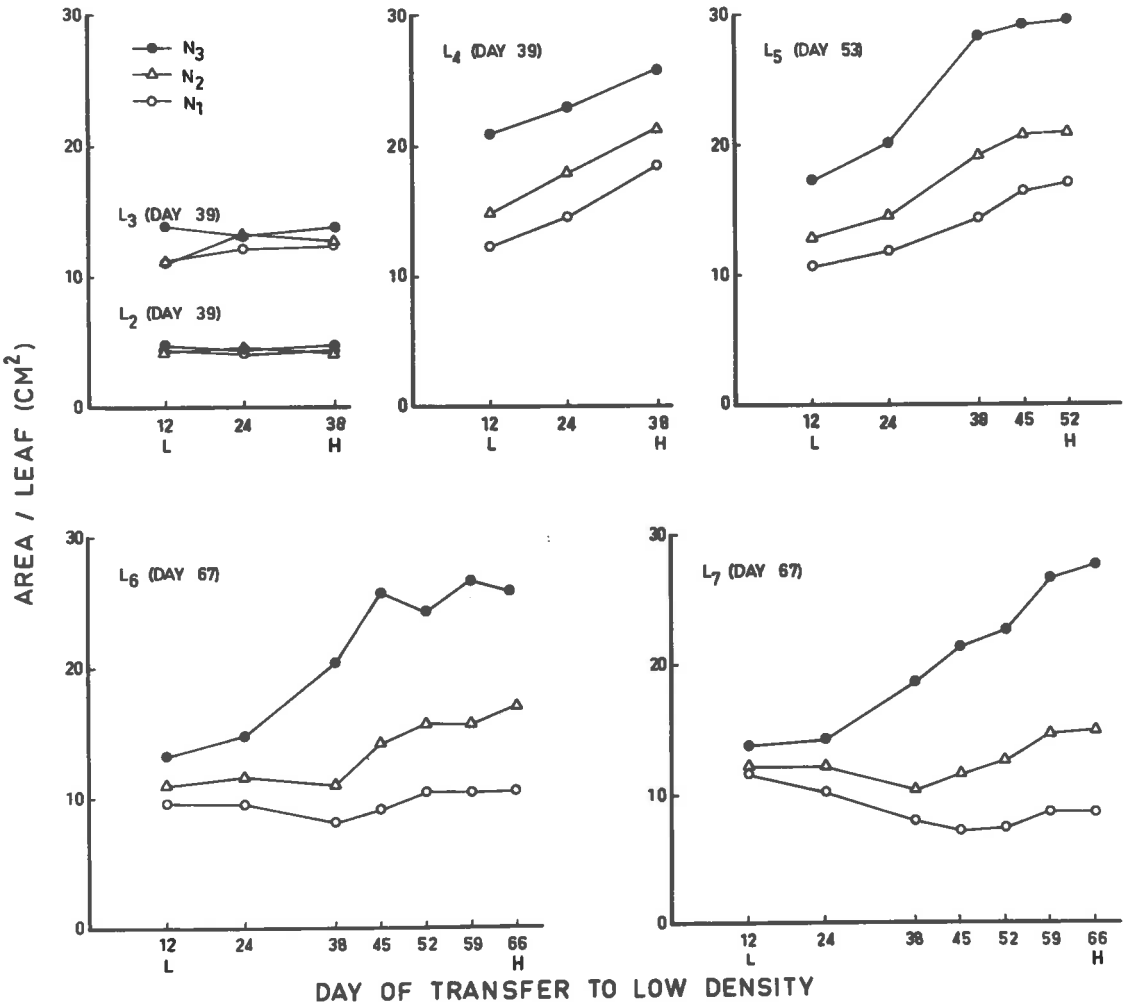
(g) Area of the individual leaves.

The mean areas per leaf for leaves 1 to 7 are shown in fig. 8 and clearly illustrate the response to high density conditions by the increased area of the leaves of later transferred plants. The values for leaf area were calculated from measurements taken after the leaves were fully expanded but before senescence commenced. It was not possible to follow the changes for many occasions of transfer with the first four leaves as they were dead or senescent by day 52.

With the later formed leaves, 5-7, the differences between leaves of plants transferred before day 24 and between those of plants transferred late was small, but for plants transferred in the intermediate period the change in area of the particular leaf with transfer occasion was considerable. This showed up particularly with N_3. Nitrogen had a considerable effect in increasing the area of the leaves and its effect was first evident with the second leaf.

It was not possible to determine from the data whether the effect of density was due to change in cell number or the degree of expansion of the cells. Friend et al. (1962 b) found by examination of the number of cells across and along the lamina that the effect of temperature and light intensity on leaf shape is primarily caused by differences in cell size rather than by changes in the number of cells present. However, taking leaf 7 of N_3 in fig. 8 as an example, it was partially or wholly covering

Figure 8. Mean area of the individual leaves. Leaves numbered in order of appearance on the main stem. The L under day 12 shows plants which remained at low density from day 12 until harvest, H shows plants which remained at high density throughout the same period.


AREA / LEAF (CM²)
N3
N2
N1
L3 (DAY 39)
L2 (DAY 39)
L4 (DAY 39)
L5 (DAY 53)
L6 (DAY 67)
L7 (DAY 67)
30
20
10
0
12
24
38
45
52
59
66
L
H
DAY OF TRANSFER TO LOW DENSITY

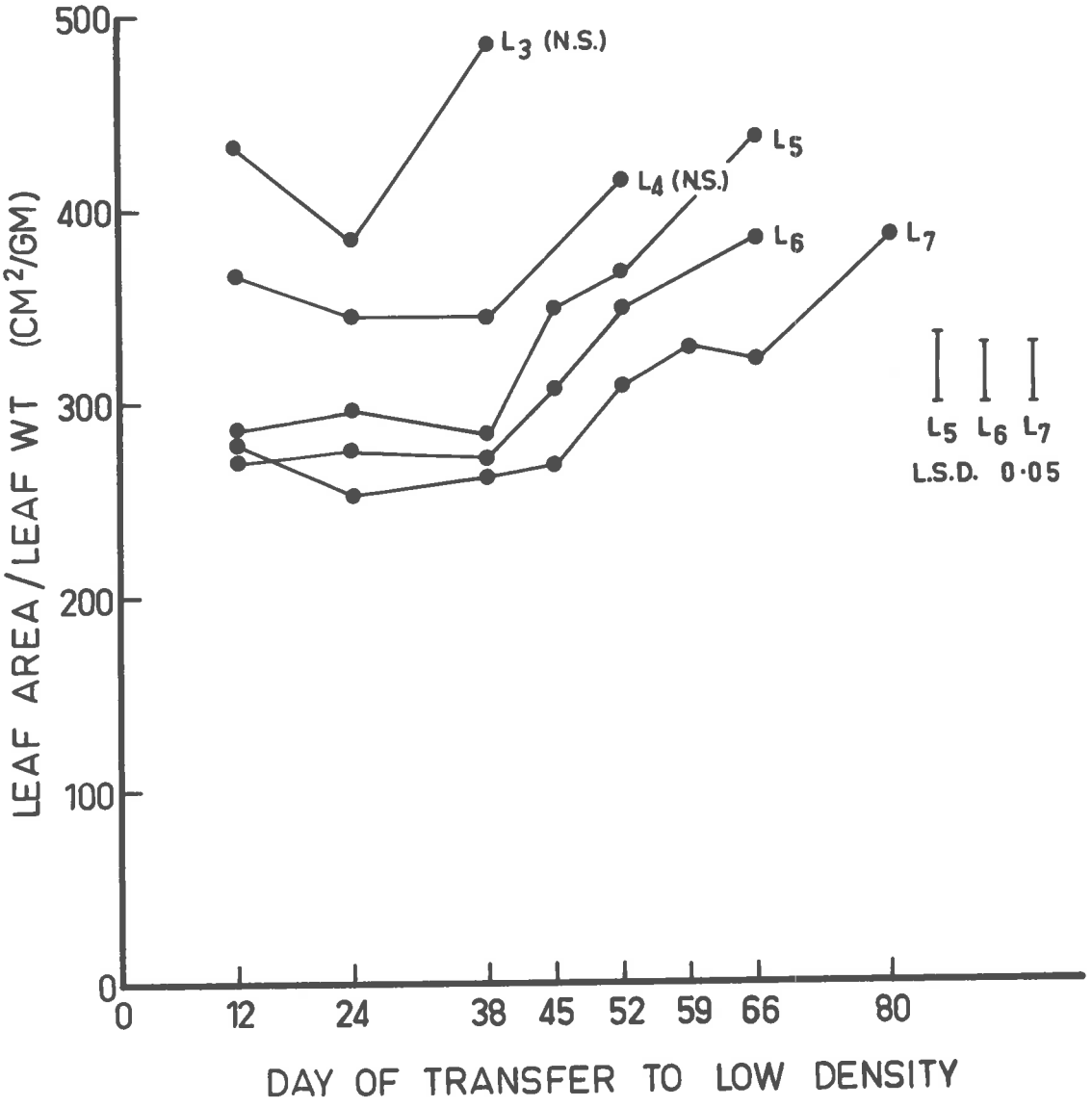
the apex on day 24 but was not visible until approximately day 54. Transferring to low density between day 24 and day 54 gave big differences in final area of leaf 7 for different days of transfer but the effect of transferring to low density was even greater at the next occasion of transfer after day 54 when the leaf first became visible. Thus the effect of density, and therefore presumably light intensity, was acting on the leaf indirectly through the plant before the leaf itself was exposed directly to light as well as immediately after the leaf emerged from the sheath.

(h) Leaf area/leaf weight ratios.

As illustrated by fig. 9 there was a considerable influence of density on the leaf area/leaf weight ratio and from this it is assumed that there was an influence on the thickness of the leaves, with the leaves of plants remaining at high density for longer periods being "thinner" than those of plants transferred to low density at an earlier date. The effect is more easily seen with the later leaves as the few occasions of transfer covered in measurement of the first formed leaves did not show significant differences.

With successive leaves the mean ratio is lower than for the previous leaves. A notable feature was that the differences due to nitrogen treatment were not significant for any particular leaf, and consequantly the graph was drawn from the combined means for each time of transfer. Leaving the plants in high density

Figure 9. Mean leaf area/leaf weight ratios for leaves 3 to 7. Leaves numbered in order of appearance on the main stem. (Mean of all nitrogen levels).


500
400
300
200
100
0
LEAF AREA / LEAF WT (CM²/GM)
L3 (N.S.)
L4 (N.S.)
L5
L6
L7
L5 L6 L7
L.S.D. 0·05
0
12
24
38
45
52
59
66
80
DAY OF TRANSFER TO LOW DENSITY

conditions had no effect on the area/weight ratio of leaf 7 up to day 45, but after day 45 the effects were considerable. As described in the previous section, leaf 7 was sufficiently advanced to cover the apex at day 24 and was first visible about day 54. Similarly there was no effect of transfer before day 38 with leaf 6 which had commenced elongation prior to day 24 and was visible at day 45. Therefore it appears that conditions during expansion are more important in determining the ultimate leaf area/leaf weight ratio than the conditions prior to leaf appearance.

(i) Apex length.

Measurements of apex length were made at the harvests on days 24, 38, 52 and 66 and the mean values are given in table 11. No differences could be determined at day 24, but by day 38 N_3 was significantly greater than N_2 and N_1 at the 1 % level and the differences were maintained at later harvests. At the harvest of day 52 the length of the apex was greater for the plants of N_3 transferred to low density at days 12 and 24 than for those remaining at high density for longer periods, but the difference was not significant over all treatments. By day 66 the length was so variable that no conclusions could be drawn other than that the length increased with increased nitrogen. The mean length of the apices for the 4 harvests was as follows.

Table 11.

Mean length of apices (mm).

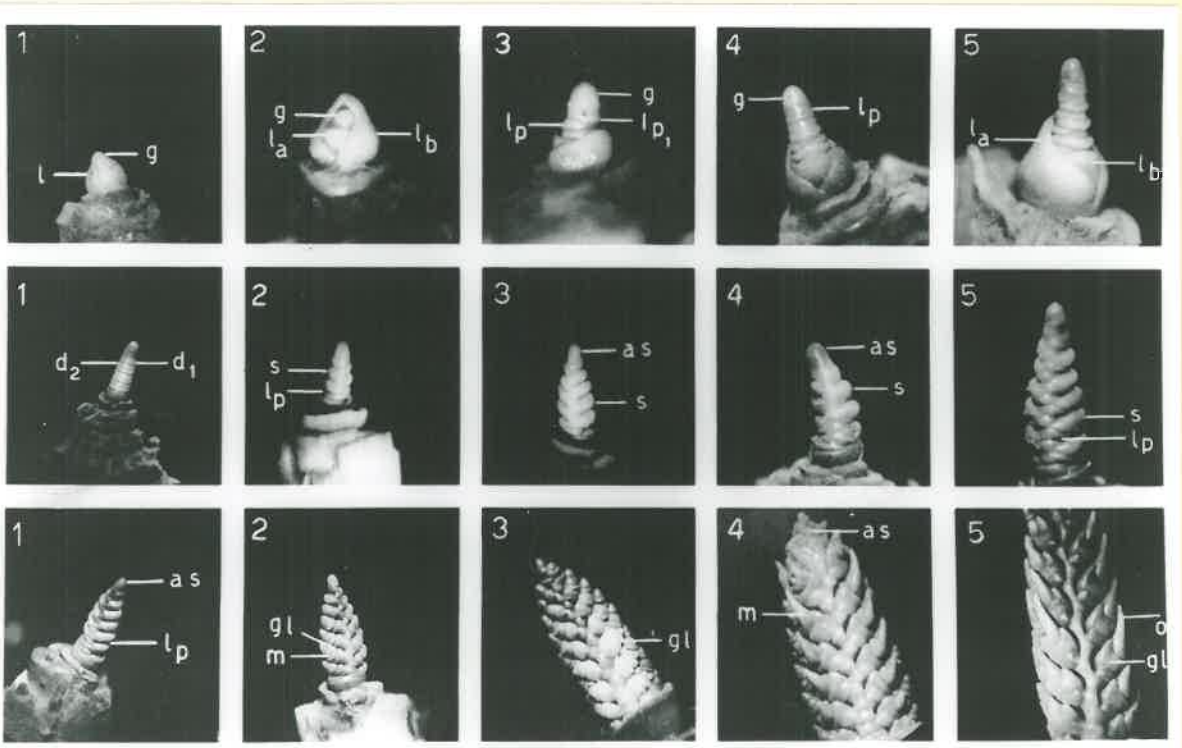
Day of harvest.	N_1	N_2	N_3	Condition of apex.
24	0.47	0.49	0.48	Vegetative.
38	1.12	1.16	1.36	Transition stage 3*.
52	3.69	4.27	7.44	Awns appearing.
66	35	40	67	Elongating.

* Plate 7.

(3) Development of the apex.

The apices were classified as to the stage of development on four occasions using Khalil's classification (1956) as a basis (plate 7). At the harvest of day 24 all plants were between stages 2 and 3 of the preparatory stage, with the apex of the vegetative axis commencing to elongate prior to spike formation (first row of photographs). There were no observable differences between nitrogen treatments. By day 38 there were still no differences between treatments, with the mean stage of development now equivalent to stage 3 of the transition stages as shown in the second row of photographs of plate 7, but with rather more spikelets than the example shown. There was variation between

Plate 7. Morphological development of the wheat apex (after Khalil 1956).



Morphological development of the wheat apex: g, growing point; lp, lp_1, leaf primordia; l, la, lb, undeveloped leaves; d_1, d_2, double ridges; s, spikelet primordium, as, apical spikelet primordium; gl, glume; m, lemma; o, own (beard)
Preparatory stage, 1–5 above. Transition stages, 1–5 middle. Developing stages, 1–5 below.

stages 2 and 4 but the spikelet primordia were developing on all the apices. Plants of the high density were slightly further advanced in N_1 than in N_2 and N_3 at day 52, but it appeared that the order was reversed in the low density. However, the mean differences were very slight and all plants had reached stages 2 to 5 of the developing stages. From then on N_3 developed more quickly, particularly with the low density plants, and the heads were much longer and further developed by day 66 than in the other two treatments. Some spikes of N_3 were beginning to fill out, while a few were almost fully elongated.

Prior to elongation of the rachis of the spike all the spikelets on the same ear appeared to be at a similar stage of development, with the basal spikelets being slightly smaller than those above. However, when elongation of the rachis commenced the sub-apical spikelets developed rapidly and a gradient of development from apex to base was formed. Once the heads started to fill out it was possible to observe the basal spikelets which would not develop, although the lowest 1 to 2 of the developed spikelets were usually smaller than those above.

By day 38 75-80 % of the eventual number of spikelets had differentiated and by day 52 all were well developed (table 12). With the data from the day 66 harvest it was not possible to draw any direct conclusions on the effect of different occasions of transfer to low density due to the extreme variability. Small changes in stage of development caused large changes in size.

Table 12.

Mean number of spikelets per ear.

(Mean of all transfer occasions).

Day of harvest.	N_1	N_2	N_3
38*	10.2	12.3	15.2
52*	15.2	16.7	19.3
135†	14.9	16.5	19.5

* Based on a sample of 10 plants.

† " " " " " 40 " .

(k) Dates of ear emergence and anthesis.

These are given in tables 13 and 14 respectively for the main stem. Both ear emergence and anthesis were delayed at high nitrogen level but the effect of density is not clear, with variation in response at different nitrogen levels. With N_3 ear emergence and anthesis were delayed by later transfer from high to low density but with N_2 and N_1 the reverse occurred. However, the overall differences were small and no direct conclusions can be drawn, particularly as the differences between replicates were marked.

(l) Length and breadth of ears.

The length, and the breadth across the widest spikelet of ears on the main stem are given in tables 15 and 16. Except for those plants with more than one tiller there was a marked increase in size with increased nitrogen and with earlier transfer to low density. When plants developed more than one tiller, ear size

on the main stem was reduced.

(m) Development of spikelets.

There was a marked nitrogen effect on the total number of spikelets produced by the ears of the main stem, with means of 14.9, 16.5 and 19.5 for N_1, N_2 and N_3 respectively. However, not all of these developed fully to produce fertile flowers. The number of rudimentary spikelets varied with treatments and were completely infertile with just a small pair of glumes (plate 8). A comparison of the total number of spikelets with the number of infertile spikelets for ears on the main stem is shown in fig. 10. Within nitrogen treatments the total number of spikelets per ear was constant except for those plants of N_2 and N_3 with tillers. However, the number of infertile spikelets increased with the longer period for which the plants remained under conditions of high density. Conversely the number of fertile spikelets decreased. The proportion of infertile spikelets was higher with low nitrogen.

(n) Number of grains per fertile spikelet.

The number of grains per fertile spikelet increased with increasing nitrogen level and with earlier transfer to low density. Means and significance levels are given in table 17. The infertile spikelets are not included in these calculations.

(o) Number of grains per ear.

Grain number per ear increased with increased nitrogen level and with earlier transfer to low density as shown in fig. 10, which also shows the effect of increased tiller number in reducing grain number in the ear of the main stem.

Plate 8. Comparisons at the final harvest of heads of the three nitrogen treatments for four occasions of transfer and plants remaining at high density throughout (H). These heads conform to the mean dimensions given in tables 14 and 15.

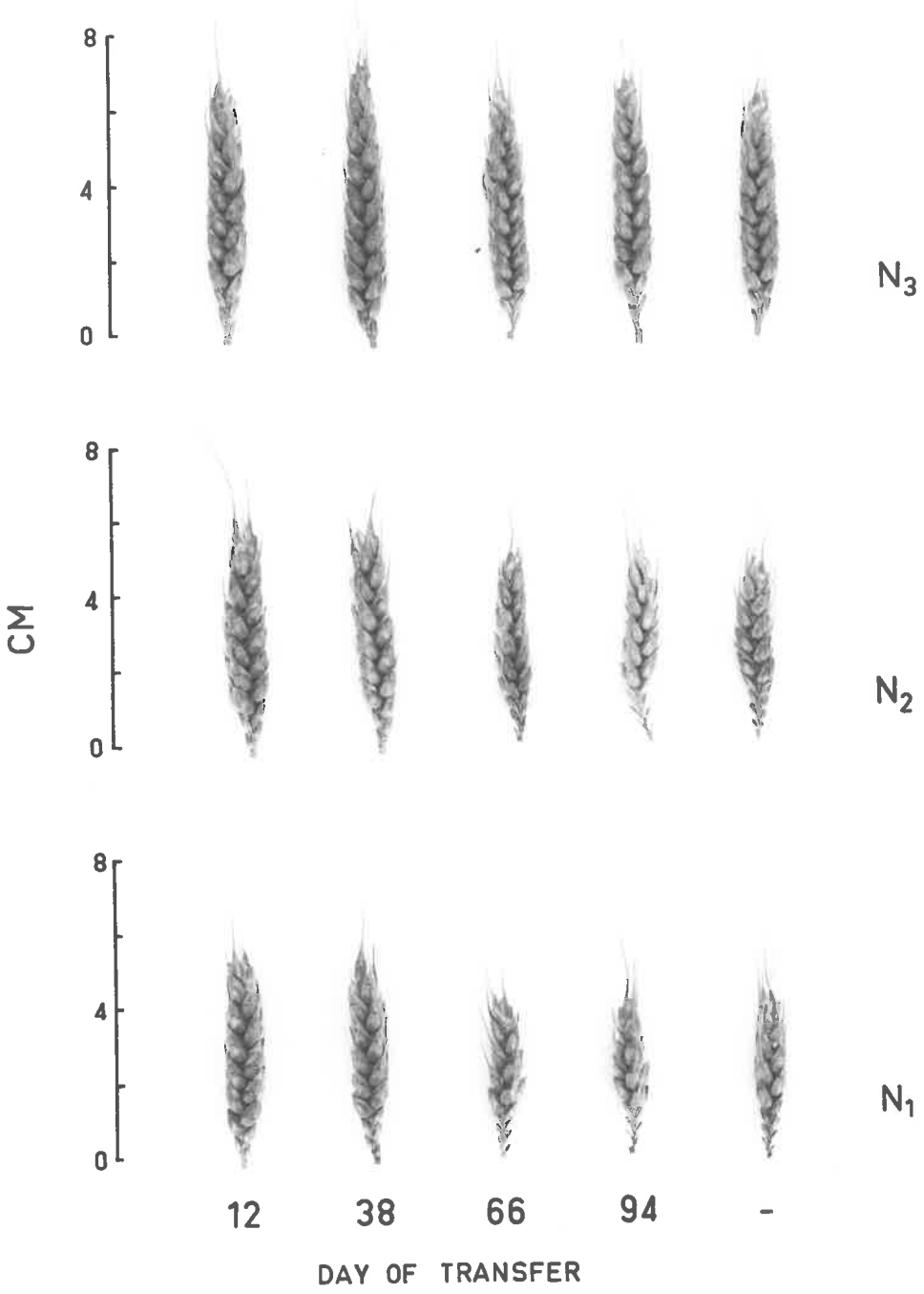

8
4
0
N3
8
4
0
CM
N2
8
4
0
N1
12
38
66
94
-
DAY OF TRANSFER

Table 13.

Date of ear appearance. (Mean September date*).

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	21.6	22.2	16.8	20.2
24	22.3	20.3	16.8	19.8
38	20.0	18.5	16.3	18.3
45	17.2	19.0	16.3	17.5
52	18.9	17.8	18.6	18.4
59	18.0	17.9	18.5	18.1
66	16.5	18.8	18.2	17.9
73	19.0	19.8	19.0	19.3
Mean	19.2	19.3	17.6	18.7

* September 18 = day 73

L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.8	1.0	1.4	0.36
Vertical Margin	1.2	1.7	-	0.59
Body of Table	2.1	2.9	-	1.03

Table 14.

Date of anthesis. (Mean September date*).

Day of Transfer to Low Density.	Treatment			Mean
	N_1	N_2	N_3	
12	28.7	29.2	24.3	27.4
24	29.2	26.8	24.5	26.8
38	26.8	26.2	23.7	25.6
45	25.1	27.0	24.3	25.4
52	26.0	25.7	26.2	26.0
59	25.2	25.3	26.9	25.8
66	24.6	27.2	25.8	25.9
73	26.8	27.8	27.2	27.3
Mean	26.6	26.9	25.4	26.3

* September 25 = day 80

L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.8	1.1	1.5	0.39
Vertical Margin	1.3	-	-	0.64
Body of Table	2.3	3.1	-	1.10

Table 15.

Mean length of ears (cm). Harvest day 135.

Day of Transfer to Low Density.	Treatment			Mean
	N_1	N_2	N_3	
12	5.82	6.12	6.90	6.28
24	5.65	6.12	7.25	6.34
38	5.47	6.10	7.75	6.45
45	4.72	5.65	7.80	6.06
52	4.42	5.42	7.60	5.82
59	4.55	4.87	7.45	5.62
66	4.45	4.95	6.65	5.35
73	4.12	4.92	6.57	5.21
80	4.02	4.82	6.52	5.12
94	4.02	4.87	6.80	5.23
H.D. throughout	4.17	4.80	6.42	5.13
Mean	4.68	5.33	7.07	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.16	0.21	0.28	0.077
Vertical Margin	0.30	0.41	0.54	0.148
Body of Table	0.52	0.71	0.93	0.256

Table 16.

Mean breadth of ears (mm). Harvest day 135

Day of Transfer to Low Density.	Treatment			Mean
	N_1	N_2	N_3	
12	12.0	11.5	12.2	11.9
24	13.0	12.2	12.2	12.5
38	11.5	12.0	12.0	11.8
45	10.2	11.5	12.7	11.5
52	10.2	11.5	12.5	11.4
59	10.7	11.0	12.0	11.2
66	10.5	11.0	12.0	11.2
73	9.5	11.0	11.7	10.7
80	9.7	10.5	12.5	10.9
94	8.5	10.5	12.0	10.3
H.D. throughout	9.5	10.5	12.0	10.7
Mean	10.5	11.2	12.2	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.3	0.4	0.5	0.135
Vertical Margin	0.5	0.7	0.9	0.259
Body of Table	0.9	1.2	1.6	0.449

Table 17.

Mean number of grains per fertile spikelet. Harvest day 135.

Day of Transfer to Low Density.	Treatment			Mean
	N_1	N_2	N_3	
12	2.14	1.85	2.06	2.02
24	2.17	2.07	1.90	2.05
38	1.85	1.84	2.04	1.92
45	1.48	2.13	2.13	1.92
52	1.71	1.65	1.81	1.73
59	1.42	1.74	1.90	1.69
66	1.37	1.44	1.52	1.45
73	1.06	1.55	1.66	1.43
80	1.27	1.41	1.56	1.42
94	1.10	1.40	1.67	1.39
H.D. throughout	0.97	1.52	1.68	1.39
Mean	1.51	1.69	1.82	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.14	0.19	0.26	0.070
Vertical Margin	0.27	0.37	0.49	0.134
Body of Table	N.S.	-	-	-

(p) Weight of grain per ear and per plant.

These both increased with nitrogen level and with earlier transfer to low density as shown in fig. 10. The weight of grain per plant was further increased in the earlier transferred plants of N_2 and N_3 by the extra tillers.

(q) Weight per grain.

Weight per grain increased with increasing nitrogen and overall with earlier transfer to low density. However, the degree of response to time of transfer depended on the nitrogen level. With N_1 and N_2 there was a large effect of occasion of transfer, grain weight falling from approximately 38 to 31 mg for N_1 and from 42 to 35 mg for N_2 whereas there was no apparent trend for N_3 (fig. 10).

(r) Percent nitrogen content.

Owing to the small amount of material available it was necessary to combine some samples for nitrogen determinations; mean figures are available for plants transferred to low density for days 18, 38, 48, 62, 76, 94, and high density throughout.

The percentage nitrogen content for all plants declined from 2.93 (for the whole plants) at the harvest of day 38 to 0.91 at maturity. Differences between treatments were very marked at the earlier harvests with N_3 having the highest percentage. However, the differences diminished at later harvests and at the final harvest plants of N_3 were lower in percent nitrogen content than N_1 or N_2 as shown by table 18.

Figure 10. Components of grain yield, the yield of nitrogen in the grain, and the number of spikelets per ear at the final harvest.

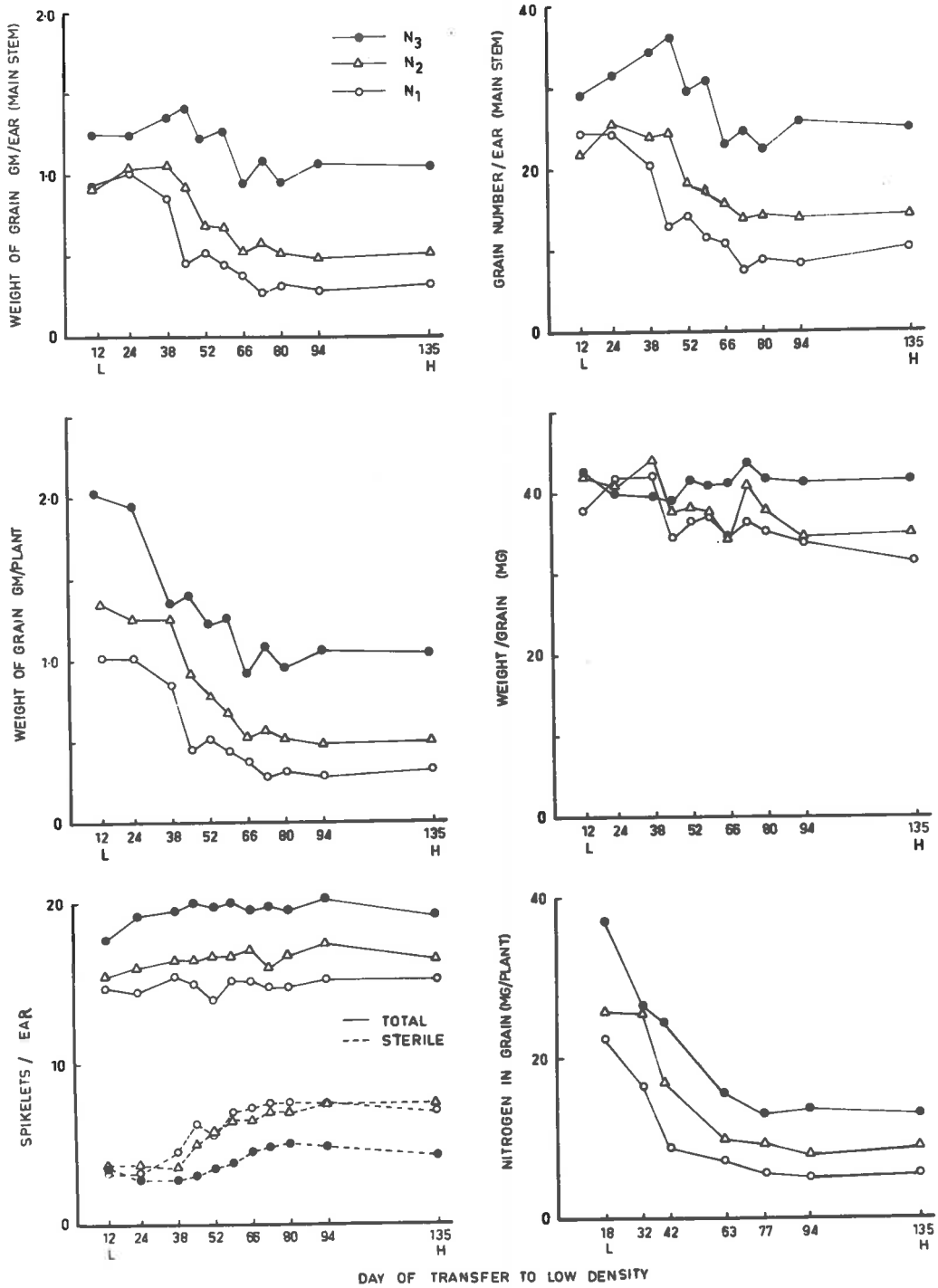

WEIGHT OF GRAIN GM/EAR (MAIN STEM)
2·0
1·0
0
N_3
N_2
N_1
12 24 38 52 66 80 94 135
L H
GRAIN NUMBER / EAR (MAIN STEM)
40
20
0
WEIGHT OF GRAIN GM/PLANT
WEIGHT /GRAIN (MG)
SPIKELETS / EAR
20
10
TOTAL
STERILE
NITROGEN IN GRAIN (MG/PLANT)
18 32 42 63 77 94 135
DAY OF TRANSFER TO LOW DENSITY

Table 18.

Percent nitrogen content of plants for three N levels (mean of all transfer occasions).

Day of Harvest.	Portion of Plant.	N_1	N_2	N_3	L.S.D. 0.05
38	Whole.	2.49	2.50	3.00	0.18
52	"	1.48	1.64	2.36	0.14
66	"	1.01	1.13	1.25	0.09
87	"	0.76	0.77	0.84	-
135	"	0.92	0.97	0.85	-
87	Leaf and stem.	0.63	0.70	0.75	0.02
135	" " "	0.34	0.36	0.31	0.01
87	Ears.	1.31	1.35	1.47	0.06
135	Grain.	1.84	1.82	1.71	0.03

The nitrogen percentage of the grain at maturity increased with earlier transfer to low density, but at the earlier harvests plants remaining at high density had a higher nitrogen content than those at low density as shown by table 19.

(s) Yield of nitrogen (g/m^2).

A comparison, for plants at high density throughout their growth, of the yield of nitrogen and of dry matter shows that whereas dry matter increase continued at a high rate until day 109, over 50 % of the nitrogen uptake had occurred by day

52 (fig. 5). The plants continued to take up nitrogen until growth ceased, but the rate of uptake was slow in the later stages. The uptake of nitrogen as percent of final uptake compared with dry weight on the same basis for five harvests is shown in table 20 as the mean of three nitrogen treatments.

Table 19.

Percent nitrogen content as affected by occasion of transfer (mean of three nitrogen levels)

Day of harvest.	Portion of plant.	Day of transfer							L.S.D. 0.05
		18	38	48	62	76	94	HD*	
38	Whole	2.62						3.25	0.15
52	"	1.64	1.56					2.29	0.14
66	"	1.13	0.87	1.11				1.42	0.11
87	"	0.87	0.74	0.80	0.76	0.80		0.96	-
135	"	0.99	0.95	0.97	0.86	0.82	0.90	0.78	-
87	Leaf & stem	0.80	0.63	0.67	0.62	0.66		0.83	0.03
135	" " "	0.28	0.27	0.36	0.38	0.38	0.37	0.31	0.02
87	Ears	1.43	1.28	1.32	1.35	1.40		1.46	0.08
135	Grain	2.00	1.93	1.87	1.72	1.72	1.67	1.63	0.04

* High density throughout.

Table 20.

Yield at five occasions as percent of final yield for high density plants. (Mean of all nitrogen levels).

	Days from sowing.				
	38	52	66	87	135
Dry matter	9.4	19.4	33.9	63.2	100
Nitrogen	38.3	60.1	65.0	77.3	100

(t) Yield of nitrogen per plant.

This reflected the differences in dry weight and percent nitrogen content. The yield of nitrogen increased with increasing nitrogen level and with earlier transfer to low density. The effect of the higher nitrogen percentage of high density plants was diminished by the increased dry weight of the earlier transferred plants. Mean yields of nitrogen and significant differences are given in tables 21 and 22.

The pattern of uptake by the low density plants differed from that of the high density plants. By day 87, up to 77 % of the final yield of nitrogen had been taken up by the plants at high density. At this time the plants transferred to low density at day 18 had taken up more nitrogen (17.2 mg cf. 10.7 mg), but this was only 61 % of the final yield.

Table 21.

Yield of nitrogen as mg/plant for three nitrogen treatments.

Day of harvest.	N_1	N_2	N_3	L.S.D. 0.05
38	3.72	4.07	6.72	0.29
52	4.10	6.12	14.30	0.38
66	5.40	7.79	14.41	0.23
87	7.14	10.19	19.55	0.30
135	13.10	19.26	28.66	0.39

Table 22.

Yield of nitrogen per plant as affected by time of transfer. (mg).

Day of harvest.	Day of transfer.							L.S.D. 0.05
	18	38	48	62	76	94	HD[x]	
38	5.55						5.47	N.S.
52	8.37	7.83					8.32	0.38
66	11.08	8.32	8.40				9.00	0.26
87	17.22	12.38	12.02	10.77	10.68		10.70	0.42
135	34.03	27.35	21.33	16.60	14.73	16.63	13.68	0.60

[x] High density throughout.

(u) Total soil nitrogen.

The technique for determination of total soil nitrogen was not entirely satisfactory but sufficed to show that the differences between nitrogen treatments diminished by the final harvest as shown by table 23.

Table 23.

Total soil nitrogen as percent x 100.

Day of sampling.	N_1	N_2	N_3	S.E.D.	L.S.D. 0.05
40	3.95	4.33	5.08	0.15	0.34
135	4.11	4.07	4.39	0.10	0.20

At day 40 the effect of the added fertilizer is still apparent, but by day 135 there was no difference between N_1 and N_2. The higher value for N_3 at day 135 may indicate that not all the hoof and horn had been mineralized.

(v) Height of stem.

The mean height of the plants increased with increasing nitrogen and with increased length of the period at high density as shown in table 24. The increased height of the later transferred plants indicates a response to competition for light.

Table 24.

Mean height of stem (cm).

Day of measurement.		Day of transfer. 12	24	38	52	66	80	94	High density
24	N_1	3.7							5.1
	N_2	4.4							5.6
	N_3	4.9							5.8
38	N_1	5.9	6.7						10.4
	N_2	7.6	7.9						13.3
	N_3	9.4	10.0						16.4
52	N_1	11.3	11.1	13.2					20.9
	N_2	12.0	12.6	15.0					23.2
	N_3	16.9	18.6	22.0					26.5
66	N_1	22.9	23.5	26.7	32.4				46.8
	N_2	24.8	27.3	32.9	34.9				47.4
	N_3	34.3	36.8	40.9	39.5				61.1
80	N_1	29.3	29.0	30.1	49.0	54.3			67.1
	N_2	37.5	29.7	47.0	52.2	62.6			75.5
	N_3	49.5	55.7	56.7	52.0	71.7			95.4
109	N_1	49.0	48.5	49.5	58.5	71.5	77.5		83.5
	N_2	48.0	57.0	56.5	65.5	77.0	88.0		96.2
	N_3	61.0	61.5	69.5	67.0	82.0	104.5		98.5
135	N_1	49.0	55.5	51.7	58.7	62.2	77.0	83.5	82.4
	N_2	52.7	58.2	63.2	61.0	70.0	87.2	92.0	103.9
	N_3	65.7	68.0	70.0	75.7	82.5	105.2	110.5	113.4

D I S C U S S I O N

(a) Tillering.

The response to reduced competition when the plants were transferred from high density to low density was less than that expected and it is suggested (section I of Results) that nitrogen limited the extent of tillering and the production of dry matter. Temperature may have been a contributing factor to limiting dry matter in that development of the plants was very rapid and spikelet initiation occurred between 24 and 36 days after sowing. Thus the vegetative stage was very short and this may have influenced the degree of tillering. All plants at high density were single stemmed and extra fertile tillers were produced only on those plants transferred to low density on day 36 or earlier, while the maximum number was three per plant. If, as suggested, nitrogen was the major factor involved, then when the plants were transferred at later occasions the main stem was already well developed and intra-plant competition would prevent further development of the tiller buds.

The plants at the low nitrogen level (N_1) remained single stemmed under all treatments, but suppression of tillering of the plants at N_2 and N_3 at high density was apparently due to the low light intensities induced by the competition of neighbours. This interpretation is supported by the observation that border plants of the high density plots produced 1-2 tillers. When removed to

low density and high light intensity, tillers were produced if the plants were transferred before day 38, but it is possible that a critical stage was reached after which transfer to low density would not overcome the effects of suppression of the tiller buds at high density. The variety used, Gabo, is not freely tillering and the tiller buds may be easily suppressed. Santhirasegaram (1962) using the same variety in the field obtained only 8.5 tillers per plant with low densities of 11 plants per metre row length in 14 inch rows while Wasserman (pers. comm.) obtained 7 tillers per plant in pot culture. Further, it was observed that the few tillers that did appear on the later transferred plants were from higher leaf axils than those tillers on the plants transferred on the early occasions. However, these late tillers were all small and soon died, thus giving support to the view that intra-plant competition was the main factor suppressing tillering at low density.

(b) Dry matter production.

Dry matter production was directly related to the degree of tillering. Thus considerable increases in dry weight were shown by the plants transferred at day 38 or sooner compared with those remaining at high density for longer periods. With plants which had only one stem the slightly increased weight of the earlier transferred plants must have been due to increased production per unit plant surface area (leaf, stem and ear surface) under the higher light intensities at low density. However, the differences between dry weights of the plants transferred after day 45 were

small. It is possible that the lower production per unit surface area of the later transferred plants may have been partly compensated by a greater leaf area per plant of the plants remaining longer at high density.

Although not directly comparable with yields in the field, the very high yields obtained with the high density plots illustrate the potential of this crop and climatic environment. The final yield for N_3 at high density, based on an area sampled near the middle of the plot, was 3,000 gm/m^2, whereas in the field at Adelaide Puckridge (1962) obtained with the variety Insignia a maximum yield of 932 gm/m^2 for the 1961 season and Wasserman (pers. comm.) a maximum of 1080 gm/m^2 for the 1962 season for the variety Gabo. Both these field experiments were at several rates of sowing and with supplementary irrigation, while the latter experiment also included two levels of nitrogen. The differences were even more outstanding when the grain yield is considered. The grain yield in the present experiment was 1170 g/m^2 for N_3 at high density. There were three reasons for this high yield; the high plant population of 1150 plants/m^2; every plant produced an ear; the ears were of good size and produced a mean of 1.04 gm of grain. In comparison a treatment with an initial plant density of 1078 plants/m^2 in a field experiment (Puckridge 1962) produced only 189 g of grain/m^2. At harvest, tiller numbers had declined from a maximum of 1400 to 600/m^2 and produced only 296 ears/m^2 with a mean of 0.62 g of grain per ear. Lodging and competition for

nutrients occurred in this instance, but comparison with the present experiment illustrates the importance of producing a high proportion of fertile tillers and a reasonable head size to obtain a high yield of grain from high sowing rates. Although the plants were mechanically supported in the present experiment and lodging did not occur, the comparison also suggests that competition for light is of doubtful significance in the yield of wheat per unit area in the field for this environment.

Competition for light was certainly severe between plants at the high denisity, but viewed as a community of tillers yield was influenced more by nutrient level. However, further experimentation is required to determine the role of competition for light at higher nutrient levels and at lower populations than those of the high density of this experiment. For instance, if a density of 383/m^2 (= 1/3 of 1150) had been used the plants may have produced a mean of three tillers per plant and consequently equivalent yields to those obtained in this experiment. However, if competition for light were to reduce the number of tillers per plant to a mean of, for example, 2.5 or 2.0 it is unlikely that increased yield per ear would be sufficient to offset the decreased number of ears. Competition for light would then be a factor in limiting the yield of grain per unit area. However, in this case the limiting effect of competition for light would not be absolute, i.e. in determining the total amount of dry matter production possible per unit area, but would depend on the ability of the plant to compensate for a

reduced number of tillers per unit area. Therefore, in theory, for varieties in which tillering was sensitive to low light intensities a dense population of single stemmed plants would be an advantage at high soil nutrient levels.

(c) The uptake of nitrogen.

The nitrogen percentage of the plants decreased from 2.93 % at the first harvest to 0.91 % at maturity (mean of all treatments). Associated with this overall decrease in percentage were differences in uptake between treatments and differences in dry matter yield and nitrogen yield.

The uptake of nitrogen by the plants at low density was greater at all stages and continued for a longer period than that of the high density plants. For example, by day 67, taking the mean of the three nitrogen treatments, plants transferred at day 18 had taken up 17.2 mg of nitrogen (61 % of the final uptake) while the plants remaining at high density throughout the experiment contained only 10.7 mg (77 % of the final uptake). At the same date the dry weight of plants transferred at day 18 was 1.97 g (58 % of the final dry weight) while that of plants remaining at high density throughout their growth was 1.13 g (66 % of the final dry weight). Thus in addition to having greater dry weights the earlier transferred plants had a higher percentage of nitrogen at maturity than those transferred later or those remaining at high density throughout the experiment.

The reason for these differences was not investigated but two possible sources of variation could be root development and energy supply. The earlier transferred plants produced roots more abundantly than those transferred later and soil exploration may have been more complete. Also energy is required for the absorption of mineral ions (Meyer, Anderson and Bohning 1960, Russell 1962). The earlier transferred plants received more light energy, the rate of photosynthesis per unit area would be higher and greater energy supplies available for nutrient uptake. Transpiration of the low density plants appeared to be greater also, and this could increase the rate of movement of salts from the xylem elements of the roots to the leaves (Meyer et al. 1960).

Although the initial nitrogen percentage was higher for N_3 plants than for N_2 or N_1 plants, the final percent nitrogen content was slightly lower for N_3. This was associated with a prolonged and greater production of dry matter and may be the result of more efficient carbohydrate production associated with delayed senescence of the leaves of the N_3 plants.

(d) Leaf development.

The major treatment effects were those on the area of the individual leaf. Leaf number increased only slightly with increased nitrogen and the only effects of time of transfer on leaf number per plant were those due to tillering. The area per leaf increased with both higher nitrogen level and with later transfer to low density. However, the leaf area/leaf weight

ratio was not affected by nitrogen supply, although it increased with later transfer to low density. This ratio was also lower for successive leaves on the main stem.

It was not possible to determine directly from the data collected whether the increase in leaf area with later transfer to low density was the result of increased cell production or differential expansion of the cells. Transferring to low density had the greatest effect on the final area of the leaf when the transfer occurred immediately after the leaf was visible above the sheath. Comparison of the area per leaf and the leaf area/leaf weight ratio with times of leaf initiation and leaf appearance showed that the effects of transferring occurred after the young leaf had completely covered the apex but within two weeks after leaf appearance. The greatest responses to changing conditions occurred immediately after the leaf's appearance. It seems from these observations that the low light intensities at high density had their main effects on the expansion of cells rather than on number of cells. This agrees with the observations of Friend et al. (1962 b). However, cell production may play a part. It was shown in fig. 8 that for N_1 the area of leaf 7 diminished with increasing time at high density up to 52 days and then slightly increased. There was some indication that the time of appearance of the later leaves was delayed in N_1 and it is possible in this case that cell formation was reduced at high density. Leaf 7 was visible at approximately day 54 and the slight increase in area

with plants transferred after this time would have been a result of increased expansion of cells after leaf emergence under conditions of lower light intensity. However, clarification of these responses would require cell counts which were not carried out with this experiment.

The Leaf Area Index (L.A.I.) was calculated for the high density plants only. For the low density plants L.A.I. would have little meaning owing to the wide spacing between plants and the small leaf area per plant. The values of L.A.I. at N_3 (max. 11.4) were much higher than at N_2 and N_1 (max. 6.9 and 4.5 respectively). The differences were almost entirely due to the increased area per leaf with increased nitrogen level. In addition to their greater area, the senescence of later leaves of N_3 was delayed compared with those of N_2 and N_1, resulting in a lengthened period of dry matter production by N_3. This increased the differences between treatments at the final harvest.

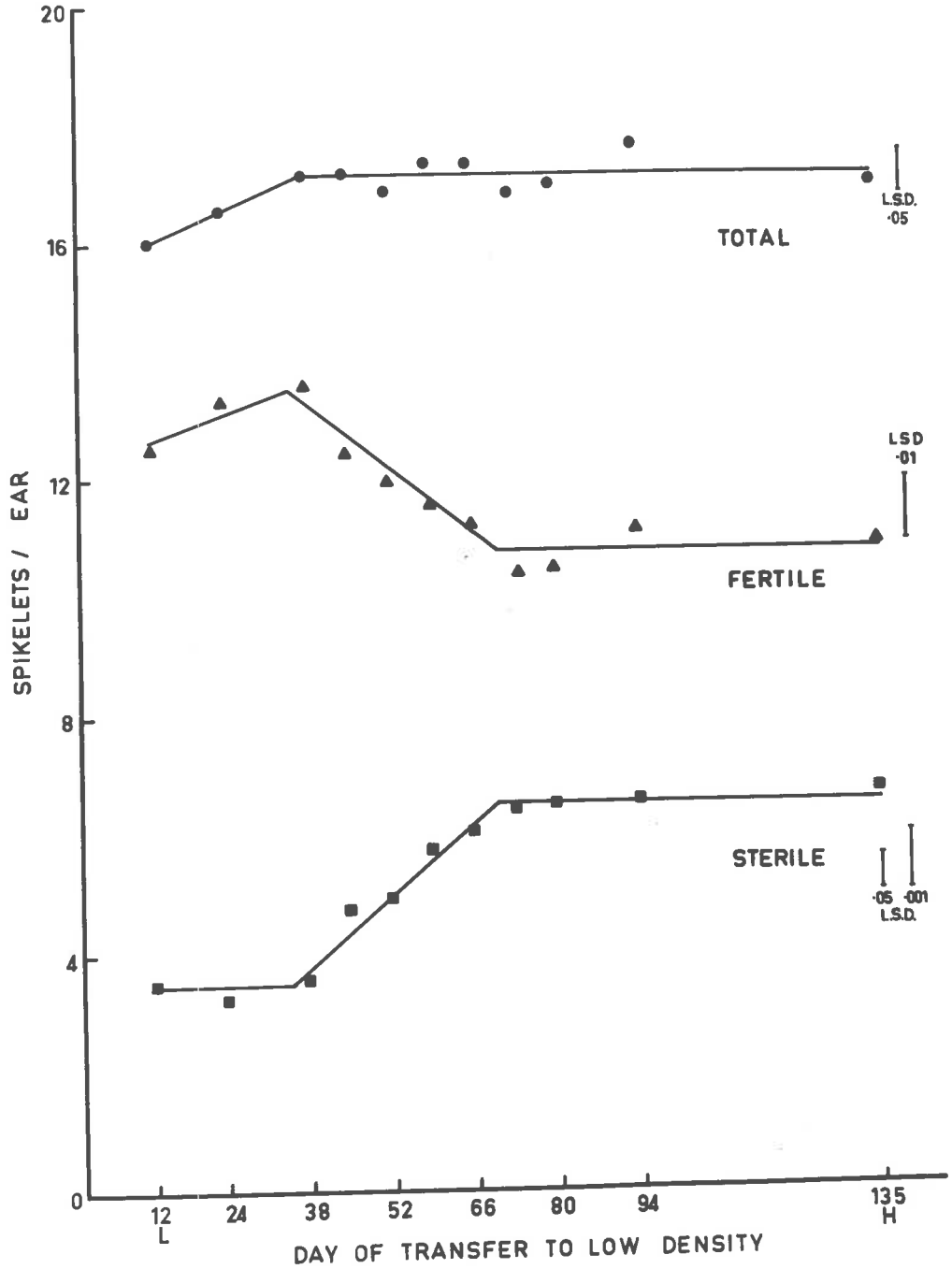
(e) Head formation.

The effect of nitrogen in increasing the size of the apex was apparent from day 38 onward with the differences becoming more pronounced as the heads developed to maturity. Associated with this was an increased number of spikelet primordia on the apices with increased nitrogen level, except for the few plants which had tillered. Here the total number of spikelets per spike was slightly reduced.

Although there was no effect of time of transfer on the total number of spikelet primordia, the number of these which fully developed to produce fertile flowers was affected by the period at high or low density, particularly at the lower nitrogen levels. Just prior to elongation of the rachis all spikelets on a spike appeared to be at a similar stage of development, and no differences indicating their future development could be observed. However, once elongation of the rachis commenced the upper spikelets developed most rapidly and it was soon possible to see that some of the basal spikelets were not developing. These usually did not increase further than just a pair of glumes and were completely sterile. Both time of transfer and nitrogen level affected the number of these sterile spikelets.

The effect of time of transfer to low density is shown in fig. 11 which gives the mean spikelet numbers for the ear of the main stem, using the combined values for the three nitrogen treatments. This figure is derived from the data shown in the bottom left graph of fig. 10. The lower number of 'total spikelets' for the first two occasions of transfer is apparently due to increased tiller number and increased competition between tillers. (There was no reduction for these two occasions with the plants of N_1 which did not tiller - see fig. 10). The graph shows that the effect of density on the number of sterile spikelets was influential for plants transferred between day 35 and day 70; this can be regarded as the critical period during which high density affected

Figure 11. The effect of time of transfer on the development of spikelets. Mean of 3 nitrogen treatments.


20
16
12
8
4
0
SPIKELETS / EAR
TOTAL
L.S.D.
·05
FERTILE
LSD
·01
STERILE
·05
L.S.D.
·001
12
L
24
38
52
66
80
94
135
H
DAY OF TRANSFER TO LOW DENSITY

the development of the spikelets. By day 35, 70-80 % of the total number of spikelet primordia could be seen on the apex and the rest soon developed. By day 52 awns had developed on the spikelets and elongation of the rachis was just commencing. The ears emerged from the sheath 4-5 days after day 70 and by this stage the number of fertile spikelets had been determined.

It would appear from the results of this experiment that those basal spikelets which failed to develop did so as a result of competition between primordia for assimilates associated with nitrogen supply. The results of Buttrose and May (1959) suggest that competition occurs between grains for assimilates from parts of the plant other than the ear itself, and it seems reasonable that competition could occur at an earlier stage between primordia in the development of the head. The supply of assimilates would be reduced by competition for light among the plants at high density, and competition for assimilates between primordia would then become more acute. Once elongation of the rachis commenced the upper spikelets developed most rapidly and apparently competed most effectively for assimilates. With later transfer to low density the amount of assimilates available for spikelet development would have been less and thus more of the lower spikelets would fail to develop. Lower nitrogen supply resulted in smaller leaf area and presumably less efficient production of carbohydrate by the leaves.

It is considered that the reduction in fertile spikelets was not an effect of shading on the apex as this is covered by the

sheath which was thicker and darker green with plants transferred to low density. Nor could the effect have been due to competition between the primordia for nitrogen alone as this would suggest that nitrogen uptake was less efficient at higher densities. The results show that the percent nitrogen content of the plants at day 66 was higher for the plants transferred at later occasions, and at day 87, while there was little difference between transfer occasions in nitrogen content of the whole plants, the percentage nitrogen content of the ear was higher for the later transferred plants.

(f) Conclusion.

It is suggested that the plants at high density were limited in their growth by competition for light. Transfer to low density removed this limitation and the plants grew at a faster rate, thus producing a greater amount of dry matter. This increased production was greatest with those plants which produced tillers. Plants at high density did not produce tillers as a result of intense competition, apparently for light. These single stemmed plants did not produce tillers if transferred to low density after day 38 and it is suggested that this was mainly due to inadequate nitrogen nutrition. Any increase in dry weight by later transferred single stemmed plants compared with those remaining at high density was due to greater production per unit leaf area.

The most interesting feature of the experiment was the effect of transferring from high to low density on the development of spikelets. The total number of spikelets per ear varied with

nitrogen treatment, being highest for N_3 and lowest for N_1, but there was no effect of time of transfer on the total number of spikelets. However, for plants transferred to low density between days 35 and 70 there was a marked increase in the number of infertile, undeveloped spikelets with later transfer to low density. The number of infertile spikelets was highest with the low nitrogen levels and it is suggested that two factors were involved. Firstly, competition for light at high density resulted in a reduced supply of assimilates to the developing apex and competition for this assimilate between spikelets. Secondly there was an interaction with nitrogen. The critical period for the continued development of the spikelets while this competition was occurring was the period from immediately prior to commencement of elongation of the rachis to ear emergence. After commencement of elongation of the rachis the uppermost spikelets developed most rapidly and there was a gradient in development from the summit to the base of the spike. It is possible that the upper spikelets were more favourably supplied with assimilates and mineral nutrients and if these were in short supply they were utilized by the upper spikelets to the detriment of the lower ones. Thus the degree of competition and the portion of the critical period during which this competition operated appeared to determine the number of spikelets which fail to develop and hence the number of fertile spikelets per ear. These effects may reduce the grain yield per ear of plants at high density to less than half of that which would be obtained if all spikelets were developed fully.

It is possible that if the experiment were conducted at a higher level of nitrogen supply, similar effects on fertile tiller production to those here reported for fertile spikelet production would have been obtained, as was intended in the design of the experiment.

APPENDIX OF NUMERICAL DATA

Table 1.

Mean dry weight per plant (g). Harvest day 52.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	0.24	0.41	0.79	0.48
24	0.32	0.38	0.84	0.51
38	0.28	0.41	0.70	0.46
H.D. throughout	0.27	0.34	0.49	0.37
Mean	0.28	0.39	0.71	0.41
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.06	0.08	0.12	0.027
Vertical Margin	0.07	0.10	0.14	0.031
Body of Table	0.12	0.17	-	0.054

Table 2.

Mean dry weight per plant (g). Harvest day 66.

Day of Transfer to low Density	Treatment			Mean
	N_1	N_2	N_3	
12	0.59	0.84	1.72	1.05
24	0.54	0.79	1.56	0.97
38	0.65	0.82	1.38	0.95
45	0.52	0.74	1.06	0.78
52	0.44	0.64	0.93	0.67
H.D. throughout	0.38	0.51	0.80	0.56
Mean	0.52	0.73	1.24	0.83
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.12	0.16	0.22	0.056
Vertical Margin	0.17	0.23	0.32	0.080
Body of Table	0.29	0.40	-	0.138

Table 3.

Mean dry weight per plant (g). Harvest day 80.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	1.00	1.47	2.88	1.79
24	0.89	1.80	2.72	1.61
38	0.79	1.34	2.27	1.47
45	0.79	1.06	1.75	1.20
52	0.82	1.09	1.76	1.22
59	0.82	1.04	1.93	1.26
66	0.81	0.97	1.83	1.20
N.D. throughout	0.67	0.84	1.38	0.96
Mean	0.83	1.13	2.07	1.34
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.12	0.17	0.22	0.059
Vertical Margin	0.20	0.27	0.36	0.096
Body of Table	0.34	0.47	0.63	0.167

Table 4.

Mean dry weight per plant (g). Harvest day 87.

Day of Transfer to low Density	Treatment			Mean
	N_1	N_2	N_3	
12	1.21	1.72	3.26	2.06
24	1.25	1.73	2.65	1.88
38	0.99	1.37	2.66	1.67
45	0.90	1.28	2.36	1.52
52	0.93	1.31	2.20	1.48
59	0.80	1.24	2.19	1.41
66	0.81	1.21	2.31	1.44
73	0.91	1.19	2.28	1.46
80	0.78	1.08	1.75	1.20
H.D. throughout	0.76	1.06	1.55	1.13
Mean	0.94	1.32	2.33	1.53
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.07	0.09	0.12	0.032
Vertical Margin	0.12	0.16	0.22	0.059
Body of Table	0.21	0.28	0.37	0.102

Table 5.

Mean dry weight per plant (g). Harvest day 109.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	2.33	2.90	4.53	3.25
24	1.70	2.32	4.08	2.70
38	1.52	2.07	3.70	2.43
45	1.29	1.67	2.76	1.91
52	1.33	1.72	3.00	2.02
59	1.16	1.53	3.15	1.95
66	1.32	1.68	2.87	1.96
73	1.10	1.52	3.19	1.94
80	1.04	1.42	3.25	1.90
94	1.00	1.52	2.85	1.79
N.D. throughout	1.12	1.38	2.41	1.64
Mean	1.36	1.79	3.26	2.14
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.20	0.27	0.36	0.099
Vertical Margin	0.39	0.52	0.69	0.190
Body of Table	N.S.	-	-	-

Table 6.

Mean dry weight per plant (g). Harvest day 135.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	2.66	3.01	4.87	3.51
24	2.30	3.05	4.73	3.36
38	1.90	2.82	3.91	2.88
45	1.22	1.93	3.30	2.15
52	1.31	1.97	3.36	2.22
59	1.27	1.62	3.13	2.01
66	1.13	1.57	2.85	1.75
73	0.97	1.42	2.85	1.75
80	1.01	1.56	2.95	1.84
94	1.01	1.56	2.94	1.84
H.D. throughout	1.02	1.40	2.67	1.70
Mean	1.44	1.99	3.42	2.28
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.25	0.34	0.45	0.123
Vertical Margin	0.48	0.65	0.86	0.236
Body of Table	N.S.	-	-	-

Table 7.

Total dry weights for high density plots (g/m^2).

Day of Harvest.	Treatment			Mean
	N_1	N_2	N_3	
24	64	64	77	68
38	161	176	234	190
52	309	380	489	393
66	490	576	987	684
80	761	930	1718	1137
87	861	1106	1862	1277
109	1297	1748	2637	1894
135	1253	1806	3001	2020

Table 8.

Mean leaf area per plant (cm^2). Day 24.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	15.7	17.0	19.3	17.3
N.D. throughout	17.3	18.7	18.3	18.1
Mean	16.5	17.9	18.8	17.7
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	1.4	1.8	-	0.71
Vertical Margin	N.S.	-	-	0.58
Body of Table	N.S.	-	-	1.01

Table 9.

Mean leaf area per plant (cm^2). Day 38.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	30.4	42.1	73.2	48.6
24	33.3	40.6	66.2	46.7
H.D. throughout	36.1	42.5	61.9	46.9
Mean	33.3	41.7	67.1	47.4
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	2.1	2.8	3.5	1.08
Vertical Margin	2.1(N.S.)	-	-	1.08
Body of Table	3.7	4.8	6.1	1.87

Table 10.

Mean leaf area per plant (cm^2). Day 52.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	43.4	64.6	113.8	74.0
24	47.4	63.8	111.0	74.1
38	39.9	54.2	97.9	64.0
45	43.7	47.6	82.0	57.0
H.D. throughout	42.3	48.8	84.3	58.5
Mean	42.9	55.8	97.8	65.5
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	3.8	5.1	6.5	1.97
Vertical Margin	4.9	6.5	8.3	2.52
Body of Table	8.6	11.3	14.4	4.37

Table 11.

Mean leaf area per plant (cm^2). Day 66.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	47.7	72.9	115.5	78.3
24	51.0	66.4	106.0	74.5
38	41.8	56.1	77.9	58.6
45	32.9	45.0	77.0	51.6
52	35.0	52.7	77.8	55.2
59	37.8	50.6	80.8	56.4
H.D. throughout	33.8	58.1	97.7	63.9
Mean	40.3	57.3	90.4	62.6
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	3.8	5.0	6.4	1.95
Vertical Margin	5.8	7.7	9.8	2.98
Body of Table	10.1	13.3	17.0	5.17

Table 12.

Mean leaf area per plant (cm^2). Day 80.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	48.2	63.4	104.5	72.1
24	40.7	52.7	82.6	58.6
38	40.4	47.6	54.8	47.6
45	28.1	42.4	63.2	44.6
52	27.7	31.1	79.5	46.1
59	25.0	35.2	64.4	41.6
66	30.5	29.1	66.3	42.0
N.D. throughout	27.4	36.6	75.3	46.4
Mean	33.5	42.3	73.8	49.9
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	7.3	9.9	13.3	3.53
Vertical Margin	11.9	16.2	21.7	5.76
Body of Table	N.S.	-	-	-

Table 13.

Mean leaf area per plant (cm^2). Day 87.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	31.4	58.5	71.7	53.9
24	32.7	45.1	54.2	44.0
38	27.0	35.2	51.9	38.0
45	23.0	37.6	54.3	38.3
52	21.1	29.6	56.6	35.8
59	18.6	30.4	58.5	35.9
66	21.8	27.5	52.7	34.0
73	21.9	30.0	61.2	37.7
80	18.9	32.8	62.4	38.1
H.D. throughout	19.2	37.5	81.5	46.1
Mean	23.6	36.4	60.5	40.2
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	3.3	4.4	5.9	1.61
Vertical Margin	6.0	8.1	10.8	2.95
Body of Table	10.4	14.1	18.7	5.10

Table 14.

Leaf area index for high density plots.

Day of Harvest	Treatment		
	N_1	N_2	N_3
24	1.85	1.84	1.84
38	4.04	4.58	6.03
52	4.87	5.06	8.34
66	4.48	6.89	11.40
80	3.08	4.71	9.07
87	2.20	4.37	9.39
109	1.67	2.64	6.06

Table 15.

Mean area per leaf (cm^2). Leaf 2, day 38 data.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	4.3	4.2	4.7	4.4
24	4.1	4.5	4.4	4.4
H.D. throughout	4.3	4.1	4.7	4.4
Mean	4.2	4.3	4.6	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.4	-	-	0.188
Vertical Margin	N.S.	-	-	-
Body of Table	N.S.	-	-	-

Table 16.

Mean area per leaf (cm^2). Leaf 3, day 38 data.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	11.2	11.1	13.8	12.0
24	12.1	13.4	13.3	12.9
N.D. throughout	12.4	12.8	13.8	13.0
Mean	11.9	12.4	13.6	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.8	1.0	1.3	0.387
Vertical Margin	0.8	1.0	-	0.387
Body of Table	1.3	1.8	2.3	0.671

Table 17.

Mean area per leaf (cm^2). Leaf 4, day 38 data.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	12.4	14.9	21.0	16.1
24	14.5	18.0	23.0	18.5
N.D. throughout	18.5	21.3	25.8	21.8
Mean	15.1	18.0	23.3	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.9	1.1	1.4	0.430
Vertical Margin	0.9	1.1	1.4	0.430
Body of Table	1.5(N.S.)	-	-	0.744

Table 18.

Mean area per leaf (cm^2). Leaf 5, day 52 date.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	10.6	12.8	17.3	13.6
24	11.9	14.5	20.1	15.5
38	14.4	19.1	28.4	20.6
45	16.5	20.8	29.3	22.2
H.D. throughout	17.1	21.0	29.6	22.6
Mean	14.1	17.6	24.9	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.7	0.9	1.1	0.343
Vertical Margin	0.9	1.1	1.5	0.443
Body of Table	1.5	2.0	2.5	0.767

Table 19.

Mean area per leaf (cm^2). Leaf 6, day 66 data.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	9.6	11.1	13.3	11.4
24	9.5	11.7	14.8	12.0
38	8.1	11.0	20.4	13.1
45	9.2	14.2	25.7	16.4
52	10.4	15.7	24.2	16.8
59	10.4	15.7	26.6	17.6
H.D. throughout	10.5	17.0	25.8	17.8
Mean	9.7	13.8	21.5	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.5	0.7	0.9	0.274
Vertical Margin	0.8	1.1	1.4	0.438
Body of Table	1.4	1.9	2.4	0.725

Table 20.

Mean area per leaf (cm^2). Leaf 7, day 66 data.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	11.6	12.2	13.8	12.5
24	10.1	12.2	14.3	12.2
38	8.0	10.4	18.7	12.4
45	7.2	11.6	21.4	13.4
52	7.4	12.6	22.7	14.3
59	8.6	14.7	26.7	16.7
H.D. throughout	8.6	14.9	27.7	17.1
Mean	8.8	12.6	20.8	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.7	0.9	1.2	0.351
Vertical Margin	1.1	1.4	1.8	0.537
Body of Table	1.8	2.4	3.1	0.932

Table 21

Mean leaf area/leaf weight ratios.

Day of Transfer to Low Density	Leaf number* (In order of appearance).					
	2	3	4	5	6	7
12	-	434	367	287	270	279
24		385	346	297	276	253
38		486	345	284	273	267
45				350	308	269
52				368	350	310
59						330
66						323
Mean for leaf	383	435	353	317	296	290
S.E.D.	-	39.4	12.2	16.9	14.5	13.9
L.S.D. .05	-	N.S.	N.S.	37	32	32
.01	-	-	-	52	44	44
.001	-	-	-	70	63	59

* Data obtained at different dates.

For leaf 2 from harvest at day 24
" leaves 3&4 " " " " 52
" " 5&6 " " " " 66
" leaf 7 " " " " 80.

Table 22.

Length of apex (mm). Harvest day 24.

	N_1	N_2	N_3
Mean	0.47	0.49	0.48

Analysis of Variance

Source	df.	S.S.	M.S.	V.R.
Total	17	0.1157	-	-
Nitrogen	2	0.0015	0.00075	0.09 N.S.
Error	15	0.1142	0.00761	

Table 23.

Length of apex (mm). Harvest day 38.

	N_1	N_2	N_3
Mean	1.12	1.16	1.36

Analysis of Variance

Source	df.	S.S.	M.S.	V.R.
Total	26	0.8315	-	-
Nitrogen	2	0.3054	0.1527	6.97**
Error	24	0.5261	0.0219	

S.E.D.	L.S.D.	.05	.01
0.108	Nitrogen	0.22	0.30

Table 24.

Length of apex (mm). Harvest day 52.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	3.41	3.88	9.78	5.49
24	3.26	4.91	8.78	5.65
38	4.16	4.47	6.52	5.05
H.D. throughout	3.94	4.43	4.68	4.34
Mean	3.69	4.27	7.44	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	1.93	2.73	-	3.89
Vertical Margin	N.S.	-	-	-
Body of Table	N.S.	-	-	-

Table 25.

Mean length of apex (mm). Harvest day 66.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	32	38	68	46
24	24	26	66	38
38	46	51	79	59
52	45	56	75	58
H.D. throughout	28	30	48	36
Mean	35	40	67	

Not analysed. (Very variable).

Table 26.

Mean number of infertile spikelets per ear. Harvest day 135.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	3.2	3.7	3.5	3.5
24	3.2	3.7	2.7	3.2
38	4.5	3.5	2.7	3.6
45	6.2	5.0	3.0	4.7
52	5.5	5.7	3.5	4.9
59	7.0	6.5	3.7	5.7
66	7.2	6.5	4.5	6.1
73	7.5	7.0	4.7	6.4
80	7.5	7.0	5.0	6.5
94	7.5	7.5	4.7	6.6
H.D. throughout	7.0	7.5	4.2	6.2
Mean	6.0	5.8	3.9	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.3	0.4	0.5	0.147
Vertical Margin	0.6	0.8	1.0	0.282
Body of Table	1.0	1.3	1.8	0.489

Table 27.

Mean number of fertile spikelets per ear. Harvest day 135.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	11.5	11.7	14.2	12.5
24	11.2	12.2	16.5	13.3
38	11.0	13.0	16.7	13.6
45	8.7	11.5	17.0	12.4
52	8.5	11.0	16.2	11.9
59	8.2	10.2	15.0	11.6
66	8.0	10.7	15.0	11.2
73	7.2	9.0	14.5	10.4
80	7.2	9.7	15.5	10.5
94	7.7	10.0	15.0	11.1
N.D. throughout	8.2	9.5	15.0	10.9
Mean	8.9	10.8	15.6	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.4	0.6	0.7	0.201
Vertical Margin	0.8	1.1	1.4	0.385
Body of Table	1.4	1.8	2.4	0.667

Table 28.

Mean total spikelet number per ear. Harvest day 135.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	14.7	15.5	17.7	16.0
24	14.5	16.0	19.2	16.6
38	15.5	16.5	19.5	17.2
45	15.0	16.5	20.0	17.2
52	14.0	16.7	19.7	16.8
59	15.2	16.7	20.0	17.3
66	15.2	17.2	19.5	17.3
73	14.7	16.0	19.7	16.8
80	14.7	16.7	19.5	17.0
94	15.2	17.5	20.2	16.7
H.D. throughout	15.2	16.5	19.2	17.0
Mean	14.9	16.5	19.5	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.4	0.5	0.7	0.182
Vertical Margin	0.7	1.0	1.3	0.348
Body of Table	N.S.	-	-	-

Table 29

Mean grain number per ear. Harvest day 135.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	24.5	21.7	29.2	25.2
24	24.5	25.5	31.5	27.2
38	20.5	24.0	34.2	26.2
45	13.0	24.5	36.2	24.6
52	14.5	18.2	29.5	20.7
59	11.7	17.7	31.0	20.2
66	11.0	15.5	23.0	16.5
73	7.7	14.0	24.7	15.5
80	9.2	13.7	22.5	15.2
94	6.5	14.0	26.0	16.2
H.D. throughout	10.5	14.5	25.2	16.7
Mean	14.2	18.5	28.5	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	1.9	2.5	3.4	0.92
Vertical Margin	3.6	4.9	6.5	1.77
Body of Table	N.S.	-	-	-

Table 32.

Mean weight of grain per ear (g). Harvest day 135.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	0.93	0.91	1.23	1.03
24	1.02	1.03	1.25	1.10
38	0.86	1.05	1.34	1.09
45	0.45	0.92	1.40	0.93
52	0.52	0.69	1.22	0.81
59	0.43	0.67	1.26	0.79
66	0.37	0.53	0.93	0.61
73	0.27	0.57	1.09	0.64
80	0.32	0.51	0.95	0.59
94	0.28	0.48	1.06	0.61
H.D. throughout	0.33	0.50	1.04	0.62
Mean	0.53	0.72	1.16	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.08	0.10	0.14	0.038
Vertical Margin	0.15	0.20	0.26	0.073
Body of Table	N.S.	-	-	-

Table 21.

Mean weight of grain per plant (g). Harvest day 135.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	1.03	1.35	2.03	1.47
24	1.02	1.26	1.94	1.41
38	0.86	1.26	1.34	1.15
45	0.45	0.92	1.40	0.93
52	0.52	0.79	1.22	0.84
59	0.43	0.67	1.26	0.79
66	0.37	0.53	0.93	0.61
73	0.27	0.57	1.09	0.64
80	0.32	0.51	0.95	0.59
94	0.28	0.48	1.06	0.61
H.D. throughout	0.33	0.50	1.04	0.62
Mean	0.54	0.81	1.30	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.12	0.16	0.22	0.060
Vertical Margin	0.23	0.31	0.42	0.114
Body of Table	N.S.	-	-	-

Table 32.

Mean weight per grain (mg). Harvest day 135.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	37.9	42.0	42.3	40.8
24	41.6	40.7	39.9	40.7
38	42.0	44.0	39.5	41.9
45	34.6	37.5	38.9	37.0
52	36.2	38.2	41.4	38.6
59	37.2	37.7	40.8	38.6
66	34.6	34.1	41.1	36.6
73	36.3	40.9	43.7	40.3
80	35.1	37.2	41.5	37.9
94	33.8	34.5	41.2	36.5
H.D. throughout	31.4	35.2	41.4	36.0
Mean	36.4	38.4	41.1	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	1.2	1.6	2.1	0.58
Vertical Margin	2.3	3.1	4.1	1.11
Body of Table	3.9	5.3	7.0	1.93

Table 33.

Mean percent nitrogen in whole plants. Harvest day 38.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18*	2.46	2.07	3.32	2.62
N.D. throughout	2.53	2.94	4.27	3.25
Mean	2.49	2.50	3.80	2.93
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.18	0.28	0.48	0.070
Vertical Margin	0.15	0.23	0.39	0.057
Body of Table	0.26	0.40	0.68	0.099

*Mean of combined samples.

Table 34.

Mean percent nitrogen in whole plants. Harvest day 52.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	1.65	1.51	1.76	1.64
38	1.19	1.41	2.07	1.56
H.D. throughout	1.61	2.01	3.25	2.29
Mean	1.48	1.64	2.36	1.83
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.14	0.20	0.30	0.060
Vertical Margin	0.14	0.20	0.30	0.060
Body of Table	0.24	0.35	0.52	0.103

*Mean of combined samples.

Table 35.

Mean percent nitrogen in whole plants. Harvest day 66.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	1.26	1.12	1.02	1.13
38	0.84	0.88	0.88	0.87
48	0.91	1.05	1.36	1.11
H.D. throughout	1.05	1.48	1.74	1.42
Mean	1.01	1.13	1.25	1.13
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.09	0.13	0.19	0.042
Vertical Margin	0.11	0.15	0.22	0.049
Body of Table	0.19	0.26	0.38	0.085

*Mean of combined samples.

Table 36.

Mean percent nitrogen in leaf and stem. Harvest day 87.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	0.95	0.84	0.62	0.80
38	0.67	0.65	0.56	0.63
48	0.54	0.68	0.78	0.67
62	0.56	0.59	0.71	0.62
76	0.57	0.63	0.78	0.66
H.D. throughout	0.63	0.81	1.06	0.83
Mean	0.65	0.70	0.75	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.02	0.03	0.03	0.009
Vertical Margin	0.03	0.04	0.05	0.012
Body of Table	0.05	0.06	0.09	0.022

*Mean of combined samples.

Table 37.

Mean percent nitrogen in ears. Harvest day 87.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	1.47	1.44	1.38	1.43
38	1.26	1.26	1.34	1.28
48	1.24	1.30	1.42	1.32
62	1.30	1.33	1.41	1.35
76	1.29	1.34	1.57	1.40
H.D. throughout	1.29	1.40	1.69	1.46
Mean	1.31	1.35	1.47	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.06	0.08	0.10	0.026
Vertical Margin	0.08	0.11	0.15	0.037
Body of Table	0.14	-	-	0.065

*Mean of combined samples.

Table 38.

Mean percent nitrogen in leaf and stem. Harvest day 135.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	0.31	0.25	0.28	0.28
38	0.25	0.32	0.23	0.27
48	0.31	0.43	0.32	0.36
62	0.36	0.43	0.35	0.38
76	0.42	0.39	0.34	0.38
94	0.37	0.36	0.39	0.37
H.D. throughout	0.35	0.34	0.23	0.31
Mean	0.34	0.36	0.31	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.01	0.02	0.02	0.006
Vertical Margin	0.02	0.03	0.04	0.010
Body of Table	0.03	0.05	0.06	0.017

*Mean of combined samples.

Table 39.

Mean percent nitrogen in grain. Harvest day 135.

Day of Transfer[a] to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	2.17	1.97	1.86	2.00
38	2.00	2.04	1.75	1.93
48	1.77	1.99	1.85	1.87
62	1.80	1.65	1.71	1.72
76	1.80	1.73	1.61	1.72
94	1.75	1.66	1.58	1.67
H.D. throughout	1.58	1.69	1.61	1.63
Mean	1.84	1.82	1.71	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.03	0.04	0.05	0.014
Vertical Margin	0.04	0.06	0.08	0.021
Body of Table	0.08	0.10	0.14	0.037

[a] Mean of combined samples.

Table 40.

Mean yield of nitrogen per plant (mg). Harvest day 38.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	3.95	3.75	8.95	5.55
N.D. throughout	3.50	4.40	8.50	5.47
Mean	3.72	4.07	8.72	5.51
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.29	0.46	0.78	0.114
Vertical Margin	0.24	-	-	0.093
Body of Table	0.41	0.65	-	0.161

*Mean of combined samples.

Table A1.

Mean yield of nitrogen per plant (mg). Harvest day 52.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	4.60	6.05	14.45	8.37
38	3.35	5.65	14.50	7.83
H.D. throughout	4.35	6.65	13.95	8.32
Mean	4.10	6.12	14.30	8.17
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.38	0.55	0.82	0.163
Vertical Margin	0.38	-	-	0.163
Body of Table	0.57	-	-	0.283

*Mean of combined samples.

Table 42.

Mean yield of nitrogen per plant (mg). Harvest day 66.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	7.20	9.20	16.85	11.08
38	5.50	7.25	12.20	8.32
48	4.35	7.25	13.60	8.40
H.D. throughout	4.55	7.45	15.00	9.00
Mean	5.40	7.79	14.41	9.20
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.23	0.32	0.46	0.104
Vertical Margin	0.26	0.37	0.53	0.120
Body of Table	0.46	0.64	0.92	0.207

*Mean of combined samples.

Table 43.

Mean yield of nitrogen per plant (mg). Harvest day 87.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	12.95	16.15	22.50	17.22
38	7.50	10.45	19.20	12.38
48	6.00	9.50	20.55	12.02
62	5.45	8.50	18.35	10.77
76	5.65	8.20	18.20	10.68
H.D. throughout	5.30	8.35	18.45	10.70
Mean	7.14	10.19	19.55	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.30	0.41	0.56	0.141
Vertical Margin	0.42	0.58	0.79	0.199
Body of Table	0.73	1.00	1.37	0.345

*Mean of combined samples.

Table 44.

Mean yield of nitrogen per plant (mg). Harvest day 135.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	26.90	30.20	45.00	34.03
38	19.20	30.75	32.10	27.35
48	11.10	21.90	31.00	21.33
62	10.15	14.25	25.40	16.60
76	8.45	13.05	22.70	14.73
94	7.75	11.90	24.25	16.63
N.D. throughout	8.15	12.75	20.15	13.65
Mean	13.10	19.26	28.66	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.39	0.54	0.73	0.189
Vertical Margin	0.60	0.82	1.11	0.288
Body of Table	1.04	1.42	1.92	0.499

*Mean of combined samples.

Table 45.

Mean yield of nitrogen per plant as leaf and stem (mg).
Harvest day 87.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	9.40	12.80	14.90	12.10
38	5.40	7.45	11.80	8.22
48	4.15	6.90	14.60	8.55
62	3.90	6.10	13.70	7.90
76	4.20	6.20	13.55	7.98
H.D. throughout	4.15	6.85	14.90	8.63
Mean	5.20	7.58	13.91	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.20	0.27	0.37	0.094
Vertical Margin	0.28	0.38	0.53	0.133
Body of Table	0.48	0.67	0.91	0.230

*Mean of combined samples.

Table 46.

Mean yield of nitrogen per plant as ears (mg).
Harvest day 87.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	3.55	4.15	7.65	5.12
38	2.10	3.00	7.40	4.12
48	1.85	2.60	5.95	3.47
62	1.55	2.40	4.65	2.87
76	1.45	2.00	4.60	2.68
H.D. throughout	1.15	1.50	3.55	2.07
Mean	1.94	2.61	5.63	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.22	0.31	0.42	0.106
Vertical Margin	0.31	0.43	0.59	0.149
Body of Table	0.55	0.75	1.03	0.259

*Mean of combined samples.

Table 47.

Mean yield of nitrogen per plant as leaf and stem (mg).
Harvest day 135.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	4.55	4.30	7.90	5.58
38	2.60	5.05	5.65	4.43
48	2.40	4.75	6.60	4.58
62	2.90	4.35	6.60	4.62
76	3.00	3.70	6.40	4.37
94	2.70	3.90	7.30	4.63
H.D. throughout	2.60	3.45	3.75	3.27
Mean	2.96	4.21	6.31	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.19	0.26	0.36	0.926
Vertical Margin	0.29	0.40	0.54	0.142
Body of Table	0.51	0.70	0.94	0.245

*Mean of combined samples.

Table 48.

Mean yield of nitrogen per plant as grain (mg).
Harvest day 135.

Day of Transfer* to Low Density	Treatment			Mean
	N_1	N_2	N_3	
18	22.35	25.90	37.10	28.45
38	16.60	25.70	26.45	22.92
48	8.70	17.15	24.40	16.75
62	7.25	9.90	18.80	11.98
76	5.45	9.35	16.30	10.37
94	5.05	8.00	16.95	10.00
H.D. throughout	5.55	9.30	16.40	10.42
Mean	10.14	15.04	22.34	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.26	0.35	0.48	0.124
Vertical Margin	0.39	0.54	0.73	0.189
Body of Table	0.63	0.93	1.26	0.327

*Mean of combined samples.

Table 49.

Yield of nitrogen by high density plots. (g/m^2).

Day of Harvest	Treatment			Mean
	N_1	N_2	N_3	
38	4.0	4.5	9.7	6.1
52	5.0	7.7	16.0	9.6
66	5.3	8.6	17.2	10.4
87	6.1	9.6	21.2	12.3
135	9.4	14.6	23.7	15.9
Mean	5.9	9.0	17.6	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.4	0.6	0.8	0.197
Vertical Margin	0.5	0.7	1.0	0.254
Body of Table	0.9	1.3	1.8	0.440

Table 50.

Total soil nitrogen (mean % x 100). Sampled day 40.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	3.60	3.95	5.20	4.25
24	4.15	4.30	5.15	4.53
38	4.10	4.75	4.90	4.58
Mean	3.95	4.33	5.08	4.45
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.34	0.49	0.74	0.147
Vertical Margin	0.34(N.S.)	-	-	0.147
Body of Table	0.59(N.S.)	-	-	0.255

Table 51.

Mean total soil nitrogen (mean % x 100). Sampled day 138.

Day of Transfer to Low Density	Treatment			Mean
	N_1	N_2	N_3	
12	3.80	4.00	4.30	4.03
38	4.10	4.00	4.40	4.17
66	4.20	4.10	4.45	4.25
94	4.10	4.05	4.20	4.12
H.D. throughout	4.35	4.20	4.60	4.38
Mean	4.11	4.07	4.39	
L.S.D.	.05	.01	.001	S.E.D.
Lower Margin	0.20	0.28	-	0.095
Vertical Margin	0.26(N.S.)	-	-	0.123
Body of Table	N.S.	-	-	-

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