THE RESPONSE OF BARLEY GENOTYPES TO AGRONOMIC MANIPULATION IN A MEDITERRANEAN TYPE OF CLIMATE

by

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To my father

CONTENTS

SUMMARY

The attainment of higher barley yields through simultaneous change in genotype and agronomic practice was investigated in South Australia between 1967 and 1970. Varieties were selected on origin, maturity and row number, and grown at a wide range of each of several environmental or cultural factors to enable comparison of their performance under conventional and optimum levels. Characteristics associated with the differential response of varieties were identified and accentuated in subsequent experiments to verify their relationship with yield determining processes.

The South Australian barley crop is planted in June or July, grows through winter, flowers in mid-October and fills grain during the spring under an increasingly severe moisture deficit. However, yields were also depressed during the winter period when moisture levels were adequate but light intensities low. Earlier planting, higher fertility or higher densities often resulted in excessive numbers of etoliated tillers that lodged prior to stem elongation with an accompanying severe reduction in ear numbers. Juvenile lodging was prevented, and ear survival increased by defoliation, application of CCC and supporting the crop. Varietal resistance to this early

lodging was associated with sparse tillering, few leaves per culm, short, wide and upright leaves and thick pseudostems. The yield of resistant varieties increased with nitrogen application up to 275 kg/ha, while susceptible varieties had an optimum at 0 kg/ha.

The number of ears surviving at high plant densities was negatively correlated with the anthesial date of varieties. Distribution of ear size became progressively more skewed to the left with increasing density and delayed maturity, eventually becoming bimodal with a large class of aborted ears. Competition for all resources apparently increased with time, and the earliest varieties suffered least. When a predetermined moisture stress was applied over set growth phases, the periods of stress were shorter in the early varieties and their yield components, and particularly grains per ear, were less affected. This advantage of earliness was lost with a late sowing in August, as all varieties then developed and flowered together.

One extremely early and sparse tillering variety had a low yield at low or conventional densities, but a very high yield at high densities. All the late flowering varieties had a much lower optimum density, but the negative correlation between yield at high and low density was broken by a profusely tillering, early variety and a temperate, late, two-row variety that had consistently high and low yields respectively.

Despite regular high vapour pressure deficits in the spring, severely shrunken grains occurred only once, after early irrigation had stimulated vegetative growth. Usually, the ranking in 1000 grain weight between varieties remained constant, and nitrogen application decreased the grain weight uniformly. Instead, moisture stress greatly reduced the number of grains set in the late, and especially two-row, varieties.

Nitrogen increased moisture usage, but although varieties occasionally differed significantly, the differences did not appear related to dry matter production or leaf area. The early varieties initially produced more dry matter and leaf area regardless of tiller number, while the late varieties continued to tiller later into the season, had greater dry weight at anthesis, but increased less in dry weight after anthesis than in grain weight. Grain growth was more rapid in the late varieties. Nitrogen application increased the LAD after anthesis, but decreased the 1000 grain weight. The grains per ear were not related to the early differences in dry weight and leaf area per tiller.

The value of the characters examined in these studies to barley breeding in a Mediterranean type of climate is discussed, together with proposed screening methods, and the concomitant changes in agronomic practice necessary for increased yields.

STATEMENT

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

C. J. Gardener

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I. INTRODUCTION

INTRODUCTION

New material in a cereal breeding programme is usually tested under agronomic conditions considered typical of the area served by the programme; the resulting selections are expected to perform well in comparison to existing varieties when released to farmers. Agronomists may test the new variety in various situations, but its commercial acceptance is likely only if it is suited to the fertility levels and plant populations already employed by the farmer. This system is proven and accepted, but it does tend to maintain the status quo and allow only slow evolution away from the varities suited to the existing conditions. Yet rapid progress seems to occur only when the new variety is such a radical departure from its predeccesor, like the semi-dwarf wheat and rice varieties, that new agronomic practices have to be employed. No such revolution has yet occurred in barley.

Discarding the genotypes not adapted to the local agronomic niche can reduce the potential of the programme, especially if agronomic practices change. Some of these types might have exceptional yields at specific plant population, soil fertility and moisture levels. Even if the existing varieties are well adepted to all conditions, and exceed the yield of those with sharp optima, the characteristics of the latter may well prove of value in the programme.

Unfortunately, it requires an enormous expenditure of time and effort to grow the world barley collection (10,000 varieties) for observation and seed preservation. Further, plant breeders are justifiably wary in using exotic material in simple crosses with adapted material. So many deleterious characters may be introduced, that huge segregating populations become necessary to provide superior recombinations. Therefore the value of exotic varieties as parents, and of segregating plants as future varieties, can be most readily assessed visually on phenotypic characters; especially if these are accentuated by extreme levels of each agronomic variable.

The object of the experiments reported in this thesis was firstly to reveal characteristics associated with success at various levels of water, nitrogen and density within a small but diverse group of barley genotypes. And secondly to seek to modify or accentuate these characteristics in order to examine further their apparent yield determining processes. The programme also permitted assessment of the effectiveness of normal plant breeding methods in evaluating introductions and the comparison, over a wide range of varieties and seasons, of the processes involved in the response to various factors.

II. LITERATURE REVIEW

II REVIEW OF LITERATURE

After the intensive study of the cereals in recent years, it is now possible to describe in part the growth and development of a crop throughout its life cycle, and the effect of environmental factors on the individual processes that collectively determine yield. Studies have also been successfully undertaken in the field on the complex relationships that exist when the environmental factors interact with one another and have a cumulative effect on each succeeding growth phase. Further expansion of such experiments to include a systematic survey of genotypic variation has, however, been rarely attempted. So that parts of this literature review are predominately physiological in content, with little reference to differences between genotypes.

Parts A - D describe the various processes during the development of the crop that determine grain yield, and how these are affected by variation in solar radiation, photoperiod, mineral nutrition, water temperature and morphological characteristics. Early vegetative growth and the subsequent attainment of a suitable leaf area are discussed in Part A, and the productivity of this canopy in terms of dry matter production in Part B. Part C deals with the conversion of this dry matter into ears and fertilised florets, while the accumulation of dry matter in these florets is covered in Part D.

The effect of manipulation of agronomic practices like irrigation, fertilisation and seeding rate on environmental factors, and the resulting interaction in grain yield when an increased supply of one resource (i.e. nitrogen) decreases the availability of another (i.e. water) is described in Part E. Examples of the differential response of varities to agronomic changes and some of the characters involved are given in Part F, the latter mainly emanating from empirical relationships with grain yield established by plant breeders.

Throughout the review, examples of crops other than cereals are used to illustrate principles where there is a paucity of information in cereals. Evidence for certain personal viewpoints has been taken from published papers and the authors acknowledged, even though the particular conclusions or deductions were not drawn by the author.

A. LEAF AREA

ENVIRONMENTAL EFFECTS. The leaf area developed by cereal crops fluctuates widely between years and sites; most commercial cereal varities being both sensitive and plastic in their response to variation in climatic and edaphic conditions, and in the agronomic practices used by farmers.

Initially the leaf area is proportional to the number of seedlings (Puckridge and Donald, 1967) and to the leaf area per seedling, which is dependent on seed size and the mobilization of seed reserves (Montgomery, 1912; Bremner et al., 1963; Demirlicakmak et al., 1963; Lexander, 1963). Thereafter until cessation, leaf growth is a cumulative process with part of the photosynthate produced being reinvested in new photosynthetic tissue (Blackman, 1919).

Generally, there is a close relationship between the per cent dry matter incorporated in new shoot and in new root growth (Troughton, 1956, 1960, 1961; Brouwer, 1962a, 1962b). However, relatively more dry matter is used in new shoot growth after defoliation or during severe mutual shading (Mitchell, 1954; Lebedev, 1963; Friend, 1966) when the amount of assimilate available for new growth is low (Milthorpe and Davidson, 1966). Conversely, a lower percentage of dry matter is incorporated into new shoot growth under low temperatures, mineral nutrient deficiencies and moisture stress (Loomis, 1953).

The actual leaf area formed from a given amount of dry matter depends on the density and thickness of the leaf tissue. Leaf cell enlargement is reduced approximately in proportion to cell turgor (Gardner and Nieman, 1964), while cell division and photosynthesis remain relatively unaffected (Slatyer, 1969), so moisture stress results in shorter, thicker leaves with more cells, stomates and venation per unit leaf area (Maximov, 1929; Whiteside, 1941). Such tissue shows an increased resistance to wilting and desiccatio during subsequent periods of moisture stress (Iljin, 1957; Asana, 1960; Henckel, 1964).

Sub-optimal temperatures and nitrogen levels result in a similar leaf morphology (Whiteside, 1941; Friend, 1966) and deficiencies in moisture (Gardner, 1942; Fischer and Kohn, 1966c) and nitrogen (Aspinall, 1963; Aspinall and Paleg, 1963) also greatly reduce the number of tillers formed per plant. High light intensities falling on individual tillers also diminish leaf size but increase the assimilate available for new growth and cause profuse tillering (Wiggans, 1939; Khalil, 1956; Friend, 1965b) if supplies of moisture and nitrogen are adequate.

EFFECT OF GENOTYPE. Although all varieties respond to improved environmental conditions with increased leaf areas, the magnitude of the increase varies considerably with variety. Further, the relative differences between varieties in characteristics like leaf length, tiller number and number of leaves per tiller are maintained under widely differing environmental conditions (Hamblin, unpubl. data).

The total number of leaves on a tiller is determined by the number of primordia not committed to spikelets at the double ridge stage, and as such, is less influenced by the local environment than by genotype and photoperiod (Nicholls and May, 1963). The variation in leaf number per main culm under long days ranges from 7 in varieties with a short life cycle to 20 in varieties with a marked response to photoperiod (Gott et al., 1955; Aspinall, 1966; Kirby and Eisenberg, 1966). However, barley behaves as a quantitative long-day plant (Johnson and Taylor, 1958; Guitard, 1960; Kirby and Eisenberg, 1966) and the leaf number falls from 7 to 6 and from 20 to 8 respectively for the two types grown under short daylengths. Varietal differences in the length of leaves are also most pronounced under short days, with the latter varieties producing successively longer leaves on a tiller until stem elongation commences (Borrill, 1959). Stem elongation is associated with higher levels of gibberellins which tend to inhibit tillering (Kirby, 1970) and early varieties have a reduced tillering potential (Asana, 1963).

OPTIMAL LEVEL OF LEAF AREA. Adequate leaf areas can be achieved in a cereal crop by high seeding rates, irrigation and fertilization to intercept practically all the incoming radiation at an early stage of growth. This prompted Watson (1952) to propose the use of these agronomic means to attain rapid ground cover and prevent wastage of light since light interception and rate of dry matter production are positively correlated (Watson, 1956; Black, 1958, 1964; Brougham,1958, 1959). Unfortunately, the early attainment of high leaf areas can also result in an earlier depletion of soil moisture (Colwell, 1963a; Barley and Naidu, 1964; Fischer and Kohn, 1966a; Luebs and Laag, 1969) and nitrogen (Puckridge and Donald, 1967) and can later lead to excessive competition for light (Puckridge and Donald, 1967). High leaf areas therefore tend to reach a very transitory peak during stem elongation (Stoy, 1965), followed by rapid senescence, when even the remaining green foliage seems to lose activity (Puckridge and Donald, 1967; Williams et al., 1968).

It may therefore be expedient to try to achieve leaf areas well below those required for complete light interception. The sacrifice in dry matter production may be small, since reducing the leaf area by half only decreases light interception from 95 to 75 per cent because of the assymptotic approach of light interception to a maximum, while the availability of the other resources per unit of leaf area is greatly increased. Clipping or grazing the crop presents one method of obtaining the desired leaf areas (Kiesselbach and Lyness, 1948; Davidson, 1965) but involves removing the youngest and most active growth first. The best method therefore appears to be the use of early, sparsely tillering varieties which have a few, short leaves per tiller. Such varieties could reach sufficiently high light interception if sown at above commercial seed rates, but should show a minimal response to improved environmental conditions.

B. DRY MATTER PRODUCTION

NET ASSIMILATION RATE. The rate of dry matter production (RDMP)[1] of a crop is equal to the mean productivity per unit leaf area (NAR)[1] times the number of units of leaf area per unit area of ground (LAI)[1]. The NAR is calculated from the RDMP and the LAI, and is therefore a rather arbitrary value, depending on, among other things, how many aging and senescing leaves were included with fully active tissue in calculating the LAI. The RDMP increases with increasing LAI until becoming asymptotic at the higher levels of

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1. The terms RDMP, NAR, and LAI are used after Blackman (1968) rather than C or CGR, E, and L because of the usage of crop growth rate for increases both in height and dry matter, parameters correlated only early in the life cycle of grain crops.

light interception. The NAR shows a similar but negative response with increasing LAI.

Watson (1947, 1952) considered that differences in the RDMP between varieties and between years, within a species, resulted mainly from differences in LAI, and that when corrected to a constant LAI, any small differences in NAR were due to differences in solar radiation. He therefore propsed leaf area duration (LAD - the integral of LAI over the whole life cycle of a crop) as the determinant of yield. However, since growth is a cumulative and initially exponential process, the value of differences in NAR can easily be underestimated. Bleasdale (1966) calculated that 10 and 1.1 per cent increases in NAR would increase yield by 230 and 10 per cent respectively in a vegetative crop, while a 10 per cent increase in LAI would increase yield only 10 per cent. The NAR of a crop depends on two factors; the net photosynthetic capacity of leaves, and the distribution of the intercepted light over their surfaces.

ENVIRONMENTAL EFFECTS ON PHOTOSYNTHETIC CAPACITY.

Environmental factors, except light, have far less influence on photosynthetic rate than on leaf expansion (Aspinall, 1965; Wardlaw,1967, 1968). For example, photosynthesis is largely independent of temperature in wheat (Downes, 1970) having a Q_{10} of only 0.2 (Stoy,1965), and remains unaffected in cotton at a leaf water content of 55 per cent (about -

50 bars) (Troughton and Slatyer, 1969). Nitrogen deficiency has only the indirect effect of hastening the decline in photosynthetic activity with age (Murata, 1965).

However, the growth (in size) of organs may not be dependent on photosynthesis; instead, photosynthesis may be dependent on growth and development (Neales and Incoll, 1968) with the leaves operating well below the photosynthetic maxima of which they are capable (Maggs, 1964). It is significant that photosynthesis in the remaining part or in an adjacent leaf is greatly increased if part of an adult leaf is removed or becomes diseased (Kiesselbach, 1948; Livne and Daly, 1966; Wareing et al., 1968). When photosynthesis in a leaf is depressed by lack of a suitable sink, the level of soluble carbohydrates in the leaf rises (Moss, 1962a) but there is no proof that the two are causally related (Neales and Incoll, 1968). Growth regulators produced by the sink may stimulate the flow of assimilate into the sink (Aronoff, 1955; Stoy, 1969), and possibly account for the increase in photosynthesis at the beginning of seed filling in soybeans (Dornhoff and Shibles, 1970).

VARIETAL DIFFERENCES IN PHOTOSYNTHESIS. The genetic variation in the maximum rate of photosynthesis of individual leaves within a species was considered small (Gregory, 1950; Winkler, 1961; Watson and Witts, 1959; Watson et al., 1963; Stoy, 1965, 1969). But recently significant and large (up to three-fold) differences have been found in maize (Duncan and Hesketh, 1968; Heichel and Musgrave, 1969), soybeans (Ojima et al., 1968; Curtis et al., 1969; Dornhoff and Shibles, 1970), wheat and oats (Sheridan, 1966, cited by Carlson et al., 1970), ryegrass (Cooper and Wilson, 1970), lucerne, birdsfoot trefoil and cocksfoot (Carlson et al., 1970). Furthermore, in all cases the photosynthetic rates were strongly positively correlated with leaf weight/leaf area ratios, a trait easily measured by leaf discs. The denser or thicker leaves had more mesophyll cells and more vascularization per unit leaf area. However, these differences when integrated with those in LAI, leaf display and sink relationships usually prevent any variations in yield being attributed to differences in photosynthetic capacity of the leaves. Only one group (Ojima et al., 1968), working with soybeans, has been able to show a close relationship between the two.

PHOTOSYNTHESIS IN INDIVIDUAL LEAVES. The photosynthetic rate of an individual leaf increases linearly with increasing intensity at low light levels, but then increases at a decreasing rate above 8.6 to 10.8 klux. Whether the rate continues to increase (non-saturated) or remains constant (saturated) at increasing levels of light intensity depends on the species. Wheat (Stoy, 1965), barley (Gaastra, 1962), and rice (Murata, 1961) occupy an intermediate position between definitely non-saturated species like corn and sugar cane (Hesketh and Moss, 1963) and those having a distinct saturation level like tobacco, red clover (Hesketh and Moss, 1963), sugar beet and turnip (Gaastra, 1959), since cereals are non-saturated at 10.8 klux but the photosynthetic rate increases only very slowly with increasing light intensity.

PHOTOSYNTHESIS IN THE CANOPY. The upper leaves in a cereal canopy normally intercept light far in excess of that required for near maximum photosynthesis, especially if they are displayed horizontally to the incoming energy. Conversely the lower leaves are severely shaded, and thus much higher light intensities are required to saturate a closed canopy than a single leaf (Boysen-Jensen, 1932; Alexander and McCloud, 1962). Davidson and Phillip (1958) estimated that a broad-leaved canopy with LAI = 9 needed 144 klux to reach maximum photosynthesis.

Warren Wilson (1960) therefore proposed a canopy arrangement with the upper leaves near perpendicular, and the lower leaves near horizontal, with respect to the incoming light. This would allow sufficient illumination of the top leaves for near maximum photosynthesis, while the greater penetration of light would enable the lower leaves to also make a greater positive photosynthetic contribution. It was also thought that more of the intercepted light would be reflected down into the canopy (Verhagen et al., 1963), but this was overestimated since Fresnel's laws of reflection were found not to apply to the microscopically rough surface of leaves (Tageeva and Brandt, 1961; Kriedemann et al., 1964).

(a) ERECT LEAF TYPE. Experimentally, upright leaved varieties of rice (Hayashi and Ito, 1962) and barley (Gardener, 1966) have shown deeper light penetration and a greater RDMP than floppy leaved varieties. And the upright one of two isogenic single crosses of maize, differing only in leaf angle, yielded 40 per cent more than its horizontal counterpart (Pendleton, et al., 1968). The increased NAR of sugar beets over wild beets was also attributed to the reduced shading of the lower leaves by the erect upper leaves (Watson and Witts, 1959) although the sugar beets may also have intercepted more light (Monteith, 1965a) and the larger sugar beet roots provided greater sinks (Thorne and Evans, 1964).

In order to avoid any pleiotropic or other genetic effects, Matsushima et al., (1964) dropped the leaf angle of an erect leaved rice variety by fastening paper clips to the leaf tips, and Pendleton et al. (1968) increased the erectness of normally droopy maize leaves by tying them to the stem above the ear. Matsushima found photosynthesis was depressed 35 per cent at his close spacing, while Pendleton increased grain yield by 14 per cent. Generally, photosynthesis should be less affected by leaf angle in crops like maize which have higher levels of light saturation in leaves. The ability of maize leaves to photosynthesize equally well regardless of whether light strikes the adaxial or abaxial surface (Moss, 1964) is also important with increased erectness.

The value of using leaf angle as a criterion for the selection of higher yielding lines has been demonstrated for wheat, oats and barley (Tanner et al., 1966) and rice (Hayashi and Ito, 1962; Jennings, 1964; Beachell and Jennings, 1965; Tanaka et al., 1966). The inclination of a leaf is dictated by two factors; the angle of insertion into the culm and the amount of bending. The former often seems simply inherited (Donald, 1963), while the latter in turn depends on the length and mechanical support of the leaves. Narrow leaves tend to be weak and bend readily (Chandler, 1969), erect leaves have greater width, are thick and short (Tanaka et al., 1966) and have a high silica content (Ishizuka and Tanaka, 1950; Iwata and Baba, 1962). These characteristics can be obtained genetically, by the use of growth retardents like CCC (Primost, 1968) or agronomically (high light intensity, low nitrogen, low water - **Part A**).

(b) OTHER CANOPY CHARACTERISTICS. A more uniform distribution of light throughout the canopy also arises from arrangement of many small leaves with a minimum of overlap (Kasanaga and Monsi, 1954; Warren Wilson, 1960). Larger leaves require greater vertical separation to have a diffuse light pattern similar to smaller leaves (c.f. sunflowers and lucerne) (Anderson, 1966). Fewer leaves per stem are therefore more preferable in dwarf cereal varieties than the same number of leaves closer together (Stoskopf et al., 1963; Donald, 1968a, b).

Planting cereals in rows causes a very uneven distribution of leaves, and this is only relieved after the onset of stem elongation. The plants are initially more erect at higher densities (Pearce et al., 1967a,b) where there is little lateral illumination, while at lower densities, the plants lack the mechanical support of their neighbours, and both tillers and leaves spread more horizontally (Saeki, 1963; Tanaka et al., 1964; Pearce et al., 1967a, b). Much more light is intercepted per unit leaf area in low density cereal crops (k = 0.7 as opposed to k = 0.25 in very dense young barley swards).*

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* k = coefficient of extinction in $e^{-k} = \frac{I}{Io} L$
where I = light intensity beneath leaf area index of L
and Io = light intensity above the crop
(Monsi and Saeki, 1953; Kasanaga and Monsi, 1954;
Davidson and Philip, 1958).

(c) MORPHOLOGICAL DISEASE RESISTANCE. Open, erect-leaved canopies have more gradual temperature and vapour pressure gradients than have canopies with long pendant leaves (Monteith, 1966) and the improved ventilation may well provide less favourable conditions to fungal spores that germinate only in a film of water (Monteith, 1969). The rotting of cotton bolls, for instance, was greatly reduced (55 per cent) by the incorporation of the super okra leaf shape which produced a far more open canopy (Andries et al., 1970). In barley, the progress of both powdery mildew and Rhynchosporium is greatly encouraged by damp, humid conditions (Crawford, 1964), and the mildew resistance rating of Proctor has shown steady decline since 1953, largely because of the more luxuriant foliage due to increased nitrogen fertilization (Howard et al., 1970). Grain yield can be reduced up to 40 per cent by powdery mildew (Lawes and Hayes, 1965) and up to 60 per cent by Rhynchosporium (James et al., 1968).

MAXIMUM PRODUCTION OF DRY MATTER. The RDMP increases with LAI until the light energy penetrating to the lowest leaves is just sufficient for their photosynthetic gains to compensate their respiratory losses (Donald, 1963). What happens when the LAI greatly exceeds this value and the light intensity is insufficient for compensation has very important practical implications. Far more caution is required in moving to higher plant populations and fertilizer rates if the excess foliage is going to greatly depress the RDMP than if it remains near maximum.

Decreases in RDMP at supra-optimal LAIs were predicted by Monsi and Saeki (1953) and Kasanaga and Monsi (1954) and have been reported in sugar beet and kale (Watson, 1956, 1958), subterranean clover (Davidson and Donald, 1958; Black, 1963), and rice (Murata, 1961; Takeda, 1961; Tanaka et al., 1966). No similar declines were observed in pastures (Brougham, 1956, 1958), rice (Tanaka et al., 1964), soybeans (Shibles and Weber, 1965) and maize (Williams et al., 1965b).

The depressions in RDMP observed by earlier authors have since been attributed to failure to include material dying between harvests, to climatic changes or nutrient deficiencies (McCree and Troughton, 1966), or to the artificial generation of differences in LAI by thinning or clipping the high LAIs obtained by high sowing rates (Brown and Blaser, 1968). Furthermore respiration, which was previously considered proportional to LAI and therefore to depress the RDMP at high LAIs (Watson, 1956, 1958), has been found proportional to gross photosynthesis itself, and to decline per unit leaf area with increasing LAI (Ludwig et al., 1965; McCree and Troughton, 1966; King and Evans, 1967; Wilfong et al., 1967).

However, whether the RDMP falls or not, depends on the magnitude of the decline in NAR, and not on the linearity or curvilinearity of the NAR (Blackman, 1968). The NAR even fell curvilinearly to below zero (a negative RDMP) in one very dense crop where mutual shading was greatly accentuated by the leaves being beaten down by rain (Blackman, 1968). Leaf senescence is also greatly accelerated by lodging at supra-optimal LAIs (Alexander and McCloud, 1962). McCloud et al. (1964) found that the lower layers of the canopy contributed negatively to the total dry matter production under low, but positively under high light intensities. And a complete, dense rice crop grown under high nitrogen lost dry weight over a period of very low solar radiation (200 cal/cm^2/day) (Murata, 1961). Chernaivskaya and Nichiporovich (1967) have reported a similar metabolic disturbance and decreased RDMP in beans and cucumbers when nitrogen supply increased without a corresponding increase in light, especially as the plants became larger.

LEAF AREA AND DRY MATTER PRODUCTION IN SOUTHERN AUSTRALIA.

Both the optimum LAI and the RDMP are dependent on the level of incoming radiation (Black, 1957, 1963, 1964; Brougham, 1960; Stern and Donald, 1961). Cereal crops planted late in the Northern spring require high LAIs for maximum RDMP (i.e. LAI = 11 with an extinction coefficient of .3) (Brown and Blaser, 1968), but the South Australian crop is planted in the autumn with the maximum LAI and potential yield being established during the winter period (July - September) when the radiation level is low.

The light intensity on cloudless days at noon in Adelaide during the winter is approximately 64 klux or about half the maximum value at midsummer (128 klux). Rain falls predominantly in the winter however, and the heavy cloud cover further reduces the mean daily maximum light intensity to 32 klux, occasionally even falling to a mean of 21 klux (160 cal/cm^2/day) over two weekly periods (Messent, pers. comm.).

The maximum RDMP obtained over a short winter period with wheat in Adelaide was therefore only 13g/m^2/day (Puckridge and Donald, 1967), compared with a maximum of 23g/m^2/day recorded in Europe (Blackman and Black, 1959; Simba, 1968). LAIs of only 3.1 and 3.0 respectively were required for maximum RDMP in wheat (Puckridge and Donald, 1967) and maximum net photosynthesis in ryegrass (Fulwood and Puckridge, 1970) during the winter period at Adelaide. LAIs above 3.1 depressed the RDMP in wheat.

C. THE NUMBER OF FERTILE FLORETS.

Providing sufficient functional foliage is retained after flowering to fill the grain without the use of assimilate previously stored in the stems, the dry matter produced prior to anthesis can directly affect grain yield only through its influence on the number of grains able to accumulate dry matter after anthesis. High yielding cereal varieties must therefore be able to produce a large number of fertile florets per unit of dry matter as well as adequate amounts of dry matter.

RELATIVE IMPORTANCE OF YIELD COMPONENTS IN CEREAL SPECIES.

Spikelet production can continue for longer in barley than in wheat, but unlike wheat, no late compensating increase in the number of florets per spikelet can arise (barley has only one floret per spikelet) (Bonnett, 1966). The potential number of grains in barley is therefore determined much earlier than in wheat, at a stage just prior to stem elongation, when the light competition within a row is most severe (Part B). The two cereals, rice and barley, in which improved light distribution within the canopy has been reported to increase yields, are also the two in which variation in ear number accounts for much of the variation in grain yield.

Rice crops seldom deviate more than 10 per cent in 1000 grain weight (Murata, 1969) and yield is largely proportional to the number of panicles (Chandler, 1969). New higher yielding varieties of barley in Ontario (Gardener, 1966) and Europe (Watson et al., 1958; Thorne, 1962a; Kirby, 1967; Cannell, 1969a) have more ears per unit area than the older varieties, especially under high nitrogen (Holm, 1970), without any completely compensating decrease in the weight of grain per ear. However, merely doubling the ear number of higher densities or highly favourable climatic conditions can be accompanied by a concomitant decrease in either both the other two components (Kirby, 1967; Nickell and Grafius, 1969) or in grains per ear along (Donald, 1963; Adams, 1967). Such compensation also explains most of the failures in the use of yield components as selection criteria. Generally yield components are less stable than yield itself (Johnson et al., 1966).

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In contrast to barley, wheat can compensate for earlier reductions in ear and spikelet numbers (Bonnett, 1966) with a potential to produce up to 9 florets per spikelet instead of the normal 2 to 4 (Hudson, 1934). For example, reductions in spikelet number produced by surgery (Lupton, 1961) or low nitrogen (Single, 1964) were counteracted by an increase in the number of florets per spikelet. The extreme plasticity in this component (Borojevic, 1968) allows the new European (Bingham, 1966b) and Australian (Rathjen pers. comm.) wheats to respond to favourable environmental conditions around anthesis, and accounts for the trend to increased ear size rather than ear numbers found in new Mexican (Thorne et al., 1969), European (Saulescu et al., 1963; Watson et al., 1963; Stoy, 1965; Bunting and Drennan, 1966; MacKey, 1966) and Australian varieties of wheat.

SURVIVAL OF FERTILE TILLERS. The number of tillers per unit area in barley rises to a maximum and then declines until ear emergence, varying little thereafter (Watson et al., 1958; Thorne, 1962a; Laude et al., 1967; Cannell, 1969a). The decline begins earlier and is much greater at high densities, although the higher densities can still finish with more ears per unit area (Kirby, 1967; Puckridge and Donald, 1967). Although the decline is accentuated by severe competition, it still occurs at low densities (Purkridge and Donald, 1967) after the tillers become autotrophic (Wardlaw, 1965; Lupton, 1966). The greatest mortality occurs in the last formed and least developed tillers (Thorne, 1962a; Krishnamurthy, 1963; Li et al., 1964; Cannell, 1969a, b).

Many of the late tillers in a dense crop never achieve an independent, positive energy balance, living from emergence to death in the partial shade at the base of the crop (Rawson, 1967). Davidson (1965) reduced the shading by regular defoliation and was able to increase the number of ears 60 per cent although maintaining the LAI at 3 instead of 12. The greater number of ears formed in an erect leaved canopy may also result from the greater quantity of light received per tiller, rather than the increased dry matter production. In fact an increased RDMP may result from the greater number of contributing tillers.

The survival of each tiller also depends on the penetration of its nodal roots to a supply of soil moisture and nutrients to enable it to become independent of parental supply (Palfi and Deszi, 1960; Aspinall, 1961; Asana, 1963). The later formed tillers have fewer or no nodal roots per tiller (Pinthus, 1969) and these have to elongate through a layer of soil increasing in apparent density as the season continues (Millington, 1959). Both ample nitrogen (Aspinall, 1961; Thorne, 1962b) and water supply (Barley and Naidu, 1964) can reduce tiller mortality by preventing sudden, severe deficiencies when tillers become autonomous.

Varieties appear to differ in the extent of competition for minerals, assimilate and water between the developing ears and the younger tillers on one plant (Aspinall, 1963; Bunting and Drennan, 1966). This intra-plant competition in barley may be regulated by the production of gibberellins from the developing ear during the period of rapid stem growth (Nicholls and May, 1964), and could be avoided by the use of uniculm varieties (Donald, 1968a, b).

The number of main nodal roots per plant is closely related to the number of tillers per plant (Pinthus, 1969; Black, 1970), and therefore root length and weight is reduced far more in nodal roots than in seminal roots by increases in plant density (Pavlychenko and Harrington, 1934). Genetic uniculm plants should be less dependent on the growth of adventitious roots as every plant possesses a seminal root system, which can supply most of the water and nutrient requirements of a single stem (Krassovsky, 1926; Troughton, 1962).

Some nitrogen but very little carbohydrate may be retranslocated from dying to living tillers (Williams, 1964; Lupton, 1966b). These nutrients move towards the base of the plant and are used for new root growth (Quinlan and Sagar, 1962; Stoy, 1965). The increases in yield from the remaining tillers after excision of late tillers (Tincker and Jones, 1931; Fairfield Smith, 1933; Hashimoto et al., 1956; Quinlan and Sagar, 1962; Birecka et al., 1963; Sims, 1963; Lupton, 1966) must therefore arise from their use of otherwise committed resources. Economy in water usage can be particularly valuable (Hurd, 1969) allowing a few tillers to reach maturity before the supply is exhausted, rather than resulting in a premature cessation of grain filling in many.

SPIKELET FORMATION. The number of unexpanded primordia available for differentiation into floral structures, depends on the rate of primordia formation, the rate of primordia differentiation into leaves, and the length of the vegetative period prior to spikelet initiation at the double ridge stage. This period is longer in main stems than in later tillers (Rawson, 1967), in early planted crops, and in later developing varieties, although the latter also form more leaves from the unexpanded primordia. New primordia continue to be formed until stamen initials appear in the developing spikelets, (Nicholls and May, 1963). The number of spikelets per inflorescence is therefore determined by the relative rates of new primordia production and spikelet development. Both processes are slowed by low temperatures, shorter light periods and moisture stress, but the total number of spikelets is increased by the first two (development slowed more than production) and decreased by the last (Nicholls and May, 1963; Friend, 1965a).

Formation of new primordia was inhibited at a soil water potential (-1 bar) which had no other apparent effect on the plant (Husain and Aspinall, 1970). An indirect effect through hormonal supply was proposed as the water content of the apex remained high. The apical meristem is also very high in nitrogen and is unlikely to make large demands on the supply (Langer, 1966). The nitrogen supply in nutrient solution had to fall from 8 to 0 ppm before the spikelet number decreased (Single, 1964); a decrease from 150 to 15 ppm had no effect (Ryle, 1964a). Perhaps very high levels of water, nitrogen and soluble carbohydrate are necessary in the apex, as there is no vascular system until stamen initiation (Aspinall, 1963; Aspinall and Paleg, 1963) and all movement is by diffusion.

Reduction in the leaf area per tiller also decreased the number of spikelets per tiller in wheat (Bremner and Ingham, 1960; Davidson, 1965) but this may have been due to fewer developing rather than fewer being produced. Puckridge (1968a) also with wheat, found that the length of time between spikelet initiation and ear emergence, during which plants suffered severe competition for light, had no effect on the total number of spikelets formed, but that the numbers remaining fertile fell with increasing period of stress, particularly at low nitrogen. The basal spikelets failed to develop and remained as a pair of glumes.

SPIKELET SURVIVAL. The number of spikelets (and the number of florets in barley) cannot be increased after stamen initiation and any adverse environmental condition like nitrogen deficiency (Kinebuchi et al., 1958; Murata, 1969) or moisture stress (Fawcett, 1964) can only decrease the survival of those remaining.

Spikelet degeneration may start immediately after stamen initiation when vascularization of the rachis occurs. The central spikelets in the spike develop most rapidly (Bonnett, 1936) and seem to restrict vascularization, both basipetally and acropetally, to other spikelets (Nicholls pers. comm.). The last formed spikelets at the tip and base of the ear often fail to develop in wheat (Opatrna et al., 1964), and 7 - 12 spikelets at the tip and 3 - 5 at the base often seem to abort in barley (Kirby, 1970; Nicholls pers.comm.).

There is always an 'overproduction' of spikelets, similar to the 'overproduction' of tillers (MacKey, 1966), and yet the last formed yield component (the grain weight) which might be expected to be greatly depressed by such 'overproduction', remains the most stable of the three. This suggests either that the grains fill relatively independently of the number of spikelets surviving; or that the genetic control of potential grain size has a pleiotropic effect, or that there is a physiological feed back mechanism that can regulate spikelet abortion.

A similar mechanism in wheat may govern the number of grains which develop per spikelet, and account for the relatively low numbers found in Australian varieties selected for their ability to form large plump grains under adverse climatic conditions. Mexican varieties have similar numbers of spikelets per ear and florets per spikelet but a much greater survival of florets (Bremner and Davidson, pers. comm.). High yielding wheat varieties in Sweden (Stoy, 1965) also set more grains per spikelet while having values of LAI, NAR and LAD before anthesis similar to lower yielding Swedish varieties.

Water stress prior to anthesis can prevent proper sexual development in all small grains (Novikov, 1952; Skazkin and Leiman, 1952; Skazkin and Zavadskaya, 1957; Bingham, 1966b) either directly or through the reduced translocation of minerals (Asana and Saini, 1958). Death of the anther wall and the prevention of carbohydrate translocation to the developing pollen (Skazkin, 1961) can result in florets becoming male-sterile but female-fertile (Bingham, 1966b). The upper florets in the ear, being unable to compete successfully for moisture against the lower florets, may die (ear tipping) under continued severe moisture stress in the late boot stage (Fawcett, 1964, 1967).

D. ACCUMULATION OF DRY MATTER IN THE GRAIN

THE COMPLEXITY OF THE PROCESS. Moving photosynthate into the fertilized florets involves an extremely complex system of five distinct steps. The photosynthate is produced in the cells of several different organs on the plant which differ in age, size and position (Step 1), and is moved out of these cells (Step II) into the conducting tissue along which it is transported towards the ear (Step III). These translocation streams vary in length (i.e. lower leaves versus awns to the developing grains), and probably compete for channels as they converge into one stream (e.g. Hartt, 1967). The sucrose is moved up the rachilla and into the cells of the grain (Step IV) where it is synthesized into starch (Step V). The grains exert a combined 'demand' on the translocate, according to their size and number, but compete with one another for the supply depending on their position in the ear.

A limitation in any one of these five steps will slow the rate of the whole process. Moisture stress, for example, can specifically effect either translocation (Yu et al., 1964; Aspinall, 1965) or movement out of the leaf (Wardlaw, 1967), but both are soon also reflected in a reduced rate of photosynthesis (Konovalov, 1959; Wardlaw, 1967). Reducing the demand for assimilate, by removing some grains from each ear, also reduces the photosynthetic rate (King et al., 1967), but increasing the assimilate supply above a certain level increases neither sucrose concentration or rate of starch synthesis in the grain

(Jenner, 1970).

SINK-SOURCE RELATIONSHIPS. The size of the 'sink' depends on all those factors like potential grain size, rate of increase in grain size, and the number of grains which affect the capacity to accept photosynthate. Likewise, Steps I, II and III are combined in the term 'source' or the capacity to supply photosynthate. The relationship between the sink and source is not constant, but varies diurnally and with the climate, micro-environment and stage of grain development.

If the capacity of a certain number of grains to accept photosynthate greatly exceeds the supply, it would seem advantageous for these grains to be dispersed over a great many culms in lax, low density, and awned ears, with several large and long-lived leaves per culm and ample reserves of mobile carbohydrate in the stem.

If the sink is the limiting factor, then the awns, the quantity of foliage per grain and the amount of solar radiation become less important, and more large grains are required per ear (as in 6-row as opposed to 2-row barleys) to utilize the excess photosynthate.

In general, increasing the number of grains per unit area reduces the likelihood of the sink becoming limiting, but increases the chance of the potential grain size not being realized. Lines with many undersized grains are selected against both by man, who requires plump grains for milling and malting, and in nature, where large grains have a competitive advantage (Donald, 1968a,b). In rice, there is a close correlation between yield and the number of spikelets when spikelet number is small, and between yield and grain size when spikelet number is large (Murata, 1969).

<u>POTENTIAL GRAIN SIZE</u>. There is very rapid division and enlargement of endosperm cells during the first 3 to 4 days after enthesis, and the grain volume increases exponentially; not until at least 6 days after anthesis does starch deposition start (Harlan, 1920; Woodman and Engledow, 1924; Hoshikawa, 1961). Growth during the initial period is highly susceptible to adverse environmental conditions, and water stress at this stage irreversibly decreases grain size and hastens maturity, despite the later resumption of optimum water conditions (Aspinall, 1965). High temperatures increase the rate of growth and the grain volume (Asana and Saini, 1962; Thorne et al., 1968; Wardlaw, 1970) but later hasten senescence thereby again reducing grain weight.

The lack of assimilate induced by shading also has an irreversible depressing effect on grain size in rice (Wang and Yan, 1965), but usually there is a surplus of carbohydrates produced between anthesis and the time of rapid increase in grain dry weight. In wheat, this is stored temporarily in the upper (Birecka et al., 1963, 1964; Stoy, 1963) or lower (Hsia et al., 1963; Wardlaw and Porter, 1967; Wardlaw, 1970) internodes and can be later retranslocated to the grain. Up to 40 per cent of the final grain weight in wheat can be due to such translocation (Birecka and Dakic-Wlodkowska, 1963, 1964). The top internode (peduncle) may also be still elongating at anthesis in some varieties, and can compete with the young developing grain for the limited supply of assimilate under low light intensities (Wardlaw, 1970).

THE DEPOSITION OF STARCH. Many authors (Stoy, 1965; Welbank et al., 1966; Bingham, 1967; Lupton, 1968; Simpson, 1968) have suggested that the increased production from more photosynthetic tissue will increase grain size. This may be true at levels of sucrose below normal (3 per cent), since the concentrations of sucrose in the rachis and endosperm, and the rate of starch synthesis are closely related (Jenner, 1970). However, increasing the levels of sucrose above normal in the rachis brought no further increase in the level in the grain. The continuity between the pericarp and the rachilla is interrupted by a core of thick-walled cells which restricts the flow of solutes to the pericarp (Zee and O'Brien 1970a). This core is surrounded by transfer cells (Pate and Gunning, 1969), that elsewhere are often concerned with the active transport of solutes.

As the grain matures, the junction of the seed coat with the pericarp is gradually sealed off by the differentiation of the pigment strand at the base of the groove in the grain (Zee and O'Brien, 1970b). This may well account for the sudden, rapid cessation in grain weight increase 28 days after anthesis reported by Jennings and Morton (1963a). Some wheat varieties continue to fill their grains after others have finished, but this has been attributed to greater longevity of starch synthesizing activity (Asana, 1963). Hillson and Penny,(1965)found maize crosses took from 53 to 61 days to reach 95 per cent physiologic maturity from silking; the longer periods may however have been caused by more kernals competing for a limited supply of assimilate.

COMPETITION BETWEEN GRAINS. At least two types of competition occur between grains in an ear of wheat, probably depending on whether the supply of assimilate is limiting or not.

All grains on the main culm have initially similar relative growth rates under English field conditions (Walpole and Morgan, 1970) suggesting carbohydrate is not at first limiting for these small sinks. But later, when the 'demand' was high, rapid senescence had decreased the supply, so that only the lowest grains on the lowest spikelets (those nearest the supply) were able to keep increasing in weight.

In a growth chamber study, Rawson and Evans (1970) found that sterilization of the basal one or two florets on central spikelets resulted in more grains being set in the upper florets and the grain yield per ear being increased by 20 per cent. The overall assimilate supply was therefore not limiting, and the domination of the earliest formed spikelets was attributed to their greater size and hormonal control of assimilate flow. The main grains (as opposed to lateral grains) in six-row barley, and the lower grains in two-row barley seem to have a similar advantage (Aspinall, 1965).

PHOTOSYNTHATE SUPPLY. Most of the dry matter accumulated in the grain is produced after anthesis by the leaf laminae and sheaths, peduncles, ears and awns. Less than 15 to 20 per cent in barley and wheat originates before anthesis and is later retranslocated to the grain (Boonstra, 1929, 1937; Archbold, 1945; Archbold and Mukerjee, 1942; Porter et al., 1950; Asana and Mani, 1950, 1955; Watson et al., 1958, 1963; Buttrose and May, 1959; Frey-Wyssling and Buttrose, 1959; Lupton, 1961; Buttrose, 1962; Stoy, 1963; Thorne, 1963a). However in rice, grain filling can be relatively dependent on carbohydrate stored before anthesis, especially in the late varieties and the tall, leafy tropical varieties which produce little dry matter after flowering (Enyi, 1962; Tanaka et al., 1966; Kawano and Tanaka, 1968; Togari, 1968). Perhaps similar reserves in barley and wheat would also be used, but for the apparent surplus of carbohydrate available for grain development.

Translocation of these stem reserves and photosynthesis in the remaining green tissue are greatly increased by shading or removal of some leaves on the stem (~~Yin et al., 1956;~~ Buttrose and May, 1959, Stickler and Pauli, 1961; Thorne, 1963a; Stoy, 1963; Birecka and **Dakic-Wlodkowski**,1964; Birecka et al., 1964; Lupton, 1969). Lupton and Ali (1966) estimated by shading the amounts contributed to the grain by the stems, leaves, ears and stem reserves and found that their sum exceeded that produced by unshaded control by 30 per cent. Most instances of compensation reported, however, occur at relatively low plant densities (i.e. 22 plants per m^2, Lupton, 1969); far less surplus carbohydrate might be available under the severe competition found at high densities.

There is indirect evidence that the sink size controls the photosynthetic rate. The photosynthesis per unit leaf area in the second leaves of young plants did not differ in diploid, tetraploid and hexaploid wheats even at high light intensities (Belikov et al., 1961). In flag leaves, at high light intensities however, photosynthesis per unit area was inversely related to the flag leaf area (Evans and Dunstone, 1970), suggesting that the similar numbers of grains per ear in all species exercised a similar demand. Further, there were no differences in flag leaf photosynthesis per unit area between species at low light intensities. And the maximum rates fell most rapidly in the species with small, quickly-filled grains.

All the techniques used to estimate the photosynthetic contribution of various plant organs to the grain have faults; shading decreases transpiration (Lupton and Kirby, 1968), excision removes a potentially mobile reserve of nitrogen (Williams, 1955; Neales et al., 1963; Nátr, 1967), and enclosure creates a changed microenvironment. So an alternative technique involving both shading the shoot and removing the developing grains from the ear has been used to estimate maximum ear photosynthesis (Buttrose and May, 1959; Lupton, 1961; Buttrose, 1962; Nösberger and Thorne, 1965). However reducing the grain number only occasionally increased 1000 grain weight (Stoy, 1965; Bingham, 1967) in the unshaded plants. Other times, it had no effect (Abolina, 1959; Buttrose, 1962) and even depressed the 1000 grain weight (Lupton and

Ali, 1966) because of the 'weaker sink' (Nösberger and Thorne, 1965). Perhaps this is another reason an increased number of grains does not decrease the 1000 grain weight proportionately.

CONTRIBUTION BY THE EARS. About 85 per cent of the assimilate in the grain of wheat and barley usually comes from above the flag leaf node (Porter et al., 1950; Quinlan and Sagar, 1962; Thorne, 1963a, 1965; Kriedemann, 1966). At low plant densities, this is presumably due to the competitive advantage of photosynthesizing tissue in proximity to the grain in supplying assimilate to the adjacent sink; in very dense stands the more juvenile flag leaves, peduncles and ears are often the only organs remaining active (Kravtsova, 1957; Shen et al., 1959; MacKey, 1966). Both erect leaves (Thorne, 1966) and erect ears (Donald, 1968a) have been extolled as advantageous in a mature crop, but this is probably only true at very high ear numbers (i.e. around 1000 per m^2). Ear photosynthesis in medium populations of ears in South Australia was in fact greater when the ears were horizontal to the incoming radiation (Puckridge, 1968a).

The ear alone in barley supplies about 45 per cent of the carbohydrate incorporated in the grain (Porter et al., 1950; Thorne, 1963a, 1965) although this contribution can probably vary, as in wheat, with the variety

(Asana and Mani, 1950) climate (Asana and Saini, 1958) and season (Buttrose and May, 1965). There is also a positive correlation between ear size and photosynthetic rate in barley (Thorne, 1963a). Generally ears supply more assimilate to the grain in barley than in wheat because of the high respiration rate in wheat ears (Kriedemann, 1966; Carr and Wardlaw, 1965; Thorne, 1965; Bingham, 1967).

Awns account for at least one third of the actively photosynthetic surface of the ear (Grundbacher, 1963) and can supply about 10 per cent of the dry matter accumulated in the grain of barley (Vervelde, 1953; Watson **et al.**, 1958). Ears of awned varieties therefore tend to contribute more assimilate to the grain (McDonough and Gauch, 1959; Asana and Mani, 1950, 1955; Birecka and Dakic-Wlodkowska, 1963; Carr and Wardlaw, 1965) resulting in greater yields (Harlan and Anthony, 1920; Atkins and Norris, 1955; Buttrose and May, 1959; Patterson et al., 1962; Suneson and Ramage, 1962) than those varieties without awns.

The awned characteristic is easy to incorporate into a breeding programme, but has also been credited with causing an unfavourable water economy in leafy hydrophilic types under semi-arid conditions (MacKey, 1966). However, awns usually seem well adapted to a warm climate, both through their xeromorphic structure and through the efficient cooling system that they provide in the floral region (Grundbacher, 1963).

PREMATURE TERMINATION OF GRAIN FILLING. Most of the assimilate from below the flag leaf node moves towards the root system (Quinlan and Sagar, 1962; Wardlaw, 1965; Lupton, 1966) where it is used for new root growth (Stoy, 1963). When there are no factors reducing the assimilate supply, root growth can be maintained at a high rate well into the grain filling period (Balazs, 1964; Walter, 1971), and the uptake of mineral nutrients continued (Watson et al., 1958, 1963; Aspinall, 1961; de Silva, 1961; Thorne, 1962b; Nathan, 1963). Lack of adequate nitrogen uptake can result in a much earlier redistribution of plant nitrogen and a premature senescence of foliage (Nathan, 1963).

The moisture supplies in the soil can also be prematurely exhausted by either excessive leaf areas (Part A), or the growth of the crop in a period of higher evaporative demand because of late planting or the use of late maturing varieties (Lehane and Staple, 1962; Colwell 1963a; Barley and Naidu, 1964; Fawcett, 1964, 1967; Fischer and Kohn, 1966a; Luebs and Laag, 1969; Nix and Fitzpatrick, 1969). Chinoy (1962), Asana et al. (1958), and May and Milthorpe (1962) found no genetic differences in drought resistance; only differences in the rates of development and the ability to escape droughts.

Later crops also suffer high temperatures and while these can also cause shrunken grain (Chinoy, 1947; Pal and Butany, 1947; Asana and Williams, 1965), the effect is probably an indirect one through lower relative humidities and increased moisture stress. Grain shrivelling did not occur at temperatures of over 40°C when moisture levels were high (Aspinall, 1965).

LEAF AREA DURATION AFTER ANTHESIS. Differences in grain yield between varieties have recently been attributed to differences either in the size or duration of the leaf area after anthesis, or in the productivity of this leaf area. (Watson et al., 1963; Stoy, 1965; Welbank et al., 1966; Simpson, 1968; Thorne et al., 1969). But these two parameters seem more dependent on growth prior to anthesis than being yield determining processes themselves. A greater survival of ear bearing tillers will increase both grain yield and LAD; more grains per ear will increase both grain yield and the amount of grain produced by the LAD. Since the number of ears and grains per ear are determined by the time of anthesis, only the 1000 grain weight can be affected by the two parameters, but even then it is possible that the size of the grain eventually determines the duration of the leaf area rather than the reverse.

In comparison, Davidson (1965) obtained by leaf defoliation, LAD values before ear emergence in the proportions of 5:3:1, and corresponding grain yields in the proportions of 5:2:1. However, the reductions in yield were not only due to reductions in numbers of grains set per m^2, but were also caused by the effects persisting after anthesis and reducing the 1000 grain weight by 50 and 60 per cent.

As a leaf ages it contributes progressively less to the grain and may become inessential before final senescence (Williams, 1964). Consequently, there may be no advantage in extending leaf life by nitrogen application (Thorne, 1962b). Rapidly growing storage structures can actually accelerate senescence (Heslop-Harrison, 1969), so it might be advantageous for leaves to have a short but active life, followed by a rapid senescence and a thorough remobilization of nutrients to the grain (Wardlaw, 1968); the complete opposite of the slow delayed senescence proposed by Watson in 1956.

E. THE INTERACTION OF AGRONOMIC AND ENVIRONMENTAL FACTORS

DENSITY. Increasing plant density increases not only the number of potential ear bearing tillers per m^2, but also the competition between tillers for the available resources, thus resulting in fewer grains per ear or smaller grains

(Kirby, 1967). This competition decreases and more or larger grains are formed when more resources are added, and the optimum density rises with increasing levels of light intensity (Willey, 1965), moisture (Bielorai et al., 1964; Toussaint and Hettinga, 1966; Fulton, 1970) and fertility (Lang et al.,1956). High densities in cereals can also compensate for the reduced ear number caused by low soil fertility (Montgomery, 1912; Boyd, 1952) or late sowing (Kirby, 1969).

PLANTING PATTERN. Competition for resources can be delayed by planting in square or trapezoid patterns which place plants the maximum distance apart for any given density. The weight of an individual plant increases approximately in proportion to the square of the distance to the nearest neighbour (Garner and Sanders, 1939). However, if the correct unit of plant population in cereals is considered to be the basic independent unit, i.e. a tiller, even a uniform pattern still gives multiple plant hills (Duncan, 1969). Holliday (1963), in reviewing the literature for wheat in Europe, found that, at a constant seed rate, decreasing the row width below 7 to 8 inches (i.e. moving towards more uniform spacing) increased yield 5 to 7 per cent, and increasing row width usually decreased yield. An exception to the latter might occur in drier environments if early competition within the row were severe enough to decrease leaf area and increase mutual shading sufficiently to conserve soil moisture. Row width, barring extremes, has less effect on yield than the seeding rate (Holliday, 1960b).

DENSITY AND UPTAKE OF WATER AND NUTRIENTS. The diffusive resistance of a crop to soil water loss depends on leaf area when the soil surface is dry (Cowan and Milthorpe, 1968). Therefore any factor which increases LAI also increases evapotranspiration provided water is available in the sub-surface soil, and the canopy is not already closed. Moderately high densities (up to about 250 plants per m^2) therefore deplete soil moisture reserves more rapidly (Fawcett, 1967; Pelton, 1969; Kirby, 1970), and can suffer moisture stress earlier (Clements et al., 1929) than lower densities, because of their deeper root penetration (Fawcett, 1967), and higher root densities (Kamel, 1959).

The root density (Kamel, 1959) and the water loss (Kirby, 1970) fall again at very high plant populations (500 to 800 plants per m^2). The severely shaded plants at these very high densities have less carbohydrate to invest in root expansion, with the resulting root system being shallower and smaller (Kamel, 1959; Duncan, 1969). Less nitrogen may be also taken up at high plant densities (Donald, 1951) because of a similar lack of efficient soil exploration, or the lack of labile organic acceptors. Generally, there is a close positive correlation between the rate at which assimilate is moved to the roots and the rate at which mineral elements are absorbed (Pristupa and Kursanov, 1957).

NITROGEN AND WATER UPTAKE. High levels of nitrogen also greatly increase the above ground competition, but shallower root systems and reductions in water use have not been reported. Perhaps this can be related to the high percentage of seminal roots at high density (400 plants per m^2) compared to the large nodal system developed after nitrogen application (Pavlychenko, 1937). Nitrogen fertilization does increase the percentage of the total weight of cereal roots in the upper horizons (Weaver et al., 1922; Crist and Weaver, 1924; Kmoch et al., 1957; Welbank and Williams, 1968), but the much greater total root weight often means that the root penetration and weight in the lower horizons is actually greater (Crist and Weaver, 1924; Kmoch et al., 1957; Grunes and Krantz, 1958; Kahari and Elonen, 1969; McNeill and Frey, 1969). Nitrogen application on cereals, therefore, often increases water use from the lower horizons of the soil (Kmoch et al., 1957; Warder et al., 1963).

Lack of other resources may limit dry matter production at the higher levels of nitrogen (Shepherd, 1960; Gasser and Iordanou, 1967), and Russell (1967) found that the grain yield with additional nitrogen increased with increased May to October rainfall. Optimum levels of both density and nitrogen vary directly with available water (Hudson, 1941a, b; Colyer and Kroth, 1968), however very few yield reductions occurred in low rainfall areas with moderate levels of nitrogen application (Viets, 1965) despite the more rapid moisture depletion, and the significant depressions in South Australia did not occur in years of extreme drought but when hot dry spring conditions followed wet winters (Russell, 1967).

F. DIFFERENTIAL VARIETAL RESPONSES TO AGRONOMIC CHANGES

DROUGHT RESISTANCE. A certain degree of drought evasion can be obtained agronomically by early seeding, lower densities, and lower nitrogen levels, but the latter two involve acceptance of lower yield potentials (fewer culms). These measures avoid drastic reductions due to drought in the number of spikelets (Asana and Saini, 1958; Asana et al., 1958), number of grains (Van der Paauw, 1949; Brouwer 1959[illegible]; Martin, 1960) or 1000 grain weight (Asana, 1962; Day and Intalap, 1970). A more difficult alternative is to breed truly drought resistant varieties.

Variations in rooting density and root distribution have been reported in varieties of wheat (Janssen, 1929; Worzella, 1932; Webb and Stephens, 1936; Hurd, 1964, 1968), barley (Hess, 1949; Lee, 1960; Hackett, 1968) and oats (Derick and Hamilton, 1942). These variations tend to be preserved in contrasting environments (Weaver et al., 1922; Weaver, 1926; Kutschera, 1960), but are small in comparison with those caused by differences in soil conditions, plant density, and mineral nutrition (Russell, 1961; Schuurman, 1965; Black, 1968). Differences in numbers of main nodal roots between varieties are usually related to the number of tillers (Paquet, 1968; Derera et al., 1969; Pinthus, 1969; Black, 1970), but root numbers and moisture loss may not be related as root pruning does not always reduce water uptake (Andrews and Newman, 1968). Varieties also differ in rate of root penetration (Pavlychencko and Harrington, 1934; Derera et al., 1969), but in South Australia both water and roots are confined to the top 3 to 4 feet of the profile. Although Derera et al., (1969) suggested improving the effectiveness of the absorbing surface of the root system, the actual capacity to remove water to a high pF seems of little importance as the water content changes little as limiting pF is approached.

Drought tolerance therefore seems largely due to foliar characteristics that prevent desiccation

(Part A) and to escape by early maturation of varieties (Part D). In northern New South Wales earliness in plant maturity accounted for up to 90 per cent of the observed variation in drought tolerance (Derera et al., 1969) and Kaufmann (1961) proposed selection on an index combining high yield and earliness in Canada.

LODGING RESISTANCE. The potential response to nitrogen application depends on the climatic conditions (Part . E). Areas favoured for high yields of cereal, like the Pacific North-West in the United States, have long, cool growing seasons with adequate moisture and very high light intensities. Yet very high wheat yields (up to 11,195 kg/ha; Briggle and Vogel, 1968) have only been obtained in these areas since the introduction of short, lodging-resistant varieties responsive to nitrogen (Van Dobben, 1966).

Lodging can reduce cereal yields up to 60 per cent (Mulder, 1954; Linser, 1968; Syme, 1968a) depending at which stage of development lodging occurred. Artificial lodging imposed after anthesis, caused shrunken grains in wheat, and decreased grain yield by 31 per cent (Weibel and Pendleton, 1964), but the effect can be further aggravated by diseases like eyespot (Cercosporella)

(Watson et al., 1963) and by mechanical losses at harvest.

Several characteristics contribute towards lodging resistance, amongst them being shorter culms, greater stem width and elasticity, tighter leaf sheaths, more nodal roots and thicker stem walls[1] (Berbigier, 1968; Chandler, 1969). All of these are important in barley, except perhaps the number of nodal roots, for it is the weakness of the straw that causes the extreme susceptibility of barley to lodging (Berbigier, 1968).

PLANT HEIGHT. Low levels of natural gibberellin or the application of antigibberellins (CCC) reduce height through a reduction in the length of the top internodes (Pugsley, 1964; Powell and Schlehuber, 1967; Berbigier, 1968; Borojević, 1968; Thorne et al., 1969); the actual number of developed or visible internodes varies little despite large differences in leaf number (between 6 and 12) and maturity (Paquet, 1968).

In wheat, it is possible to combine short straw with normal length ears, since both spikelet number and ear density (length of rachis internodes) are independent of plant height (Borojević, 1968; Briggle and Vogel, 1968; Paquet, 1968). Unfortunately, the semi-dwarf varieties of barley also have increased ear densities (10 per cent),

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1. The difference between the outer and inner dimensions of the culm.

fewer grains per spike (10 per cent) and smaller grains (14 per cent). They have a lower yield potential than standard height varieties, only surpassing them in grain yield when lodging occurs (Berbigier, 1968).

The number of ears per m^2 also tends to increase when height is reduced (Gandhi et al., 1964; Paquet, 1968), but the effect may be indirect, as correlations can also exist between short plants and short leaves (Chowdhry and Allan, 1966), and short leaves and number of ears (Hamblin, unpubl. data). Shorter stems tend to be thicker (Primost, 1968) and more completely covered by leaf sheaths (Wünsche, 1970), but the laminae are proportionally wider and greatly encourage foliar disease (Briggle and Vogel, 1968) when many are inserted into the stem over a short distance. Vogel et al. (1963) therefore specified medium leaf size, medium culm diameter and medium semi-dwarf height characteristics in lines developed for the Pacific North-West. Later when yields rose above 5,500 kg/ha, Briggle and Vogel (1968) found they needed even shorter and stronger straw to avoid lodging.

INHERENT YIELD CAPACITY. The incorporation of resistance to drought, lodging, shattering and disease constitutes breeding for yield stability (Stoskopf et al., 1963) or defect elimination (Donald, 1968a), and this accounts for most or all of varietal differences in yield, despite the tremendous effort devoted to increasing the inherent yield capacity.

For example, neither Yugoslav (Borojević, 1968) nor Indian (Anonymous, 1968) semi-dwarf wheats have a higher yield potential than tall local wheats, but they can respond to nitrogen application without lodging. Even the tall and leafy variety of rice Peta (usually considered as typical of the low yielding types) gave a grain yield nearly as high as IR8 (the very high yielding new variety) when the plants were tied up to prevent lodging (Chandler, 1969). The yield differences between old and new varieties of barley, apparent with machine harvesting, also disappear when all the grain is gathered from the plots by hand (Kirby, 1967; Cannell, 1969a).

HARVEST INDEX.[1] Pugsley (1964) found semi-dwarf wheat varieties, which were 35 to 50 per cent shorter than standard varieties, had much higher harvest indices (40 instead of 28 per cent). However, the extra efficiency does not add to grain yield unless the reduced demand of the stem for carbohydrate during elongation allows more spikelets to develop. Likewise, the reduction in number of sterile tillers proposed by several authors (de Silva,

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[1] Harvest Index is the term used by Donald (1962) for the percentage of total dry matter utilized in economic yield; a ratio previously developed by Beaven (1947) and Nichiporovich (1954).

1961; Watson et al., 1958; Thorne, 1962a; Kirby, 1967) will increase the harvest index, but will not effect yield unless more heads or spikelets survive to use the additional resources available. Both circumstances do eventuate however, and the higher harvest indices found in newer varieties coincide with either unchanged (Watson et al., 1958; Sims, 1963; Van Dobben, 1966; Kirby, 1967; Cannell, 1969a) or higher (Watson et al., 1963; Stoy, 1965; Bingham, 1967) yields of total dry matter.

The harvest index usually shows a parabolic response when plotted against variations in total dry matter (Medinets, 1967). When the total biomass is large, it becomes increasingly difficult to obtain high harvest indices because lodging, drought, mutual shading and insufficient nutrient supply are more likely to occur. Medinets also found that the newer varieties were more resistant to these factors and could reach higher values of total dry matter before the harvest index declined.

VARIETAL RESPONSE TO DENSITY. The differential response of cereal varieties grown at different densities (Immer, 1941; Frey and Maldonado, 1967; Koller and Scholl, 1968; Giesbrecht, 1969) seems attributable to three factors. Firstly, some varieties lodge badly at high densities (Kirby, 1967) causing an interaction similar to that between varieties and nitrogen (Vogel et al., 1963; Jensen and Federer, 1964; Porter et al., 1964; Tanaka et al., 1964; Woodward, 1966; de Datta et al., 1968; Kawano and Tanaka, 1968; Reid et al., 1969). Secondly, an early maturing sorghum hybrid used less water, and had peak yield at a higher density, than a late maturing hybrid (Blum, 1970). Thirdly, some varieties, especially those with a longer period for ear formation (Krishnamurthy, 1963) tiller and yield more at low densities, but this tillering ability has little effect in determining their yield at high density (Lupton, 1961; Adams, 1967; Kirby, 1967).

In fact, several authors (Wiebe et al., 1963; Tanaka et al., 1964; Donald, 1968a; Hurd, 1969) have suggested selecting from segregating populations the lower yielding lines because their characteristics, like low tillering capacity, small leaf size, short height, and non-spreading habit, should also provide the minimum interference to neighbours when grown at high density (Donald, 1968a). However experimental evidence suggests that there may not be a useful inverse correlation between tillering capacity at moderate density and performance as a single culm in a dense crop as short, upright-leaved, heavy-tillering indica types of rice are high yielding both in 20 by 25 cm hills, and when seeded directly at 100 kg/ha (Chandler, 1969).

SHADE TOLERANCE AND FERTILITY. The competitive ability of cereal varieties has sometimes appeared unrelated to any observable morphological differences (Sakai and Gotoh, 1955; Pal et al., 1960), suggesting differences in shade tolerance similar to those found in maize. Stinson and Moss (1960) found the grain yield of maize hybrids tolerant of dense planting was significantly (20 per cent) higher than intolerant hybrids when both were grown under shade. The two groups had similar yields in the absence of shade, and the differences under shade resulted more from differences in ear barrenness (16 per cent) than in ear weight. The barrenness was caused by less sucrose being available for silk development, with silk maturation being delayed beyond the period of pollen shedding (Moss and Stinson, 1961; Williams et al., 1968).

Defoliation increased barrenness more in an intolerant than in a tolerant hybrid (Pendleton and Hammond, 1969), and moisture stress, possibly through a reduction in sucrose translocation (**Part D**) can also increase infertility (Robins and Domingo, 1953; Denmead and Shaw, 1960; Grinfeld, 1965). The upright leaf type, on the other hand, can greatly alleviate barrenness in intolerant hybrids (Pendleton et al., 1968). Barley is not, however, a dioecious crop, and while moisture stress can adversely affect reproductive development (**Part**

C), the actual fertilization seems insensitive to most factors (Heslop-Harrison, 1969).

PLASTICITY OF EAR SIZE. Free tillering varieties can compensate sufficiently for differences in rainfall, through tiller number, to always produce maximum grain yield at a low density (Karper, 1929). However, the optimum seeding rate of low tillering or uniculm types varies each year with the moisture supply. Donald (1968a) points out that modern, non- or weak-tillering varieties of sorghum carry sufficient plasticity in the ear to be grown successfully in both irrigated and low rainfall areas, and that perhaps this could be developed in wheat and barley as well.

Certainly genetic selection for increased ear size would become more effective in uniculm plants, as culm number is divorced from the reciprocal relationship with ear number (Donald, 1968a) which seems greatly affected by variations in microenvironment (Frankel, 1935; Lupton and Whitehouse, 1957; Adams, 1967; Rasmusson and Cannell, 1970).

G. SOME FEATURES OF BARLEY PRODUCTION IN SOUTH AUSTRALIA

Barley is grown in South Australia on mallee (solonized brown) soils and red-brown earths in areas normally receiving more than 400 mm of rain. These soils are naturally low in organic matter, nitrogen and phosphorus, and intensive use under a wheat-fallow system depleted the fertility even further in the period before 1940 (Cornish, 1949). However since World War II, the fertility has been improving due to an increased use of superphosphate and the successful introduction of medics and subterranean clover. Barley is now grown either alternatively with a medic pasture, or after a wheat crop that follows several years of medic or subterranean clover pasture (French et al., 1969). Between 90 and 240 kg/ha superphosphate (with a mean of 100 kg/ha) is applied at seeding (French and Rudd, 1967), but nitrogen fertilizer is rarely used since a good subterranean clover pasture can add 165 kg/ha nitrogen in each of its first two years of growth (Goode, 1963).

Seventy per cent of the highly variable annual rainfall occurs between April and October, and barley is sown throughout June and into July at approximately 55 kg seed per ha. The crop then grows slowly throughout the winter period, flowers in October, and matures in November. Rain rarely delays the harvest in December, but strong winds and high temperatures can cause severe neck breakage and loss of ears. The major variety grown during the last 60 years, Prior, is very susceptible to neck breakage, and rolling the crop before maturity has been used as a preventive measure. Currently Prior is being replaced by Clipper, a variety with improved resistance to neck breakage, lodging and mildew. Earlier sowing with chemical weed control has been recommended for Clipper, but unfortunately the new variety is susceptible to Rhynchosporium during the cool, damp winter period.

Six-row varieties, like Cape and Coast that grow fairly vigorously during the winter period, are commonly used for winter grazing but their grain ~~growth~~ does not fulfil the local malsters' requirements and can only be used for stock feed. The average grain yield for Prior between 1951 and 1961 ranged from 800 to 1800 kg/ha depending on the locality (French et al., 1969) but individual yields of up to 4500 kg/ha have occasionally been realized.

III. PRESENT INVESTIGATIONS

A. OBJECTIVES

B. SELECTION OF VARIETIES

C. GENERAL EXPERIMENTAL INFORMATION

III. THE PRESENT INVESTIGATIONS

A. OBJECTIVES

Although genetic diversity exists for each character in barley, only one variety was used in the majority of references cited for this species. Most of the other authors examined either closely related, locally adapted commercial varieties, or the progeny from a single cross. Only very rarely was any exotic material included in a trial (Kirby, 1967). Therefore, while deficiencies in water, nutrients, light and assimilate are known to adversely affect growth processes at every stage of development, little is known about the differential responses that exist within this species. Comparison of a wide range of genetic material in agronomic and physiologic studies is also more likely to reveal the characteristics associated with such differential responses and greatly broaden the inference of the findings. In the present investigations a group of 12 varieties was selected from the world collection at the Waite Institute to provide a wide range in genetic origin, yield and maturity.

The relative yields of these varieties had already been established under the agronomic conditions of the South Australian barley districts, during the

Waite Institute breeding programme. The varieties with high yields in these conditions were therefore well adapted to the local agronomy, but it was not known whether those with lower yields had an intrinsically lower potential or could also give high yields when grown in an appropriate agronomic niche.

The objectives were:-

(1) To see if varieties differed in their optimum requirements of water, nitrogen and plant density for maximum yield. It was also important to determine whether the yields at the respective optima differed, and whether varieties had very specific optima or had high yields over a wide range of conditions.

(2) To reveal the processes involved in the responses. Both nitrogen and density greatly increase the LAI, and it was important to determine whether lodging dictated the response to these factors or whether increased competition for light during the winter or moisture stress in the spring became the principal determinants of yield.

(3) To identify the plant characteristics associated with the differential response between varieties. These might be morphological characteristics such as upright leaves, physiological characteristics such as the differential removal of water from the soil profile, biochemical characteristics such as an increased resistance to shading,

or ontogenetic characteristics such as early maturation and escape from intense competition for light, water or nutrients.

(4) To study these characteristics in further experiments (i) to confirm that they are truly involved in yield-determining processes and

(ii) to determine whether they could be used in a breeding programme.

This thesis is a consideration of all the factors affecting the yield of the 12 varieties when water, nitrogen, density and light are varied with a view towards the simultaneous manipulation of both agronomy and genotype to raise barley yields in South Australia.

B. SELECTION OF VARIETIES

A random sample of 277 varieties was taken by Finlay and Wilkinson (1963) from a world barley collection for testing at 7 sites in South Australia. The environment at each site was graded quantitatively by use of the mean yield of all varieties (after Mooers, 1921, 1933; Yates and Cochran, 1938; Walton, 1957), and then the 7 individual yields for each variety were plotted against the 7 site means (Figure 1a). The resulting regression coefficient provides an index of varietal responsiveness to improving environmental conditions, in addition to

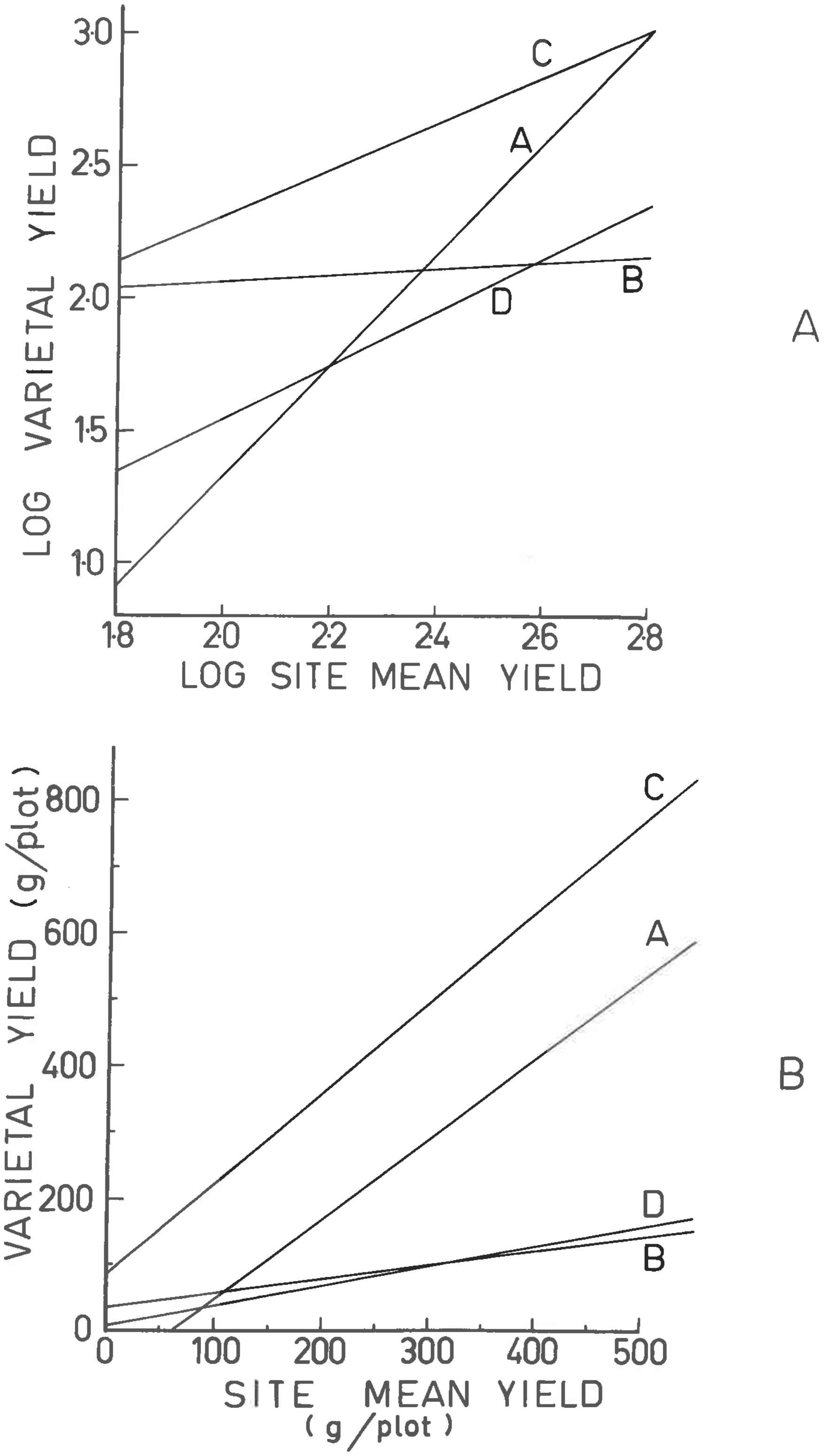


Figure 1. Regression lines of individual varietal yields on site mean yield (A) on log data after Finlay and Wilkinson (1963) and (B) on natural data after Eberhart and Russell (1966).

usual varietal mean yield. The varieties used in the experiments reported in this thesis were selected on the basis of these two parameters, and to give equal numbers of 2 - and 6 - rowed varieties, a range of maturity (Table 1) and a wide diversity of origin (Table 2).

Two of the varieties, Proctor and Maraini, were selected as being particularly responsive to improved conditions, with a high regression coefficient similar to line A in Figure 1a. Two other varieties, Bankuti and Excelsior were selected for their stability or lack of responsiveness (line B in Figure 1a). The remaining eight varieties in decreasing order of yield, Arivat, CI 3576, Vaughn, Prior A, Velvon II, Drake, Princess and BR1239 all showed an average responsiveness (lines C and D in Figure 1a) but differed greatly in mean yield (Table 1).

However, the selection of varieties on regression coefficient and mean yield, as two independent parameters, does not now seem justified. The original analysis (Finlay and Wilkinson, 1963) was performed on logarithmically transformed data to provide homogeneity of experimental error. Unfortunately the transformation both failed in this purpose (Lawrence, 1970), and greatly emphasized the differences between varieties in low yielding environments, since 1 to 10 kg/ha is equal to

5.2. EXPLORATORY PRODUCT STUDIES OF ARYL RADICAL CYCLIZATION REACTIONS

The effluent obtained after the measurement of the e.p.r. spectrum of the o-allyloxyphenyl radical, formed by the reduction of o-allyloxybenzenediazonium borofluoride (83a) with titanium (III) ethylenediaminetetraacetic acid at ~ pH 8, was extracted with ether; the ethereal layer was concentrated and subjected to short-path molecular distillation. Unfortunately only a very small amount of volatile product was obtained, thus showing that this method is not suitable for product analysis. In an attempt to increase the yield of monomeric products, several reducing agents were used for reduction of the above diazonium salt viz.:-

(i) A stirred two-phase system, with cyclohexane as the organic layer, using titanous ion as the reducing agent. It was hoped that the cyclohexane would act not only as a good hydrogen-atom donor but that it would also remove the products from the aqueous reaction phase thereby preventing further reaction of the products with radicals that are formed subsequently. Again volatile products were formed in a very low yield.

(ii) Two similar reductions with titanous chloride were carried out with ethanol present in the reaction mixture instead of cyclohexane. These

TABLE 2

Origin and ancestry of the 12 varieties used in investigations

	Country of State of Origin	Release Date	Ancestry	Developed from land races in
ARIVAT	California, USA	1940	Atlas x Vaughn	N.Africa, Lower Egypt, S. Russia
CI3576	Egypt	-	Land race	Egypt
VAUGHN	California, USA	1935	Lion x Club Mariout	S. Russia, Lower Egypt
PRIOR A	Australia	1904	Chevallier selection	England
PROCTOR	England	1953	(Plumage x Archer)x (Binder x Gull)	England, Moravia, Gotland
MARAINI	Italy	1912	Unknown	Unknown
DRAKE	Sweden	1930	Gull x early 6-row-barley	Gotland and N.E. Sweden
VELVON 11	Utah, USA	1935	(Coast x Lion) x Trebi	N.Africa, S.Russia, Asiatic Turkey
PRINCESS	Sweden	1928	Archer selection	England
EXCELSIOR	Central Asia	-	Land race	Central Asia
BR1239[1]	Manitoba, Canada	1942	(Manchuria x Lion)x OAC21)xPeatland)x OAC21)	Manchuria, S.Russia, Switzerland.
BANKUTI	Hungary	1939	Hungarian Commercial Selection	Hungary

1. Tested widely but never released or grown commercially

100 to 1000 kg/ha on a logarithmic scale. The regression coefficient of each variety on log data is therefore mainly dependent on its yield at the sites with low mean yield, and gives the impression of independence between yield and responsiveness (Figure 1a). But when the same data ~~is~~ are presented on a natural basis after Eberhart and Russell (1966), the regression value is positively correlated with mean yield (Figure 1b).

The use of the mean yield of a group of common varieties (Walton, 1957) to classify a site also has limitations. Two vastly different environments, such as drought and flooding could well have the same site mean yield, and the ranking of varieties is unlikely to be the same at both. Finlay and Wilkinson probably obtained such good linear fit to their data only because yields were dictated by a simple factor, namely the supply of moisture. Further additions of water and fertility could not be expected to promote a continued linear response (Russell and Eberhart, 1968), as response curves tend to become parabolic over a wide range of inputs.

The mean yields of the 12 varieties shown in Table 1 were obtained at 3 locations in the South Australian cereal belt in 3 years, one of which was a drought. The material was grown in 3 row plots with 17.8 cms between rows and 35.6 cms between plots. Weeds were mechanically controlled between plots, and a seed rate of approximately 80 kg/ha used throughout. This is slightly above the normal commercial rate of 55 kg/ha. Standard local cultivation and fertilization practices were undertaken by the co-operating farmer. Superphosphate was the only fertilizer applied, so that the major source of nitrogen originated from the legume content of previous pastures. The nitrate level was probably low in the year following the drought, and generally is kept low in barley crops grown for malting.

Two distinct groups of varieties appear among the 12 selected. The first group consists of Arivat, Vaughn, Velvon II and CI 3576, all of which were derived in part from material originating in the Mediterranean areas of North Africa (Table 2). The first three were developed from material taken to California by the Spaniards. Arivat and Vaughn were grown there under irrigation, but with CI 3576, were among the highest yielding varieties grown under dry land conditions in Finlay and Wilkinson's trials (Table 1). All the high yielding material in the collection, except CI 3576, had six-rows and was obviously well adapted to South Australian conditions.

The second group is comprised of 2-row varieties derived from the temperate regions of Europe (Proctor, Princess, Drake and Prior A). Prior A is a back cross derivative from Prior which is the standard commercial variety used for malting in South Australia. Both Proctor and Princess are later than Prior A and often suffer yield reduction through flowering at a time of increasing temperature and moisture stress.

The remaining 2-row variety Bankuti Korai, flowers exceptionally early, is weak tillering and has very sparse foliage; probably as a result of it being selected as a nurse crop for red clover. It was also grown as a main crop in the drier and less fertile areas of Hungary, again presumably because of its rapid development.

All the three other varieties have in common is the 6-row characteristic. BR 1239 was selected in Western Canada from a cross including 85 per cent Manchurian material. The rachis is extremely fragile and tends to fracture under arid conditions. This loss may have resulted in the grain yield (Table 1) being underestimated, since BR 1239 matures well before other varieties and is left in a brittle condition for a longer period.

Little is known about the ancestry of Excelsior and Maraini. Both are later maturing and also lose grain; Maraini by neck breakages, and Excelsior by weak attachment of the grains to rachis. Maraini is sown in the

Autumn in Italy, and was selected especially for drought resistance, but in South Australia was the latest of the 12 varieties.

Since the four 2-row varieties derived from European germplasm also suffer from neck or rachis breakage, the 12 varieties were never harvested together in the experiments reported here but soon after each was estimated to have reached physiologic maturity. Staggered harvesting considerably reduced the 5-fold yield differential previously found among varieties (Table 1); delayed harvesting only has merit in a breeding programme aimed at improving grain retention after maturity.

The group of varieties allowed comparisons to be made not only on the basis of yield, but also between two-and six-row varieties and between early and late varieties. If any differences in drought resistance exist then they should be revealed in such a microcosm. Likewise the varieties came from areas of greatly differing soil fertility, and seemed likely to have different nitrogen requirements. The varieties were also known to vary greatly in morphologic characteristics, like leaf number, and therefore possibly in the density required for optimum yield. Conversely, similarities in response among such a diverse group of varieties would be significant. North African, Northern European, Manchurian, and

Southern European varieties had not previously been compared agronomically.

C. GENERAL EXPERIMENTAL INFORMATION

Techniques common to several experiments and cultural practices are covered in this part of the thesis. Methods unique to particular experiments are described and discussed at the relevant places throughout the text.

PLANT ESTABLISHMENT. All plots were sown by hand and the whole plot covered with coarse sand to a depth of approximately 2 cm, except those in 1967, the first experimental year. In 1967 the plots were covered with loose soil, but even the few light showers in that dry year were sufficient to break down the unstable soil aggregates and increase the density of the surface soil. This had no appreciable effect on seedling establishment at the high density, while at low density any empty sites were filled with transplants grown under similar conditions. In the following seasons two or three seeds were planted at each position and thinned to one after germination at all low densities and in precision plantings. A seed rate of 100 kg/ha (approximately 250 seeds/m^2) in 17.8 cm (7 inch) rows was adopted as a standard in all experiments not of varying density, to conform with the present plant breeding methodology at the Institute.

WEED CONTROL. Excellent control of all broadleaved species resulted in all four years from the use of Buctril MA at the rate of 1 to 2 l/ha. Buctril MA contains 20 per cent Bromoxynil and 20 per cent MCPA and no damage to the barley was observed in any year. Annual winter grasses were effectively controlled by hand hoeing or pulling, but were only a problem in 1967.

DISEASE CONTROL. Powdery mildew infestation occurs regularly during the cool wet winter at Adelaide, and so the experiments were sprayed regularly to avoid the problems associated with the differential resistance of varieties. Pipron 25W (3 (2-piperidino) propyl 2, 4-dichlorobenzoate) was used in 1967 and 1968 until the supply in Australia was exhausted. This was followed by Morestan 25WW (6-methylquinoxaline-2, 3-cyclicdithiol carbonate) in 1968 until two new systemic fungicides, Benlate 50WW (1-(butylcarbamoyl)-2-benzimidazole carbamic acid) and Milstem (5-n-butyl-2-ethylamino-4-hydroxy-6-methy-pyrimidine) became available. All four were applied by a mist blower at the rate of .5 kg/ha every two weeks, and while outbreaks of mildew did occur, they were quickly suppressed. However in 1969 when unsprayed controls were included for the first time, no yield advantage was gained by spraying despite the disease having a devastating appearance on the controls. Barley scald (*Rhynchosporium* spp) also occurred in one year, 1969, but no significant amount of other diseases ~~were~~ was recorded.

LEAF AREA INDICES. The LAIs were calculated by one of two methods depending on the stage of the crop. Before stem elongation, the leaves were detached from the stems at the ligules and a sample fed through a belt-fed optical planimeter (Wilkinson and Silsbury, 1966) to give the ratio of leaf area to leaf weight. The total weight of leaves was then multiplied by this ratio and divided by the area occupied by the sample.

At anthesis and thereafter, the LAI was calculated from the mean of measurements taken to describe random culms. The leaf area per culm was obtained by adding the area of green leaves (width x length x .75, Stoskopf pers. comm.) to the area of the stem considered as half a cylinder (.5 x Π x diameter x height), the area of one side of the ear considered as a simple rectangle (length x breadth), and the area of one side of the awns. The sum was then multiplied by the number of culms in a square meter.

LIGHT PENETRATION. The percentage of light penetrating to the base of the crop was calculated by dividing the value recorded at the base of the crop by the value outside the crop. Each measurement was the integrated value over a 23 cm length of a probe with 6 silicon photovoltaic cells connected in parallel and covered by opaque perspex for cosine correction. The probe design resulted in only the near vertical component of the incoming radiation being recorded. Readings were taken within one hour of true solar noon, and only on bright cloudless days since a uniformly overcast day proved to be entirely theoretical at Adelaide. Cloudless, windless days were rarities however in the winter period, especially in 1968 when only 5 such days occurred in the period critical for light prior to stem elongation. Readings were taken across the rows to sample both intra- and inter- row shading. The row direction was North-South in 1967 and 1969 and East-West in 1968.

SOIL MOISTURE CONTENTS. The amounts of moisture remaining in the soil after differential rates of extraction by treatments and varieties was measured indirectly throughout 1967 and 1968 by the neutron scattering method. The moisture meter (Model Number 8402 Nuclear Enterprises Ltd. Edinburgh) comprised a portable scaler (NE5011) and a moisture probe (NE5592) with a 45 mc Americium/Beryllium source. Access tubes were made from polyvinyl chloride, and counts taken at 15 cm (0-30 cm), 45 cm (30-60 cm) and 75 cm (60-90 cm) depths, which coincided with the A horizon and the upper and lower parts of the B_1 horizon. A layer of gravel restricted the maximum depth to 90 cm in 1967 but this probably had little effect on the comparisons between varieties and between treatments, as the wetting front reached only 90 cm in 1967 and deeper tubes in 1968 showed relatively little water taken up below 90 cm. The counts per minute were transformed into volumetric water contents from a calibration curve (Burford, 1969) with the formula:- $\ln \frac{(C-B)}{N-B} = -0.1869 + 0.9094 \ln (MC)$

where MC = moisture content

C = counts/min in soil

N = counts/min in water

B = counts/min in air

MORPHOLOGIC AND YIELD MEASUREMENTS.

Tiller Numbers - only those tillers clearly protruding between leaf sheath and subtending leaf were included.

Height - was taken from ground level to the tip of the elongating leaves or awns depending on stage of development.

Stem length - was taken from ground level to the collar of the ear.

Ear length - was measured from the pedicel or collar to the tip of the terminal grain.

Leaf length - was measured from the auricle to leaf tip.

Leaf width - was taken at the widest part of the leaf.

Anthesis - was recorded when approximately 30 per cent of the florets on the main culms had released pollen from their anthers inside the glumes.

Total dry weights - included all above-ground material, including all dead leaves and tillers on the ground surface of the area harvested, and was obtained after dehydration at 62° C for one to three days depending on the bulk of the sample.

Grain weight per ear - was derived from the grain dry weight per unit area and the number of ears.

Number of grains per ear - was derived from the 1000 grain weight and the grain weight per ear.

STATISTICAL ANALYSIS. All analyses of variance were carried out on a CDC 3200 computer using the GENSTAT general programme. Regression analyses were performed on a CDC 6400 using STATSCRIPT and various specialized programmes. Throughout this thesis, the least significant difference (LSD) has been used in preference to multiple range test of Duncan (DMR) when the F test is significant, despite the need to compare 12 varieties and numerous treatments. This decision was taken after a computer simulation (Atkinson and Chambers, unpubl.) had shown that the LSD had classified no more events significant than the DMR when no significance was present, but indicated more events significant when they were actually significant. The values of any variable that are followed by different alphabetical letters therefore differ by more than the appropriate LSD.

The data showing the response of varieties to nitrogen and density ~~was~~ were fitted by computer using linear and quadratic terms, and the fitted curves plotted directly by computer. The individual points about these lines have been ommitted due to the large number (up to 1440) in each figure, but the equation for each line has been included in the appendix, together with the amount of variability accounted for by the two terms (R^2) and their significance (F- test). The curves in the remaining figures were hand fitted and the individual points included.

IV. ENVIRONMENTAL CONDITIONS AND ONTOGENETIC DEVELOPMENT IN 1967, 1968, 1969 AND 1970

IV. ENVIRONMENTAL CONDITIONS AND ONTOGENETIC DEVELOPMENT IN 1967, 1968, 1969 AND 1970

EDAPHIC CONDITIONS. All experiments but one were grown in the field at the Waite Agricultural Research Institute ($34^{\circ}58'$S, $138^{\circ}38'$E, 123m above sea level). The other was grown in a glasshouse at the Institute. The soil at the Institute is a red brown earth (Urrbrae fine sandy loam) with over 40 per cent fine sand and 20 per cent clay in the cultivated layer (Table 3).

TABLE 3

Characteristics of the Urrbrae fine sandy loam (Litchfield, 1951)

Depth (cm)	0-15	15-30	30-90	90-180
Horizon	A1	A2	B1	B2
pH	5.7	5.9	6.6	
% coarse sand	2.5	2.2	0.9	0.7
% fine sand	40.9	40.0	17.1	21.7
% silt	33.3	31.7	14.6	30.6
% clay	20.2	24.6	65.3	34.3
Structure	crumbly	nutty	prismatic	nodular

In its native state, Urrbrae loam is well textured and friable, but after continued cultivation, the aggregates become unstable (Clarke and Marshall, 1947) and break down with continued rainfall (Millington, 1961). The apparent density of the surface soil therefore increases as the season progresses, from 1.2 up to 1.6 g/cc, and Millington (1961) reported a yield reduction with wheat of 215 kg/ha for every 1 cm of rain falling in the month after seeding because of reduced seedling establishment. The aeration is impaired, and denitrification rapidly exhausts the nitrate available to the plant in mid-winter (Burford, 1969). The experimental areas in 1967, 1968 and 1970 had a poor surface structure, and nitrogen deficiency symptoms appeared in plots receiving no nitrogenous fertilizer. In 1968, the soil structure was excellent and even the incorporation of chopped straw, to reduce the level of nitrogen available in the soil, did not induce any deficiency symptoms.

FERTILITY. Nitrogen was always applied as calcium ammonium nitrate, broadcast on the soil surface soon after seeding. Details of the amounts applied to each experiment are given in the description of individual experiments. Since high nitrogen levels relative to phosphorus can depress barley yields (Gregory, 1949), approximately 500 kg/ha superphosphate (50 kg/ha P) was worked in over the whole experimental area each year. About 100 kg/ha superphosphate had also been applied to every cereal and pasture crop previously grown in each area (Table 4). The pastures were usually sown to subterranean clover, but there was a succession to broadleaved weeds, and the soils showed less build up of nitrogen than would be expected. Potassium is rarely deficient, but 120 kg/ha muriate of potash was incorporated each year.

CLIMATIC CONDITIONS. 1967 was the driest year on record at the Waite Institute with a total rainfall of 325.7 mm. Only in one month (July - Figure 2A) did the rainfall exceed the pan evaporation. Both temperatures and solar radiation were consistently above average but still only 168.3 cals/cm^2

TABLE 4

History of experimental areas used in 1967, 1968, 1969 and 1970 over the previous ten years

Number Years Previous	1967 area	1968 area	1969 area	1970 area
10	pasture	pasture	pasture	pasture
9	wheat	pasture	pasture	pasture
8	cereals	pasture	pasture	fallow
7	pasture	pasture	cereal hay	fallow
6	pasture	pasture	cereal hay	pasture
5	pasture	pasture	fallow	pasture
4	fallow	pasture	cereals	pasture
3	wheat	pasture	fallow	fallow
2	peas	pasture	peas, fallow	wheat
1	wheat	cereal hay	peas, fallow	t~~h~~ick beans
Sowing date	June 25	July 9	June 13	June 25

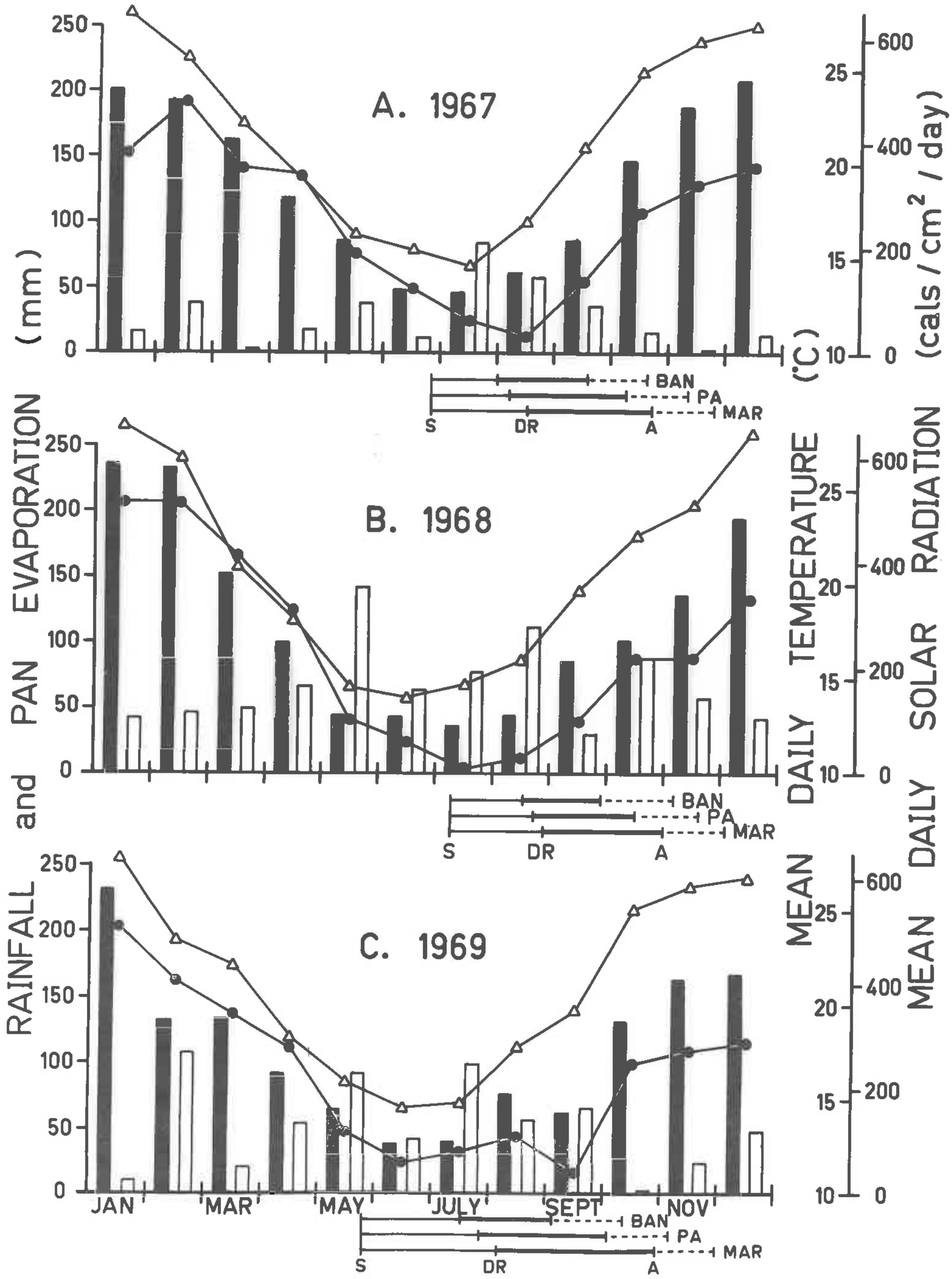


Figure 2. Rainfall (open column), pan evaporation (closed column), solar radiation (open triangle) and temperature (closed circle) for A. 1967, B. 1968 and C. 1969.
The dates of sowing (S), double-ridge (DR), anthesis (A) and maturity are indicated for Bankuti (BAN), Prior A (PA) and Maraini (MAR).

were received per day during July compared with a potential of 306 for that month or 832 for December (Figure 3C) (.8Q, Messent, pers. comm).

1968 was the wettest year recorded at the Institute with a total rainfall of 820.5mm; 202mm above normal with an exceptionally wet period between May and August (Figure 2B). Leaching may have added to denitrification losses and nitrogen deficiency became most apparent. Solar radiation fell as low as 5 cals/cm^2/day in June and 9 cals/cm^2/day in August and averaged only 145 cals/cm^2/day throughout June. The mean daily temperature in July was only 10°C, below which a substantial check to growth occurs (Trumble, 1948).

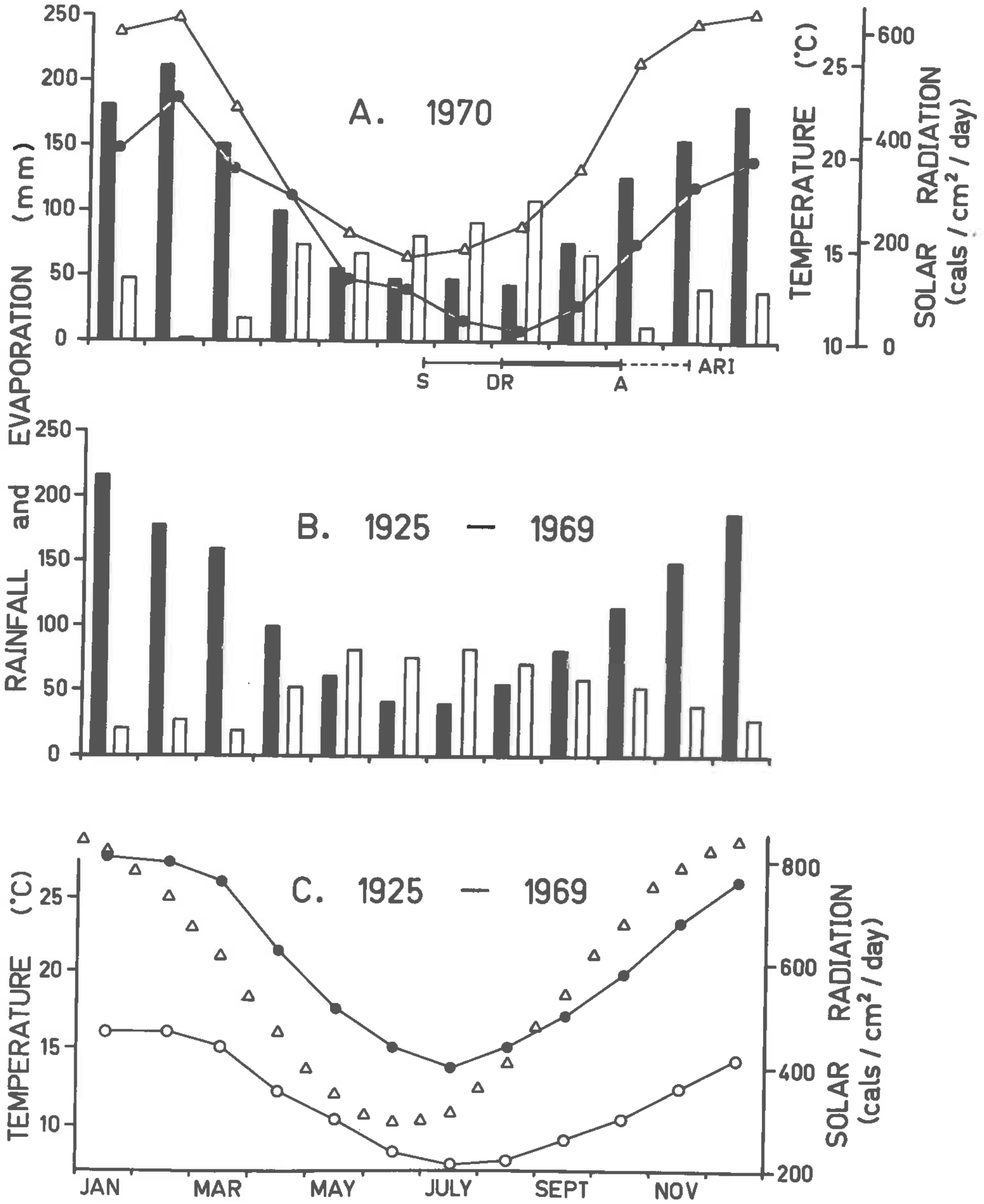
1969 (Figure 2C) and 1970 (Figure 3A) had near average rainfall, 623 and 653mm respectively, and approached a 'typical' year (Figure 3B) in the Adelaide type of Mediterranean climate. Adequate rain fell during the cold and cloudy days of May, June, July and August while the light intensity and temperature increased rapidly in October coupled with a sudden decrease in precipitation.

ONTOGENETIC DEVELOPMENT. Though all varieties in a trial are subject to the same environment, developmental rates vary so that very different environmental conditions may exist at the same growth stages of particular varieties (Johnson, 1953). Bankuti, the earliest variety, always

Figure 3. A. Rainfall (open column), pan evaporation (closed column), solar radiation (open triangle) and temperature (closed circle) for 1970. Date of sowing (S), double ridge (DR), anthesis (A) and maturity are indicated for Arivat (ARI).

B. Mean rainfall and pan evaporation for 1925-1969.

C. Mean maximum (closed circles) and mimimum (open circles) for 1925-1969, and maximum daily solar radiation (open triangles) on cloudless days (by ½-monthly periods).


A. 1970
B. 1925 — 1969
C. 1925 — 1969
RAINFALL and EVAPORATION (mm)
0
50
100
150
200
250
TEMPERATURE (°C)
10
15
20
25
SOLAR RADIATION (cals / cm² / day)
0
200
400
600
800
S
DR
A
ARI
JAN
MAR
MAY
JULY
SEPT
NOV

reached anthesis during September (Figures 2A, B, and C) and usually matured before severe vapour pressure deficits developed. The latest variety, Maraini, flowered in late October, and was subjected to higher evaporative demand during November, and occasional hot, dry winds during grain filling.

Maraini responded very strongly to photoperiod as anthesis took place on October 29 in 1969 and October 30 in 1968, despite planting on June 13 and July 9 respectively in the two years. In contrast, Bankuti reached anthesis on September 3 and September 28 for the same two planting dates, and appeared insensitive to daylength.

The effect of sowing date on flowering date was followed more systematically in 1969, when one adjacent 2 metre row was planted every 3 days between May 16 and July 24 in 4 replications of 6 varieties (Figure 4). A delay in sowing of 69 days delayed anthesis in Bankuti by 57 days but in Maraini by only 16 days. The departures from linearity in the lines (Figure 4) disappear when the horizontal axis is changed to degree days instead of planting date, and the varietal lines can be extrapolated to a point at the end of August where all varieties flower together. This simultaneous flowering actually occurred in a similar experiment with wheat varieties of less extreme maturity (Gardener and Rathjen, unpubl.), and suggests the practice

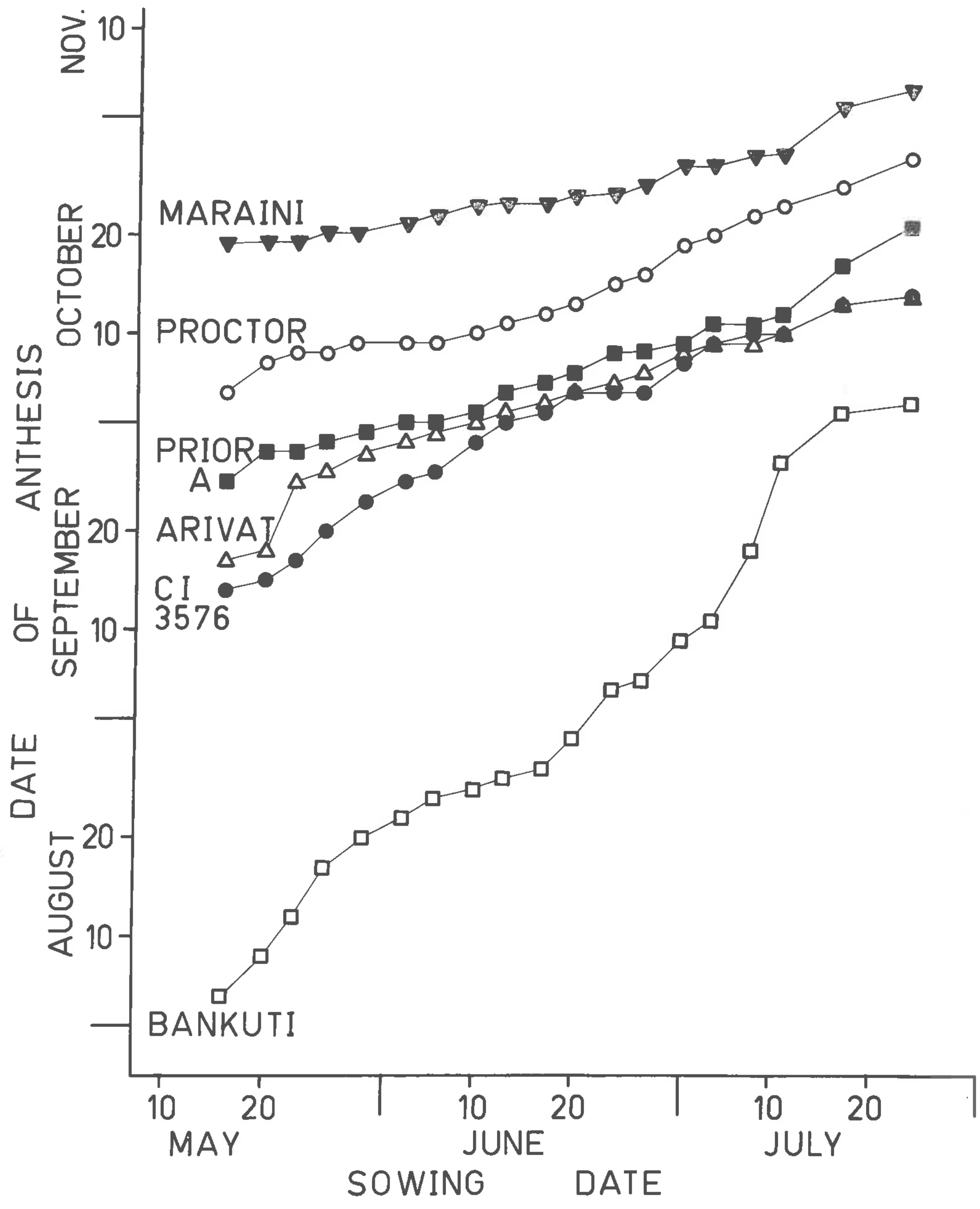


Figure 4. The effect of sowing date on the date of anthesis in six varieties of barley.

of using earlier varieties to escape the drought encountered by late planting in August is as erroneous as the idea that late varieties benefit most from an early planting.

Various other agronomic treatments employed during the three years also significantly affected the length of the period up to flowering, but the effect was relatively small and apparently inconsistant (Figure 5). Very high plant densities and low nitrogen levels both hastened anthesis by 4 days in 1968 (Figure 5A), and a combination of high moisture and nitrogen levels with the higher density gave a similar result in 1967 (Figure 5B). High densities always seem to speed development (Kirby, 1967), presumably because of the suppression of tillering, since uniculm lines are always much earlier than their parents.

These differences in development due to agronomic practice were, however, swamped by the varietal differences (Figure 5C). The sequence of varieties was relatively constant with the ranking upset only by CI3576 flowering before BR1239 and Arivat, and Princess after Excelsior and Velvon, in 1967 and 1968. The differences in flowering date between varieties were not entirely due to differences in the length of the period from sowing to floral initiation, as only 3 weeks separated the floral initiation of Bankuti and Maraini, but during this period, far more primordia were committed to leaf structures in the later

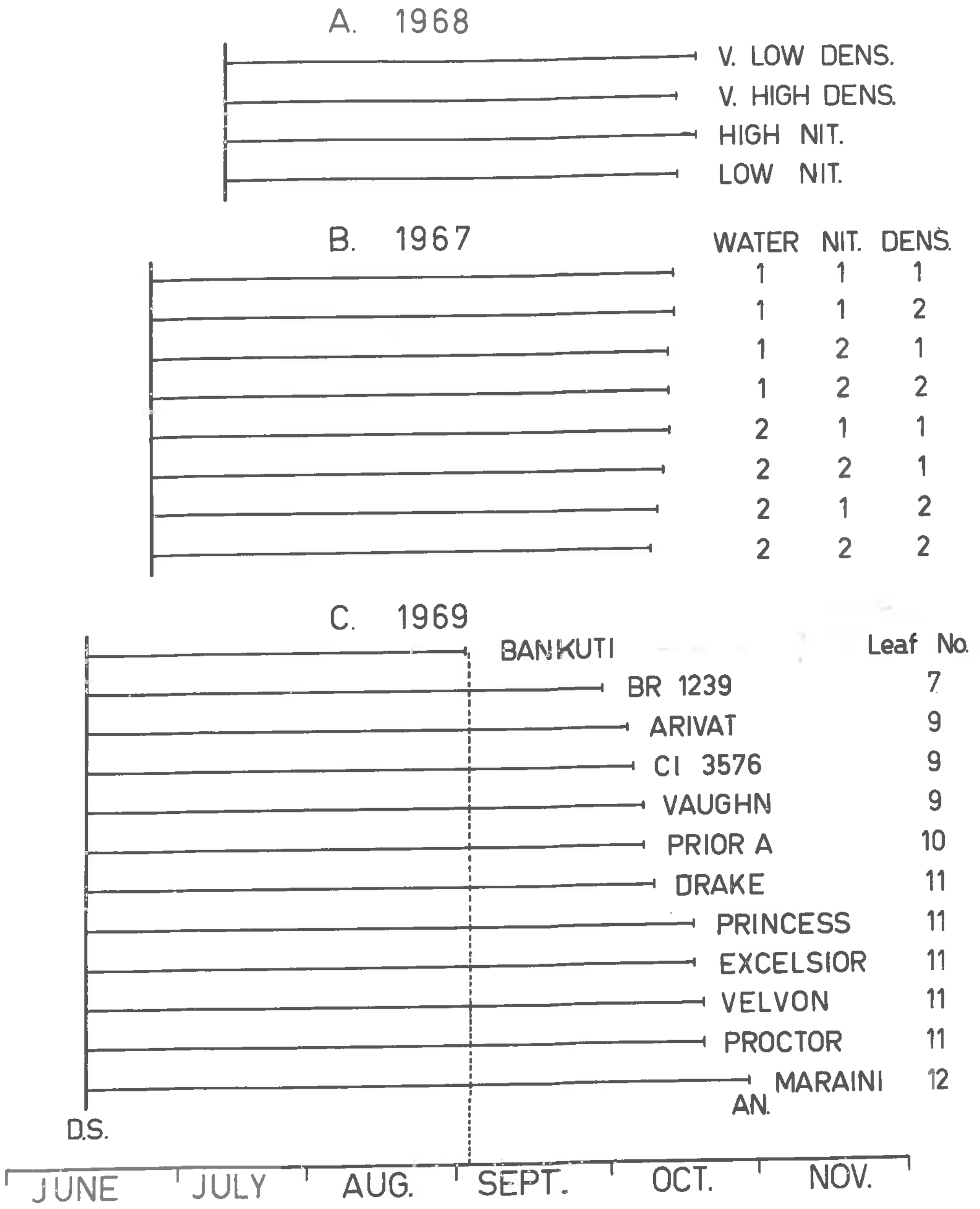


Figure 5. Differences between agronomic treatments, between varieties, and between years in the length of period from sowing (D.S.) to anthesis (AN.).

varieties. The number of leaves and length of the pre-anthesis period were closely related (Figure 5C), as found by Gott et al. (1955), with Maraini having 12 leaves on the main culm and Bankuti seven from the June 13 planting. The leaf number in Maraini, however, decreased to eight at the latest planting (July 24), compared to six for Bankuti.

V. THE DIFFERENTIAL RESPONSE OF VARIETIES TO NITROGEN

V. THE DIFFERENTIAL RESPONSE OF VARIETIES TO NITROGEN.

Improving the nitrogen nutrition of a crop can increase all three yield components, but can also result in increased competition for light and for water. Varietal differences in both aspects of competition were investigated concurrently in adjoining sets of plots in 1968.

METHODS

Experiment 1. One experiment was specifically designed to show pictorially the response of each variety, in terms of the three yield components, straw and grain yields and harvest indices, to a wide range of nitrogen levels (Table 5). Nine levels were considered necessary to depict the parabolic response of each variety as no previous knowledge of varietal requirements was available.

TABLE 5

The nine rates of nitrogen used in 1968

N Level	Rate (kg/ha)	Comments
1	0	Usual farm application in South Australia
2	10)	Possible commerical levels
3	25)	
4	50)	
5	75	
6	100	
7	150	Extracted by a high yielding crop
8	200)	Possibly yield-depressive levels
9	275)	

The 12 varieties were planted in three-row plots, 9m in length, and then, two weeks after planting, the nine nitrogen levels were applied as 1m strips at right-angles to the rows. The 12 varieties were randomized within each replication, but the 9 strips of nitrogen were always arranged systematically, from 0 to 275 kg/ha. Hence 0 and 10 kg/ha were always adjacent as were 200 and 275 kg/ha. This reduced the need for very wide borders without much danger of serious influence from neighbouring plots, and enabled the centre 0.5m of each sub plot or 50 per cent of the available material to be utilized. A substantial degree of protection was achieved by the use of eight replications to smooth out fluctuations in individual replications, and the alternation of highest and lowest levels of nitrogen at any one end in adjacent replications (with gradients running alternatively east to west and west to east).

Experiment II. Rather than disperse the neutron access tubes throughout the quite large area of experiment I with the attendant dangers of increasing soil heterogeneity (Kirby, 1970), the soil moisture measurements were located together in the second experiment. Arivat, Proctor, Excelsior and Princess were selected as varieties likely to differ in water use and 0, 50, 100, and 200 kg/ha nitrogen was again applied 2 weeks after planting. The sixteen combinations were randomized within each of the three replications, and each plot was 2m square with the access tube at the centre.

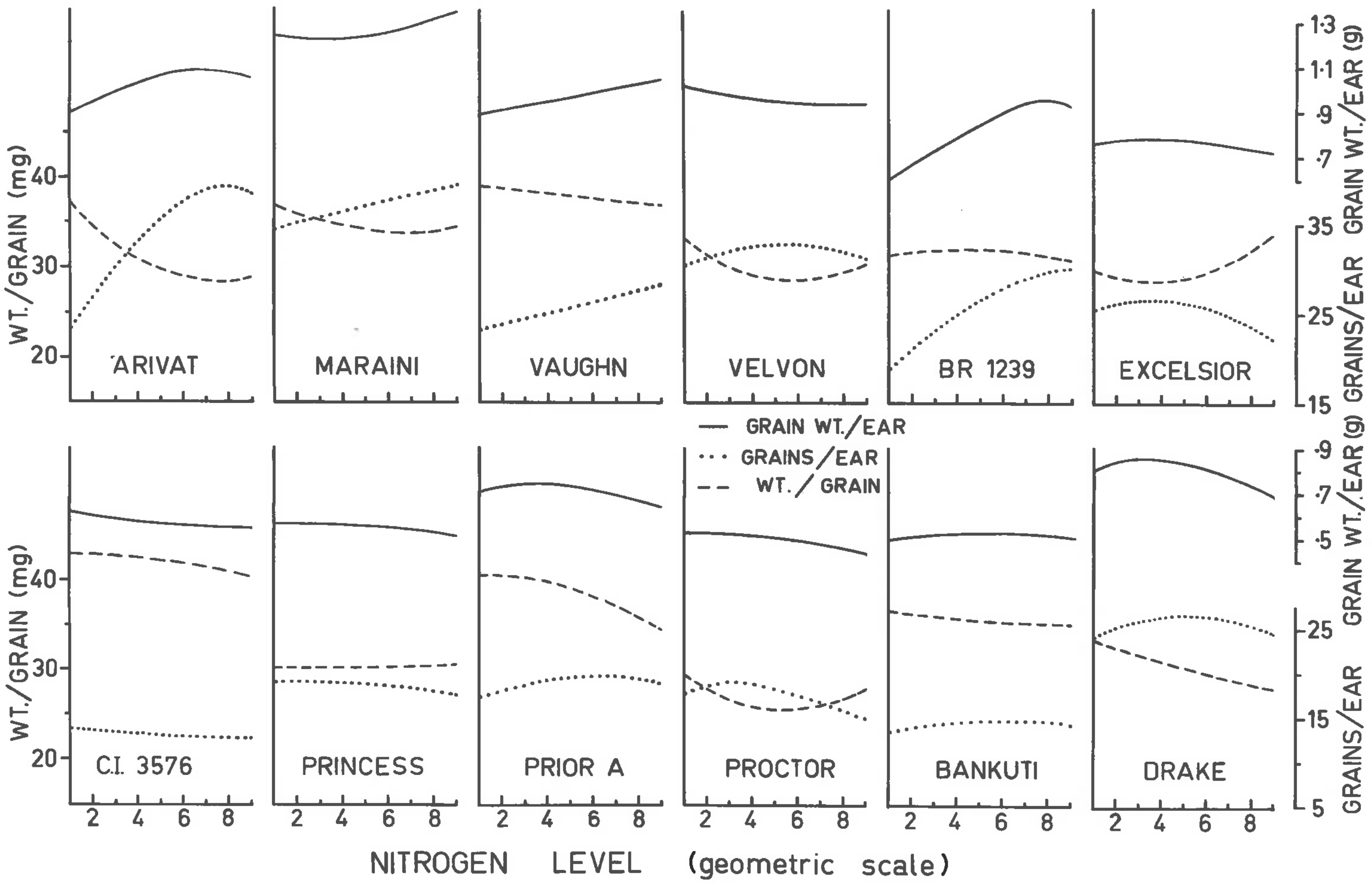
RESPONSE OF VARIETIES.

(1) Weight per grain, grains per ear and grain weight per ear. The number of grains per ear increased with increasing nitrogen application up to the fifth level (75 kg/ha) in ten out of the twelve varieties (Figure 6). Above this level, the number of grains per ear fell in eight and continued to rise in four varieties. The weight per grain showed the reverse tendency, falling with increasing nitrogen application until the fifth level in ten varieties and then rising again in four.

The grain weight per ear therefore tended to remain constant over the nine levels of nitrogen in every variety, except BR1239, with variation in weight per grain being almost exactly compensated for by variation in number of grains per ear. Also, the grain weight per ear was similar between Vaughn and Velvon and between CI3576 and Princess despite the many small grains of Vaughn and CI3576 and fewer large grains of Velvon and Princess. The weight of grain per ear in the six-row varieties was approximately twice that in the two-row varieties because of the greater number of similar sized grains of the former.

The exception to the relative constancy of grain

Figure 6. The reciprocal relationship of weight per grain and number of grains per ear at nine levels of nitrogen. The consequent tendency to constant yield per ear is indicated. Computer fitted curves (equations given in Appendix C).

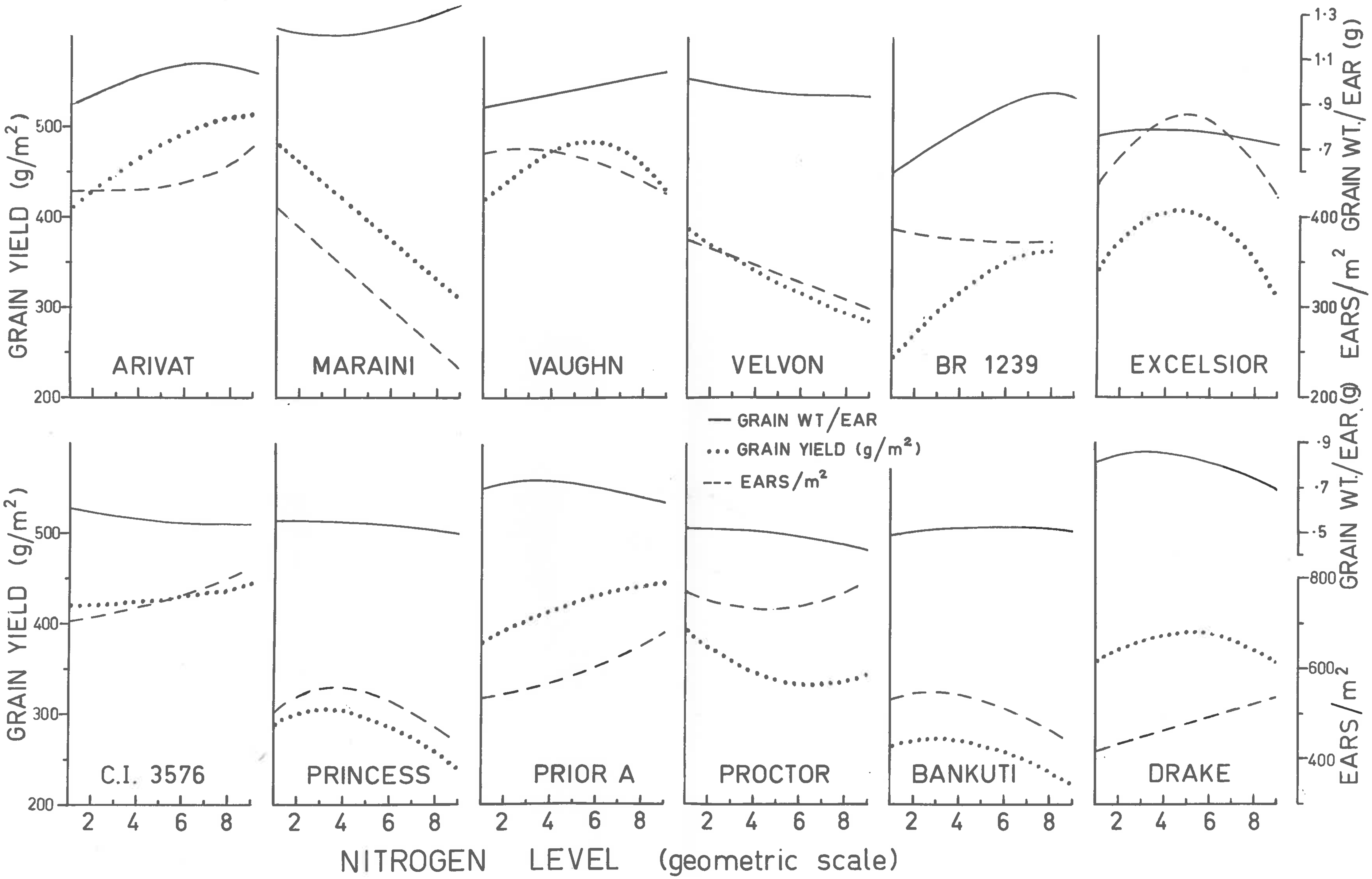

ARIVAT
MARAINI
VAUGHN
VELVON
BR 1239
EXCELSIOR
C.I. 3576
PRINCESS
PRIOR A
PROCTOR
BANKUTI
DRAKE
WT./GRAIN (mg)
20
30
40
GRAIN WT./EAR (g)
1·3
1·1
·9
·7
·5
GRAINS/EAR
35
25
15
5
GRAIN WT./EAR
GRAINS/EAR
WT./GRAIN
2
4
6
8
NITROGEN LEVEL (geometric scale)

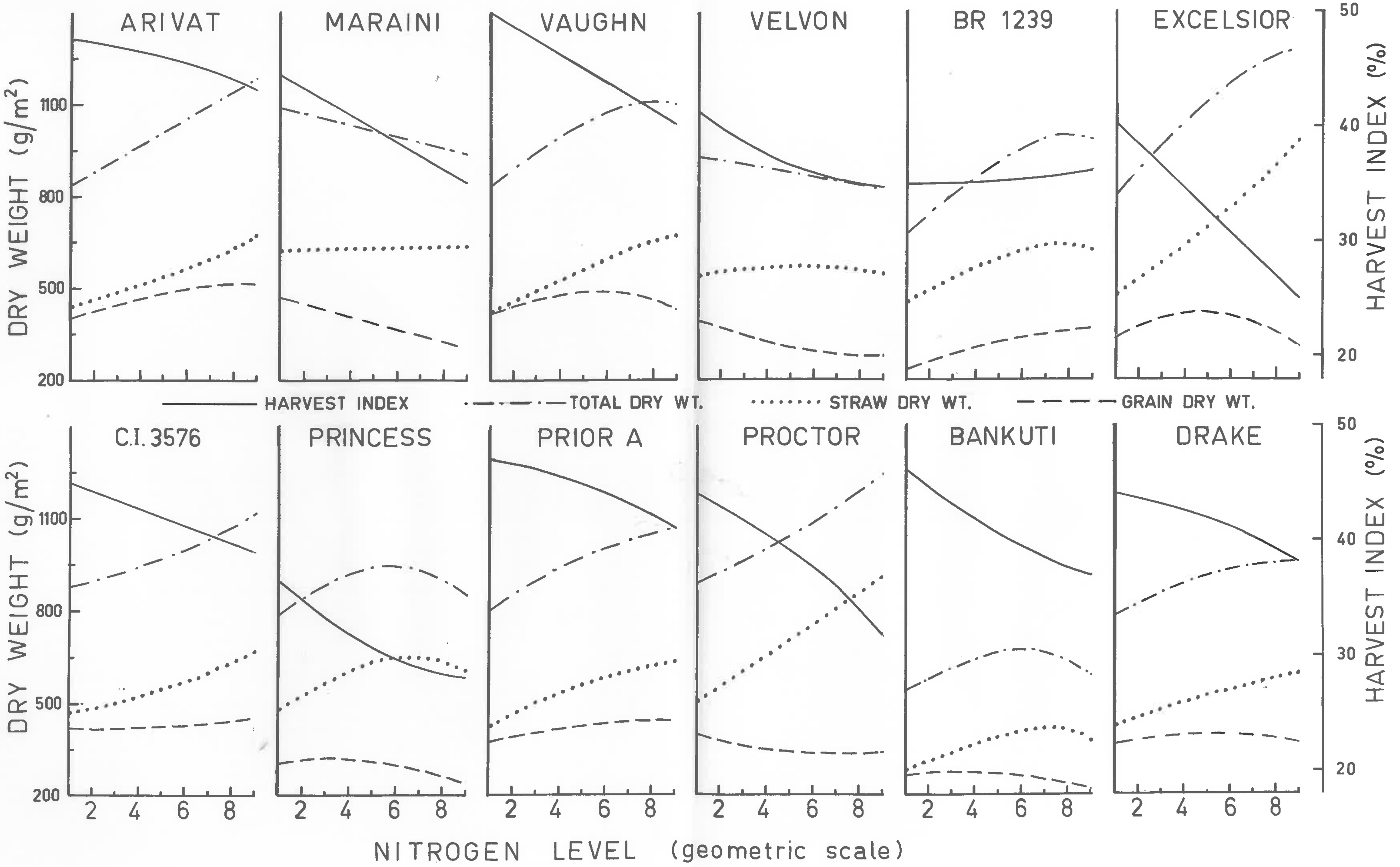
weight per ear with increasing level of nitrogen was BR1239, which previously had been observed to show readily symptoms of nitrogen deficiency. In this experiment BR1239 again appeared slightly chlorotic at the lower nitrogen levels and at 0 kg N/ha had only a similar number of grains per ear to the two-row varieties. Both the increase of grain weight per ear and the increase in grain yield (Figure 7) with increasing nitrogen level were solely attributable to this increase in number of grains per ear. BR1239 is the only variety in the group derived from the Manchurian lines of barley, but its failure at low nitrogen levels may alternatively result from its selection under the extremely fertile Prairie conditions.

(2) Number of ears per m^2 and grain yield. With relative stability in the weight of grain per ear, the change in grain yield with nitrogen application was largely determined in all varieties, except BR1239, by change in number of ears per m^2 (Figure 7). The ear numbers of both two- and six-row varieties showed responses of a similar magnitude, but since the six-row varieties had heavier ears, they were far more responsive to changes in nitrogen level. The range from lowest to highest grain yield in the six-row varieties was approximately twice the range in the two-row varieties.

The variation in the direction of the response

Figure 7. The relationship of grain yield to number of ears per m^2 and weight of grain per ear in twelve varieties at nine levels of nitrogen. Computer fitted curves (equations given in Appendix C).


GRAIN YIELD (g/m²)
500
400
300
200
ARIVAT
MARAINI
VAUGHN
VELVON
BR 1239
EXCELSIOR
1·3
1·1
·9
·7
GRAIN WT./EAR (g)
400
300
200
EARS/m²
— GRAIN WT/EAR
••• GRAIN YIELD (g/m²)
--- EARS/m²
GRAIN YIELD (g/m²)
500
400
300
200
C.I. 3576
PRINCESS
PRIOR A
PROCTOR
BANKUTI
DRAKE
·9
·7
·5
GRAIN WT./EAR (g)
800
600
400
EARS/m²
2
4
6
8
NITROGEN LEVEL (geometric scale)


ARIVAT
MARAINI
VAUGHN
VELVON
BR 1239
EXCELSIOR
C.I. 3576
PRINCESS
PRIOR A
PROCTOR
BANKUTI
DRAKE
DRY WEIGHT (g/m²)
200
500
800
1100
HARVEST INDEX (%)
20
30
40
50
HARVEST INDEX
TOTAL DRY WT.
STRAW DRY WT.
GRAIN DRY WT.
2
4
6
8
NITROGEN LEVEL (geometric scale)

is remarkable even in a group of varieties selected for genetic diversity. Three varieties had their maximum yield at 0 kg N/ha, four at 275 kg/ha, and five at intermediate levels. Obviously there is great scope for selecting varieties suited to particular nitrogen levels. Arivat appears well adapted to those areas which have excellent legume growth, for a well established clover sward can add 225 kg/ha nitrogen to the soil in a good year (Sims, 1953), although the grain yield of even Arivat was depressed by nitrogen application under conditions of higher natural fertility in later experiments (Section VI and VII). Only BR1239 consistently responded with higher grain yields to levels of nitrogen supra-optimal for other varieties. Maraini and Velvon are well suited to nitrogen deficient areas which are unable to grow pasture legumes. The high yield of Maraini at 0 kg/ha was surprising and when its response curve is taken with those of Arivat and Vaughn, a common parabolic curve seems to emerge with all four varieties having the same intrinsic yield at their differing optimum levels. Choice of Arivat alone for nitrogen experimentation might have led to the conclusion that it would be economic to apply high rates of nitrogen to deficient soils in areas with adequate rainfall, whereas use of Maraini without fertilization would prove economically advantageous.

(3) Total dry matter, straw and grain. The weight of straw increased in all varieties with increasing nitrogen level, regardless of the direction of response of grain yield (Figure 8). The total dry matter similarly rose in all varieties except in Maraini and Velvon where the reduction in ear numbers and grain yield at higher nitrogen levels was sufficient to depress the total yield. In all varieties, except BR1239, the weight of straw progressively exceeded the weight of grain, and the harvest index fell with increasing nitrogen level. The late flowering varieties (Maraini, Velvon, Excelsior, Princess and Proctor) tended to have lower harvest indices at all nitrogen levels indicating either heavier stems or a greater number of sterile tillers, since the mean ear size was similar to the early varieties. In some varieties, slight lodging did occur just before maturity, but the weight per grain was not differentially reduced. It was therefore important to know the cause of the differential ear survival between varieties.

REMOVAL OF SOIL MOISTURE. Significant differences in soil water contents were expected to show up between the four varieties, or at least in the variety x nitrogen interaction for the following reasons:-

1. Highly significant differences occurred in the amount of solar energy being intercepted for foliar

Figure 8. The relationship of grain yield, straw yield, total yield and harvest index in twelve varieties at nine levels of nitrogen. Computer fitted curves (equations given in Appendix C).

evaporation by the four varieties at the four nitrogen levels (Table 6).

2. Varieties differed in stage of development at any one date, and the three later varieties continued to transpire after Arivat matured.

3. Between September 25 (Date 1) and December 13 (Date 7) the soil surface was often dry, thereby decreasing evaporation from the soil, while the sub-surface moisture was subject to removal by transpiration.

4. Varieties differed greatly in grain yield (highest, Arivat, Figure 6), straw and total dry matter (highest, Excelsior, Figure 8) and number of ear bearing culms (highest, Proctor, Figure 7).

However at no time during the season did the differences in soil water content between varieties reach the 5 per cent level of significance (Table 7). The highest F value on October 21, when the ears had emerged on all varieties and the light readings given in Table 6 were taken, was 2.37 which was significant at the 10 per cent level only. The mean varietal values are given for this date (Table 8) because the trend resembles the significant differences found between varieties in 1967 discussed in Section X with the early developing variety, Arivat, having removed more soil moisture than the three later varieties.

TABLE 6

Percent light interception in 4 varieties at 4 nitrogen rates on October 21, 1968 when all ears had fully emerged

Variety	Nitrogen (kg/ha) 0	50	100	200	Variety Mean
Arivat	65.8	75.6	81.7	85.3	77.1
Excelsior	79.3	82.3	88.4	90.2	85.1
Proctor	57.4	82.7	85.2	88.6	78.5
Princess	82.3	86.2	88.6	91.8	87.2
Nitrogen Mean	71.2	81.7	86.0	89.0	82.0

L.S.D. = 5.3

TABLE 7

F values for soil moisture contents, on 7 occasions in 1968: mean of 3 depths

	Date of Readings						
	Sept. 25	Oct. 9	Oct. 21	Nov. 4	Nov. 15	Nov. 26	Dec. 13
Variety	.34	1.24	2.37	.63	.25	.12	.39
Nitrogen	3.08*	5.20**	7.82**	3.12*	2.54	2.89	5.29**
Var. x Nit.	1.05	1.14	1.13	1.17	.95	1.89	1.64

* = .05 significance

** = .01 significance

The differences do not appear related to number of ears or weight of straw, since Proctor and Excelsior have similar soil water contents but different ear numbers and straw weights,nor are they related to light interception (Table 6) since Arivat and Proctor have similar light interception but different soil water contents. In fact, the only clear difference between varieties was the 2 week earlier stem elongation of Arivat. Foliar evaporation has been correlated positively with plant height in maize (Tanner and Lemon, 1962) and wheat (El Nadi and Hudson, 1965). Plant height apparently influences evaporation by the greater interception of advected heat and by creating greater turbulence (Lemon et al., 1957; Bowers et al., 1963), and such effects are greater in smaller areas than areas of extensive fetch.

TABLE 8

Mean soil water contents (% v/v) for
4 varieties on October 21, 1968

Variety	Arivat	Excelsior	Proctor	Princess
Soil Moisture content (v/v %)	25.3	25.9	26.2	26.3

F .05 N.S. L.S.D. .05 = .4

Unlike the F values for varieties, those for nitrogen were significant except at two November readings

(Table 7). The soil water contents on four dates are shown in Figure 9. The application of up to 100 kg/ha increased moisture loss by September 25 and October 21 although this effect diminished as the soil dried out. The apparent anomalies in F values were created by the much lower total moisture loss on all four dates at 200 kg/ha nitrogen.

The analysis of the water content of the soil for the 3 depths at the third date, which is typical of all seven dates, is given in Table 9. The 200 kg/ha level followed the overall pattern of more rapid depletion of soil moisture in the top 30cm with increasing nitrogen level, but extracted far less moisture between 30 - 60cm and 60 - 90cm than the 100 kg/ha level.

TABLE 9

The effect of 4 nitrogen levels on soil water content (% v/v) at 3 soil depths on October 21, 1968

Nitrogen (kg/ha)	Depth (cm) 0-30	30-60	60-90
0	15.6	26.7	39.5
50	12.0	26.7	39.4
100	11.0	25.3	39.0
200	10.1	29.2	40.6

L.S.D. = 1.4

Nitrogen has previously been found to increase

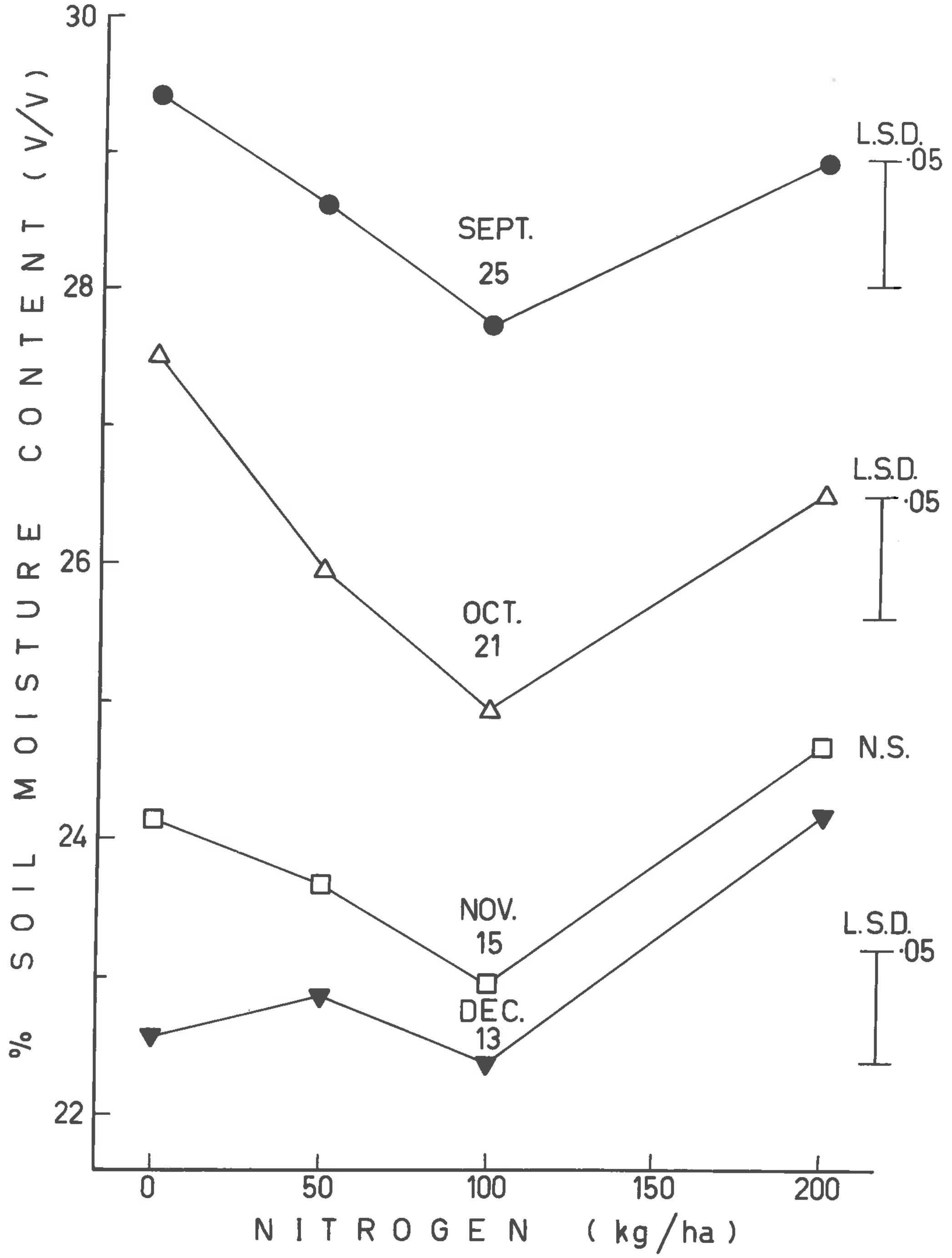


Figure 9. Soil moisture contents for four nitrogen rates on four occasions, 1968: each point being the mean of 3 depths, 3 replications and 4 varieties.

the percentage of roots in the surface horizon but moisture usage is usually increased from both upper and lower levels (Kmoch et al., 1957; Warder et al., 1963; Olson et al., 1964). No workers have yet associated an increased concentration of surface roots with reduced extraction of subsoil or total moisture. But, a 7850 kg/ha grain crop of oats was grown with 50 per cent of the total root weight above the 8cm depth and no root penetration below 68cm (Foth et al., 1964), so the effect of shallow rooting on the crop presumably depends on the degree of moisture stress induced by the climatic conditions.

The varieties developing later at a time of increasing moisture deficit might have been expected to suffer most stress but their 1000 grain weights were not depressed, possibly due to an above average rainfall in the latter half of October. Neither was moisture usage connected to the differential survival of ears.

JUVENILE LODGING - A YIELD DEPRESSING PROCESS. The crop grew luxuriantly in the latter part of July and during August at the high levels of nitrogen with a lack of any growth retarding moisture stress. Tillering was profuse and leaves were long,narrow (Table 10) and drooping, and the potential yield appeared excellent in all varieties. Then a southerly wind brought driving rain that beat down some varieties at the high nitrogen levels. A research worker experienced with local conditions stated lodging at this stage was a common and transient occurrence that would be rectified with the onset of stem elongation. This proved correct, but it was later found that the ear number was drastically reduced in areas which had previously suffered lodging.

TABLE 10

Morphological characteristics of the 12 varieties at the highest level (275 kg/ha) of the nine rates of nitrogen

	Severe Juvenile Lodging	Number Leaves/ Main Culm	Longest Leaf. Mean Length cm	Leaf (6th) Width cm	Number Tillers per m^2
Arivat	No	9	30.0	.69	840
Bankuti	Yes‡	7	25.0	.83	443
BR1239	No	9	29.0	.86	683
CI3576	No	9	29.6	.74	849
Drake	No	11	28.9	.69	858
Excelsior	Yes	11	34.4	.68	1089
Maraini	Yes	12	35.7	.63	876
Prior A	No	11	28.3	.58	840
Proctor	No	11	27.8	.53	858
Princess	Yes	11	29.9	.64	895
Vaughn	Yes‡	10	32.2	.66	923
Velvon	Yes	11	32.1	.77	766

‡ very short duration only

Figure 10A shows this temporary collapse prior to stem elongation, in the following year 1969, compared with an unlodged stand on the right where lodging was prevented by CCC application (see Section VII). The lodging was multi-directional, resulting in some parts of the plot heavily overlying other parts which were almost totally killed out (Figure 10B) and which greatly increased individual plot variability.

The lodging seemed largely attributable to the weakness of the pseudostems (leaf sheaths) which became excessively etoliated with the low light intensities penetrating through the canopy, both from the low solar radiation in July and August and the severe mutual shading at high nitrogen. No variety was entirely immune from the collapse, but the early varieties suffered for a shorter period as stem elongation was earlier. The etoliation of the pseudostem also tended to be more severe in the latest varieties as they produced more leaves before stem elongation, had a greater tillering capacity (Excelsior compared with Bankuti and BR1239, Table 10) and had longer leaves (Velvon and Maraini, Table 10).

It seems possible that on at least some of the occasions when yield reductions in late varieties have been attributed to the crop running out of water, the yield was depressed at a much earlier stage of growth

Figure 10. A. Plot badly lodged on August 20 prior to stem elongation in 1969. Lodging has been prevented in the plot on the right by the application of CCC.

B. Two samples taken after anthesis from a plot with severe juvenile lodging 6 weeks earlier. Both came from the same sized areas, but the one on the left was overlain by lodged material.

A.

B.

during the wet and overcast winter, especially when the crop was sown early at high densities with high fertility. In this experiment, the contrasting response curves of varieties to nitrogen were obtained in the absence of any differential use of soil moisture (Table 7).

VI. VARIATION IN JUVENILE LODGING AND EAR NUMBER

A. NITROGEN

B. DENSITY

VI. VARIATION IN JUVENILE LODGING AND EAR NUMBER

Although lodging in the juvenile stage and depression in ear number occurred together in the nitrogen trial (Section V), there was no proof of a causal relationship. It was therefore decided both to prevent and encourage juvenile lodging by mechanical and chemical means, and to compare the effect on ear number with an otherwise identical control.

A. NITROGEN

METHODS. To reduce the level of naturally available soil nitrogen, 6300 kg/ha of finely chopped straw was incorporated into the soil before seeding (June 13) in 1969, and three levels of nitrogen applied (0, 100 and 200 kg/ha). Only two levels were required (a low and a high), but it was feared that a severe deficiency might result in the death of many plants at 0 kg/ha, so 100 kg/ha was included as a low level alternative. However, tremendous nitrification must have occurred naturally in the soil, for the plots at 0 kg/ha in 1969 morphologically resembled the crop grown at high nitrogen in 1968. Therefore, 0 and 200 kg/ha were used as the low and high nitrogen levels respectively.

Two six-row varieties were grown at each nitrogen level; Arivat which had responded positively to nitrogen fertilization and Velvon which had responded negatively.

Each varietal sub-plot was further split into the following six treatments:-

1. Control.

2. CCC. (Figure 11C). Tolbert (1960~~a, b~~) found that CCC could prevent or delay the lodging of etoliated seedings in the laboratory, but considered this inapplicable to field conditions. Subsequent workers have used CCC to reduce mature height and prevent lodging in the adult crop (Linser, 1968). CCC was applied in this experiment, to obtain an effect similar to Tolbert's, only in [illegible] ? a little later ontogenetically, and under field conditions. Two applications, each of 3 kg active/ha, were made at the four (August 1) and six (August 15) leaf stages.

3. Mechanical Support. (Figure 11A). A grid made from 5 mm square welded wire mesh was placed about 30cm above the crop on August 10 to support the crop. Juvenile lodging was prevented, but later during grain filling, there was some breakage of culms over the grid by strong winds.

4. Defoliation. (Figure 11B). Grazing early sown, six-row barley crops is common practice in South Australia, and has sometimes been followed by high grain yields. Defoliation has also reduced lodging in adult crops (Thatcher, 1947; Cutler et al., 1949). All the foliage above the 20cm height level was therefore removed,

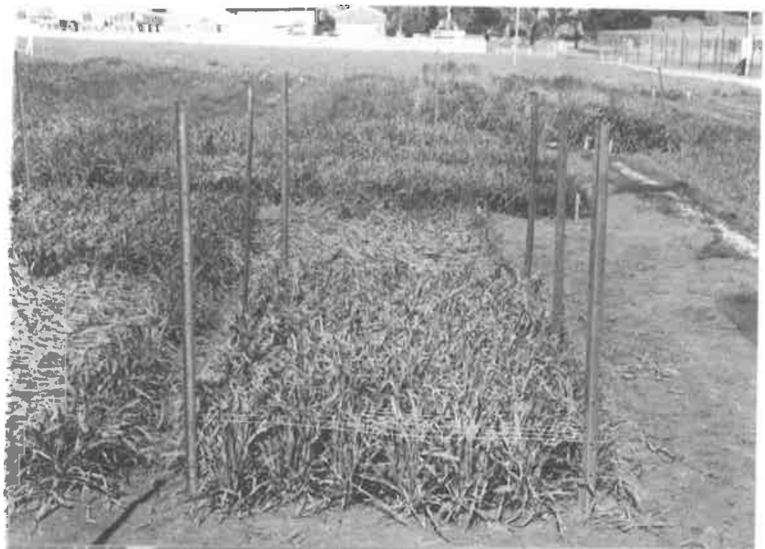
Figure 11. Three attempts to prevent juvenile lodging.

A. Supported by a 5mm square grid.

B. Excess foliage removed.

C. Sprayed with CCC.

A.



B.

C.

leaving mainly pseudostems and the first two leaves. The apices were undamaged, still being near ground level, and an extra 50 kg/ha nitrogen was applied to replace the nitrogen calculated to have been removed in the foliage.

5. Mechanical Lodging. (Figure 12B). A 20cm square welded mesh grid was laid over the upright crop and movedlaterally to artificially simulate juvenile lodging. The grid remained in place on the crop between August 10 and September 1.

6. Shading. (Figure 12A). The plots were covered over a three-week period with a shade cloth allowing 48 per cent light transmission, to determine if the effect of lodging was accentuated by a further reduction in light intensity.

Experimental Details. The plots were arranged in a split-split-plot design with 4 replications, 2 main plots (nitrogen), 2 sub plots (variety) and 6 sub-sub plots (treatments). All sub-sub plots were 2.5m long, 1.25m wide and comprised 7 rows. Only the middle 1.5m section of the centre 3 rows was harvested.

RESULTS AND DISCUSSION.

Expression of juvenile lodging. The crop germinated evenly, and prolific tillering gave further uniformity in each plot. The coefficient of variation was only 2.08 per cent for tiller counts on August 10

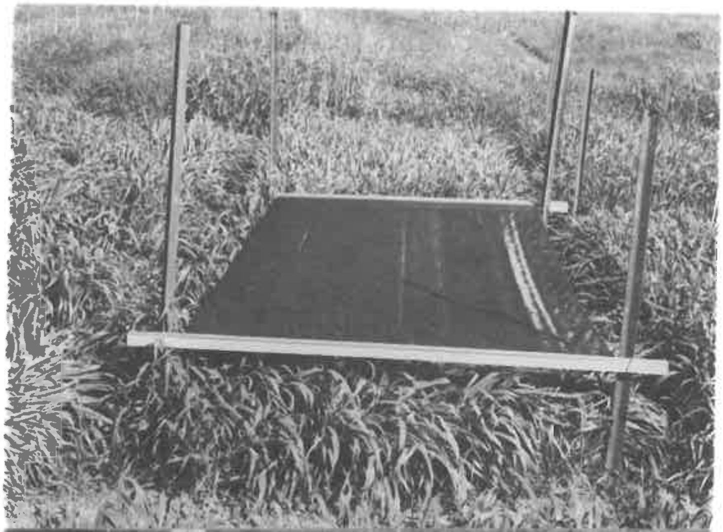
Figure 12. Two attempts (A and B) to promote and accentuate the process of juvenile lodging.

A. Reducing the light intensity by 52%.

B. Artificially lodging the crop with a 20mm square grid.

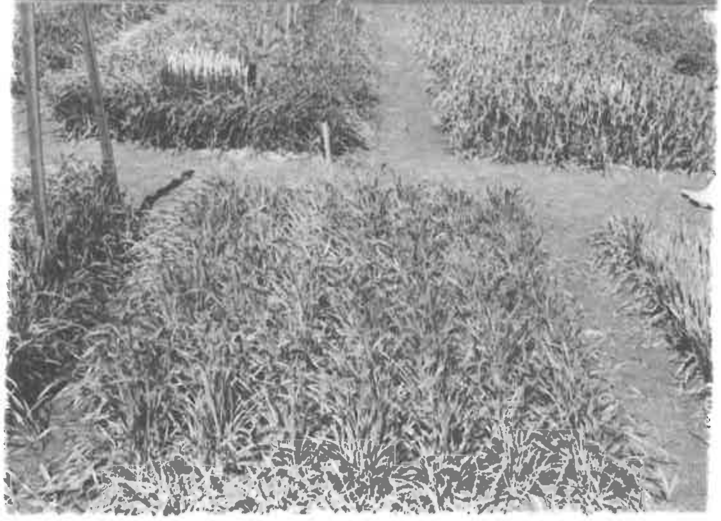
C. Control plot at low nitrogen. Compare with lodged control at high nitrogen (Figure 10A).

A.



B.

C.



and the counts shown in Table 11 for four adjacent sections of row in one plot are representative of the low variability throughout the whole experiment. The plots at high nitrogen then lodged severely on August 11 and remained lodged for approximately 3 weeks (in Arivat) until the commencement of stem elongation. By maturity, the previously uniform sections at high nitrogen showed a 40 fold variation in ear number and a 100 fold variation in grain yield (Table 11). This excessive within-plot variability was caused not only by the death of the overlain tillers, but also by the above average survival of ears in the overlying sections. The latter had both better illumination and later, a reduced competition for all resources from adjacent areas.

TABLE 11

Variability at two stages of development in 4 adjacent 60cm lengths of row in an Arivat plot at high nitrogen

		1	2	3	4
Tillers Aug 10		189	183	195	189
Ears	Maturity	6	88	80	2
Grain, g/61cm		1.4	98.0	73.8	.1
Straw g		25.0	128.0	158.0	16.0
Unreproductive tillers		90	140	132	100

Varieties and Nitrogen. Application of 200 kg/ha increased the number of tillers similarly in both varieties, and these tillers contained a higher moisture percentage and were more etoliated than those at 0 kg/ha (Table 12). The varieties did not differ in tiller number, but both leaves and pseudostems were longer in Velvon than Arivat, despite the later development of Velvon and the similar number of leaves per tiller on August 10. In fact, Velvon lodged in the juvenile stage at both high and low nitrogen levels, while Arivat lodged only at high nitrogen.

TABLE 12

Morphological data and leaf area removed by defoliation on August 10 for 2 varieties at 2 nitrogen levels

	Low Nitrogen		High Nitrogen		
	Arivat	Velvon	Arivat	Velvon	LSD
Tillers per m^2	1255	1181	1587	1596	126
Length of Pseudostem (base to top auricle)cm	11.1	13.3	14.7	16.3	1.9
Length of fifth leaf cm	27.0	31.2	32.1	34.7	2.5
Leaf area/leaf weight ratio cm	321	333	337	363	33.3
% Moisture in tillers	89.1	89.8	90.3	90.8	1.3
LAI removed	1.76	2.02	3.30	4.05	

The two varieties responded differentially to nitrogen application in grain yield, with Arivat showing a much greater decrease from low to high nitrogen (377 down to 269 g/m^2 or 29 per cent) than Velvon (249 down to

203 g/m^2 or 19 per cent). The varietal differences in ear number were almost identical in magnitude to the differences in grain yield, and the reductions in grain yield were also reflected in a significant variety x nitrogen interaction in harvest index. Apart from a variety x treatment interaction for number of grains per ear, no other interactions were significant, so only the main effects for nitrogen, varieties and treatments are presented in the remaining tables in this section.

The significant increase in the number of tillers with nitrogen application (Table 12) was associated with a significant decrease in ear number (Table 13). The weight of straw however remained constant and neither 1000 grain weight or number of grains per ear were affected by nitrogen fertilization. The large reduction in yield (28 per cent) therefore resulted solely from the decrease in ear number (30 per cent).

Grain yield and ear number were also significantly (**) lower in Velvon than in Arivat, but in addition, Velvon had fewer grains per ear and a higher 1000 grain weight (Table 13). In other years, Arivat and Velvon set a similar number of grains per ear, so the lower value of Velvon in this experiment may indicate increased moisture stress at anthesis, which occurred 14 days later in Velvon. In comparison, nitrogen application, shading and CCC only delayed anthesis by two days.

TABLE 13

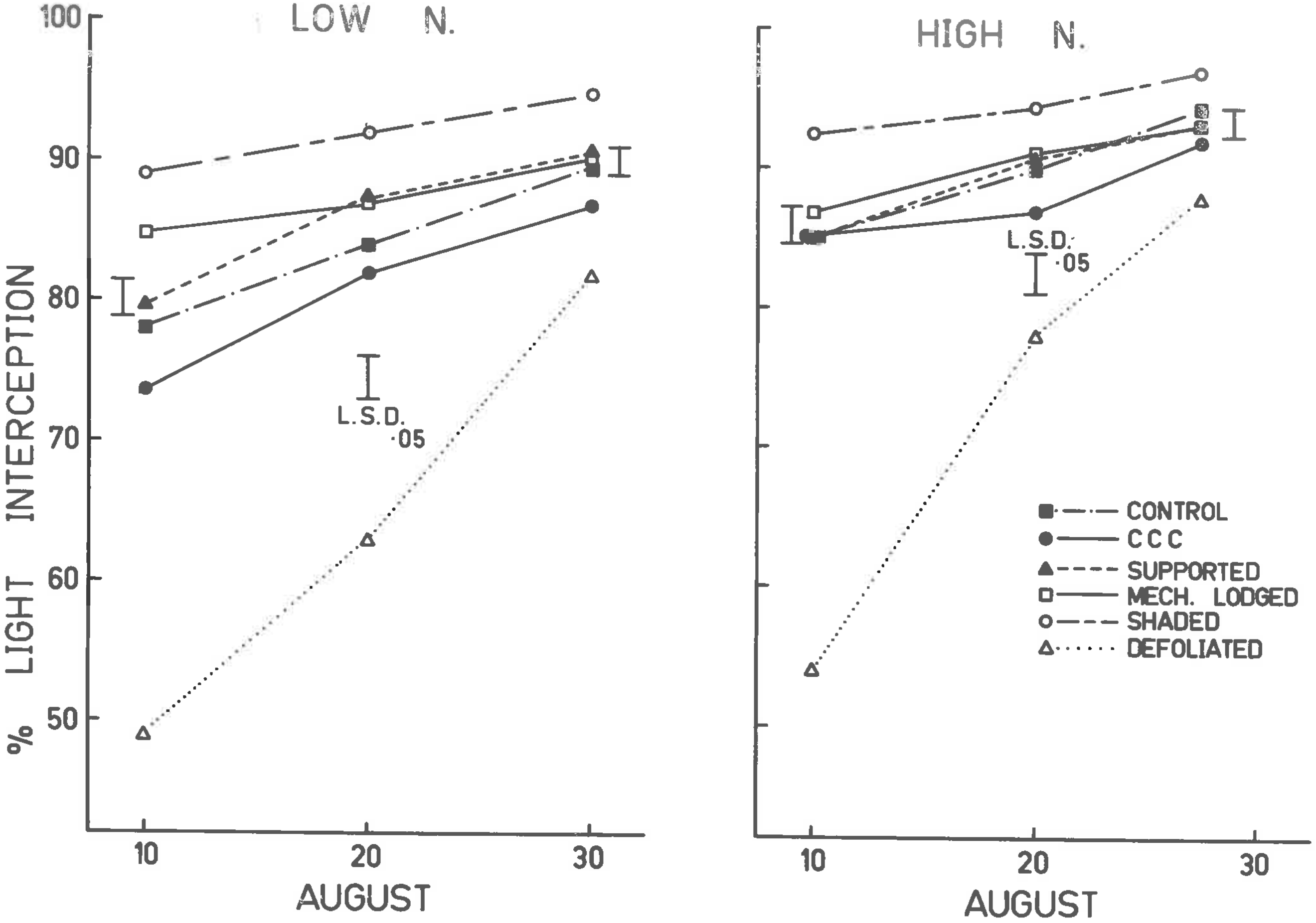
Yield components, grain, straw and total dry weights, and harvest indices for 2 nitrogen levels and 2 varieties

	Low Nitrogen	High Nitrogen	LSD	Arivat	Velvon	LSD
Number ears/m^2	347.2	250.2	61.0	330.8	266.6	20.0
Grains/ear	32.1	32.0	NS	34.1	30.0	1.3
1000 Grain weight	29.0	28.5	NS	27.9	29.6	1.5
Grain yield g/m^2	323.2	226.0	75.6	313.4	237.8	23.8
Total dry weight g/m^2	1082.0	979.6	NS	1052.4	1009.2	NS
Straw weight g/m^2	758.8	753.6	NS	739.0	773.4	NS
Harvest index	29.7	23.0	3.13	29.5	23.1	2.0
Date of Anthesis (Oct.)	11.5	13.5	.8	5.7	19.3	.5

Treatments.

(a) Light. Light interception differed most between treatments at the lower nitrogen level (Figure 13) as more variation in light regime was possible in the less dense crop, but generally treatments were ranked in similar order at both levels. The shaded and defoliated plots intercepted respectively more and less light than the control, and while the other 4 treatments did not differ significantly from the control on any one date, over the whole period the mechanically lodged and supported plots intercepted

Figure 13. The percent light interception on 3 dates for 6 treatments at 2 nitrogen levels.


LOW N.
HIGH N.
100
90
80
70
60
50
% LIGHT INTERCEPTION
L.S.D. ·05
L.S.D. ·05
10
20
30
AUGUST
10
20
30
AUGUST
■ CONTROL
● CCC
▲ SUPPORTED
□ MECH. LODGED
○ SHADED
△ DEFOLIATED

more light than the control, which in turn, had greater light interception than the plots receiving CCC.

(b) Height. There were two and one half fold differences in height when lodging occurred (Figure 14). The canopy height of the mechanically supported, CCC and defoliated plots increased steadily from seedling to maximum height; it decreased in the control and shaded plots with increasing severity of lodging, until their height was similar to the artificially lodged treatment at the end of August. These differences between treatments progressively disappeared during September after onset of stem elongation, until only the previously shaded plots were shorter than the other treatments at maturity.

The two early applications of 3 kg/ha CCC neither reduced final height nor prevented adult lodging after physiologic maturity. Elsewhere, CCC has been found far more rapidly metabolized in barley than in wheat leaves (Škopík and Cervinka, 1967), and the decline is often followed by the enhanced synthesis of gibberellic acid (Linser and Kühn, 1962; Bohring, 1965). Larter (1967) needed three applications, each of 3 kg/ha, to reduce the height in barley to 75 per cent of the control.

(c) Ear Number. CCC significantly increased, and shading significantly decreased, the number of ears relative to the control (Tables 14 and 15). Defoliation and mechanical

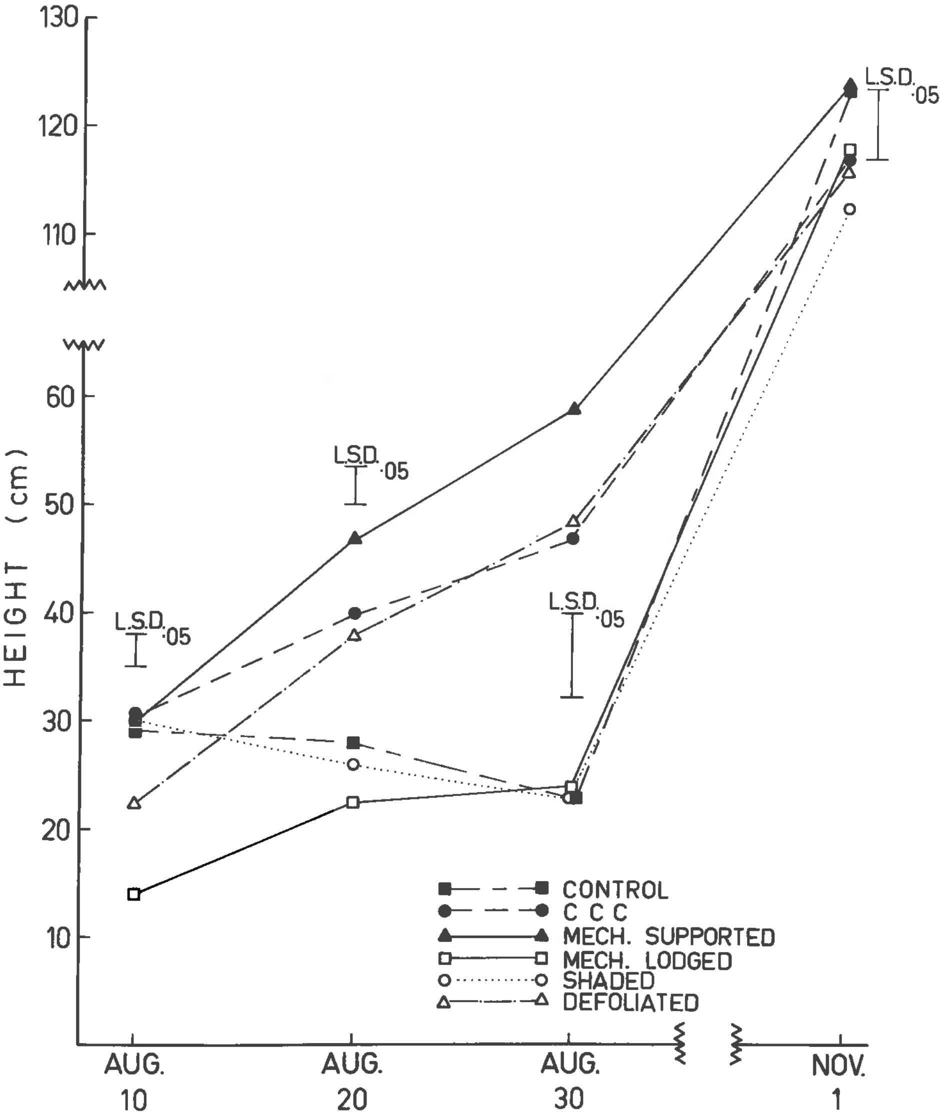


Figure 14. The effect of the six treatments on height of crop; Arivat at the high level of nitrogen.

support also increased the ear number but only to the 10 per cent level of significance. Deliberately lodging the crop had little effect, as juvenile lodging occurred naturally on all plots except Arivat at low nitrogen. When juvenile lodging, scored on a visual basis on August 23, is plotted against the number of ears produced by each treatment, a strong negative effect is revealed (Figure 15). The relationship is good considering the diversity of the treatments upon which it is based.

The differences in ear number were reflected in grain yield in the CCC and shaded treatments (Table 14). However compensating changes in the other two yield components nullified the effect in both the defoliated and supported treatments.

TABLE 14

Yield components, grain, straw and total dry weights, harvest indices and dates of anthesis for the six treatments; mean over 2 nitrogen levels and 2 varieties

	Control	CCC	Support	Defol.	Lodged	Shade	LSD
Number ears/m^2	284.3	335.3	314.7	316.0	297.5	244.4	36.6
Number grains/ear	33.4	33.5	31.9	31.5	31.3	30.7	NS
1000 grain weight	29.0	28.3	27.6	28.1	29.4	30.1	1.2
Grain yield g/m^2	278.7	317.8	276.4	280.0	268.1	226.5	35.8
Total dry weight	1044.6	1157.4	1069.3	1030.0	1049.7	834.0	80.0
Straw weight	765.9	839.5	792.8	750.0	781.7	607.5	57.5
Harvest index %	26.1	27.2	25.6	25.2	27.0	26.8	NS
Anthesis, Oct.	11.6	14.1	11.1	12.3	12.1	13.9	.6

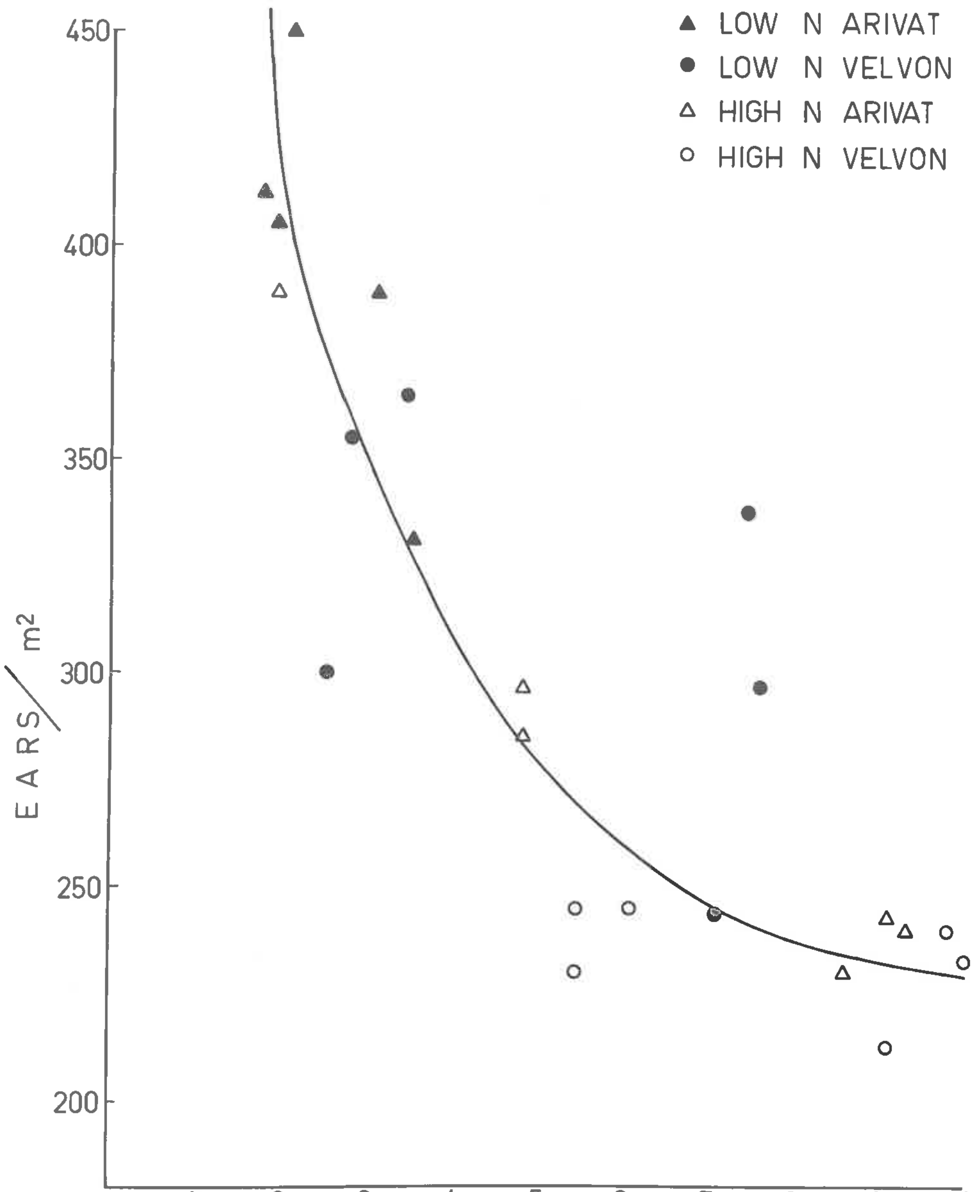


Figure 15. The effect of juvenile lodging on number of ears at two levels of nitrogen, 2 varieties and 6 treatments. 1 = no lodging, 10 = very severe complete lodging. Hand fitted curve.

TABLE 15

The actual values in Table 14 expressed as per cent deviation from the control

	CCC	Support	Defol.	Lodged	Shade
Number ears/m^2	+17.9	+10.7	+11.1	+ 4.6	-14.1
Number grains/ ear	+ 0.5	- 4.2	- 5.5	- 6.3	- 8.0
1000 grain weight	- 2.5	- 4.8	- 2.9	+ 1.5	+ 3.9
Grain yield g/m^2	+14.0	- 0.8	+ 0.5	- 3.8	-18.7
Total dry weight	+10.8	+ 2.4	- 1.4	+ 0.5	-20.2
Straw weight	+ 9.6	+ 3.5	- 2.1	+ 2.1	-20.7
Harvest index	+ 4.2	- 1.9	- 3.4	+ 3.5	+ 2.7

(d) CCC.

TABLE 16

The effect of CCC on the morphology of the main culm: mean over 2 nitrogen levels and 2 varieties on August 24

	Control	CCC	LSD
Length of pseudostem, cm	20.8	11.8	4.0
Diameter of pseudostem, cm	.47	.39	.04
Length of sixth leaf, cm	36.8	31.4	2.4
Width of sixth leaf, cm	1.22	1.12	.08
Leaf area/leaf weight, cm/g	345	280	59
Dry weight per tiller, g	1.30	.92	.24
% Dry matter in weight of tiller	14.8	16.3	N.S.

Twenty-four days after the first CCC application, the morphology of the tiller had altered considerably (Table 16) and virtually no lodging was present (Figure 11C) compared with the control (Figure 10A). CCC reduced the length of the pseudostem by nearly one half, and resulted in shorter and more dense or thicker leaves (Table 16). It did not significantly increase the per cent dry matter in the tiller; it reduced the diameter of the pseudostem, leaf width and the weight of individual tillers (Table 16) along with length. The reduced tiller weight had no effect, however, on the number of grains per ear (Tables 14 and 15), presumably because of the improved illumination of individual tillers.

All the increased ear number due to CCC was attributable to Arivat (Table 17) despite the variety x treatment interaction being non-significant over all treatments. No juvenile lodging occurred in Velvon when CCC was applied, but the compact, closed canopy, resulting from the shortened pseudostems and long leaves (Table 17), provided a microclimate with far less ventiliation, that greatly encouraged Rhynchosporium. This disease has drastically reduced ear numbers elsewhere at the Institute, and probably resulted in the lack of response in ear number in Velvon, which is a highly susceptible variety.

The effect of the extra ear production in Arivat was somewhat negated by their smaller size, but CCC increased the number of grains per ear in Velvon with the ear number remaining constant (Table 17) (the variety x treatment interaction for grains per ear was significant). This suggests that CCC may have increased drought resistance of the later developing variety. Certainly in wheat, CCC has increased resistance to drought (Plaut and Halevy, 1966; Kaul, 1968) through increased root growth (Hanus, 1967) delaying the onset of moisture stress (Humphries, 1968a, b) and increasing the number of grains per ear (Humphries et al., 1965; Wünsche, 1970).

TABLE 17

The effect of CCC on the yield components, grain yield and morphology of Arivat and Velvon

	Arivat		Velvon		LSD
	Control	CCC	Control	CCC	
Grain yield, g/m^2	329.7	382.7	227.7	252.9	50.6
Number ears/m^2	307.5	407.1	261.2	263.4	51.8
Grains/ear	38.3	34.5	28.4	32.6	3.6
1000 grain weight	27.9	27.1	30.1	29.4	1.7
Length of 6th leaf, cm	35.5	29.8	38.0	32.9	3.4
Length of pseudostem, cm	21.0	11.5	20.6	12.2	5.6

(e) Mechanical support. The marginally significant increase in ear number obtained by supporting the crop was not reflected in the final grain yield for two reasons. First, was a non-significant decrease in the 1000 grain weight caused by the breakage of some culms over the single grid after anthesis. Second, was a non-significant decrease in grains per ear. This may have been occasioned by the more rapid exhaustion of soil moisture by plots taller than all surrounding plots (Figure 14) as discussed previously.

? removed

(f) Defoliation. A drop in the number of grains per ear also erased the advantage of more ears in the defoliated plots. Davidson (1965) obtained a similar result with wheat, and it seems likely that the reduction in grains per ear was caused by the lack of available assimilate both through removal of the most actively photosynthetic tissue, and through the increased demand of rapid foliar regrowth. Elsewhere, defoliation has resulted in a cessation or marked reduction in root growth (Crider, 1955; Jacques and Schwass, 1956; Baker, 1957a, b; Troughton, 1957) decreasing both nutrient and water uptake in dry conditions (Oswalt et al., 1959), and defoliation has been used in an attempt to reduce excessive early moisture use (Dann, 1968).

Grazing of wheat is recommended in rank-growing crops on very fertile soils (Kiesselbach and Lyness, 1948), and will not cause a reduction in yield if carried out when the crop is 10 - 20 cm high (Crawford, 1964). When vegetative growth is not excessive (e.g. semi-dwarf wheats), the deleterious effect of clipping increases with severity or lateness (Mathur and Bhatnagar, 1968; Pumphrey, 1970). Here, grain yield remained unaffected despite the removal of LAIs between 1.76 and 4.05; indicating that, at least, there was a considerable amount of foliage superfluous for the environmental conditions.

(g) Mechanical lodging. Deliberately lodging the crop only appreciably reduced the grain yield on the Arivat plots at low nitrogen where juvenile lodging did not naturally occur.

(h) Shading. Shading decreased the grain yield in both varieties at both nitrogen levels, but the greatest reduction again occurred in Arivat at low nitrogen. Juvenile lodging apparently caused an initial reduction in grain yield, and further shading has less effect. The effect of shading remained after removal of the shade cloths, probably through a lack of labile carbohydrate reserves, and the final height was significantly reduced along with ear number, grain yield, and straw yield.

Juvenile lodging and its implications. The results indicate that juvenile lodging depresses ear number, but exactly how the process causes the additional tiller death is not clear, and indeed, would be hard to isolate. Obviously the light relationships in the canopy are drastically changed, but then so is canopy ventilation, evaporation and temperature gradient. When an adult plant lodges, a burst of new tillering commences, and there may be similar physiological changes in the juvenile plant. The overlain foliage would also be more open to attack by weak parasites like *Alternaria* and *Fusarium*, which colonize senescent tissue which is becoming progressively less physiologically active (Stringfield, 1964).

The biochemical processes are greatly disturbed in beans and cucumbers when the supply of nitrogen is increased without a corresponding increase in light (Chernaivskaya and Nichiporovich, 1967) resulting in a pathological depression of the RDMP, especially when the plants increase in size. Similarly, rice plants lost dry weight under high nitrogen when the solar radiation fell below 200 cals/cm^2/day (Murata, 1961), and juvenile lodging might be merely coincidental with such a process rather than the causative agent. However the surviving parts of the crop appeared healthy, and the mechanically supported plots also had a high nitrogen status. Neither did pathological symptoms appear in the defoliated treatment, in which an increase in nitrate levels might be expected to occur, as the incorporation of nitrate into organic forms slows with the reduced assimilate availability (Alberda, 1957; Milthorpe and Davidson, 1966).

Juvenile lodging could also be responsible for some of the reports of optimum LAIs in pastures beyond which the RDMP decreases, as juvenile lodging has been noticed frequently in pastures (Carter, pers. comm.; Alberda, pers. comm). Certainly it seems to be the dominant factor in deciding the optimal nitrogen level and density for each barley variety in Adelaide.

B. DENSITY.

Introduction.

The amount of juvenile lodging also increased with increasing plant density in an experiment containing three densities on the highly fertile soil in 1969, although the severity depended on variety. No varieties lodged at the low density (2.69 plants/m^2), despite a mean length in the sixth leaf of 30.6cm, all varieties lodged at the high density (1560 plants/m^2), and most varieties showed signs of lodging at the intermediate density (156 plants/m^2).

The response in ear number for CI3576 (the most prolific ear producer) in 1969 is compared in Figure 16 with the response in 1968 when juvenile lodging was prevented by supporting the plots with wire grids. Nearly all the plants at high density in 1968 survived, producing one miniscule ear per plant, but in 1969 a 10-fold increase in population (156 to 1560/m^2) depressed ear number by 14 per cent; leaf length increased from 28.7 to 32.1 cm.

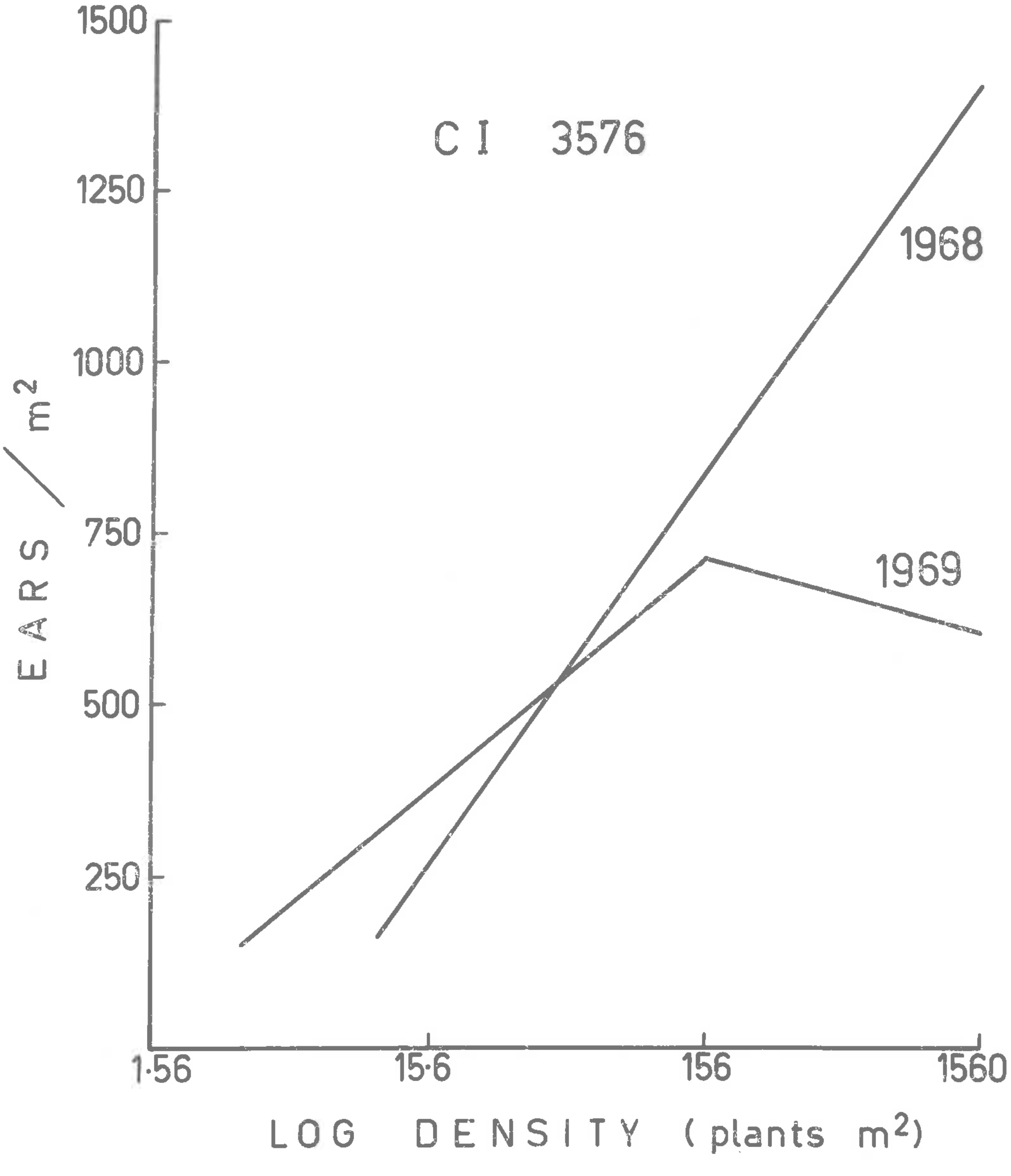


Figure 16. The response of CI3576 in ear number to density (log scale) in 1968 and 1969.

The effect was even more pronounced in other varieties and leaf lengths up to 44 cm were recorded at the highest density in 1969.

TABLE 18

Morphological characteristics of tillers of Arivat at 3 densities in 1969

	Density (plants/m^2)			LSD
	2.69	156	1560	
Length of pseudostem, cm (base to auricle)	12.3	17.9	21.7	2.8
Pseudostem diameter, cm	.45	.40	.32	.07
Length of 6th leaf, cm	26.4	31.7	33.8	2.8
Width of 6th leaf, cm	1.03	.92	.82	.16
Dry weight/tiller, g	1.12	1.09	.93	.09
% Dry weight	16.0	14.3	13.6	1.1
Total length/dry weight cm/g	34.2	45.9	59.5	3.9

The plants became increasingly etoliated with increasing density in 1969, and this was reflected in a progressively larger ratio of length/dry weight for individual tillers (i.e. Arivat, Table 18). The larger ratio resulted both from a slightly decreased weight per tiller, and from longer and narrower pseudostems and leaves. The tillers at high density therefore lacked structural support and tended to lodge easily.

Methods

Therefore it was decided to repeat the 1969 experiment on ear survival in 1970 with 3 densities instead of 2 nitrogen levels. The three densities were 31, 156 and 780 plants/m^2, and each density was broadcast over 6 replicated areas 8m long and 2½m wide (18 main plots). Each main plot was divided into 4 sub plots (2m x 2½m) from which the centre 1.25m square was harvested. The four treatments were:-

1. Control.
2. CCC - 2 x 3 kg/ha at 4 and 6 leaf stages.
3. Supported with two 5mm grids.
4. Deliberately lodged with a grid.

Arivat was again selected as the test variety because of its general resistance to disease. Detailed morphological measurements were not taken, but were generally thought to be less extreme than those for 1969 (Table 18) since the 100 kg/ha nitrogen application was withheld in 1970 until August 7, when the natural fertility had been assessed.

Results

Juvenile lodging occurred at the high density in 1970, but not for so long or as severely as in 1969, probably due to the lack of abundant nitrogen in early August. There was a large increase in plant mortality as density was raised from 156 to 780 plants/m^2, but sufficient ears survived to increase significantly the number of ears at high density (Figure 17). The advantage of extra ears, was outweighed however by a large decrease in number of grains/ear, and a small but significant decrease in 1000 grain weight so that yield of grain fell.

TABLE 19

Yield components, grain, straw and total dry weights, harvest indicies and heights for 4 treatments applied to Arivat in 1970. Means of 3 densities, as density x treatment interaction NS

	Treatment				
	Control	CCC	Supported	Lodged	LSD
Ears/m^2	228	239	266	209	36
Grains/ear	33.6	34.9	36.9	37.5	NS
1000 grain weight	35.9	35.8	36.0	34.6	NS
Grain yield, g/m^2	269	290	323	263	43
Straw weight, g/m^2	617	618	683	591	NS
Total weight, g/m^2	886	901	1005	855	101
Harvest index	33.3	34.6	33.3	33.1	NS
Height, cm	96.8	95.8	104.2	78.5	4.5

The crop artificially lodged for three weeks prior to stem elongation did not differ significantly from the control in 1970, presumably because the control also lodged at the high density, and because lodging had no deleterious effect at low density. The latter indicates

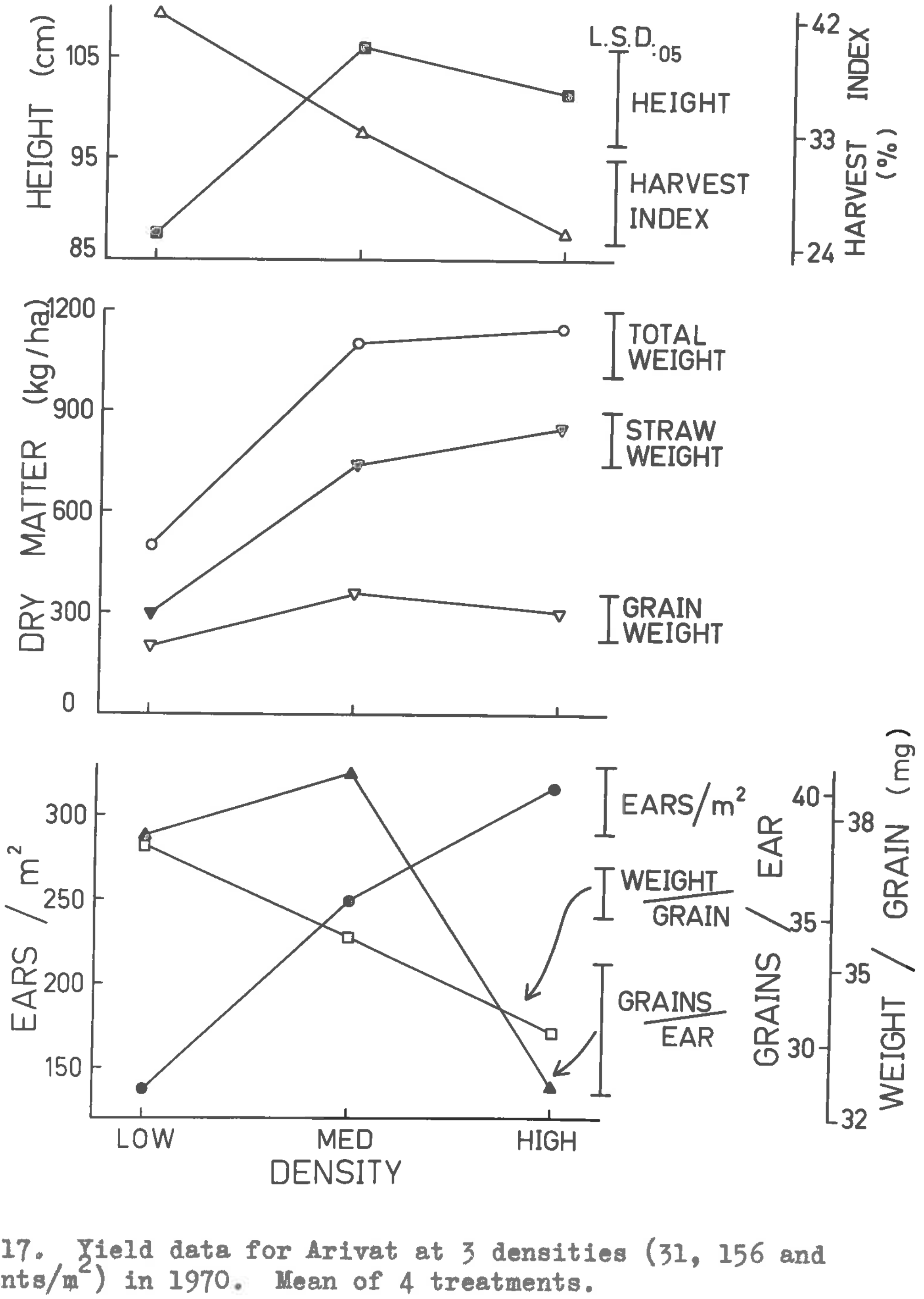


Figure 17. Yield data for Arivat at 3 densities (31, 156 and 780 plants/m^2) in 1970. Mean of 4 treatments.

that juvenile lodging does not upset the hormonal balance as postulated previously since relatively little light and temperature stress would have been present in the lodged crop at low density.

Mechanically supporting the crop significantly increased ear number and grain yield (Table 19) in 1970, as this time there was no reduction in grains/ear or weight/grain due to breakage of culms over the wire grid; a second grid, placed above the first in late September, prevented much lateral movement of ears. While the density x treatment interaction for ear number was non-significant overall, mechanical support only significantly increased ear numbers at high density, thus offsetting the reduction in number of grains per ear. The amount of total dry matter was also increased significantly with ear number by the mechanical support at high density.

The response of grain and total dry weight to increasing density in Figure 17B conforms to the relationship proposed by Holliday (1960a, b, c, 1963) where the total dry weight reaches a plateau asymptotically, but the grain yield is parabolic. The unstated implication is that the weight of straw increases with density and exactly compensates for the reduction in grain weight. This happened in 1970 (Figure 17B and C) when the number of ear-bearing tillers increased with density, and provided more straw to offset the reduction in grain number and yield. However, the ear number was also decreased along with the other two yield components at the high density in 1969 (Figure 16) when juvenile lodging was prevalent; as the yield of straw is dependent on the developed ear-bearing culms rather than the numerous aborted tillers, the total dry weight fell at the high density in 1969 (Figure 18).

The extent of the decrease depended on variety (Figure 18), with Velvon showing the greatest depression and CI3576 the least. The weight of grain and straw, and the ear number for Velvon and CI3576 are shown in Figure 19. The straw weight did not increase with density in 1969 but decreased along with the grain weight and number of ears. The effect of increased ear survival at high densities on straw and total weight is discussed in a later section.

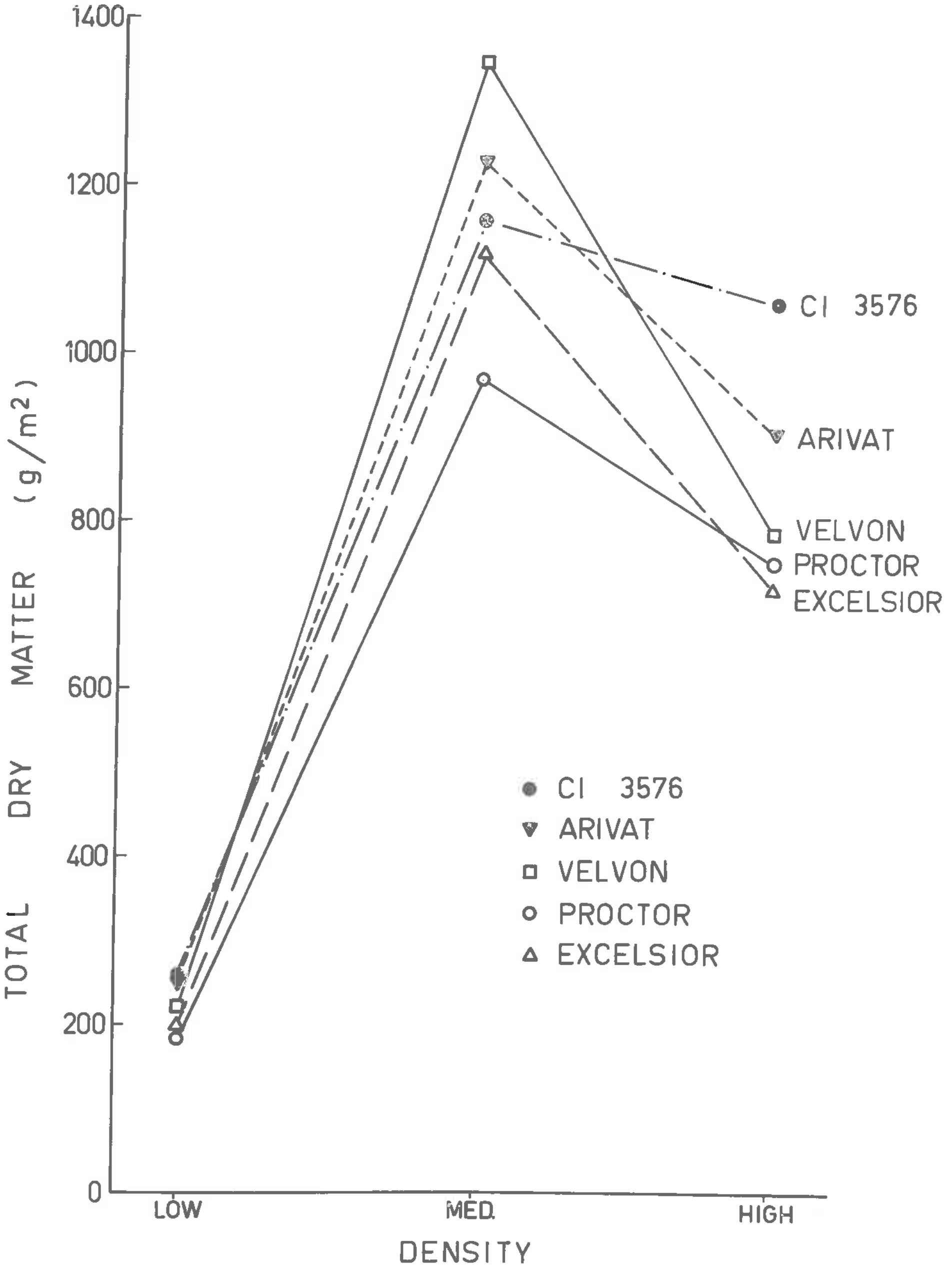


Figure 18. Total dry weight for 5 varieties at low (2.69 plants/m^2), medium (156 plants/m^2) and high (1560 plants/m^2) density in 1969.

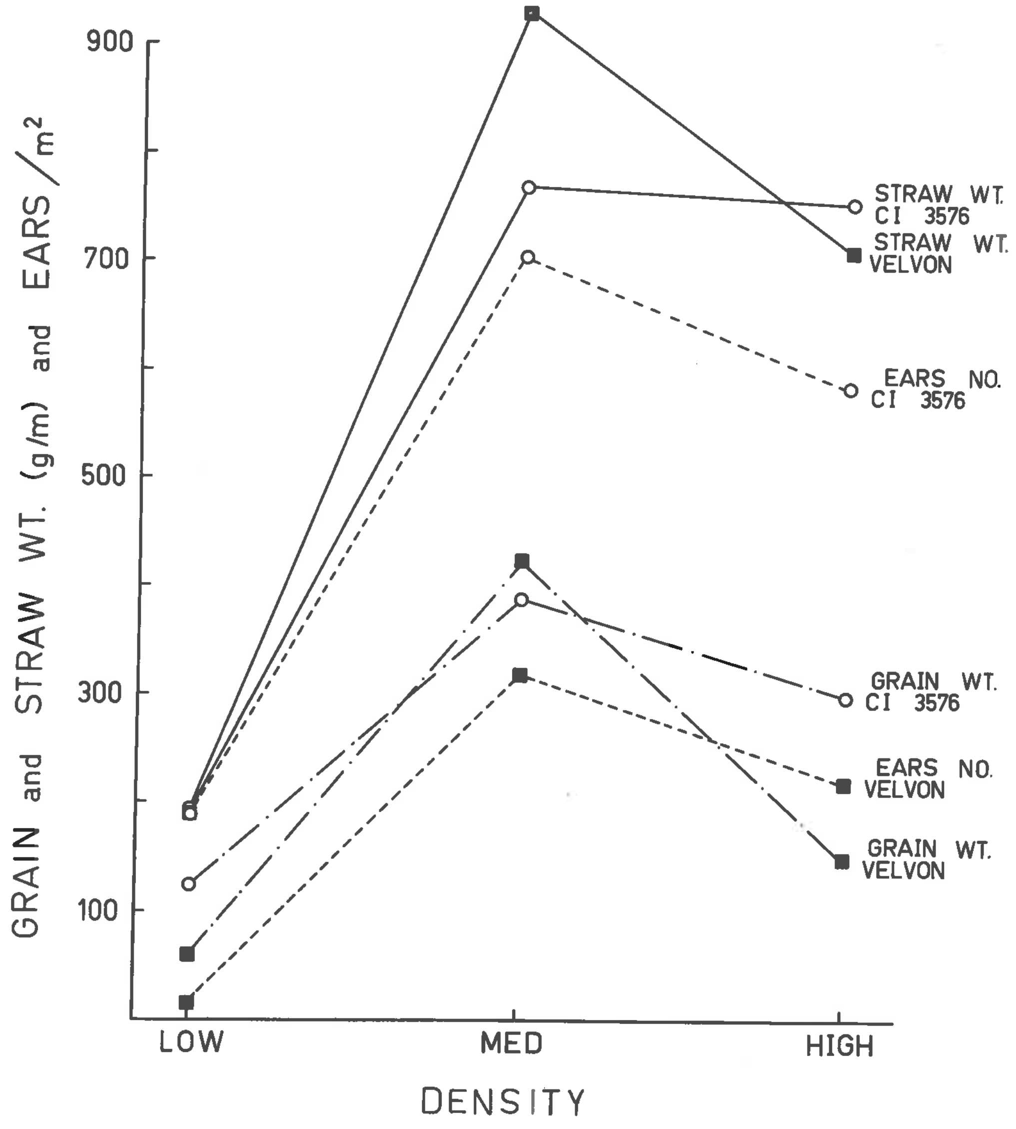


Figure 19. Number of ears and weights of grain and straw for 2 varieties at low, medium and high density (2.69, 156 and 1560 plants/m^2 respectively) in 1969.

VII. THE EFFECT OF VARYING COMPETITION FOR LIGHT AT VARIOUS ONTOGENETIC STAGES

A. THE INFLUENCE OF SHADING

(I) Light interception by barley cultivars

(II) Shading during initiation

(III) Shading during grain filling

B. THE INFLUENCE OF LIGHT ENRICHMENT

VII. THE EFFECT OF VARYING COMPETITION FOR LIGHT AT VARIOUS ONTOGENETIC STAGES

A. The influence of shading.

Both the number of tillers and leaf area of a crop increase with the increasing availability of nutrients and moisture, and a successful variety must be able to evade or tolerate the severe competition for light that can develop under such conditions. Evasion of mutual shading can be achieved by having fewer, smaller and more upright leaves per tiller, thus improving the illumination of all tillers. Toleration consists of maintaining a high percentage of fertile tillers and spikelets under increasingly intense shading. Varietal differences in both processes were investigated in this experiment in 1969.

Experimental techniques. Four replications of the twelve varieties were planted at an 8cm x 8cm square spacing in plots 10m long and 2m wide. Each plot contained 7 sub-plots, each comprising 36 plants (6 x 6). The long axis of the main plots ran north-south, and the treatments were always arranged in the same order, with the sub-plot covered by a shade cloth after anthesis always casting its shadow over sub-plots already harvested.

The tolerance of varieties to shading was tested over two ontogenetic periods; during the stage of ear initiation and during grain filling. Testing the young plants ideally required a source of shade which was constant and increased progressively towards the ground. This ruled out the use of either overhead shade cloths or of neighbouring plants, since the former cause a reduction in ambient light, and the latter change concomitantly with the shaded plants, as well as competing for other factors. Therefore 10mm diameter dowels, 56cm in length, were inserted between the plants in a sub-plot, so that each plant was surrounded by 4 dowels (Figure 19A). Each sub-plot was additionally surrounded by a shade cloth to prevent lateral penetration of light to the shaded plants. The dowels intercepted approximately 50 per cent of the light at ground level, and cast a sun-fleck shadow quite similar to that cast by plants but removed no water or nutrients from the soil. Dry matter harvests of shaded and non-shaded (control) sub-plots were taken at the time of insertion of dowels (July 26); after ear initiation (August 25), and at anthesis.

The last of these also provided the basal harvest for the period of shading during grain filling between anthesis and maturation. The sub-plots were covered by a 1.5m square shade cloth (48 per cent light transmission) stretched across a square wooden frame and suspended just above the tips of the awns. Shade cloths were used in

Figure 19A. Dowels, 56cm in height, inserted into the crop to increase shading.

this case, because of the necessity of reducing the light intensity at the sites of the most active photosynthesis (awns, ears, flag leaves and peduncles).

The light interception was measured in the unharvested controls, and related to the total dry matter at that ~~this~~ time, the number and size of tillers, height and morphology of the canopy and leaf size and LAI.

RESULTS AND DISCUSSION

1. Light interception by barley cultivars. The interception of light by the 12 varieties closely followed their various patterns of growth. The initial seedling weights obtained from a preliminary harvest 23 days after emergence showed a good relationship with the 1000 grain weights of the seed sown (Figure 20) although BR1239, Bankuti, Drake and Vaughn were well above the regression line and Proctor and Prior well below it. The reason for this deviation from the regression became apparent in the analysis of the harvest taken at the time of insertion of the dowels (34 days after emergence - harvest 1) when Bankuti, BR1239, Drake and Vaughn produced significantly more leaf area per gram of dry matter used for leaf growth than Proctor and Prior (Figure 21A). BR1239, Drake, CI3576 and Vaughn had the highest LAI at harvest 1 (Figure 21B) and also intercepted the most light (Figure 21C). These four varied greatly in their morphological composition however, as BR1239 had very few, extremely large tillers, Vaughn very

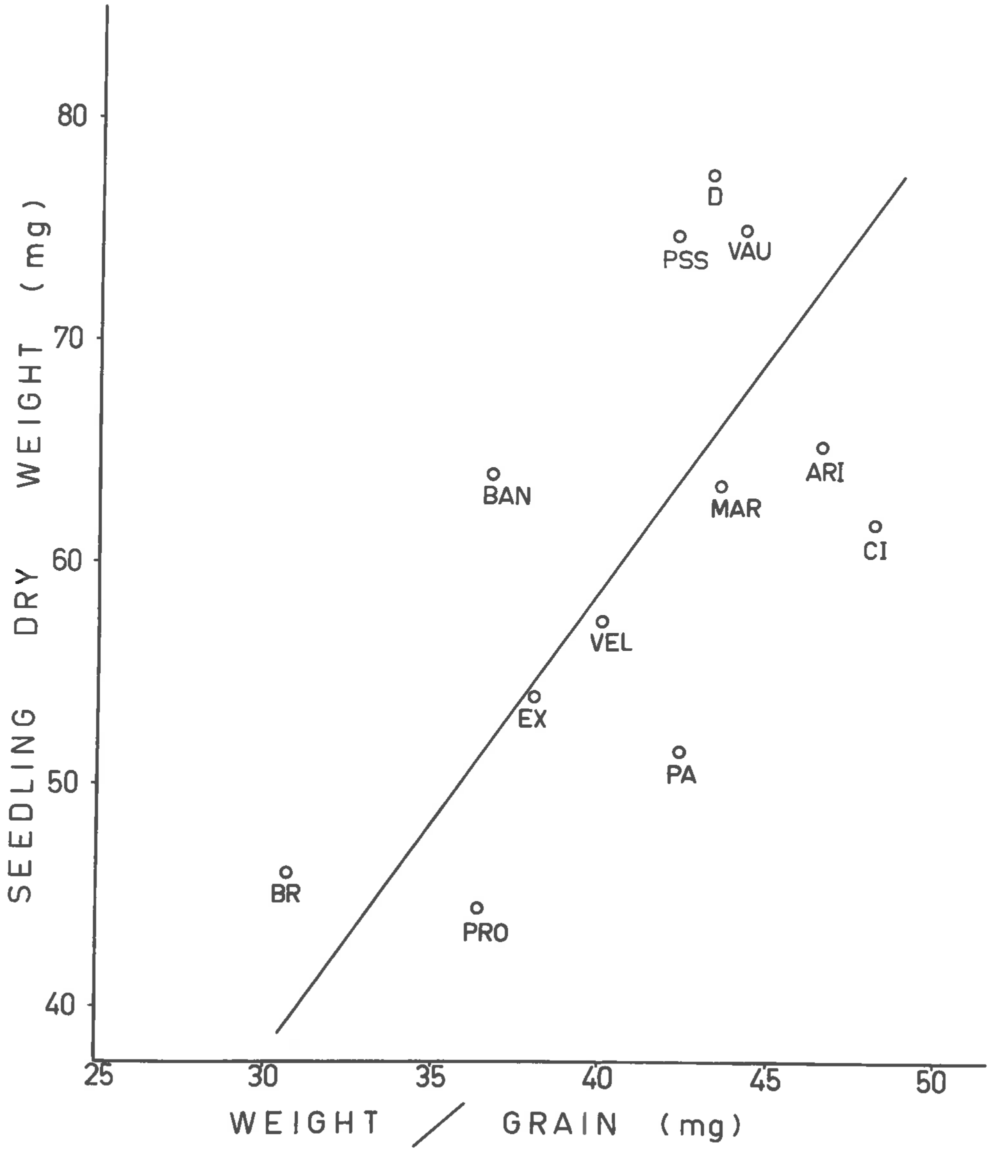


Figure 20. Dry weight of seedlings 23 days after emergence (32 days after planting) plotted against weight/grain of seeds sown, 1969. Regression line hand fitted.

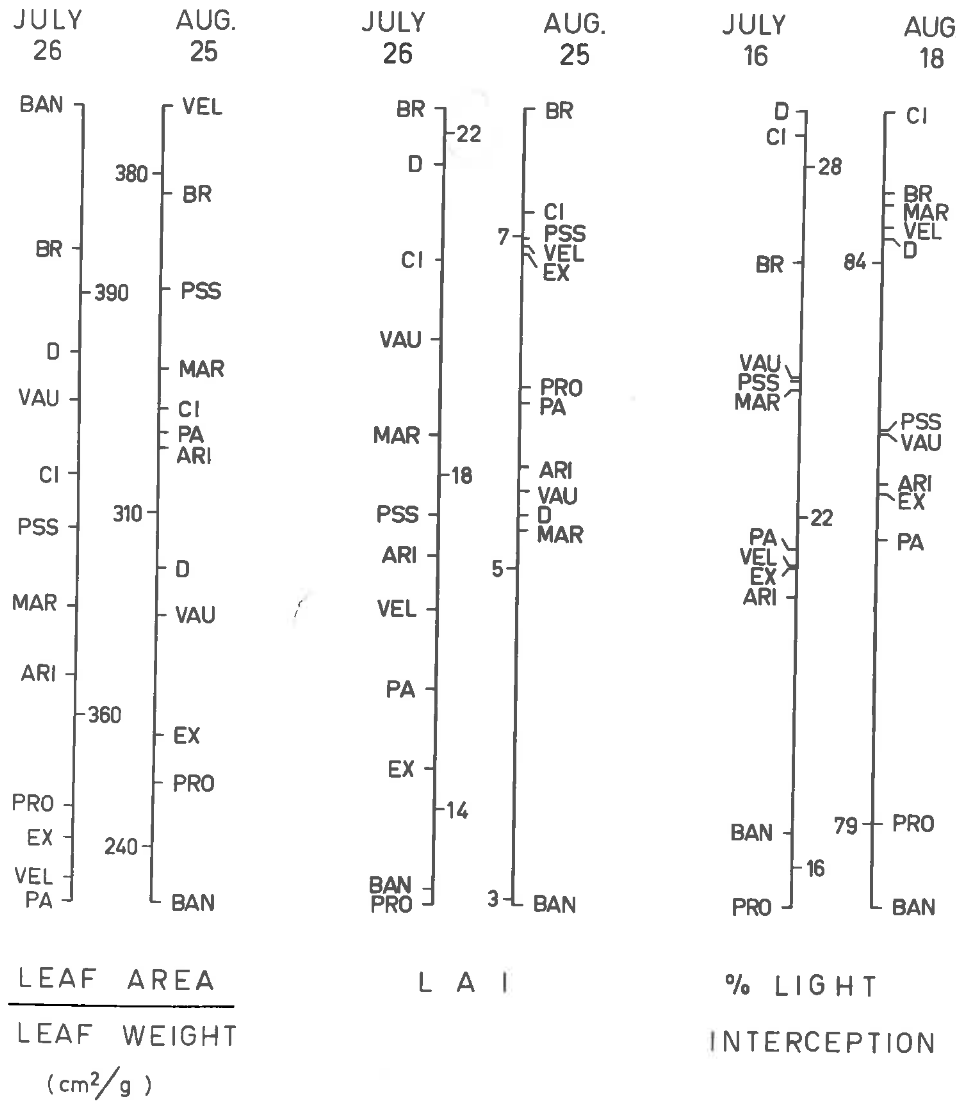


Figure 21. Leaf area/leaf weight ratio, LAI and percent light interception for 12 varieties at harvest 1 (July 26) and harvest 2 (August 25).

many extremely small tillers and Drake and CI3576 were intermediate (Figure 22B and C).

By the time of the second harvest, 64 days after emergence, the later varieties with low seedling weights, Proctor and Excelsior, had greatly increased their production of dry matter relative to the other varieties (Figure 22A). While the ranking of the dry weight of individual tillers changed little between the two harvests (Figure 22B), Proctor and Excelsior produced many additional tillers during the period (Figure 22C). Conversely, the early varieties, Bankuti, BR1239, and CI3576 added few extra tillers. Therefore by the end of August no difference existed between the varieties in LAI and light interception (Figure 21B and C) except for Bankuti and Proctor.

Bankuti showed a remarkable shift in leaf area/ leaf weight ratio, moving from highest at the first harvest to lowest at the second (Figure 21A). This bore out previous observations that early leaf growth in Bankuti was very thin and pale yellow-green in colour, but later that the leaves appeared very thick and blue-green, possibly through absence of severe mutual shading.

The amount of light intercepted by each of the 12 varieties on days near the two harvests is plotted against the LAI in Figure 23. Any varieties above the visually fitted regression line intercept relatively more light per

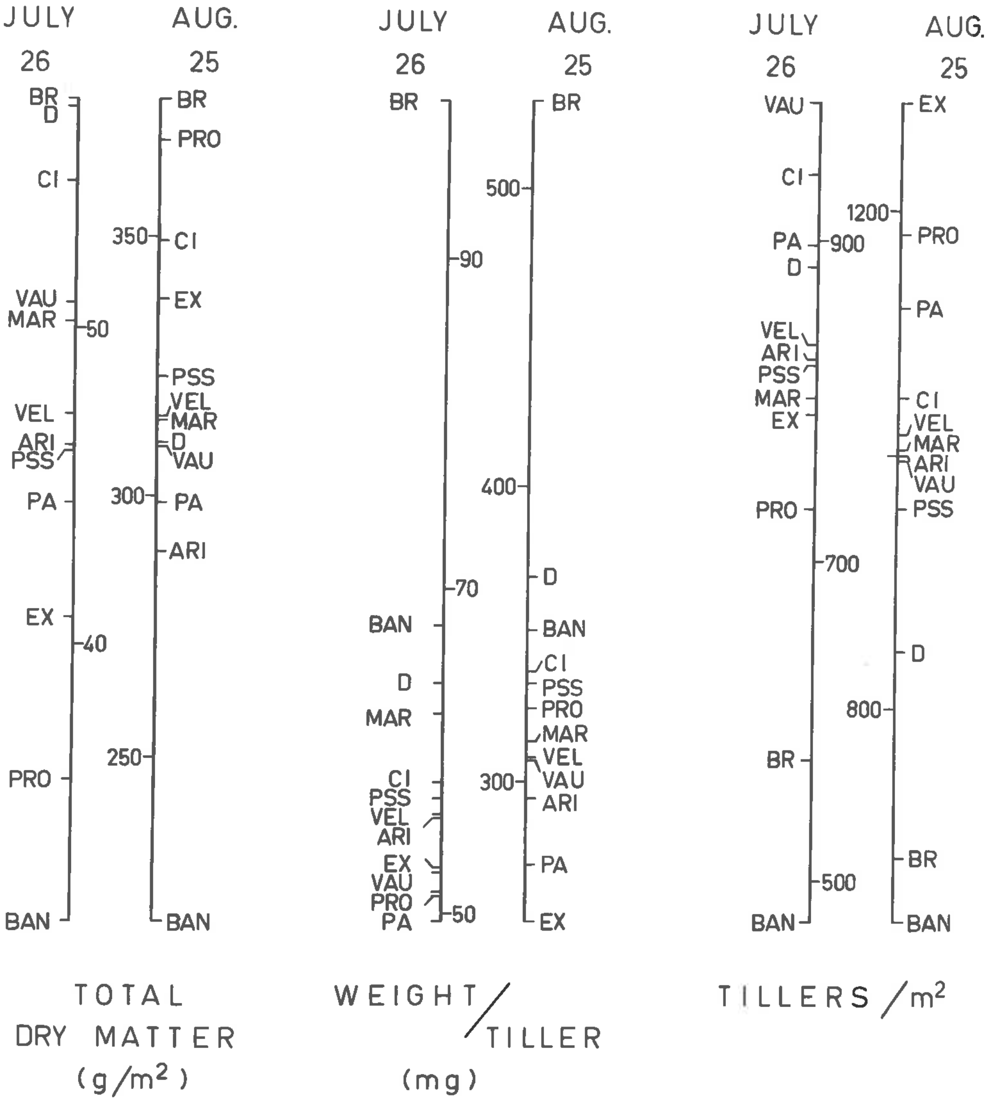
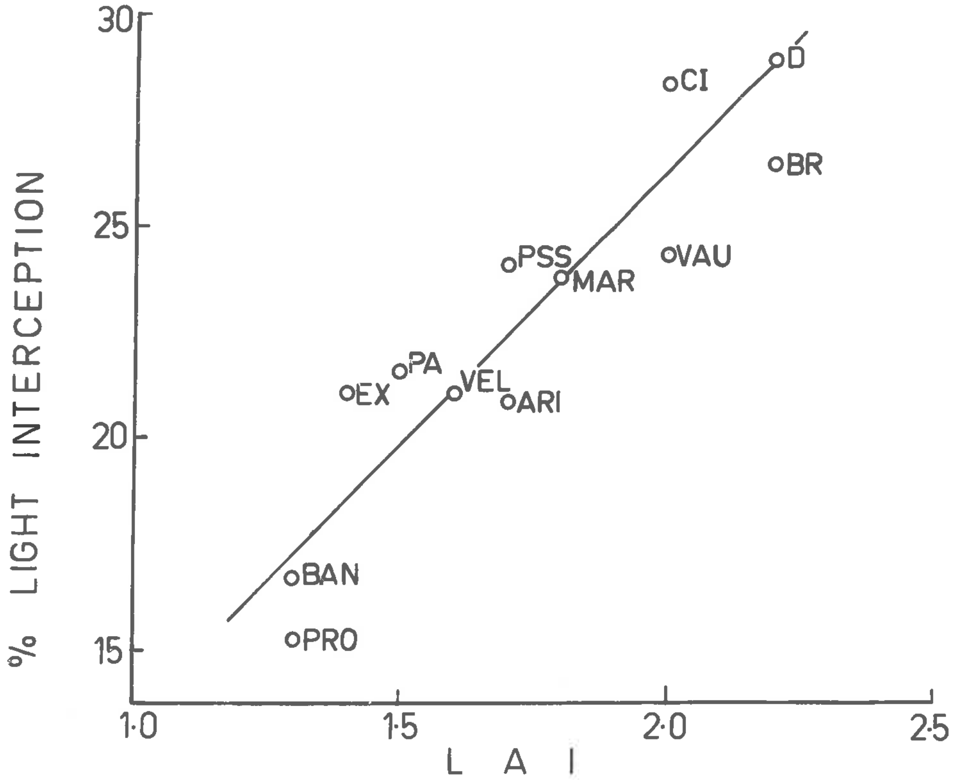
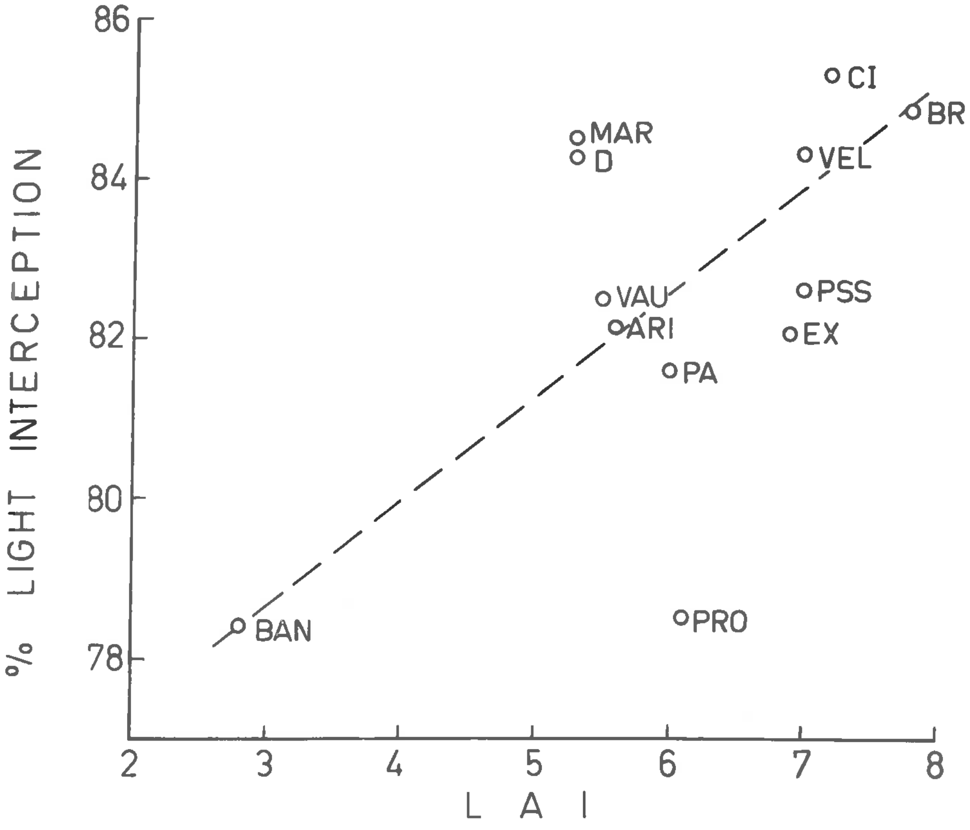


Figure 22. Number of tillers, weight per tiller and total dry weight for 12 varieties at harvest 1 (July 26) and harvest 2 (August 25) in 1969.

Figure 23. The percent light intercepted on (A) July 16 and (B) August 18 plotted against the LAI on (A) July 26 and (B) August 25 for 12 varieties. Regression lines hand fitted.


% LIGHT INTERCEPTION
L A I
30
25
20
15
1·0
1·5
2·0
2·5
D
CI
BR
VAU
PSS
MAR
PA
EX
VEL
ARI
BAN
PRO


% LIGHT INTERCEPTION
L A I
86
84
82
80
78
2
3
4
5
6
7
8
CI
BR
MAR
D
VEL
VAU
ARI
PSS
EX
PA
BAN
PRO

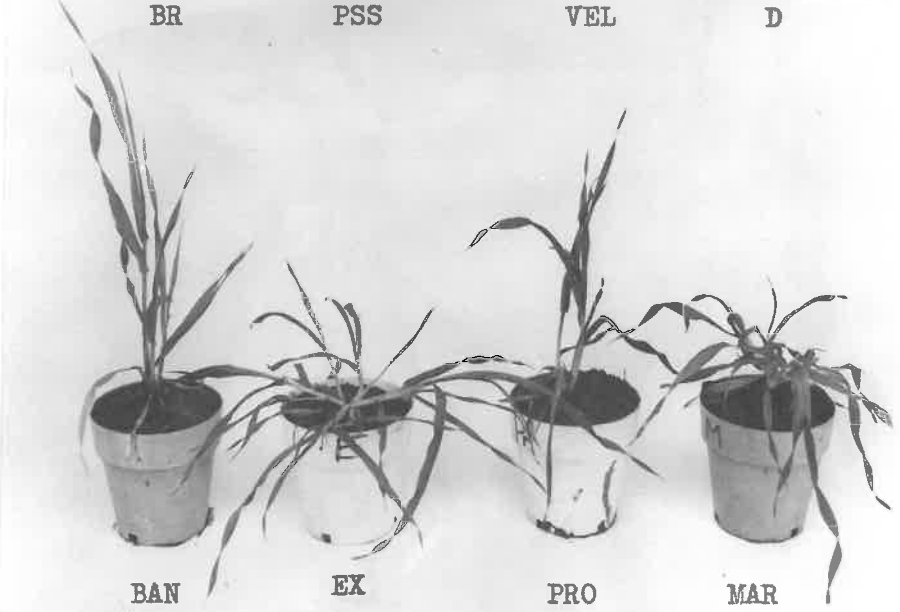
unit leaf area, any below it intercept relatively less. However, there was little deviation from the line at the first harvest (Figure 23A) despite very large differences in the initial growth habit (Figure 24 and Table 20). Two varieties, Excelsior and Vaughn, grew horizontally along the ground until the tillers overlapped each other. Others, like Bankuti, BR1239, Proctor and Princess grew erectly. This strongly influenced the canopy height, with short culmed varieties like CI3576 and Proctor having relatively tall canopies.

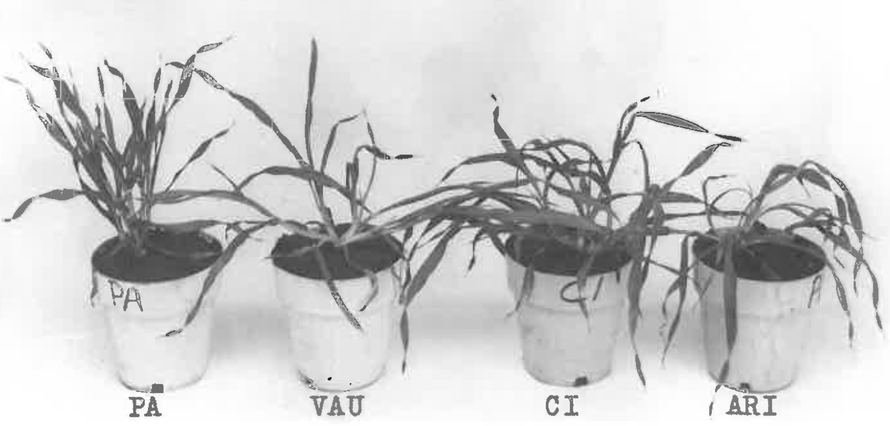
At the second harvest there was far more deviation from the line of best fit. The three varieties, Excelsior, Proctor and Prior A, which had many small tillers (Figure 22B and C) and also rather narrow leaves (Table 20) intercepted less light per unit leaf area (Figure 23B). Drake with fewer large tillers and Maraini with wide and long leaves both intercepted more light per unit leaf area. BR1239, with few very large tillers and wide leaves, was on the regression line because of the much shorter leaves and erect leaf type (Table 20). The different types of canopy before stem elongation are shown in Figure 25. Despite these differences in canopy architecture, and the large range of LAIs (2.9 to 7.8), variation in percent light interception was comparatively small (78.4 to 85.4), resulting from the asymptotic extinction of light. Leaves

Figure 24. The growth habit of the 12 varieties at approximately the time of floral initiation. Plants were grown at normal densities in rows, removed in blocks of soil that were placed in pots and photographed immediately.

(Top)	BR1239	Princess	Velvon	Drake
(Centre)	Bankuti	Excelsior	Proctor	Maraini
(Bottom)	Prior A	Vaughn	CI3576	Arivat


BR
PSS
VEL
D


BAN
EX
PRO
MAR


PA
VAU
CI
ARI

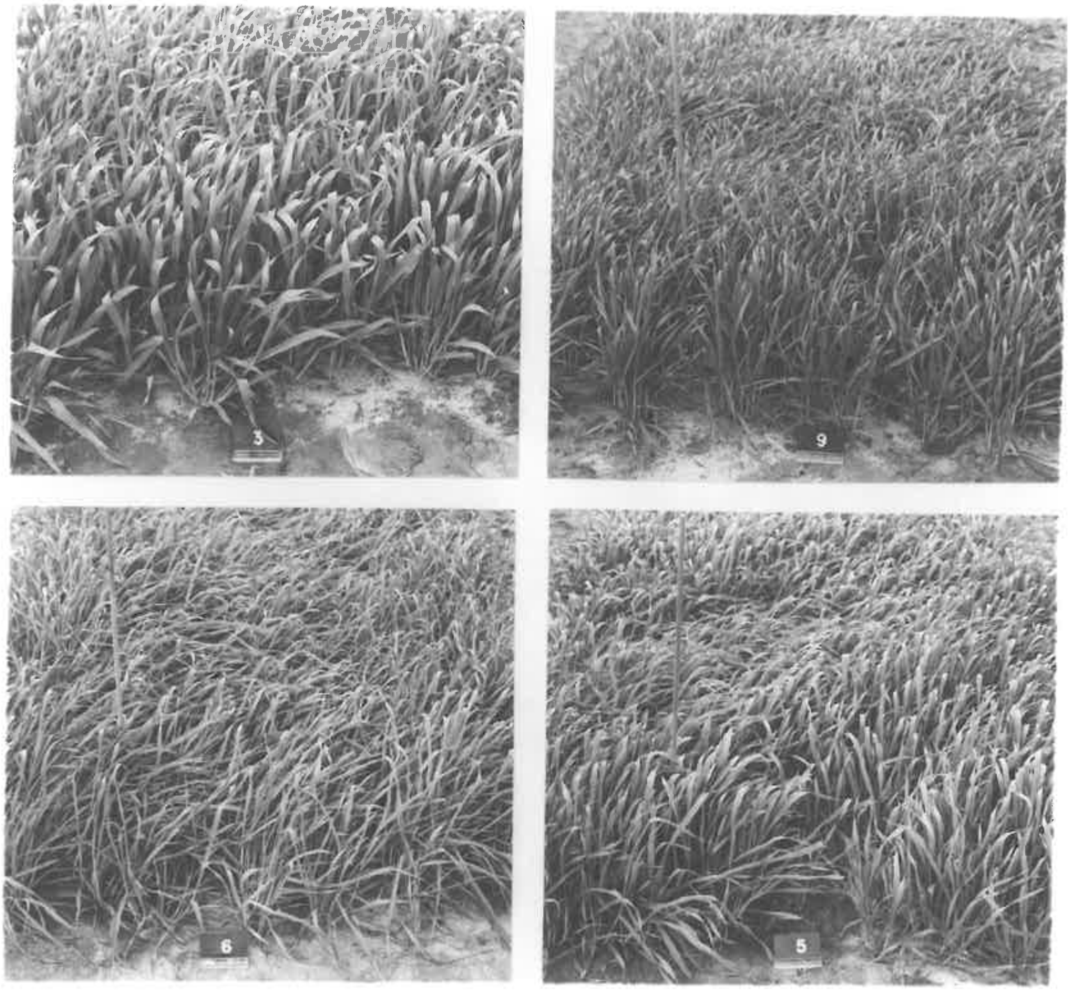


Figure 25. The varying types of canopy of BR1239 (3), Proctor (9), Excelsior (6) and Drake (5) on August 15. Excelsior and Drake lodged soon afterwards. The distance between lens and canopy is the same in all four photographs.

on varieties with low LAIs seemed to occupy positions with minimum shading from surrounding leaves. More light penetrated per unit leaf area at the higher LAIs because of the increasing erectness of leaves. This decrease in the extinction coefficient (k) with increasing LAI has also been reported by Saeki (1963), Pearce et al. (1967b) and Brown and Blaser (1968).

TABLE 20

Early growth habit, leaf angle, canopy height and leaf size for each of 12 varieties, 1969

	Growth Habit*	Leaf Angle **	Canopy Height Aug.22	Fifth Leaf	
				Length cm	Width cm
Bankuti	8.0	7.8	63.0	31.7	1.3
BR1239	8.0	8.5	57.8	28.9	1.4
CI3576	6.6	7.5	48.8	33.9	1.0
Proctor	6.6	6.0	43.8	32.8	.9
Drake	8.0	6.5	43.3	34.9	.9
Arivat	8.0	5.5	43.3	33.9	1.0
Maraini	6.6	5.3	39.8	33.8	1.3
Princess	6.6	4.8	38.0	34.9	.8
Prior	8.0	4.8	35.8	34.6	.8
Velvon	7.0	3.0	33.0	34.7	1.3
Vaughn	3.0	2.8	31.0	34.8	.9
Excelsior	3.0	1.3	28.5	38.2	.8
LSD	2.2	2.0	5.3		

* 1 = completely prostrate to 10 = tillers vertical
** 1 = leaves horizontal to 10 = leaves erect

the same procedure as described above for the preparation of (92a), o-allyloxyiodobenzene was obtained as a colourless liquid (48%), b.p. 141-144°/18mm. (Found: C, 41.5; H, 3.4; I, 48.5. C_9H_9IO requires C, 41.6; H, 3.5; I, 48.8%), ν_{max} 3070 and 3020 ($CH=CH_2$), 1645 (olefinic C=C), 1245 (C-O), 990 and 925 ($CH=CH_2$) and 745cm^{-1} (aromatic 1,2 disubstitution), δ 7.9 - 6.2 (m, 4H, aromatic H), 6.2 - 5.5 (m, 1H, $C\underline{H}=CH_2$), 5.5 - 5.0 (m, 2H, $CH=C\underline{H_2}$) and 4.7 - 4.3 (m, 2H, $O-C\underline{H_2}$), m/e 260, G.C.$^{A}_{135^o}$ one peak.

3-Methylbenzofuran

The sequence described in Organic Syntheses[115] was used without modification.

(a) Ethyl α-chloroacetoacetate was obtained as a slightly yellowish liquid (93%) b.p. 85-89°/17mm (lit.[115] b.p. 85-89°/17mm).

(b) Ethyl α-phenoxyacetoacetate was prepared from ethyl α-chloroacetoacetate and sodium phenoxide and used in the next step without purification.

(c) Ethyl 3-methylcoumarilate was obtained, from cyclization of ethyl α-phenoxyacetoacetate, as a colourless liquid (53%), b.p. 123°/1.8mm (lit.[115] b.p. 162-167°/16mm).

(d) 3-Methylcoumarilic acid, obtained by hydrolysis of the above ester, was a colourless crystalline solid (74%), m.p. 192-193° (lit.[115] m.p. 192-193°).

Decarboxylation of 3-methylcoumarilic acid at 280° gave

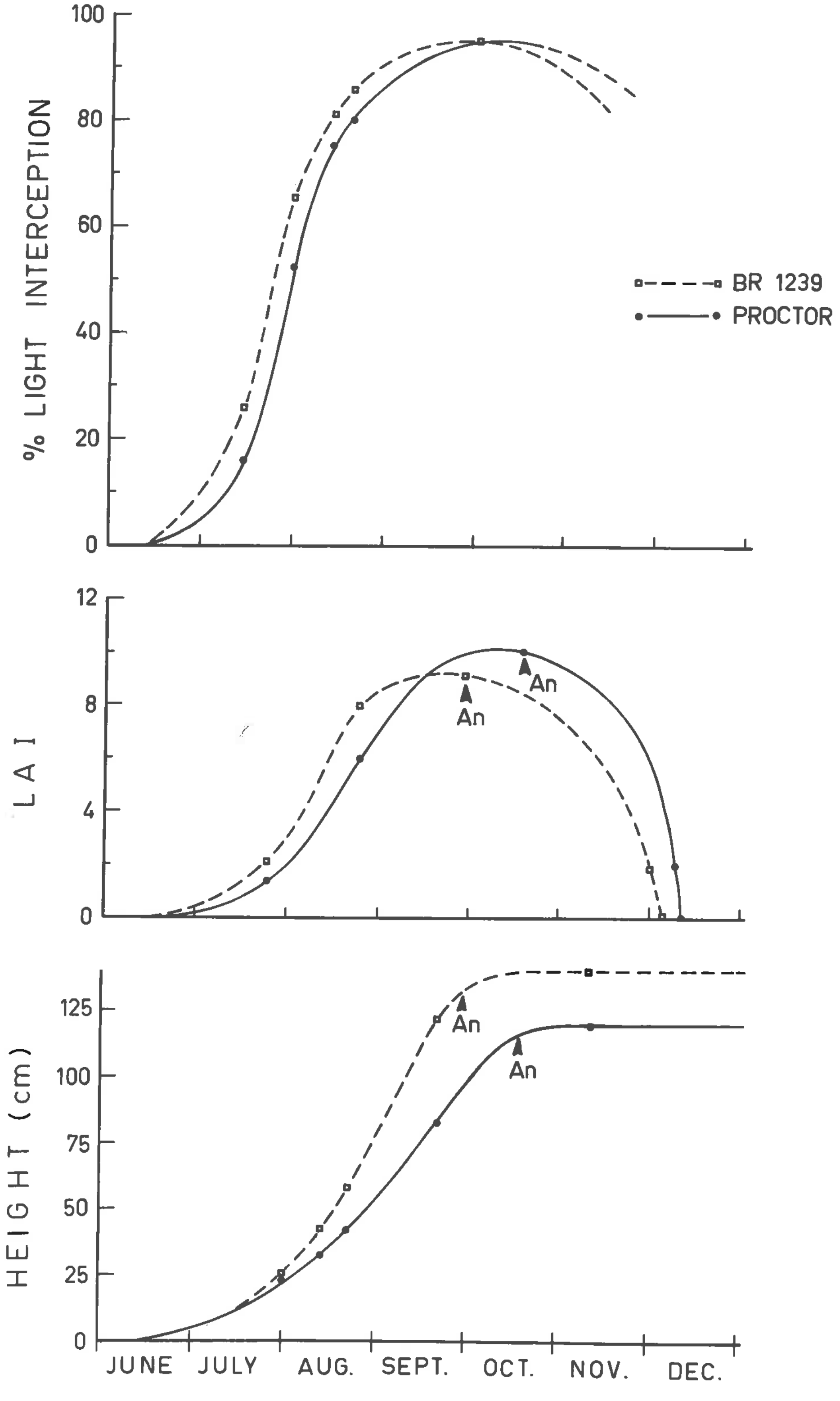
TABLE 21

The influence of floret production, floret fertility, ear survival and grain size in determining final grain yield in each of the 12 varieties.

	Normal Crop						After lodging at 6-leaf stage				
	Florets 0000s/ m^2	Ears/ m^2	Florets per ear	Grains per ear	% Fertile Florets	Grains 0000s/ m^2	%Ears‡ Surviving after lodging	Grains 0000s/ m^2	1000 grain wt.mg.	Grain Yield g/ m^2	Yield Ranking
VAUGHN	3.76	680	55.3	40.2	72.7	2.73	50.4	1.38	28.7	396	4
MARAINI	3.13	495	63.3	43.8	69.2	2.17	47.3	1.03	35.0	359	8
VELVON	2.97	414	71.7	46.3	64.6	1.92	76.8	1.47	33.4	492	1
EXCELSIOR	2.51	492	51.0	35.7	70.0	1.76	75.8	1.33	30.0	400	3
BR1239	2.34	310	75.7	35.7	47.2	1.11	100.0	1.11	30.7	339	10
ARIVAT	2.32	437	53.3	44.3	83.1	1.94	89.7	1.74	28.0	486	2
PRINCESS	1.74	605	28.7	24.2	84.3	1.46	71.6	1.05	32.9	344	9
DRAKE	1.63	437	37.3	27.7	74.3	1.21	72.8	.88	27.5	243	12
PROCTOR	1.61	570	28.3	18.7	66.1	1.07	100.0	1.07	28.4	303	11
PRIOR A	1.58	590	26.7	20.8	77.9	1.23	96.6	1.19	30.7	364	7
CI3576	1.48	681	21.7	15.5	71.4	1.06	100.0	1.06	36.9	390	5
BAŃKUTI	.91	407	22.3	25.0	112.1	1.02	100.0	1.02	35.9	365	6

‡ Difference between plots supported with dowels and unsupported plots. See Table 23.

Figure 26. Light interception, LAI, and height for BR1239 and Proctor in 1969. Lines hand fitted. Other varieties fell between these two extremes.


% LIGHT INTERCEPTION
100
80
60
40
20
0
BR 1239
PROCTOR
LAI
12
8
4
0
An
An
HEIGHT (cm)
125
100
75
50
25
0
An
An
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.

directly responsible, through the increased etoliation of the shaded pseudostems, for the increased losses from lodging in Vaughn, Maraini, Princess and Drake. Vaughn has been regarded previously as a highly variable variety (Finlay pers.comm.) and this contention is supported by comparing the high potential yield (37,600 florets per m^2) with actual number of grains set (13,800 per m^2) (Table 21). Arivat is far more reliable (23,300 to 17.400/m^2) and Bankuti completely attained its early potential. Therefore the range in grain numbers set was less than in the potential yield, and the final ranking of grain yields closely reflected the numbers of grains per m^2 with minor shifts due to differences in 1000 grain weight.

2. Shading during ear initiation

TABLE 22

The effect of shading the crop with dowels over a 30 day period between July 26 and August 25

(a) Mean of 12 varieties on August 25.

	Control	Shaded	LSD	% Change
Total dry weight, g/m^2	317	272	26.5	-14.3
Weight/tillers, mg	335	309	21	- 7.7
Tillers/m^2	984	906	NS	- 7.9
Leaf area/leaf wt.cm^2/g	315	326	NS	+ 3.6
LAI	6.0	5.3	NS	- 12.2

(b) Mean increase for 12 varieties from July 26 to August 25

Total dry weight, g/m^2	270	225		-16.7
Weight/tiller, mg	274	248		- 9.5
Tillers/m^2	186	108		-41.9
LAI	4.3	3.6		-16.3

The 12 varieties did not differ significantly in their response to being shaded by dowels. The total dry matter of all varieties on August 25 was reduced after the 30 day period of shading by a mean of 14.3 per cent (Table 22). This was less than expected, since initially the crop was growing at approximately half normal light intensity, though receiving more adequate illumination at the end of the period when the crop neared the top of the dowels. However throughout the experiment, differences in dry matter production were correlated with numbers of tillers produced, and there were relatively few tillers produced in the period of shading. The ~~mean~~ tiller number increased very rapidly under the fertile, moist conditions, from an initial density of 156 seedlings/m^2 to 797 tillers per/m^2 on July 26. From then until August 25 (the period of shading) 186 tillers were produced in the control compared to 108 in the shaded plots (a decrease of 41.9 per cent). The weight per tiller in the control, over the same period, increased from 61mg to 335mg, so the significant reduction of 26mg caused by shading was 9.5 per cent of the increase for the period.

The reductions in tiller number and weight did not, however, decrease either the size or numbers of ears. The number of florets per ear was, in fact, significantly increased from 44.7 to 49.1 by shading, and appeared similar for all varieties. The effect was not related to varietal differences in ear number, and the earlier reductions in LAI and total dry matter seem insufficient to allow conservation of soil moisture. The most likely explanation is that stamen initiation in lateral spikelets was slowed more by the lower light intensity than spikelet formation, resulting in the production of more spikelets, similar to the effect of decreasing daylength (Nicholls and May, 1963; Friend, 1965a).

TABLE 23

The number of ears/m^2 produced at anthesis after shading with dowels

	Control	Dowels	Difference
Arivat	392	437	+ 45
Vaughn	343	680	+337
CI3576	681	538	-143
Prior A	570	590	+ 20
Velvon	318	414	+ 96
Drake	318	437	+119
Princess	433	605	+172
BR1239	310	295	- 15
Proctor	570	570	0
Maraini	234	495	+261
Excelsior	373	492	+119
Bankuti	407	376	- 31
LSD			±127

Varieties responded differentially in ear number to shading, reflecting again the extent of juvenile lodging (Table 23). Varieties such as BR1239 and Bankuti in which no juvenile lodging occurred showed a non-significant decrease in ear number after being shaded. Ear number of varieties like Vaughn, Maraini and Princess which had lodged severely by August 24 were significantly increased where lodging was prevented by the structural support of the dowels. In retrospect, perhaps a second control was needed; plots with thin upright wires had cast little shade but which also support the crop. CI3576 was the only variety to show a significant decrease in ear number due to shading.

3. Shading during grain filling. Theoretically the only yield component that should be affected by shading after anthesis is the weight per grain, and this was confirmed by the present results. Significant changes were obtained in weight per grain leading to changes in grain yield and harvest index. Once again there was no variety x shade interaction.

Shade only reduced the final 1000 grain weight from 31.5g to 29.0g, but the end result included two compensating processes. Firstly, the weight per grain increased much more slowly under 48 per cent daylight; at their maximum point of divergence, the weight of the shaded treatment was only 75 per cent of the control (Figure 27A). But secondly, the shaded treatment continued to increase in weight after the control had reached a plateau, and had nearly equalled the latter at physiologic maturity. The leaves of the shaded plots remained green two days longer, and the stems and ears four days longer, but this could have been due either to the sink remaining unfilled, or to the cooler, moister conditions prevailing under the shade cloth. Surprisingly, shading did not decrease straw weight, so apparently no stem reserves were mobilized to replace the theoretical loss of photosynthate. Also the earlier difference in grain weight between shade and control may have been maintained if the control had not been subjected to more arid conditions.

B. <u>The influence of light enrichment</u>. The previous experiment has shown that shading the crop during early development resulted in a greater reduction in yield than shading during grain filling, and a second experiment was run concurrently on an adjoining area to see if reducing the competition for light also varied in importance at different stages.

Two methods of reducing light competition were used together on each plot. One was the technique used by Clements et al. (1929) of bending the neighbours away from the test plants. This was achieved by surrounding

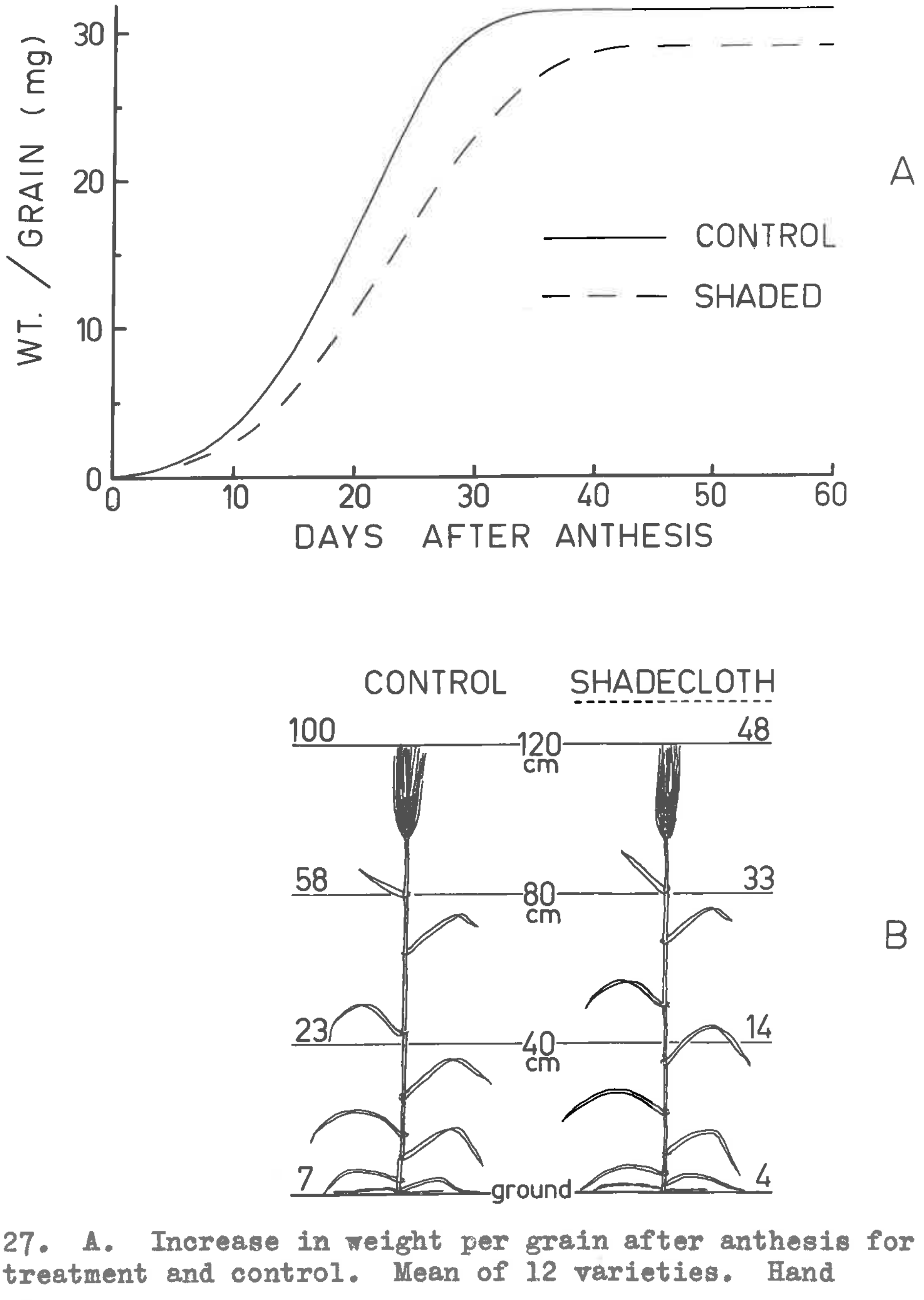


Figure 27. A. Increase in weight per grain after anthesis for shaded treatment and control. Mean of 12 varieties. Hand fitted curves.

B. Percent penetration of light to 3 levels in the canopy under shade and control. Mean of 6 varieties immediately after anthesis.

the test plants with an open ended, truncated and inverted pyramid moulded from 5cm mesh chicken wire (Figure 28). The secondary effects on growth and mineral uptake of the neighbours was minimized by the short duration of the treatment, and the high fertility of the soil. No additional rainfall was deflected onto the test plants. The second technique used to increase light availability was to place a small reflector at one side of the test plot (Pendleton et al., 1967). The reflector was concave, covered with a high gloss white paint and positioned on the south side of the plot. The net effect of each of these measures was a two-fold increase over the control in the light penetrating to ground level.

The 8cm x 8cm square planting giving 156 plants/ m^2 was again used, 30 kg/ha nitrogen applied, and two varieties grown. CI3576 and Arivat were selected as most likely to respond to improved light conditions because of their usually high yield potential. There was no variety x treatment interaction, except when only CI3576 produced late ears under decreased competition for light during grain filling. There were four replications, 2 main plots (varieties) and 3 sub-plots (periods of light enrichment). Each test plot consisted of only four plants but these were surrounded by a 1m border. Sub-plots were chronologically harvested from south to north to avoid the shadow

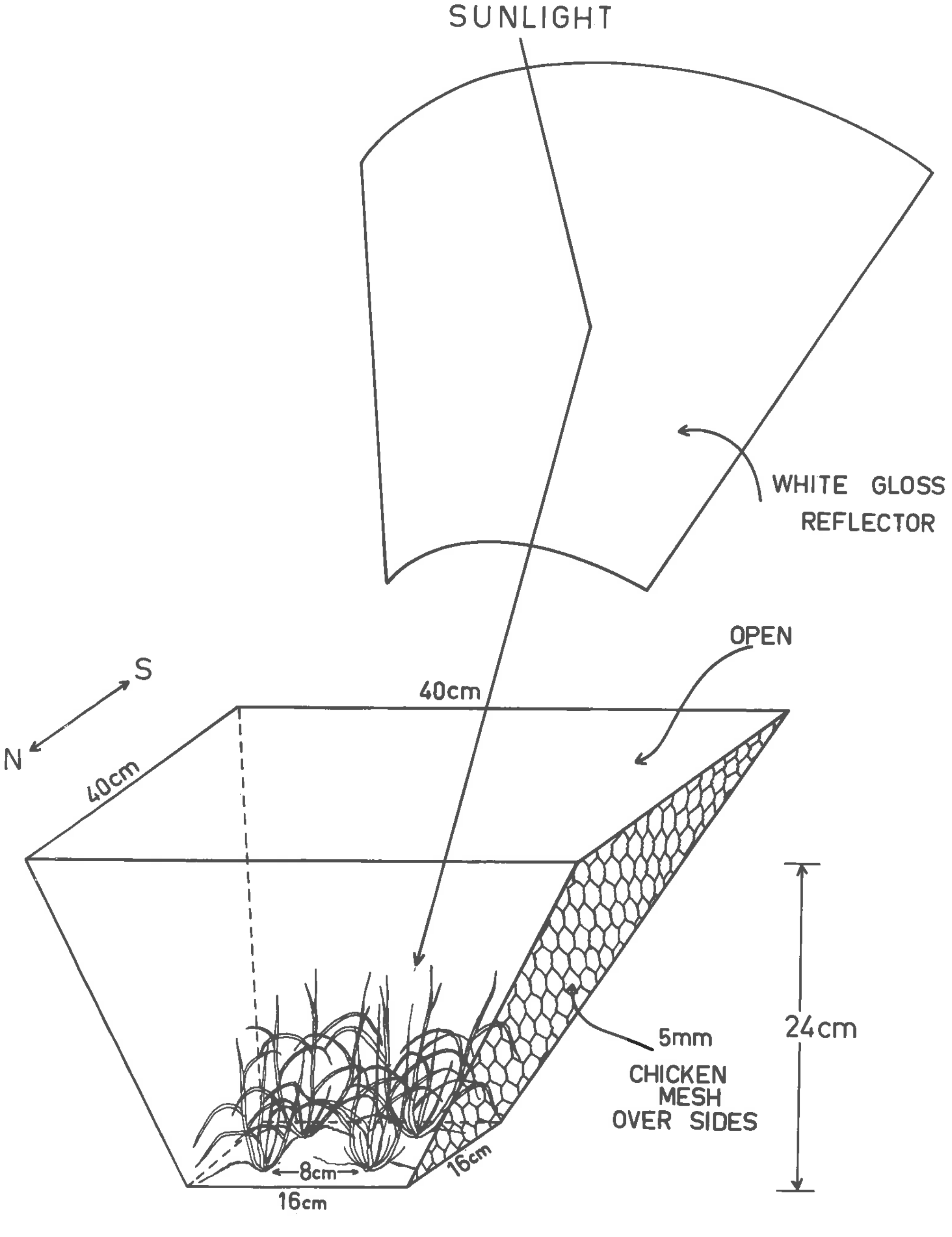


Figure 28. Truncated and inverted mesh pyramid and reflector used to increase the amount of light available to the four test plants.

of the reflector falling on future sub-plots.

The first period of light enrichment was from the fifth leaf stage (August 17) to the start of stem elongation (September 3) for a total of 17 days. The second period was 31 days long from September 3 to anthesis on October 4. The third period covered the whole of grain filling from October 4 to December 4, but grain filling was probably only rapid over the first 30 days.

RESULTS

The increased availability of light was of most value to the crop in the progressively earlier stages of development. Light enrichment increased the yield of dry matter by 56.7 per cent in the first period of 17 days, by 65.6 per cent in the 30 days of the second period, and by 24.7 per cent during the 61 days of grain filling (Table 26). And the latter only reached this percentage because of the late burst of tiller and ear production by CI3576. Light enrichment during grain filling did not increase the number of ears of Arivat, or the 1000 grain weight or number of grains per ear of either variety. The 1000 grain weights were low for both control and light enrichment suggesting that the water supply was limiting starch deposition in the grain. Conversely there was sufficient moisture and nutrients available for late tillering and ear production; exactly the opposite to what one might expect from reviews of the literature. (Slatyer, 1969). When the support of the surrounding plants was removed at anthesis, the test plants did splay out, so perhaps both occurrences were the result of the 'breaking of apical dominance'.

The large increase in dry matter in the first period was associated with an increase in the weight per tiller rather than an increase in tiller number. In the first part of this section, tillering in the early varieties like Arivat and Vaughn was found to slow greatly after the end of July and the death of tillers then accelerate. Apparently improved light conditions late in August just before stem elongation do not then reinitiate renewed tillering, but did allow more existing tillers to survive and raise the mean weight per tiller.

Light enrichment after the start of stem elongation both initiated the production of more small tillers, and allowed more earlier tillers to develop into ears. The mean weight per tiller therefore remained unaltered and only the distribution of individual tiller weights changed.

TABLE 24

Change in dry weight and various components per plant after 3 periods of light enrichment (August17 - September 3, September 3 - October 4, October 4 - December 4)

	Control	Light Enrichment	% Increase	LSD
	August 17 - September 3			
At September 3				
Number tillers/plant	7.7	9.1	18.2	NS
Weight/tiller, g	.38	.52	36.2	.07
Total weight/plant, g	3.0	4.7	56.7	1.3
	September 3 - October 4			
At October 4				
Number tillers/plant	8.4	13.8	64.3	3.6
Weight/tiller, g	.81	.84	3.7	NS
Total weight/plant, g	6.1	10.1	65.6	2.5
Number ears/plant	3.6	5.6	55.6	.7
Florets/ear	30.1	34.4	14.3	NS
	October 4 - December 4			
At December 4				
Number ears/plant	4.1	5.1	24.4	.7
Grains/ear	26.2	28.5	8.8	NS
Weight/grain, mg	26.0	28.1	8.1	NS
Grain yield/plant, g	2.6	3.6	38.5	.6
Total weight/plant, g	9.3	11.6	24.7	1.5

Stages of growth

August 17	6-leaf
September 3	Stem elongation
October 4	Anthesis
December 4	Maturity

VIII. AWN AND LEAF REMOVAL UNDER FIELD CONDITIONS

VIII. AWN AND LEAF REMOVAL UNDER FIELD CONDITIONS

With the realization that most of the dry matter in the grain is derived from current photosynthesis, much work has been devoted to assessing the relative contributions of assimilate to the grain by the various photosynthesing organs. Few workers, however, have compared a range of genotypes under field conditions, especially at commercial plant densities. The resulting discussion has therefore centred on the validity of the various techniques used in the estimates, rather than on the amount of genetic diversity available to the plant breeder in the species.

Experimental Technique. Three replications of the 12 varieties (36 main plots) were sown at 100 kg seed/ha in 1969 in 4 row plots, each 3m in length with 17.8 cm between rows. The area received 30 kg/ha nitrogen and the fertility was high. Forty culms were selected for uniformity of size at anthesis in the centre 2m of the inside rows of each plot, and these culms randomly allocated one of 4 treatments (each of 10 culms) applied as each variety reached anthesis;

(1) Control, with leaves, stems[1], ears and awns.

(2) Removal of all leaf laminae, leaving stems, ears and awns.

---

[1] Stems here include both leaf sheath and peduncle.

(3) Removal of all awns, leaving laminae, stems and ears.

(4) Removal of awns and leaf laminae, leaving only stems and ears.

The defoliated culms and their controls were surrounded by dense populations of intact culms with a mean LAI, including all green parts, of about 10. The grain was therefore developing under a normal micro environment, although some carbohydrate may have moved from the undefoliated culms to the more carbohydrate deficient, defoliated culms as found by Fairfield Smith (1933), Thorne (1962a) and Natr (1967).

The surface area per ear-bearing culm (Table 25) was calculated (Section IIIC) from length and width measurements of the top five leaves, awns, ears and stems (leaf sheaths and peduncles) taken at anthesis on fifteen of the selected culms in each variety. Not all of this area was photosynthetically active ~~however,~~ and the area of each organ visually estimated to be senescent was omitted from the photosynthetic area available for grain filling (Tables 26 and 27).

Results and Discussions. The size and proportion of the foliar organs varied considerably (Table 25). The flag leaves of Drake, for instance, had nearly 5 times the area of those of Prior A and CI3576; the six-row varieties had

TABLE 25

The surface area+ of photosynthetic organs on ear-bearing culms for 12 varieties at anthesis (cm^2)

	Flag Leaf	Second* Leaf	Third Leaf	Fourth Leaf	Fifth Leaf	Stem	Ear	Awns	Total	Ears/ m^2	LAI
6-row											
Maraini	20	34	34	32	28	140	5	71	364	184	6.7
Velvon	23	43	41	33	34	119	9	61	362	318	11.5
Excelsior	16	30	27	26	23	144	6	61	332	270	9.0
Arivat	13	29	30	31	25	124	5	71	328	362	11.9
Vaughn	13	31	33	26	23	118	5	71	320	379	12.1
BR1239	14	29	30	30	28	112	6	54	302	320	9.7
MEAN	16	33	32	30	27	126	6	65	335	306	10.2
2-row											
Drake	34	39	28	19	21	80	7	22	251	372	9.3
Princess	19	26	26	20	21	91	7	32	242	440	10.6
Bankuti	25	40	31	23	14	68	4	22	226	511	11.5
Proctor	15	25	25	22	21	77	5	27	217	481	10.4
Prior A	6	18	20	21	21	90	5	29	210	503	10.6
CI3576	6	17	20	24	20	71	5	19	183	707	12.9
MEAN	17	27	25	21	20	80	5	25	222	502	11.1
L.S.D.	6	10	8	8	8	18	1	8	46	107	

+ Total including both green and senescent area.

* Leaves are numbered in this table from the top downwards.

both taller and thicker stems, and more awns than the two-row varieties. The areas of ears given in Table 25 underestimate the true values, since the surfaces of ears are not simple rectangles but have a complex geometry with many facets. The values do, however, indicate the relative size of ears between varieties, although the varieties also differed greatly in ear shape (Figure 29). Varieties such as Drake and Princess have very long, narrow and lax ears while Maraini and CI3576 have shorter, wide and compact ears with a high density of grains.

The percentage total area attributable to the stems ranged from 30 per cent for Bankuti up to 43 per cent for Excelsior, or slightly less than the 40-50 per cent reported for wheat (Ross and Nilson, 1967[illegible]). The percentage rapidly increased however, with the senescence of leaf laminae, until the stem contribution to the grain must have been important, despite the low light interception and the higher respiration rate (and lower photosynthetic rate per unit area) compared with leaf laminae and ears (Stålfelt, 1935; Gabrielsen, 1942; Thorne, 1959, 1963a, 1965; Stoy, 1965).

The earlier varieties produced fewer leaves per culm, so the areas of their top five leaves given in Table 25 are actually for leaves developed earlier in the growing

Figure 29. The extremes in ear type within the twelve varieties. (Left) Drake, a lax-eared 2-row with deciduous awns. (Centre) Maraini, a club-eared 6-row. (Right) Excelsior, a 6-row with strongly attached awns.

TABLE 26

Photosynthetic area per ear-bearing culm (cm^2) at anthesis for 12 varieties, after removal of awns or leaves or both

	Number of rows	Control	No Leaves	No Awns	No Awns No Leaves
Arivat	6	311	200	241	129
Maraini	6	311	216	240	145
Vaughn	6	304	195	232	123
Velvon	6	301	188	241	128
Excelsior	6	300	210	240	150
BR1239	6	293	172	239	118
Bankuti	2	220	94	199	72
Drake	2	205	109	183	87
Princess	2	204	131	172	99
Prior A	2	182	125	152	95
Proctor	2	170	110	142	83
CI3576	2	156	95	137	76
Mean		246	154	201	109

TABLE 27

Photosynthetic area per grain being filled (cm^2) at anthesis for 12 varieties after removal of awns or leaves or both.

	Number of Rows	Grains/ ear	Control	No leaves	No Awns	No leaves No Awns
Bankuti	2	19.3	11.4	5.0	9.5	3.6
Excelsior	6	34.7	8.7	5.6	7.2	3.8
Princess	2	24.4	8.4	4.8	6.7	3.4
CI3576	2	20.7	7.5	4.9	5.9	3.3
Proctor	2	24.9	6.8	4.5	5.3	3.9
Prior A	2	27.7	6.6	4.5	5.3	4.0
Drake	2	32.3	6.3	3.7	5.7	2.8
Vaughn	6	48.4	6.3	4.4	5.9	3.3
Arivat	6	51.1	6.1	4.0	5.2	3.0
Velvon	6	52.4	5.8	4.4	6.3	3.0
Maraini	6	57.3	5.4	4.0	4.3	2.8
BR1239	6	54.3	5.4	3.3	5.3	2.6
Mean		37.3	7.1	4.4	6.1	3.3

season. However, the five top leaves of Bankuti were all functional (green) at anthesis giving an area of 220cm^2 per culm at anthesis (Table 26) compared with a 'maximum' of 226cm^2 in Table 25. In comparison, some of the lower leaves of Velvon, Maraini, Proctor and Princess had already senesced by anthesis and their total leaf area per culm had fallen (Table 26). All the six-row varieties still had greater leaf areas per culm than the two-row varieties although the LAIs were similar because of the greater ear number of the latter. When the leaf area per culm was divided by the grains per ear in each treatment to give the leaf area supplying each grain, the ranking changed completely (Table 27) with only Excelsior, which has low grain numbers for a 6-row variety, interposing between the 2-row varieties, all of which had a high leaf area per grain. These values were positively related to the final weight of individual grains (Figure 30), with a fivefold increase in leaf area per grain being associated with a doubling in grain weight. In did seem, however, that the area per grain could fall from 11.5cm^2 to 6cm^2 before a severe decline in grain weight occurred. Lowering the cm^2 per grain further from 4.5 to 2.5 then decreased grain weight from 31 to 18mg.

Notwithstanding the overall effect of leaf area per grain on grain weight, the twelve varieties responded

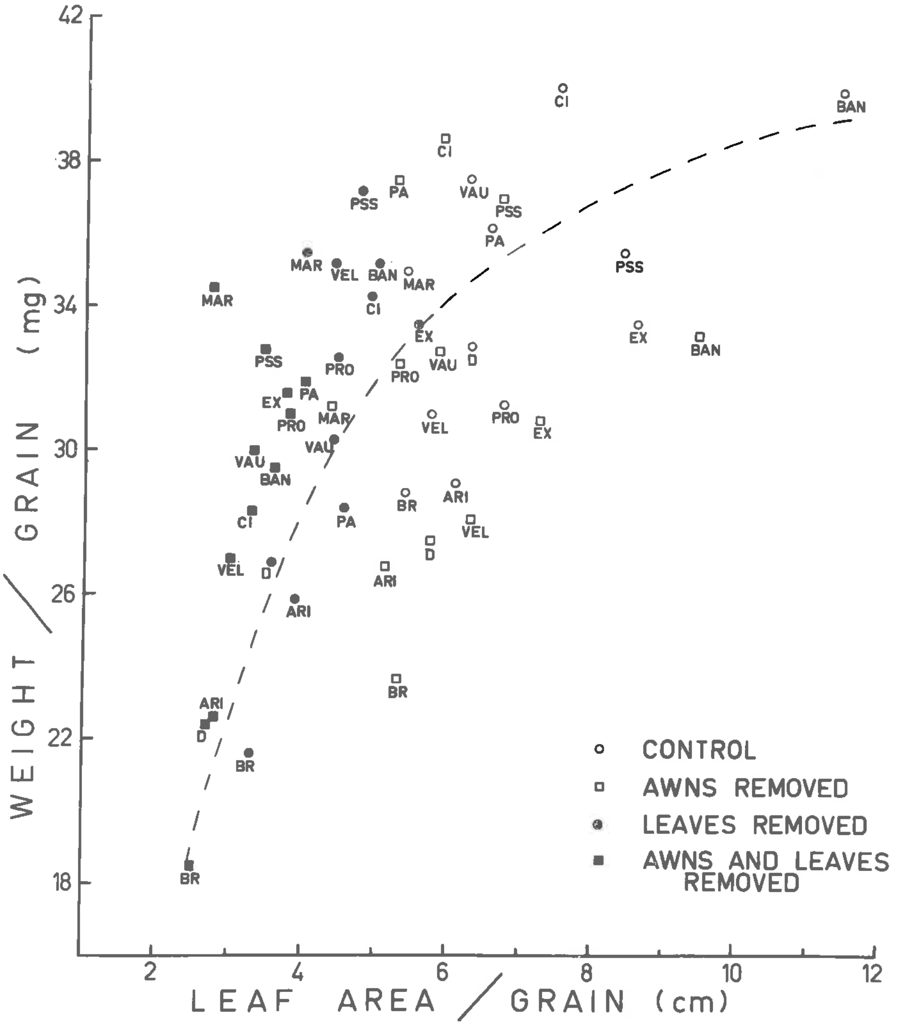


Figure 30. The weight per grain (mg) produced by the leaf area per grain at anthesis. Leaf area varied by leaf and awn removal. Hand fitted curve.

differently to defoliation both in the number of florets becoming infertile, and in the individual weights of those grains fertilized.

TABLE 28

The effect of leaf and awn removel on the number of fertile and infertile florets per ear
Mean of 12 varieties

	Control	No Leaves	No Awns	No Leaves No Awns	LSD
Fertile	37.3	35.6	34.6*	34.0*	2.1
Infertile	6.1	6.9	8.6*	8.7*	1.0
Total	43.4	42.5	43.2	42.7	NS

* Treatments differing significantly from the control

Only the awn removal and the awn and leaf removal significantly reduced the number of fertile grains in an ear (Table 28), suggesting surgical damage to the florets, but the awns were clipped off approximately 5mm from the top of the lemma to avoid such damage. The increased sterility was most likely caused by adverse temperature or water relations in the florets developing and flowering after the mean anthesial date. The variety x treatment interaction was not significant for the number of fertile florets per ear, only the number of infertile florets (Table 29). This seemed due to the greater potential existing for floret abortion in the six-row varieties. For example, as many florets aborted in BR1239 and Velvon as were present in the whole ear of Bankuti. Two defoliation treatments increased fertility in BR1239 (Table 29); for it to happen twice in one variety and no other almost eliminates a chance happening, but no explanation can be offered other than BR1239 obviously has very precise requirements for fertilization.

The varieties differed widely in their response in weight per grain to the removal of foliage an anthesis. The reduction ranged from 37.8per cent in BR1239 down to only 1.0 per cent in Proctor when both leaves and awns were removed (Table 30). Removal of awns alone only significantly reduced the grain weight of Bankuti, but removing the leaves alone had a significant effect on BR1239, Drake, CI3576, Vaughn and Prior A. However, the leaves accounted for approximately twice the leaf area of the awns.

It was expected that the combined leaf and awn removal would cause a greater reduction in grain weight than the sum of the two individually, as the excess photosynthetic capacity of the plant could compensate for the loss of either one alone, but not for the loss of both. However the two individual effects appeared to be additive, and their sum did not differ significantly from the combined effect in any variety.

Another theory, which was not substantiated, was

TABLE 29

Number of infertile florets per ear for 12 varieties after removal of leaves and awns.

	Control	No Leaves	No Awns	No Leaves No Awns	Total Florets per ear
BR1239	17.9	11.3*	11.4*	20.8*	71.6
Velvon	14.9	14.1	19.7*	16.8	67.2
Excelsior	10.6	16.7*	17.6*	15.6*	45.3
Vaughn	7.0	8.9	13.2*	10.9*	55.4
Maraini	5.8	9.9	14.9*	11.9*	63.0
Arivat	5.2	8.1	13.3*	14.9*	56.3
Princess	4.0	3.6	3.0	4.2	28.4
Proctor	3.0	2.2	3.4	2.3	27.9
Drake	1.7	4.6	2.0	2.0	34.0
Prior A	1.5	1.7	1.8	2.0	29.2
CI3576	1.2	1.8	1.0	2.3	. 22.0
Bankuti	.7	.6	1.7	1.0	20.0

LSD = 3.4 * = differs significantly from control

based on observations made in 1967. Under the arid conditions of that year, the awns of Drake, Princess, Proctor and BR1239 broke off soon after anthesis (e.g. Drake in Figure 29), while the leaves of Excelsior senesced very early and apparently left grain filling dependent on the assimilate from the bright green awns. Under the less arid conditions of 1969, removing the awns had most effect (nearly significant) in Drake followed by Excelsior, Proctor and Princess. The

TABLE 30

Weights per grain (a) in grams and (b) percent change from control for 12 varieties after the removal of leaves and awns.

	Type	Control	No Leaves	No Awns	No Leaves: No Awns	No Leaves	No Awns	No Leaves: No Awns
			(Grams)			(% Change)		
BR1239	Early 6-row	28.9	21.6*	24.3	18.0*	-25.2	-16.0	-37.8
DRAKE	Medium 2-row	32.9	26.9*	27.6	22.6*	-18.1	-16.2	-31.3
CI3576	V.early 2-row	41.0	34.4*	38.7	28.3*	-16.2	- 5.6	-30.9
BANKUTI	V.V.early 2-row	40.1	35.2	33.2*	29.5*	-12.3	-17.2	-26.4
ARIVAT	Early 6-row	29.1	25.8	26.8	22.6*	-11.4	- 8.0	-22.2
VAUGHN	Early 6-row	37.6	30.3*	32.8	30.0*	-19.3	-12.8	-20.2
VELVON	Med.late 6-row	31.1	35.3	28.1	27.0	+13.5	- 9.4	-13.1
PRIOR A	M.early 2-row	36.2	28.5*	37.6	31.9	-21.4	+ 3.7	-11.8
PRINCESS	Late 2-row	35.5	37.2	37.0	32.8	+ 4.9	+ 4.2	- 7.5
MARAINI	V.late 6-row	35.1	35.5	31.3	34.5	+ 1.2	-10.7	- 1.6
EXCELSIOR	Med.late 6-row	33.6	33.5	30.8	31.6	- .3	- 9.3	- 5.8
PROCTOR	Late 2-row	31.3	32.6	32.4	31.0	+ 4.0	+ 3.5	- 1.0
MEAN		34.4	31.4(*)	31.7(*)	28.3(*)	- 8.7	- 7.9	-19.5
	LSD = 5.9							

* = differs significantly from control

(*) = LSD = 1.7

observations were therefore either misleading in 1967, or the contribution of the various foliar organs to grain filling alters markedly in each variety with changes in environment; both seem likely to be true.

Neither does the severity of reduction in grain weight seem related to the leaf area per culm, leaf area per grain, number of culms or number of infertile grains in a variety. True, BR1239 with the lowest leaf area per grain suffered the greatest reduction, from further loss of foliage, but the next three varieties, Drake, CI3576 and Bankuti, all had relatively large leaf areas per grain. In fact, the only consistent relationship was between date of anthesis and effect of defoliation, with the four late varieties, Proctor, Excelsior, Maraini and Princess showing no adverse effects from any of the three treatments; while all the early varieties were affected significantly. At first this seems illogical, since the earlier varieties should be able to continue grain filling for a longer period and thus be able to compensate for the reduced capacity, but two pieces of evidence tend to support the findings.

Firstly, the later flowering varieties produced less dry matter after anthesis than early varieties, and often less than the amount accumulated in their grain (Figure 31). This was found under the favourable climatic conditions of 1968 when 4 replications of 10m long plots

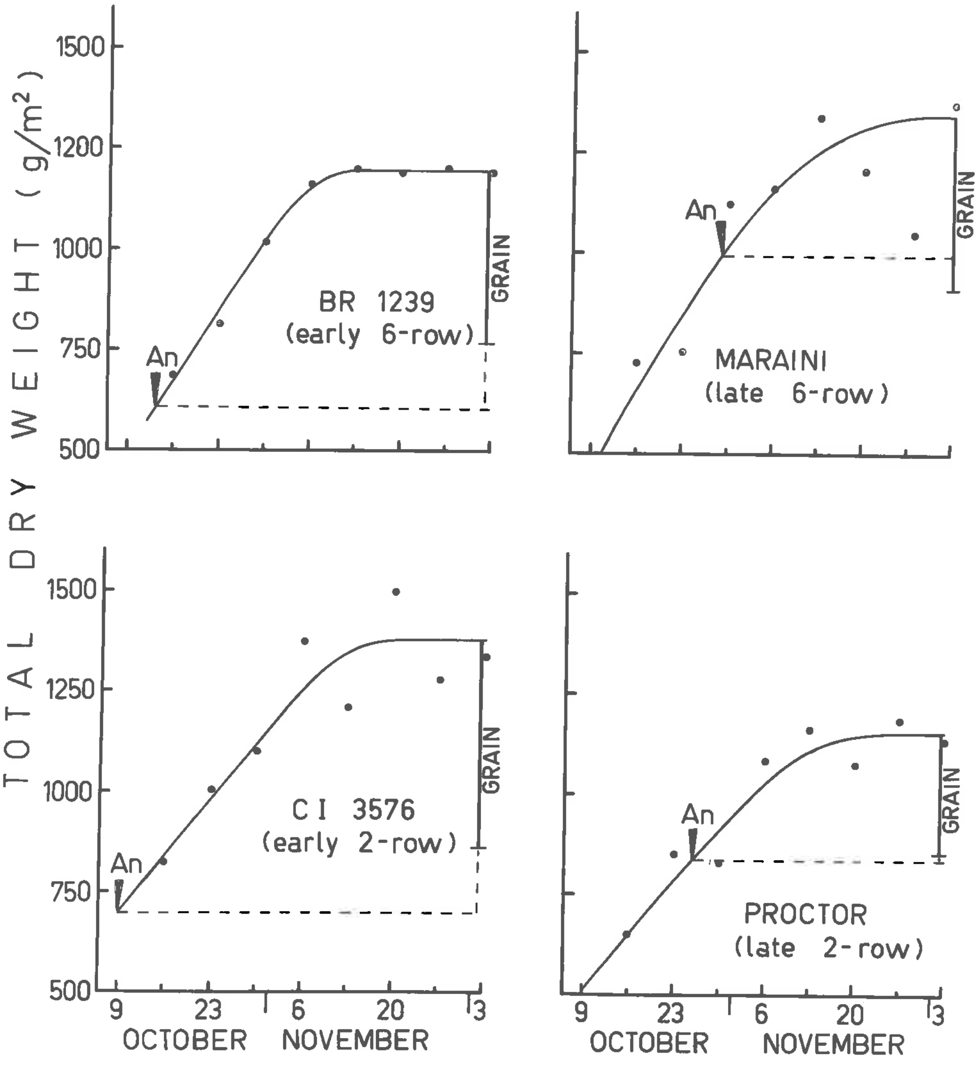


Figure 31. Increase in total dry weight over an eight week period for CI3576, BR1239, Maraini and Proctor in 1968. Arrow indicates date of anthesis. Hand fitted curves.

were destructively sampled on eight weekly occasions starting on October 16. Excelsior behaved similarly to Maraini (Figure 31) by increasing in grain weight far in excess of the increase in total dry weight after anthesis; Princess and Velvon resembled Proctor where the dry matter increase after anthesis just equalled grain weight; and Arivat, Vaughn, Bankuti, Drake and Prior A resembled CI3576 and BR1239 in producing more dry matter after anthesis than was used in grain production.

The net decrease in straw weight of Excelsior and Velvon might be indicative of higher respiration losses under the warmer temperatures later in the season, but could also indicate a greater mobilization of assimilate, stored in the stem just prior to anthesis, into the grain. The later flowering varieties do have a longer period between stem elongation and fertilization, when, presumably, production of photosynthate remains high.

Secondly, even a small quantity of carbohydrate available immediately after anthesis might negate the effect of defoliation and allow the formation of grains of normal size or volume (e.g. Aspinall, 1965) in the later varieties. Whereas, in the earlier varieties, during this period, the rapidly developing grain could be competing against the still elongating stem for a supply of assimilate reduced by defoliation.

Under irrigated conditions in 1967 (Section X for experimental details), the grain weight increased after anthesis more rapidly in later flowering varieties (Figure 32), with the latest variety in 1967, Princess, having a threefold greater grain weight ten days after anthesis than the earliest variety, BR1239 (Bankuti was ommitted from the 1967 results). The complete ranking of varieties at that stage, in increasing order of grain weight was BR1239, Arivat, Vaughn, CI3576, Prior A, Drake, Velvon, Excelsior, Proctor, Maraini and Princess, but it is merely supposition to credit this more rapid weight increase to an increased availability of stem reserves or less competition with the elongating stem. Both temperature and solar radiation are higher during the grain filling period of the later flowering varieties and could affect the increase in grain dry weight.

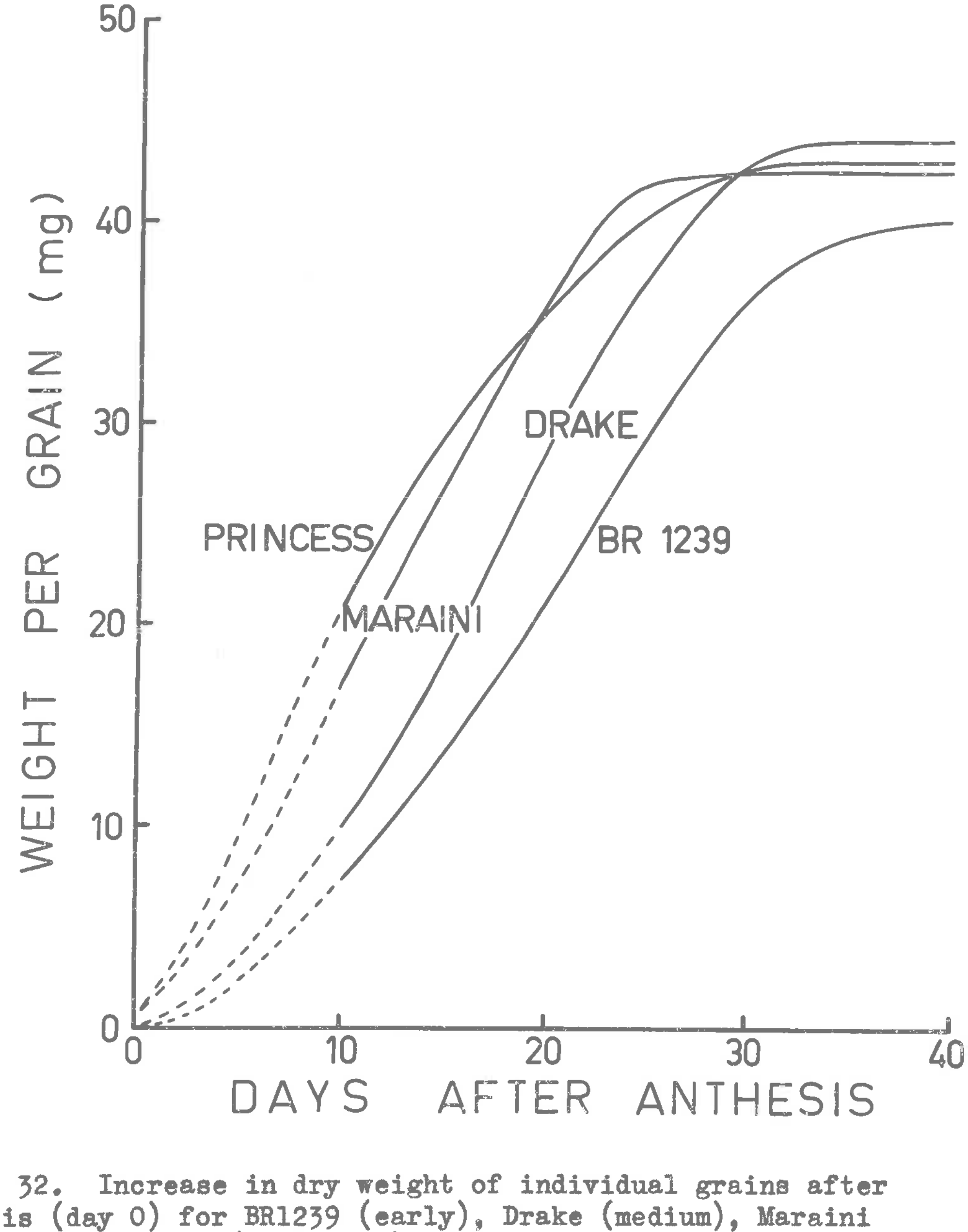


Figure 32. Increase in dry weight of individual grains after anthesis (day 0) for BR1239 (early), Drake (medium), Maraini (late) and Princess (very late) in 1967. Irrigated block, means of 12 plots. Computer fitted curves.

IX. VARIETAL TOLERANCE TO CROWDING

IX. VARIETAL TOLERANCE TO CROWDING

The large differences in tillering capacity between varieties suggested that they might differ considerably in the density required for maximum grain yield. However, neither the extent of these differences nor the actual values were known. Commercial densities vary from 600 plants/m^2 for European varieties grown in the moister areas of the British Isles (Boyd, 1952), down to 40 plants/m^2 for varieties grown with only 150mm rainfall in North Africa (Nassef pers. comm.), so the experimental range had at least to exceed these limits. This virtually precluded the use of large conventional plots, because the large area then involved was neither practical nor statistically desirable. Therefore the varieties were compared in the 'fan' or 'cartwheel' design successfully used for sorghum (Blum, 1970), maize (Duncan, 1969) and vegetable crops (Bleasdale, 1967).

In the fan (which is a partial cartwheel) design, presented by Nelder in 1962, the grain is planted in rows that radiate out from the centre or hub like the spokes of a wheel. The plants are set further apart by equal logarithmic intervals as the distance from the centre increases, leaving each plant essentially in the centre of a trapezoid that diminishes in area towards the centre of the wheel.

Conversley, the density gradually decreases by a geometric progression towards the outside of the wheel.

This systematic design allowed 30 densities to be tested and had a range from 9 to 4200 plants/m^2. The highest seven densities were all in excess of 1000 plants/m^2, and their use was inspired by the observation that plants growing in the large clumps resulting from seed spillages, often managed to produce miniature culms each bearing only one or two grains. This suggested the possibility of screening varieties on their ability to survive and produce at very high plant populations. Maize breeders already test inbreds for barreness by planting 15 to 20 seeds per hill, and plant ecologists often use densities, huge by commercial standards, in studying plant growth. Hozumi et al. (1955) for instance, in their studies on competition, grew maize plants only 2cm apart and Blackman (1968) increased the density of corn cockle (Agrostemma) and brassica (B. oleracea) up to 1549 plants/m^2.

The densities in the fan design are probably not directly comparable with those in conventional plots, especially at high densities. More sunlight penetrated 'between the spokes' towards the higher densities, for example, than if they had been surrounded by a large area of similar density. The cartwheels did, however, provide an excellent method for comparing the response of different varieties to density.

Experimental design and technique. Each fan comprised 36 spokes with $5^{\circ}\ 42'$ between each spoke (e) and thus covered an arc of just over 205°. Four varieties were grown in each fan, each having an eight row plot, with the two outside varieties having an additional two rows to provide a border. An access path ran between adjacent fans to facilitate spraying and observation. Three fans constituted a replication, and there were six replications. The six plots of each variety were assigned to the eight positions available in the 360° so that no variety occurred in the same position twice. This orientation prevented any variety gaining an advantage through an increased percentage in any one row direction.

Thirty-five plants were arrayed along each spoke, although the data for only 30 ~~is~~ are presented here, as the outermost and four innermost arcs were designated as borders, In addition, seed was broadcast at the highest density inside the innermost circle to maintain competition. The distance between plants on each spoke decreased by a factor of .9 towards the centre of the fan (Table 31), while area per plant decreased by .81. The area per plant was calculated according to the formula :- $An = r_n^2\ \theta\ (\alpha^2 - 1)/2\alpha$

(Bleasdale, 1967) where An = Area per plant at arc n

r_n = distance from centre of arc n

α = constant rate of change of spacing

Each arc was harvested separately and consisted of the centre six plants, as the two outside spokes in each plot were left as borders.

TABLE 31

Number of plants per m^2, area per plant, and distance to next plant along an arc (from the outside to the centre) for the 30 densities in 1968. r_o = 15.1 cm.

Plants/ m^2	Area/Plant cm^2	Distance to next arc, cm	Plants/ m^2	Area/Plant cm^2	Distance to next arc, cm
9	1070	31.8	220	45.5	6.6
12	867	28.7	272	36.8	5.9
14	707	25.8	336	30.0	5.3
18	569	23.2	415	24.1	4.8
22	461	20.9	512	19.8	4.3
27	373	18.8	632	15.8	3.9
33	302	16.9	780	12.8	3.5
41	245	15.2	963	10.3	3.1
50	198	13.7	1189	8.41	2.8
62	161	12.3	1468	6.81	2.5
77	130	11.1	1812	5.52	2.3
95	105	10.0	2237	4.47	2.1
117	85.5	9.0	2762	3.62	1.9
145	69.0	8.1	3413	2.93	1.7
179	55.9	7.3	4202	2.38	1.5

The experiment was carried out in 1968, the year of record rainfall, so use of irrigation to prevent the domination of optimum density by moisture availability never became necessary. Nitrogen fertilization presented a problem in that the requirements both of varieties and densities probably varied and could effect the response to density. BR1239 at high density for example might be expected to have a greater requirement than Maraini or Velvon at low density. The supply was kept at an adequate but not abundant level by applying 40 kg/ha nitrogen at seeding and again 6 weeks after seeding. The latter was applied when the plant nitrate status as indicated by the diphenylamine test on leaf tissue, fell to low levels at the high densities in pilot fans planted 3 weeks before the main experiment. The marginal nitrogen status probably indirectly resulted in high grain yields, as no lodging occurred before supporting grids were fixed over the high density areas of each fan. Without lodging, either early or late, it was possible to see which yield components failed at really high densities. Kirby (1967), for instance, found that the ear numbers per m^2 continued to increase up to 800 plants per m^2, although the grain yield had started to fall due to reductions in both grain number and weight, so it was interesting to see if this pattern continued or whether ear number would also suddenly decline.

A problem arises with the graphical presentation of data from such a wide range of densities. When the horizontal scale is treated arithmetically, a typical yield depression at high density is sometimes revealed, but the performance at low density is completely obscured (Figure 33 top). When the axis is geometric (i.e. equal spacing between each density, as the percent increase in density was constant), the performance at low density is shown, but the grain yield appears to increase linearly at high densities (Figure 33 middle). No transformation of density showed clearly the performance at both high and low densities, so the data is presented in a composite form with geometric scaling between 12 and 180 plants/m^2 and arithmetic scaling between 180 and 4202 plants/m^2.

RESULTS AND DISCUSSION

Grain yield. The twelve varieties are ranked on grain yield at three densities in Table 32, and it is apparent that no single relationship exists between the relative performance of varieties at low, medium and high densities. Bankuti and Drake performed poorly at low density but did very well under high density (Table 32), and would conform to the picture of the poorly competitive ideotype presented by Donald (1968a, b). Conversely, Arivat and Velvon performed better at lower than higher densities. This inverse relationship between performance at high and low density did not extend to CI3576, which had the highest yield at both low and high density, or to Proctor and Princess, which

Figure 33. Grain yield for BR1239 plotted against density with the horizontal axis expressed (Top) arithmetically, (Middle) geometrically, and (Bottom) geometrically up to 180 plants/m^2 and arithmetically between 180 and 4202 plants/m^2.

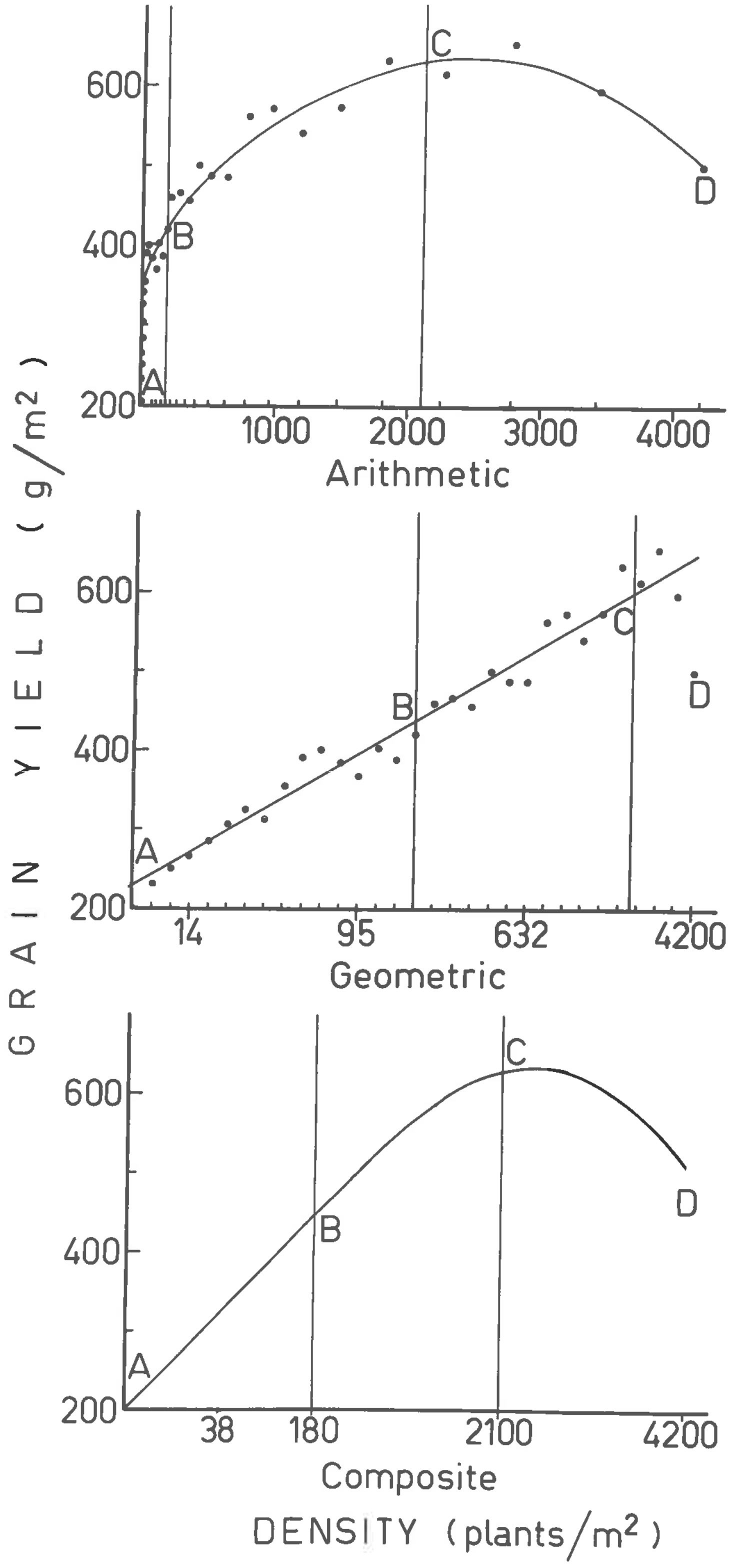

GRAIN YIELD (g/m²)
600
400
200
A
B
C
D
1000
2000
3000
4000
Arithmetic
600
400
200
A
B
C
D
14
95
632
4200
Geometric
600
400
200
A
B
C
D
38
180
2100
4200
Composite
DENSITY (plants/m²)

TABLE 32

Grain yields of the twelve varieties at three of the thirty densities (12, 220 and 4202 plants/m^2). Varieties are presented in order of yield.

Low density (12 plants/m^2)			Medium density (220 plants/m^2)			High density (4202 plants/m^2)		
Var.	Type‡	Yield (g/m^2)	Var.	Type‡	Yield (g/m^2)	Var.	Type‡	Yield (g/m^2)
CI3576	2-VE	410	ARIVAT	6-E	627	CI3576	2-VE	883
ARIVAT	6-E	388	MARAINI	6-VL	593	DRAKE	2-M	800
VELVON	6-ML	346	VELVON	6-ML	563	BANKUTI	2-VVE	783
VAUGHN	6-E	330	VAUGHN	6-E	533	PRIOR A	2-ME	720
BR1239	6-VE	330	EXCELSIOR	6-ML	537	VAUGHN	6-E	683
EXCELSIOR	6-ML	322	CI3576	2-VE	500	EXCELSIOR	6-ML	553
PRIOR A	2-ME	322	DRAKE	2-M	500	ARIVAT	6-E	552
MARAINI	6-VL	298	PRIOR A	2-ME	477	PRINCESS	2-L	550
DRAKE	2-M	218	PROCTOR	2-L	467	BR1239	6-VE	526
PRINCESS	2-L	210	PRINCESS	2-L	458	VELVON	6-ML	460
PROCTOR	2-L	204	BR1239	6-VE	403	PROCTOR	2-L	420
BANKUTI	2-VVE	122	BANKUTI	2-VVE	383	MARAINI	6-VL	208

‡ 2- or 6- indicates 2-row or 6-row varieties

V = Very
E = Early Flowering
M = Medium Flowering
L = Late Flowering

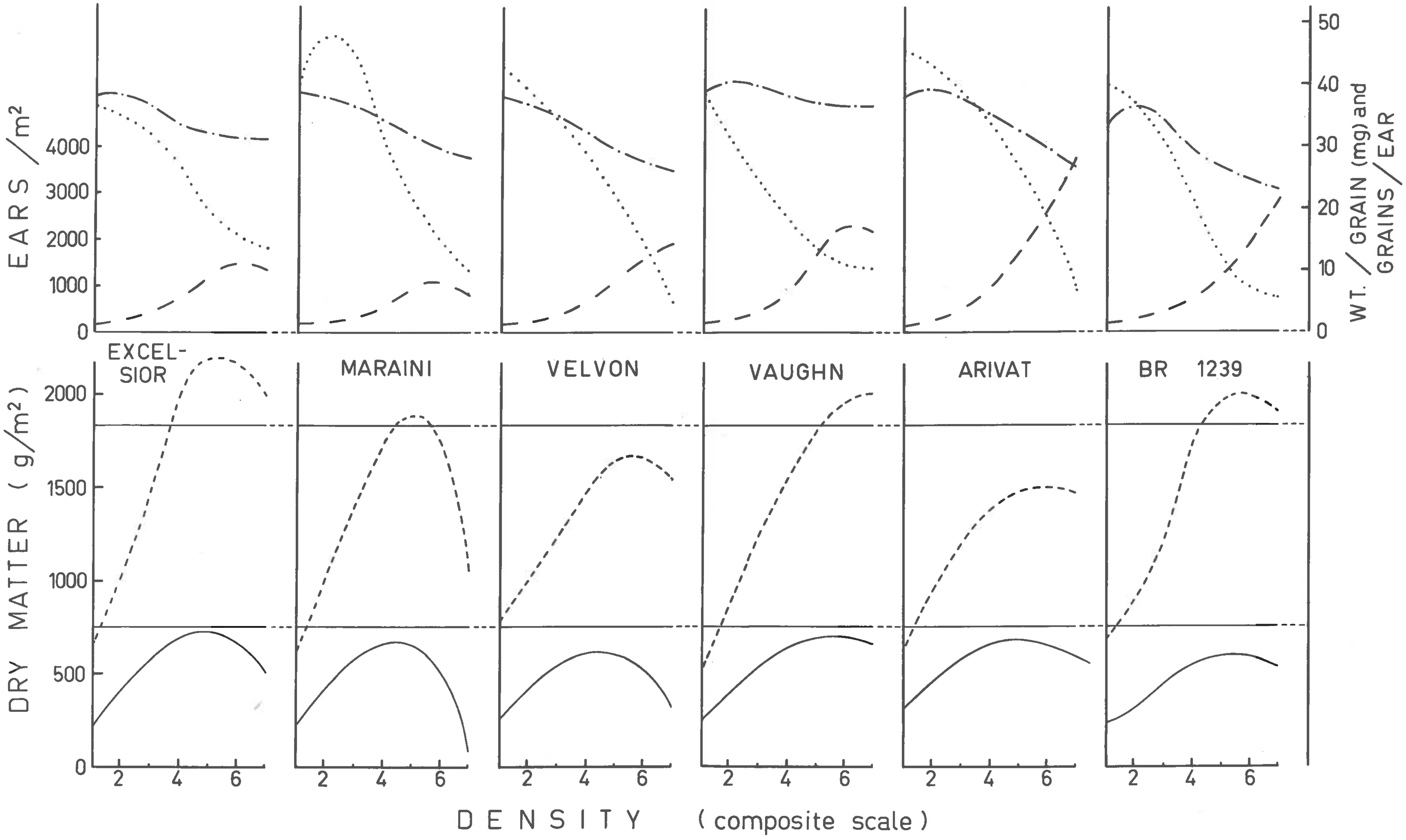
performed poorly at all densities (Table 32). CI3576, in its ability to do well over a range of densities, resembled the short and heavy-tillering indica types of rice which are well suited to both spaced hills and direct seeding (Chandler, 1969).

The optimum density differed between varieties, 6-row varieties producing maximum yield at lower densities than 2-row varieties (compare Figures 34 and 35). Consequently at low densities, yields of 6-row varieties exceeded those of every 2-row except CI3576, which produced many ears per plant at wide spacing (Table 33). At the high densities, more plants survived to produce ears in the 2-row varieties (Table 33) and since the grain weight per ear was similar in both types (Table 33), the 2-row varieties had the highest yield.

The maximum grain yields varied at the different optima. The earlier varieties within each type (i.e. Bankuti, CI3576, Vaughn) tended to have high optimum densities and high maximum yields compared with the later varieties (Princess, Proctor, Maraini, Velvon) (Figures 34 and 35). Generally the maximum yield at any density was positively related to its optimum density (Figure 36), indicating the potential for high cereal yields lies in varieties with high optimum densities.

Figure 34. Grain yield, total dry matter and yield components for six 6-row varieties grown at 30 densities. Lines computer fitted (equations given in Appendix D).

Grain yield	———————
Total dry matter	- - - - -
Ears/m^2	—— —— ——
Grains/ear	·········
Weight per grain	— · — ·


EARS /m²
0
1000
2000
3000
4000
WT. / GRAIN (mg) and GRAINS / EAR
0
10
20
30
40
50
EXCEL-SIOR
MARAINI
VELVON
VAUGHN
ARIVAT
BR 1239
DRY MATTER (g/m²)
0
500
1000
1500
2000
2
4
6
DENSITY (composite scale)

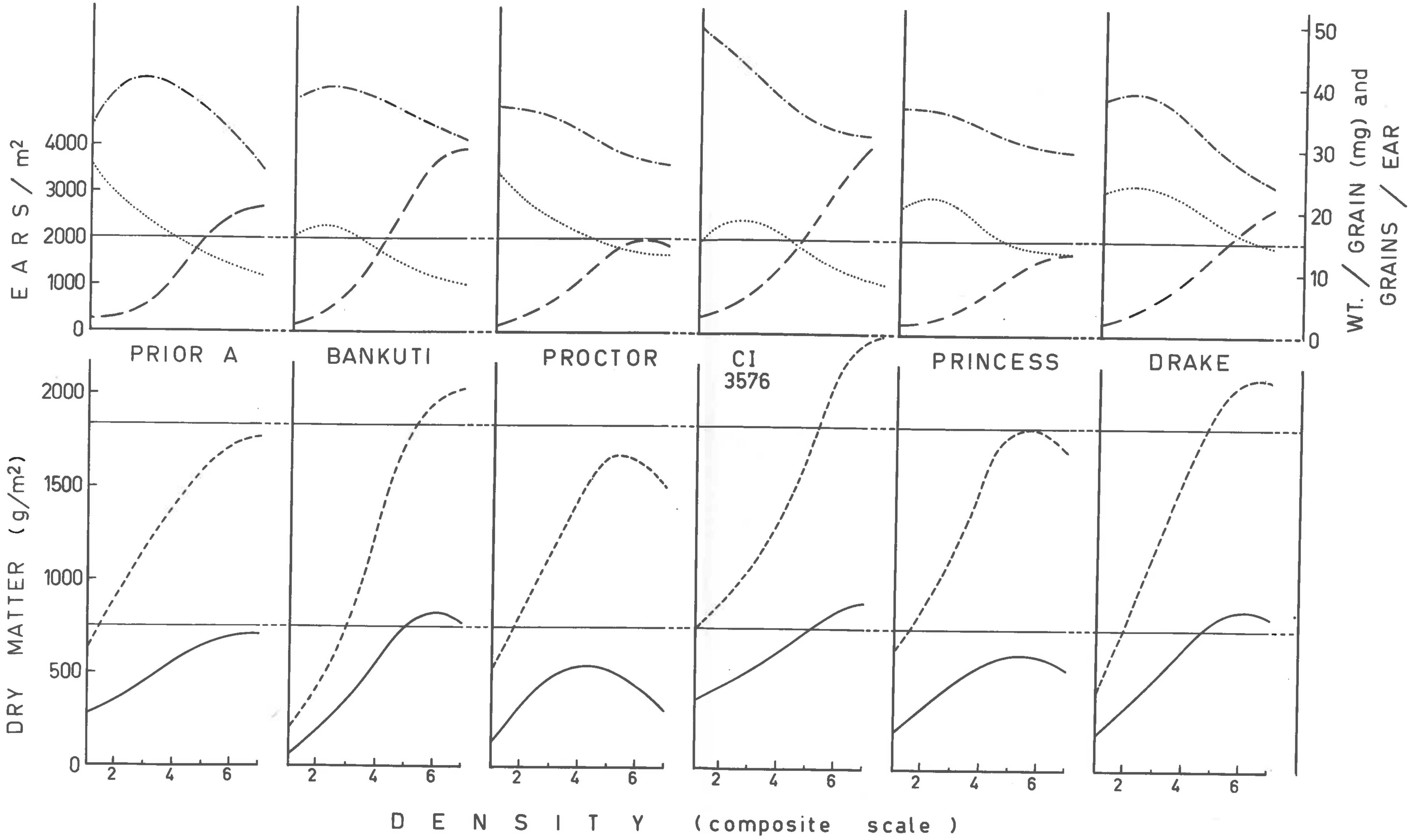

E A R S / m²
4000
3000
2000
1000
0
WT. / GRAIN (mg) and GRAINS / EAR
50
40
30
20
10
0
PRIOR A
BANKUTI
PROCTOR
CI 3576
PRINCESS
DRAKE
DRY MATTER (g/m²)
2000
1500
1000
500
0
2
4
6
D E N S I T Y (composite scale)

Figure 35. Grain yield, total dry matter and yield components for six 2-row varieties grown at 30 densities. Lines computer fitted (equations given in Appendix D).

Grain yield	————
Total dry matter	- - - - -
Ears/m^2	— — —
Grains/ear	....
Weight per grain	— . — .

TABLE 33

Breakdown of grain yields shown in Table 32 into ears per m^2 and weight of grain per ear, for 12 varieties at three densities (12, 220 and 4202 plants/m^2). Rank given is on grain yield.

	Low density (12 plants/ m^2)			Medium density (220 plants/m^2)			High density (4202 plants/m^2)		
	Rank	Ears per m^2	Gr.wt. per ear	Rank	Ears per m^2	Gr.wt. per ear	Rank	Ears per m^2	Gr.wt. per ear
2-rows									
Bankuti (VVE)	12	194	.63	12	660	.58	3	3632	.22
CI3576 (VE)	1	438	.94	6	746	.67	1	4150	.21
Prior A (ME)	6	292	1.10	8	653	.73	4	2583	.28
Drake (M)	9	250	.87	6	568	.88	2	2334	.34
Proctor (L)	11	212	.96	9	834	.56	11	1667	.25
Princess (L)	10	282	.74	10	636	.72	8	1733	.32
MEAN	8.2	278	.87	8.5	683	.69	4.8	2683	.27
6-rows									
BR1239 (VE)	4	148	2.20	11	370	1.09	9	2833	.19
Arivat (E)	2	194	2.00	1	468	1.34	7	3679	.15
Vaughn (E)	4	194	1.70	4	507	1.09	5	2233	.31
Excelsior (ML)	6	190	1.69	5	479	1.12	6	1181	.47
Velvon (ML)	3	216	1.60	3	433	1.30	10	1875	.25
Maraini (VL)	8	162	1.83	2	366	1.62	12	763	.27
MEAN	4.5	184	1.84	4.3	437	1.26	8.2	2094	.27

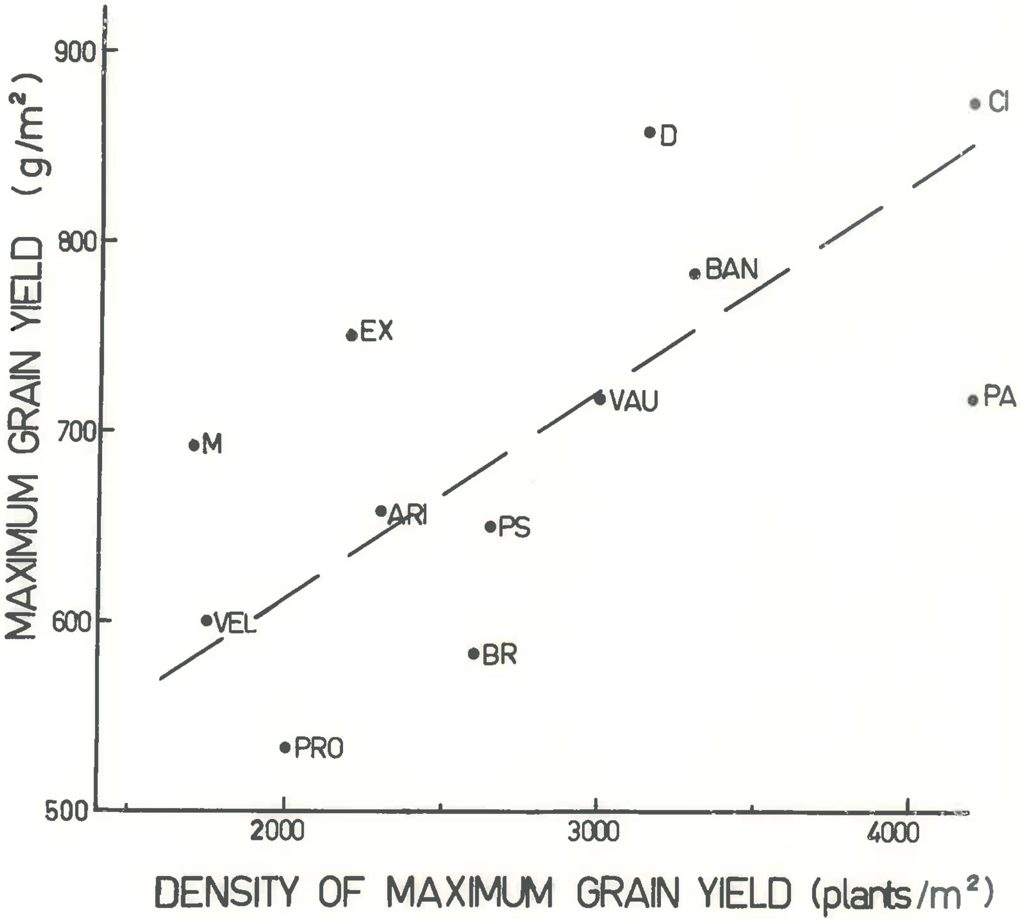


Figure 36. The relationship between maximum yield at optimum density and optimum density for the twelve varieties.

The success of Bankuti at very high densities is particularly interesting as it was the only variety to be specifically bred as a weak competitor. Bankuti[1] was grown in Hungary at quite high densities (500 plants/m^2), and yet was used as a cover or nurse crop for red clover and lucerne. It was therefore selected as being very early, weak tillering, drought resistant and having large grains. The extreme earliness seemed valuable in this experiment, as the yield-controlling processes were subjected to the least severe competition for the shortest possible duration.

Comparisons between varieties were clearly misleading if not made between comparable positions on the population response curve, as proposed by Willey and Heath (1969). At the densities (300 plants/m^2) used by Finlay and Wilkinson (1963) to test the collection in the field, Arivat, Vaughn, CI3576 and Prior A had the highest yields; the yields of Excelsior, Maraini, and Velvon were declining at this density while those of Bankuti and Drake were still rising. The standard methodology failed to delineate the tremendous potential of early 2-row varieties at high density. Very early and morphologically different

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1. Information on Bankuti gratefully received from:-
Dr. E. Bócsa, Agricultural Research Institute, Kompolt, Heves, Hungary: Dr. G. Lörincz, University of Agricultural Sciences, Gödöllo, Hungary: Dr. S. Rajki, Hungarian Academy of Sciences, Martonvásár, Hungary: Dr. A. Jánossy, National Institute of Agrobotany, Tápiószele, Hungary.

varieties like Bankuti would tend to be discriminated against by screening techniques using normal Australian farming densities, which tend to protect standard types from displacement. Demirlicakmak et al. (1963) proposed having the seeding rates of variety trials conform to the commercial rates if varieties responded differentially to density, but this would only be a sound policy if grain yields at the different optima were similar. If the potential yields at the various optima differ, then it seems logical to change farming practice to the optima with the highest yield.

Yield components. At establishment, the plants at even the highest densities suffered no more competition than plants grown at commercial densities in rows. Plants in the fan arrangement had an advantage in that the distance to the next plant was always at a maximum while the distribution in row plantings is unequal. All plants in the fan therefore had a remarkably uniform start with the precise planting, depth, grain size and edaphic conditions, and, as found by Kirby (1969), the initiation of tiller buds was little affected by density. Vestigial tillers actually emerged on plants of all varieties at high densities, but died with sudden onset of competition, leaving a dense population of single-culmed plants. Survival of these single-culmed plants to produce ears varied greatly between varieties, nearly all surviving in CI3576, Bankuti and Arivat and very few in Excelsior and Maraini (Figures 34 and 35). But while it was aesthetically pleasing to see so many small ears survive, they were not necessarily reflected in greater grain yields (Table 34). The grain number per ear and weight per grain of Excelsior, for instance, were reduced far less by increasing density than those of Arivat, and the two varieties had similar response curves for grain yield. Drake maintained fewer but larger ears than CI3576 and Bankuti, and had a similar high grain yield.

However, certain generalizations could be made over all varieties.

TABLE 34

Grain yield and yield components for two 2-row and two 6-row varieties at high density (4202 plants/m^2)

	Grain yield	Ears/m^2	Grains/ear	Weight/ grain
2-rows: Bankuti	783	3632	7.0	30.8
Drake	800	2334	14.4	23.8
6-rows: Arivat	552	3679	6.2	24.2
Excelsior	553	1181	15.5	30.2

Both the weight per grain and the number of grains per ear fell with increasing density, either from the very lowest density, or after a slight, initial increase. The latter was caused by late ear-bearing tillers developing on the widely spaced plants at low density, which reduced the mean weight per grain and ear size. The six-row varieties naturally had more grains per ear at low densities, but the number often fell below that of the two-row varieties at high densities (Table 33), when the six-row varieties only set grains at two to four rachis nodes. In this, their feed-back mechanism seemed to 'over react', as the response curves for weight per grain did not seem to differ between the two types (Figures 34 and 35).

The moisture stress presumably increased with time at the higher densities, but the weight per grain was not differentially reduced in the later varieties. Vaughn (early) showed a similar reduction to Excelsior (late), as did Bankuti and Princess (late). However, the number of ears at high density was negatively related to anthesial date with the order in decreasing numbers being CI3576, Bankuti, Arivat, BR1239, Drake, Prior A, Vaughn, Proctor, Velvon, Princess, Excelsior and Maraini (Table 33).

Frequency distribution of ear size. After the uniform start of growth, competition quickly increased at the highest densities and was revealed in the greater height at the centre of the cartwheel, as the elongation of the leaves and pseudostems increased with the amount of mutual shading. This co-operative interaction between plants (Hozumi et al. 1955) did not last for long, however, as the maximum elongation rates of the centre plants, limited by the restricted supply of resources, soon fell below those of plants at intermediate densities. From then on the plants at high density appeared starved and spindly, and despite their initial uniformity, their equilibrium was unstable (Duncan, 1969), and it only needed a chance occurrence for one plant to dominate and suppress those surrounding it. No plant mortality was observed after ear emergence.

The distribution of ear size of early varieties like CI3576 and Arivat was therefore skewed away from normal by an increase in density (Figure 37), but far less so than for the late varieties, Proctor and Maraini. The latter appeared bimodal having a strong mode in the left hand class containing ears of zero size, or all those plants which had failed to survive to maturity. This is akin to the self thinning reported by Koyama and Kira (1956) and Yoda et al. (1963), and the former authors also found that the distribution of total dry weight of maize and horticultural crop plants became increasingly skewed with density and time, as individual plants gained an increasing share of the factors in short supply. Obeid et al. in 1967, working with flax, proposed the skewness in a population as an indicator of the intensity of interference.

Height. The plants at the centre of the fan, after their initial rapid increase in height, fell behind those at

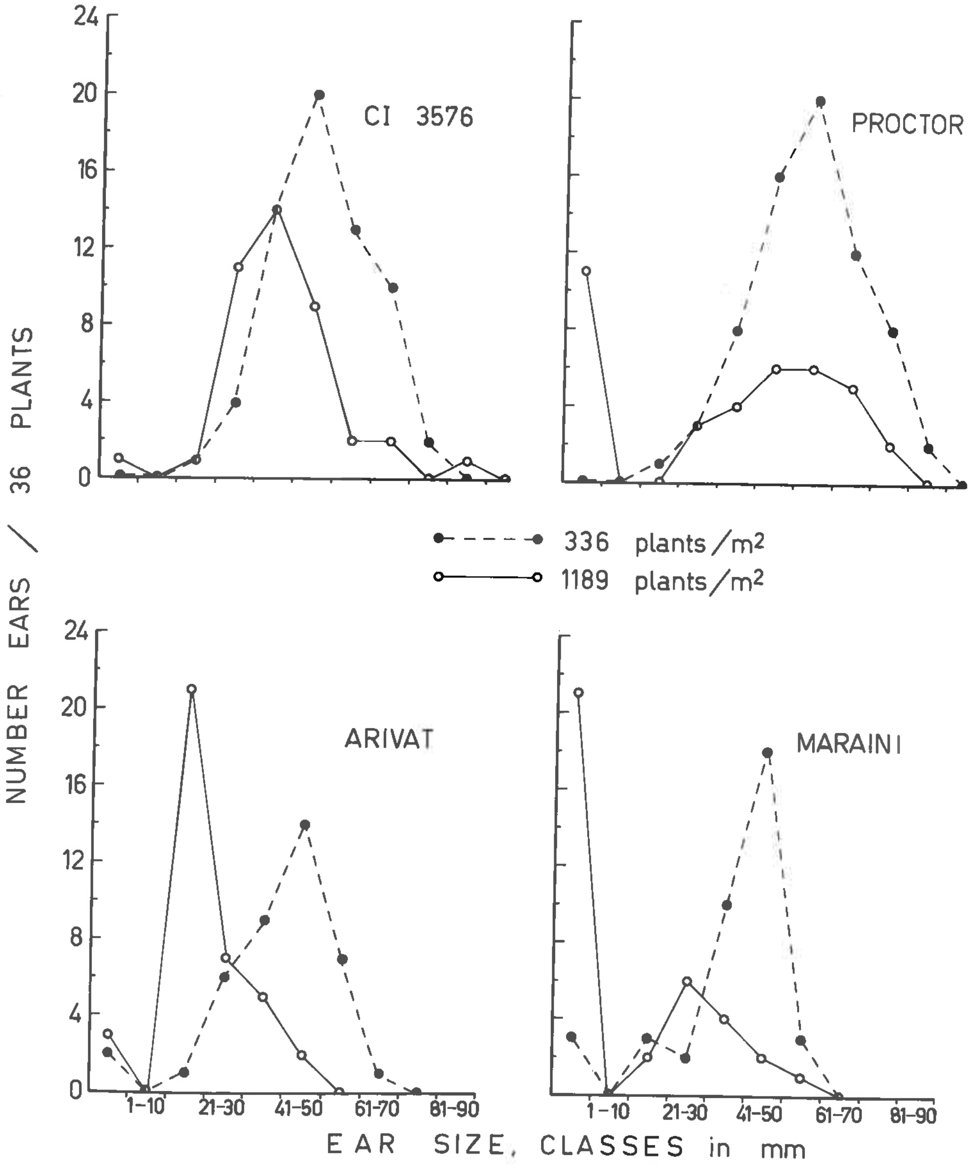

Figure 37. The distribution of ear size at two densities (336 and 1189 plants/m^2) for two 2-row varieties (CI3576 and Proctor) and two 6-row varieties (Arivat and Maraini).

intermediate density (Figure 38). The normal genotypic differences in height between varieties were largely suppressed at high densities, probably because the maximum rate of stem elongation was dictated by the availability of resources; there was not even any difference in height between early and late varieties (Figure 38A and B).

Varieties did respond differentially in height when density was increased from the very low to intermediate levels. The stems of Bankuti and BR1239 did not show any increased elongation with the increase in shading and decreased in height linearly with increasing density (Figure 38C). Prior A, Drake and Vaughn had a slight plateau before falling (Figure 38D) and the other seven varieties all initially increased in height with increasing density before falling (Figure 38A and B). Not increasing in height under increased light competition and causing still further competition, generally seems a highly desirous trait and one easily measured. It seems more than coincidence that the five varieties showing this characteristic all performed excellently at high densities. Bankuti especially showed an independence of a changing microclimate in maintaining height, ears per plant, grains per ear and weight per grain.

Total dry weight. The varieties were ranked on decreasing

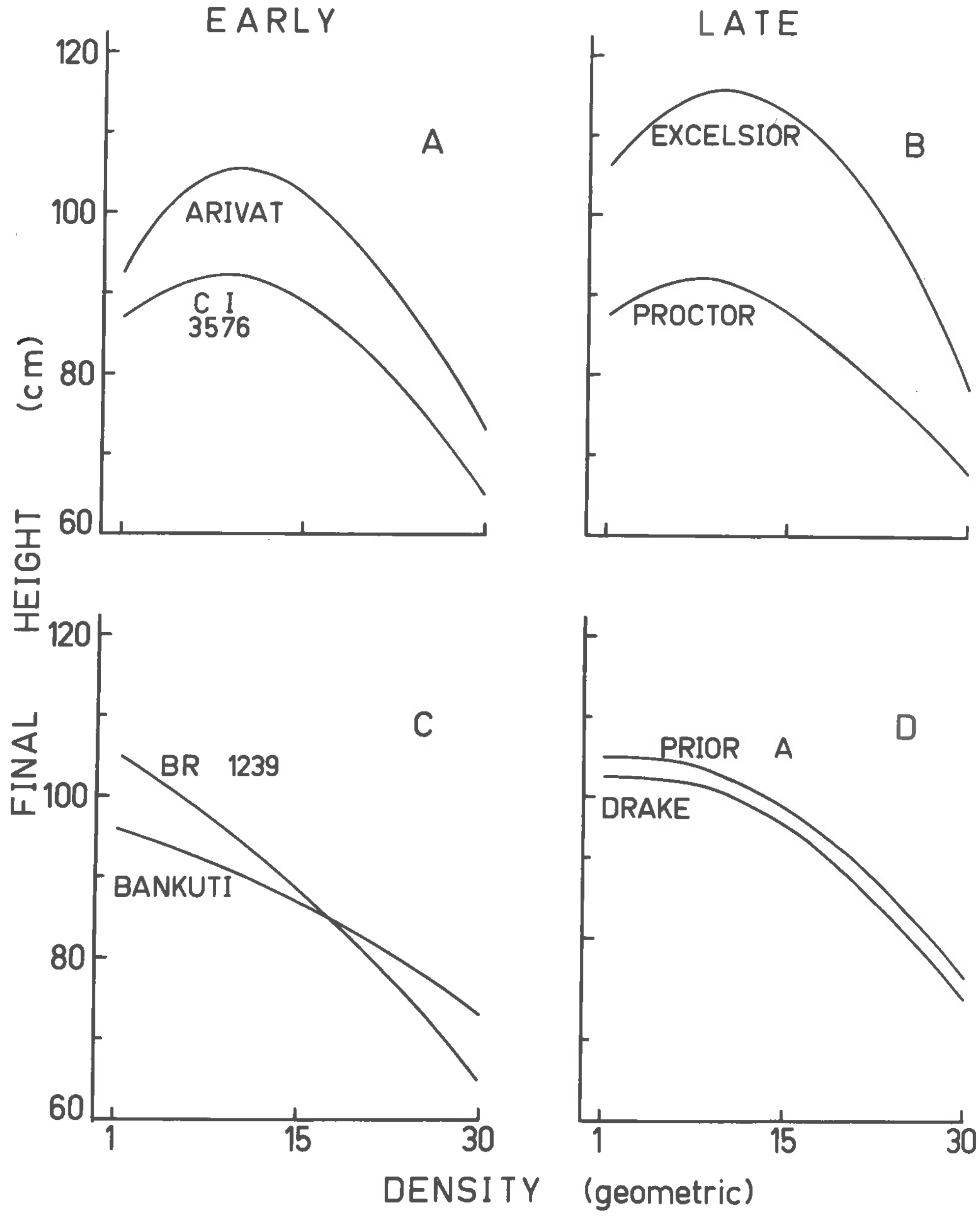

Figure 38. Mature height of eight varieties at 30 densities. Computer fitted lines (equations given in Appendix D). (A) Arivat and CI3576 (early varieties). (B) Excelsior and Proctor (late varieties). (C) BR1239 and Bankuti. (D) Prior A and Drake.

order of maximum total dry matter production:- CI3576, Excelsior, Vaughn, Drake, Bankuti, BR1239, Maraini, Princess, Prior A, Velvon, Proctor, Arivat (Figures 36 and 37). Allowing for the greater straw production of the six-row varieties, the ranking in peak total dry matter and in peak grain yield were similar, but there was little relationship between number of ears and the production of dry matter, since many more ears survived in CI3576 and Arivat than in Excelsior.

Holliday in 1960 (a,b and c) proposed a relationship in which, with increasing density, the total dry matter rose asymptotically, while the grain yield was parabolic. Here, while the grain yield always declined more than total dry matter with increasing density with a resultant increase in the percentage of straw, all the inflexions in the response curve for grain were mirrored in the curve for total dry matter. There are two possible reasons for the present exceptions to Holliday's generalization.

Firstly, the range of densities used here was far greater than those demonstrating Holliday's conclusions (Haynes and Sayre, 1956; Rennie, 1957; Wasserman, 1964; Bremner, 1969b). It is unlikely that the total dry matter could remain on the plateau indefinitely however, and it also fell at the high densities of both Kamel (1959) and

Puckridge and Donald (1967). Secondly, no adult lodging occurred in this experiment, and lodging would seem to reduce grain yield greatly, while having no effect on the weight of straw which itself tends to increase with density.

Arivat was by far the most efficient variety in terms of the amount of grain produced per unit of dry matter, while other six-row varieties like Excelsior, Vaughn and BR1239 were less efficient and had low harvest indices (Figure 39). The high harvest index was, however, of little value to Arivat, even at the high densities, since both Vaughn and Excelsior had higher grain yields.

All varieties had lower harvest indices at low and high densities than at intermediate densities, although this was less pronounced in some two-row varieties like Prior A (Figure 39). The low harvest indices at low densities indicate a surfeit of carbohydrate relative to floret and grain production, and Willey (1965) found little effect in shading these densities. Carbohydrate production and grain production become more balanced at intermediate densities where intra-plant competition is still minimal (Donald, 1963), but the highest grain yields were obtained by prodigous numbers of depauperate plants bearing miniscule ears at the high densities. At these densities, when lodging is prevented, the demand for assimilate with such an

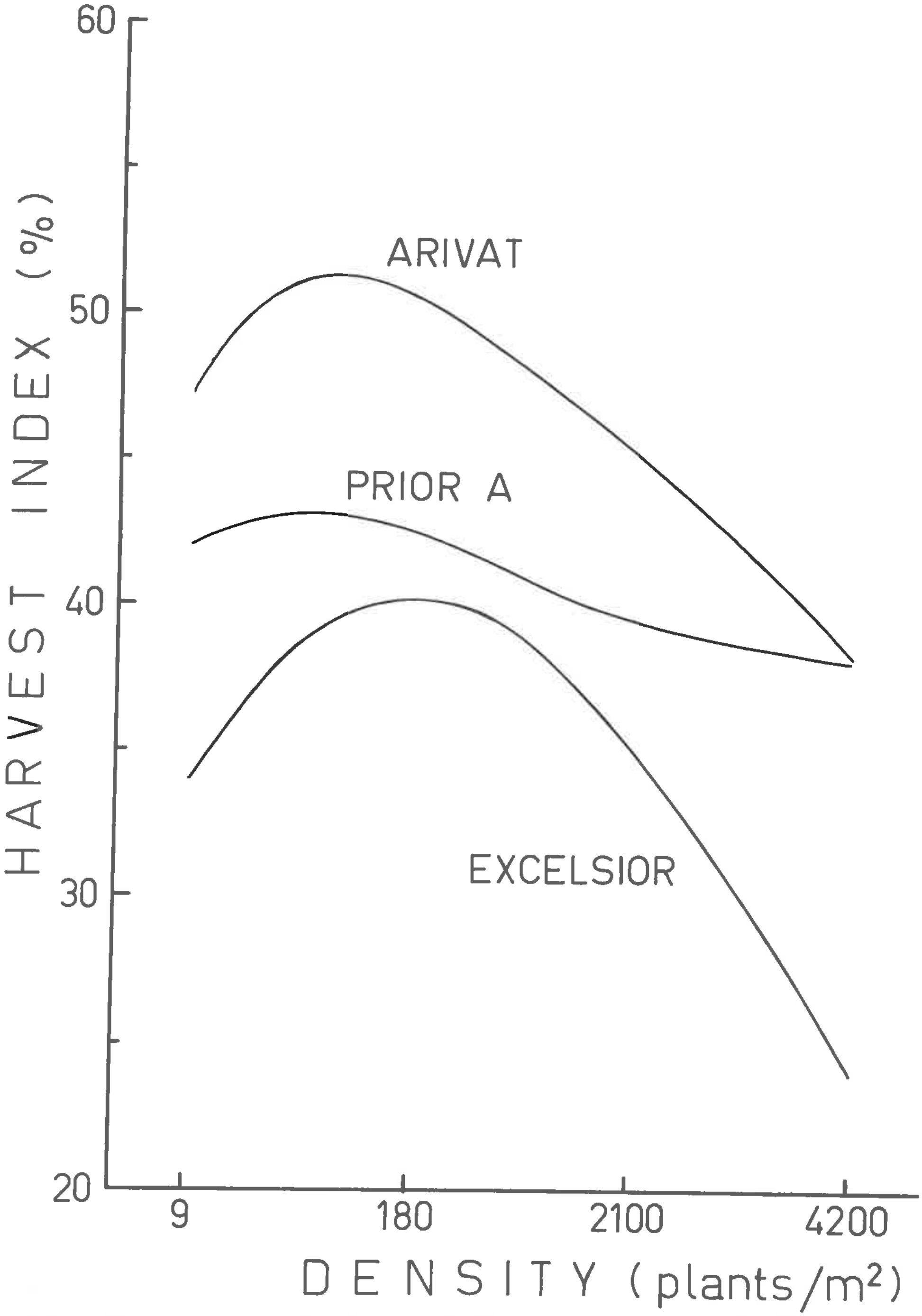

Figure 39. The harvest indices of three varieties at 30 densities. Curves computer fitted (equations in Appendix D).

abundance of sinks (i.e. up to 4,000 apices per m^2) must exceed the supply.

The total dry matter produced by varieties did not seem related to differences in either canopy type or length of life cycle. All varieties had erect leaves at high densities, and while there were differences in the amount of light intercepted (Figure 40), they appeared more as a result of varietal differences than causative of them. The relatively small differences at high density were related to numbers of culms surviving to cast shade (i.e. CI3576 compared to Proctor, Figure 40), while the differences at low density were related either to the tillering ability of varieties like CI3576, or to the large tillers and leaves of BR1239, as found previously at an intermediate density (Section VIII) but much earlier in the growing season.

Small and narrow leaves did ~~not~~ appear to confer resistance to crowding, at least in this restricted collection of varieties, and while soil moisture measurements were not taken because of lack of fetch in the systematic design, the differential varietal response to density seemed more of a differential tolerance to a restricted supply of resources rather than to a differential use of the supply.

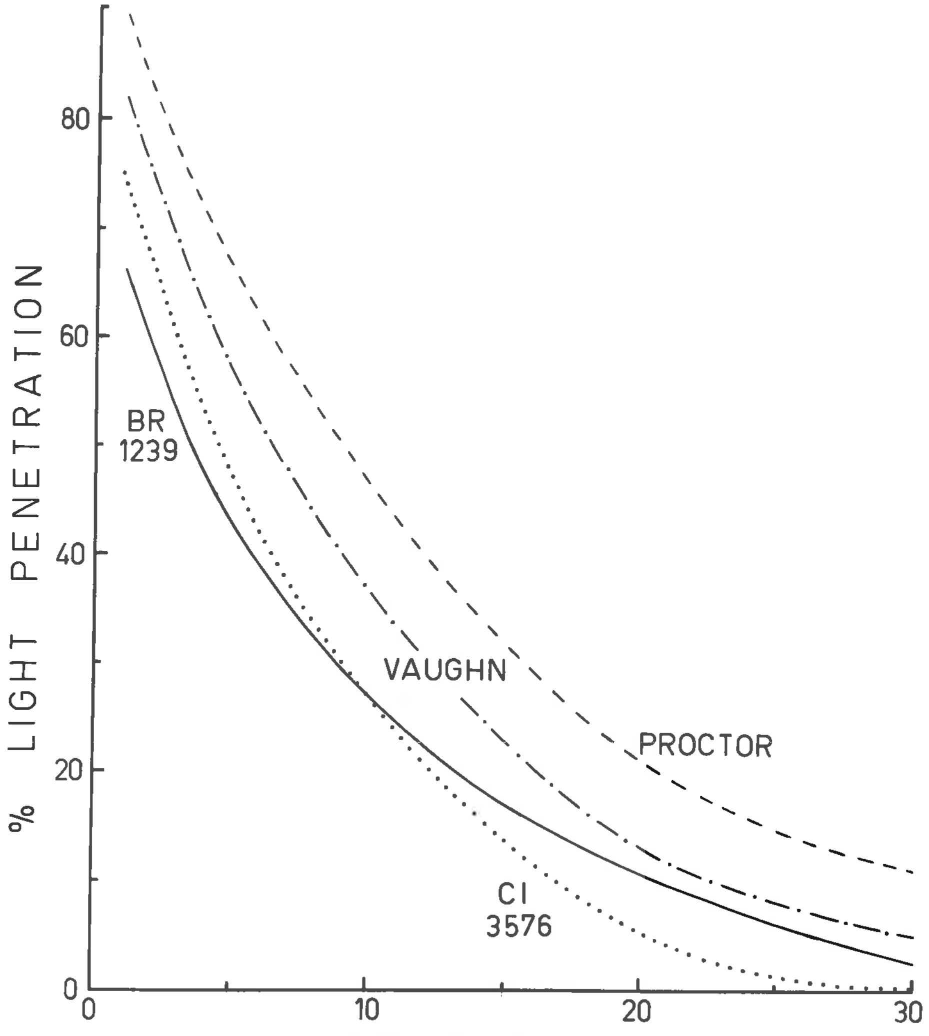

Figure 40. The percent light penetrating to ground level at 30 densities on September 16, 17 and 18, 1968. Proctor, CI3576 and BR1239 are the varietal extremes, with all other varieties falling within these boundaries. Computer fitted curves.

X. THE RESPONSE OF VARIETIES TO IRRIGATION

X. THE RESPONSE OF VARIETIES TO IRRIGATION

The extremely low total rainfall (326mm) received in 1967 provided an opportunity to examine the response of the varieties to irrigation. However, the above-ground climate in 1967 also differed greatly from that of the other three years of experimentation. The relative humidity was lower, the cloud cover less, the light intensities higher and the evaporation greater (Figure 2). Both leaf expansion and tiller production were somewhat inhibited even at the high levels of water and nitrogen; neither juvenile or adult lodging occurred in the resulting well lit and ventilated canopy.

Experimental design and methods. The experiment consisted of two adjoining square blocks, irrigated and non-irrigated, each containing 3 replications x 2 nitrogen levels (main plots) x 2 densities (sub-plots) x 11 varieties[1] (sub-sub-plots). The two levels of water are confounded with any edaphic variation, but this was small in 1967 compared with the response to water (Table 35) and was outweighed by the following advantages. Firstly, as a sprinkler-irrigation system was used, spray did not drift onto non-irrigated plots. Secondly, a much smaller land area was required

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[1] Bankuti has been ommitted as the seed source was found to be impure.

than if water levels had been replicated and large border areas included to avert runoff. Thirdly, the blocks presented two relatively uniform microenvironments instead of a heterogeneous mixture.

The irrigated block received an extra 311mm water during the growth of the crop, almost twice the amount of rainfall in 1967. Six irrigations were applied on:-

June 27	40mm
September 11	25mm
September 27	50mm
October 4	65mm
October 13	65mm
October 29	65mm

The water pressure in irrigation lines was reduced sufficiently to allow large droplets to be thrown from the sprinklers (instead of a fine mist), and this gave an even distribution of water as measured by rain gauges. It also indirectly resulted in a higher infiltration percentage, as the system had to run for longer periods to apply the desired amount of water.

The nitrogen and density treatments were included to vary both LAI and moisture loss and to extend the range of environments. The treatments consisted of 20 and 170 kg/ha nitrogen, and 31 and 156 plants per m^2; the higher density being dictated by the availability of seed supplied in 1967.

The plots were superimposed exactly on the previous years wheat plots, thus avoiding the increased variability that might have arisen if the previous pathways had crossed the plots. In addition to the remaining wheat stubble, 3400 kg/ha of chopped straw was incorporated into the soil with a rotary hoe 3 weeks before sowing, to reduce the availability of nitrogen to the crop. The 170 kg/ha nitrogen was split into three applications; 70 kg/ha at sowing (June 23), 50 kg/ha 57 days after seeding, (August 19) and 50 kg/ha 75 days after seeding (September 6). The low nitrogen treatment also received 10 kg/ha on each of the latter two occasions when both the diphenylamine test and visual symptoms indicated that the nitrogen deficiency was becoming severe.

Each plot consisted of nine rows, 17.8 cm apart and 3m long with no unplanted rows between adjacent plots. Four samples, 61cm long and 3 rows wide, were taken from each plot during the season; two from rows 2, 3 and 4 and two from rows 6, 7 and 8. The first sample was taken on September 18, the second as each plot reached anthesis, and the third and fourth on the same date at maturity in December. In addition, ten ears were removed every 3 days from a well bordered section of each plot, between the twelth day after anthesis and physiologic maturity, to give the daily increase in dry weight of the grain.

The area of green plant parts was measured at anthesis (Section IIIC) and their senescence recorded daily to enable calculation of the LAD.

Neutron access tubes were installed in all eleven varieties in each of four sub-plots; high and low levels of nitrogen at high and low levels of water. Light readings were taken at ground level at anthesis.

RESULTS AND DISCUSSION

A. The eight treatments or 'sites'. The eight treatment means are set out in Table 35 in order of increasing grain yield. Predictably in such a dry year, irrigation increased both the grain and total yield, all three yield components, the LAI and light interception. It was unexpected, however, that the four combinations of nitrogen and density would behave so alike within the two water regimes (Table 35). This similarity suggests that the amount of water available was limited at both water levels, for although the irrigated block received nearly twice the amount of water, the LAI was also much higher. The low nitrogen and low density combination had the lowest grain yields, because the increased grain numbers per ear and heavier weights per grain, resulting from the reduced competition for water, did not entirely compensate for the low numbers of ears produced. Increasing density alone proved to be the most effective and economical means of increasing grain yield, as the increased ear number

TABLE 35

Yields of grain, straw and total dry matter, yield components, LAIs and dates of anthesis at eight 'environmental sites'. Mean of 11 varieties. Sites presented in order of grain yield.

Water	Low	Low	Low	Low	High	High	High	High	LSD*
Nitrogen	Low	High	High	Low	Low	High	High	Low	
Density	Low	High	Low	High	Low	High	Low	High	
Grain, g/m^2	117	131	137	173	249	301	305	341	46
Ears/m^2	151	248	209	248	233	329	310	324	42
Grains/Ear	26.8	19.6	22.8	22.7	31.5	28.8	29.7	29.8	4.4
Grains/m^2	4058	4851	4768	5618	7330	9478	9192	9667	744
Wt./grain, mg	31.1	28.8	29.5	30.3	39.9	34.0	35.1	38.1	3.8
Harvest Index	35.2	24.7	27.8	32.8	39.8	30.3	32.2	39.7	5.3
Straw, g/m^2	221	390	350	352	388	675	642	522	96
Total D.M., g/m^2	338	521	487	525	637	976	947	863	
LAI Anthesis	1.9	3.5	3.3	4.0	3.6	6.8	6.4	5.1	1.6
LAD, m^2 days/m^2	342	644	605	694	870	1729	1553	1295	280
Light Interception %	39.1	62.8	55.1	58.5	58.2	87.0	79.2	75.2	10.2
Anthesis, Oct	15.9	15.0	15.0	15.8	15.2	12.4	14.2	12.6	1.4
Abbreviation	$W_1N_1D_1$	$W_1N_2D_2$	$W_1N_2D_1$	$W_1N_1D_2$	$W_2N_1D_1$	$W_2N_2D_2$	$W_2N_2D_1$	$W_2N_1D_2$	

* For comparison of four treatments within each level of water

was not accompanied by a depression in weight per grain similar to that found at the two high nitrogen levels.

Usually, a reduction in weight per grain, after nitrogen application, has been related to a premature ripening of the grain because of excessive moisture usage (Section II, part D), but this does not appear to have happened in this experiment, as nitrogen delayed senescence at both water levels. Further, this was **most** pronounced at the high water level where the reduction in weight per grain was greatest. Therefore, when the LAD per grain is plotted against the weight per grain (Figure 41), nitrogen increased the LAD per grain and decreased the grain weight in every variety. In comparison, irrigation increased both the LAD per grain and the grain weight, so it appears that LAD and weight per grain are not necessarily related. Both LAD and LAD/grain would thus be a very misleading character on which to base yield selection.

A likely explanation for the depression in grain weight is that nitrogen induced sufficient additional moisture stress to slow the early growth of the grain and limit its final volume (Aspinall, 1965), whilst later promoting and prolonging leaf activity. Support for this hypothesis comes from two sources. Firstly, nitrogen application did increase water use (Figure 42), especially in the irrigated block, since a given quantity of water was

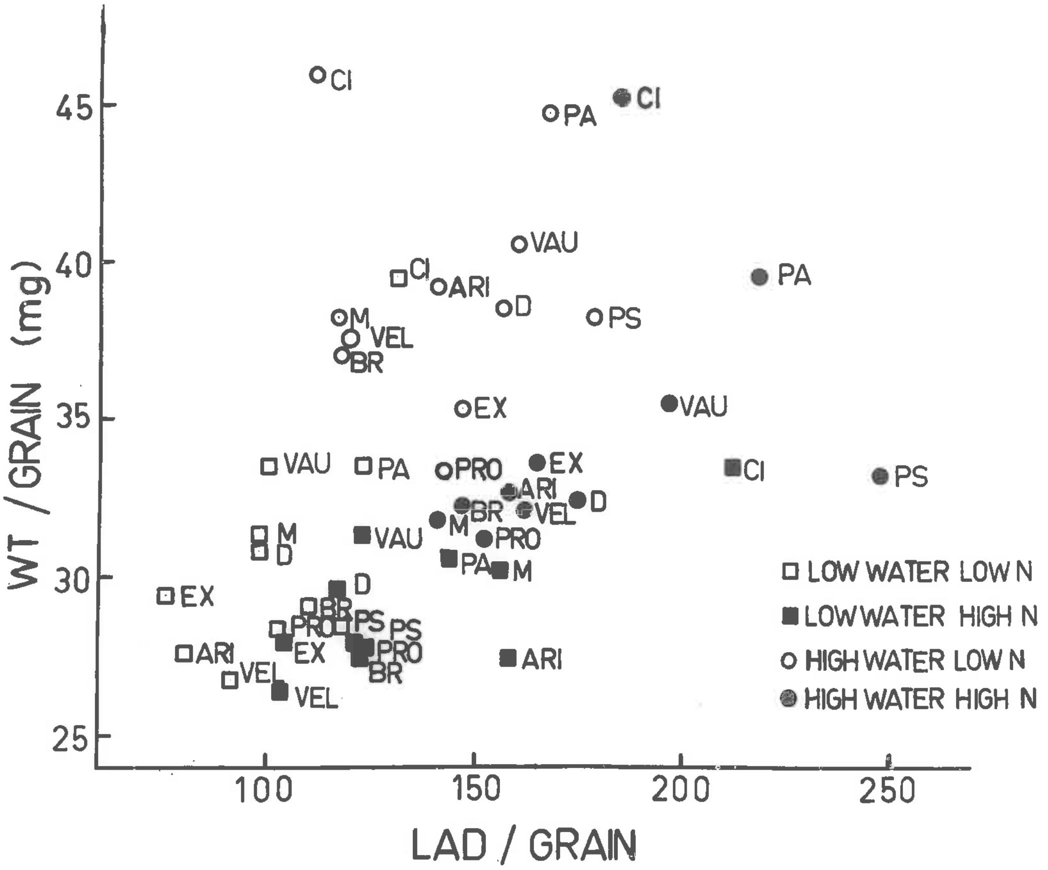


Figure 41. The effect of LAD/grain on weight per grain for 11 varieties grown at four agronomic treatments.

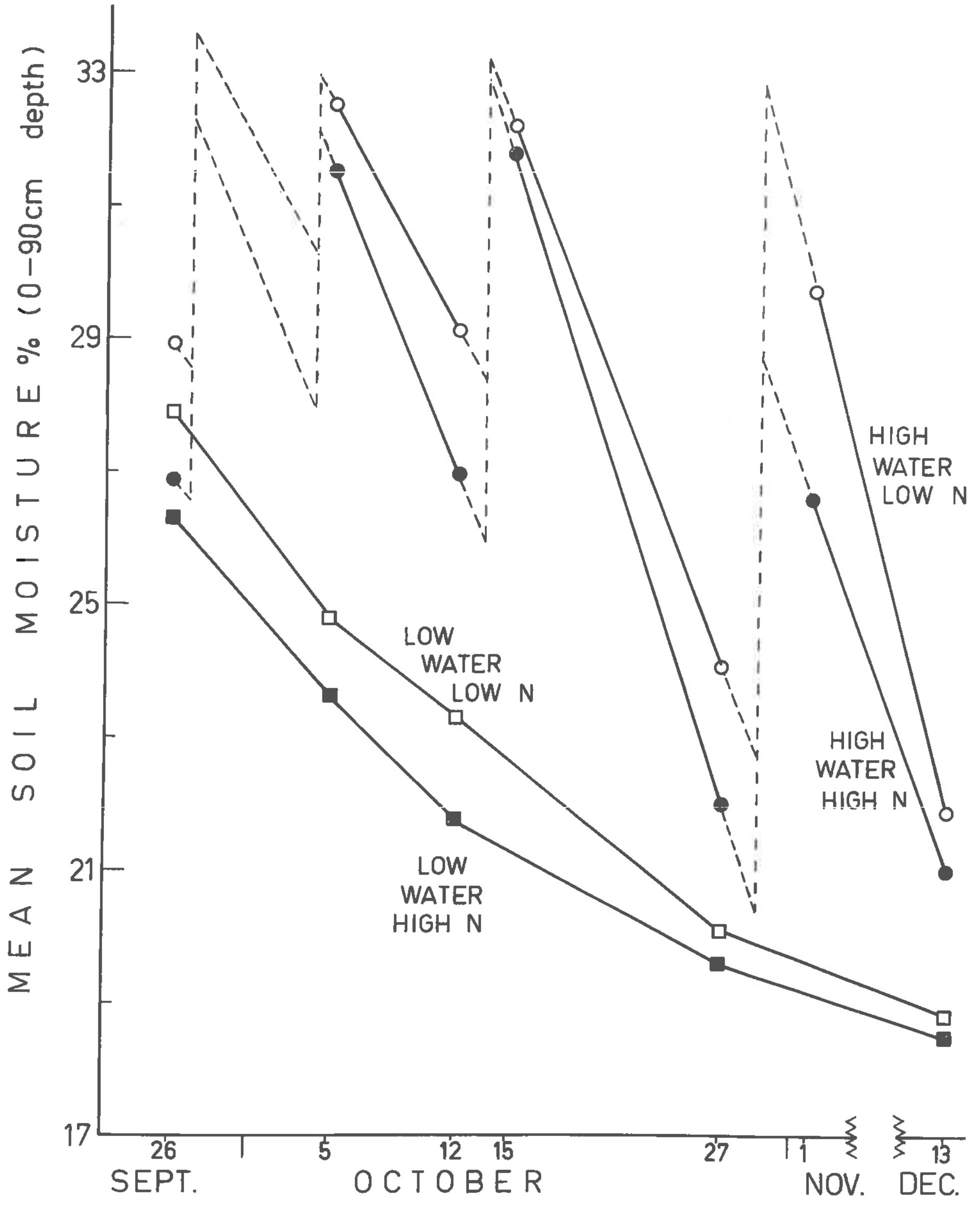


Figure 42. Mean percent moisture (v/v) in top 90cm of soil for high and low nitrogen levels at high and low water levels. Means of 11 varieties and 2 densities.

applied overall rather than maintaining treatments at a specific moisture level. Secondly, irrigation did not differentially increase the grain weight of the later varieties (Table 36), indicating that the stress occurred during early grain growth and that each variety reached the potential grain weight established soon after anthesis. Neither did the ranking of varieties on weight per grain change much with treatment (Table 36), implying that the genetic differences remained constant while environmental effects controlled the potential. That the grains appeared small and plump at the lower water level, instead of large and shrivelled, also supports the argument.

B. The eleven varieties. The ranking and relative grain yields of the eleven varieties remained remarkably constant in all eight environments, despite a threefold variation in 'site' mean yield (Figure 43). Velvon and Maraini performed slightly better, and BR1239 slightly worse, at the high as opposed to the low water level, but otherwise, any statistical interaction was due to the scale of the response and not to a change in the order. The grain yield of the late varieties, for example, fell by a greater amount, when irrigation was withheld or nitrogen applied, than that of the early varieties (Figure 43).

The constancy of the varietal ranking again suggests that competition for one factor was the dominant process,

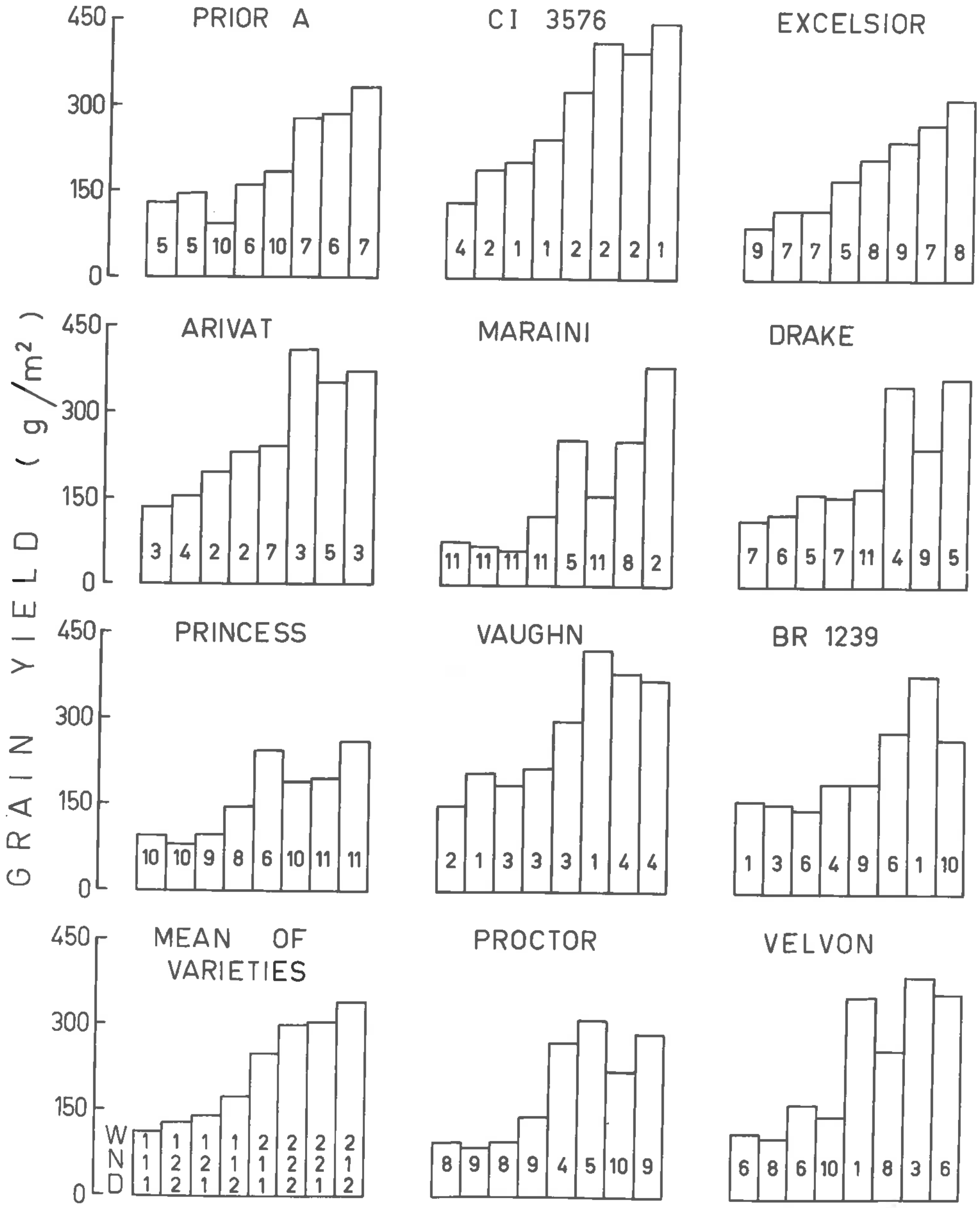


Figure 43. The grain yield (histogram) and rank (inset number) of 11 varieties at eight agronomic treatments, 1967.

TABLE 36

Weight per grain for 11 varieties grown at high and low nitrogen under two levels of water. Varieties arranged in order of reaching anthesis. Figures in brackets indicate ranking on weight per grain within each treatment

	HIGH WATER			LOW WATER			PERCENT CHANGE	
	N_1	N_2	Mean	N_1	N_2	Mean	N_1 to N_2	W_2 to W_1
BR1239	37.1(9)	32.2(9)	34.6	29.0(7)	27.4(9)	28.2	-9.8	-18.5
CI3576	46.0(1)	45.4(1)	45.7	39.4(1)	33.4(1)	36.4	-7.7	-20.4
ARIVAT	39.3(4)	32.7(6)	36.0	27.6(10)	27.4(9)	27.5	-10.2	-23.6
VAUGHN	40.6(3)	35.7(3)	38.2	33.5(2)	31.6(2)	32.5	-9.2	-14.9
PRIOR A	44.8(2)	39.5(2)	42.1	32.5(3)	30.6(3)	31.6	-9.3	-24.9
DRAKE	38.8(5)	32.4(7)	35.6	30.8(5)	29.2(5)	30.0	-11.5	-15.7
VELVON	37.5(8)	32.3(8)	34.8	26.8(11)	26.4(11)	26.6	-8.7	-23.6
EXCELSIOR	35.2(10)	33.9(4)	34.5	29.7(6)	28.1(6)	28.9	-4.4	-16.2
PRINCESS	38.1(6)	33.4(5)	35.8	28.7(8)	28.1(6)	28.4	-7.9	-20.7
PROCTOR	33.4(11)	31.0(11)	32.2	28.2(9)	28.0(8)	28.1	-4.2	-12.7
MARAINI	38.1(6)	31.8(10)	34.9	31.4(4)	30.3(4)	30.8	-10.6	-11.7

LSD = 4.5

and the mean varietal yields (Table 37) are in a similar order to that found by Finlay in Table 1 (Section III). Vaughn, Arivat and CI3576 again had the highest yields, and Princess performed poorly. Only Excelsior and BR1239 improved on their past performance, and this was probably a result of the elimination of ear breakage by harvesting immediately after maturity. Finlay and Wilkinson (1963) also considered moisture supply to be the dominant factor controlling grain yield in their trial over 7 sites, and it seems likely both experiments were conducted with water levels in the linear phase of response curve for water. Competition for light was less severe in 1967, than in 1968, 1969 and 1970, as the light interception only reached 87 per cent.

Under these arid to semi-arid conditions, the early varieties had higher grain yields than the late varieties, but this was not strongly correlated with greater weights per grain (Table 37), although as found previously under moister conditions (Section IX), CI3576 and Vaughn had high weights per grain. Similarly, neither the number of ears per m^2 nor the number of grains per ear seemed individually related to grain yield, but there was an excellent positive relationship between grain yield and their product, the number of grains per m^2.

TABLE 37

Yields of grain and straw, yield components and leaf areas of 11 varieties. Means over eight treatments

	Grain Yield g/m^2	Ears per m^2	Grains per ear	Grains per m^2	Weight per grain	Anthesis Oct.	Straw g/m^2	Harvest Index %	LAI anthesis	LAD anth. m^{2}days/m^2
CI3576	291	383	18.6	7124	41.0	4	403	41.9	4.5	1165
VAUGHN	275	256	30.9	7910	35.3	9	443	39.0	5.3	1352
ARIVAT	262	239	35.3	8437	31.7	8	450	36.9	4.2	1141
VELVON	235	227	32.5	7378	30.8	20	520	29.8	4.3	950
BR1239	221	179	39.6	7088	31.4	7	421	35.0	3.9	949
DRAKE	211	278	23.6	6561	32.8	12	441	32.6	4.2	864
PRIOR A	202	278	19.5	5421	36.8	10	368	35.2	3.7	995
EXCELSIOR	194	211	28.1	5929	31.7	20	461	29.5	4.1	829
PROCTOR	187	360	16.8	6048	30.1	23	428	29.8	4.8	855
MARAINI	171	167	29.4	4910	32.9	24	501	23.6	3.7	671
PRINCESS	163	291	17.1	4976	32.1	23	431	27.1	4.8	862
LSD	29	38	2.7		2.1		51	2.2	.9	160

It appears that some intrinsic mechanism, here operative especially in the later varieties, reduces either the number of ears or the grains per ear to a number low enough to allow the probable formation of plump grains with normal weights. Further, this regulation of grain numbers is based on the moisture stress existing before stem elongation starts when the survival of tillers and spikelets is determined. Irrigation allowed many more of these tillers and florets to develop, but they could then become fertilized and filled only with continued irrigation.

C. <u>The induction of 'haying off' by early irrigation</u>.

An additional four replications of the 11 varieties were grown alongside the irrigated block to supply material for transplanting, apical dissections and early harvests of dry matter. They were treated identically to the high nitrogen, high density treatment in the irrigated block, except that only the first 3 irrigations were applied; a total of 115mm over June 27, September 11 and September 27.

Up until the beginning of October, these four replications appeared very healthy, but then suddenly became severely wilted on days with high vapour pressure deficits. (This was in sharp contrast to the crop in the non-irrigated block which never appeared wilted, although it was stunted and 'spiky'). Ears in the early varieties, like CI3576, were able to emerge before the wilting became permanent, but their fertilization was impaired, the grains shrunken (Table 38) and the grain yields greatly reduced when compared with those of both continually irrigated and non-irrigated plots (Figure 44). Stem elongation in the late varieties, like Proctor and Princess ceased, and the ears failed to emerge from the boot and became completely sterile (Figure 45).

This dramatic setback in development closely resembled the 'haying off' of wheat crops described by Storrier (1962) and Dann (1969) when the excessive vegetative growth caused by high nitrogen prematurely exhausts soil moisture. Wheat crops in New South Wales and Queensland often rely heavily on water stored in the soil at the beginning of the growing season, and therefore may 'hay off' in dry seasons similarly to a crop receiving rainfall or irrigation only during the early vegetative growth.

The leaves were thinner and more succulent than those in the non-irrigated block, and seemed far more susceptible to desiccation. It is possible that the foliage may also have died at a higher relative water content before the crop was able to deplete the soil moisture down to the extremely low levels found in the late varieties grown without irrigation.

D. Dry matter, leaf area and water use. The weight of the seedlings was proportional to the seed weight, as was also found in 1969 (Section VII), but again BR1239 increased

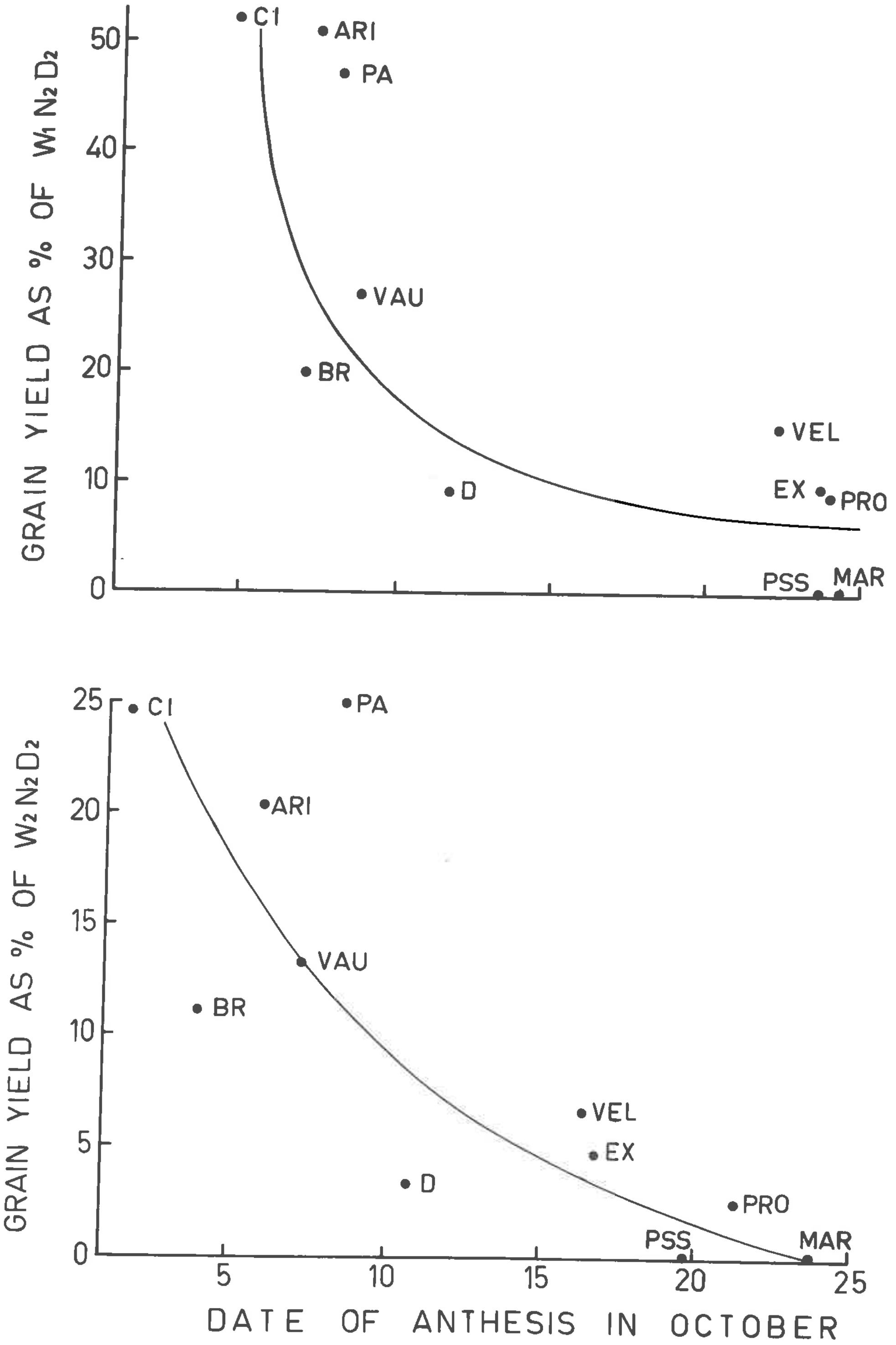


Figure 44. The grain yield of the 'hayed off' plots expressed as a percentage of the grain yield of the plots receiving (Top) no irrigation, (Bottom) continuous irrigation, and plotted against the anthesial date of each variety. Line hand fitted.

Figure 45. 'Hayed off' material on the right, irrigated control of same variety (Princess) on the left. Haying off induced by early irrigation.

TABLE 38

Varietal yields after the crop had 'hayed off' as a result of early, discontinued irrigation. Varieties arranged in order of reaching anthesis

	Grain Yield g/m^2	Total Yield g/m^2	Harvest Index %	Weight per grain,g *
CI3576	100.7	307	32.1	28.6
BR1239	31.2	201	16.2	21.0
Arivat	82.7	301	26.3	23.0
Vaughn	55.4	322	16.9	26.9
Prior A	69.2	253	27.6	23.4
Drake	11.7	261	4.2	28.7
Excelsior	11.6	266	4.6	20.3
Velvon	17.8	263	7.1	22.4
Princess	0	207	0	-
Proctor	7.6	216	3.4	16.8
Maraini	0	240	0	-
LSD	34.0	73	8.4	4.3

* Does not include the many empty husks that failed to fill.

in leaf area and dry weight more rapidly than Proctor, so that by August 20, the four earliest varieties again differed significantly from the later varieties (Table 39). However on this occasion, the varieties did not differ in the leaf area/leaf weight ratio which was much lower (a range of 211 to 267 cm^2/g) than in the more humid year of 1969. The leaves were also much shorter in 1967. The more rapid increase in dry matter in the early varieties was therefore initiated either by greater amount of soluble nitrogenous substances and reducing sugars in the seed (Lexander, 1963) or by more assimilate being reinvested in top growth than in root growth.

TABLE 39

Total dry weight, LAIs and crop characteristics of 10 varieties on August 20, 55 days after sowing. Maraini is missing,

	TDW g/m	LAI	Tillers per m^2	Leaves per plant	Length 4th Leaf
CI3576	45.0	1.0	859	4.9	14.6
Arivat	44.3	1.1	781	5.1	16.0
Drake	44.0	1.0	969	5.5	13.9
BR1239	35.2	.9	563	4.4	16.6
Vaughn	34.4	.7	719	4.7	17.6
Excelsior	33.9	.7	682	4.8	16.2
Velvon	33.1	.8	692	4.9	13.9
Prior A	22.4	.6	651	4.8	14.~~8~~2
Princess	22.1	.5	615	4.8	14.2
Proctor	15.6	.4	474	4.1	14.9
LSD	13.9	.3	255	.4	2.2

Twenty-nine days later on September 18, the later varieties had caught up slightly but the order showed little change (Table 40). The first set of soil moisture readings were taken eight days after this harvest, on September 26 but showed only a poor correlation with dry matter and leaf area. The three late varieties, Proctor, Excelsior and

Maraini had used the least water, but two others, Velvon and Princess, along with the early varieties, Prior A and BR1239 had used the most.

TABLE 40

Total dry weignt on September 18 and an anthesis, LAI on September 18 and mean soil moisture on September 26

	Sept. 18		Sept. 26	Anthesis	
	TDW g/m^2	LAI	Mean Soil Moisture %v.v.	TDW g/m^2	Date Oct.
BR1239	150	4.1	26.8 ab	349	7
CI3576	147	3.3	27.7 ab	329	4
Vaughn	132	2.9	27.0 ab	375	9
Drake	130	3.2	27.4 ab	405	12
Arivat	129	3.5	26.9 ab	336	8
Velvon	116	2.7	25.3 b	514	20
Maraini	108	2.6	28.9 a	526	24
Princess	103	2.4	26.9 ab	471	23
Prior A	103	2.7	25.4 b	323	10
Excelsior	101	2.1	28.3 a	454	20
Proctor	96	2.4	27.8 ab	412	23
LSD	31	.7	2.9	62	

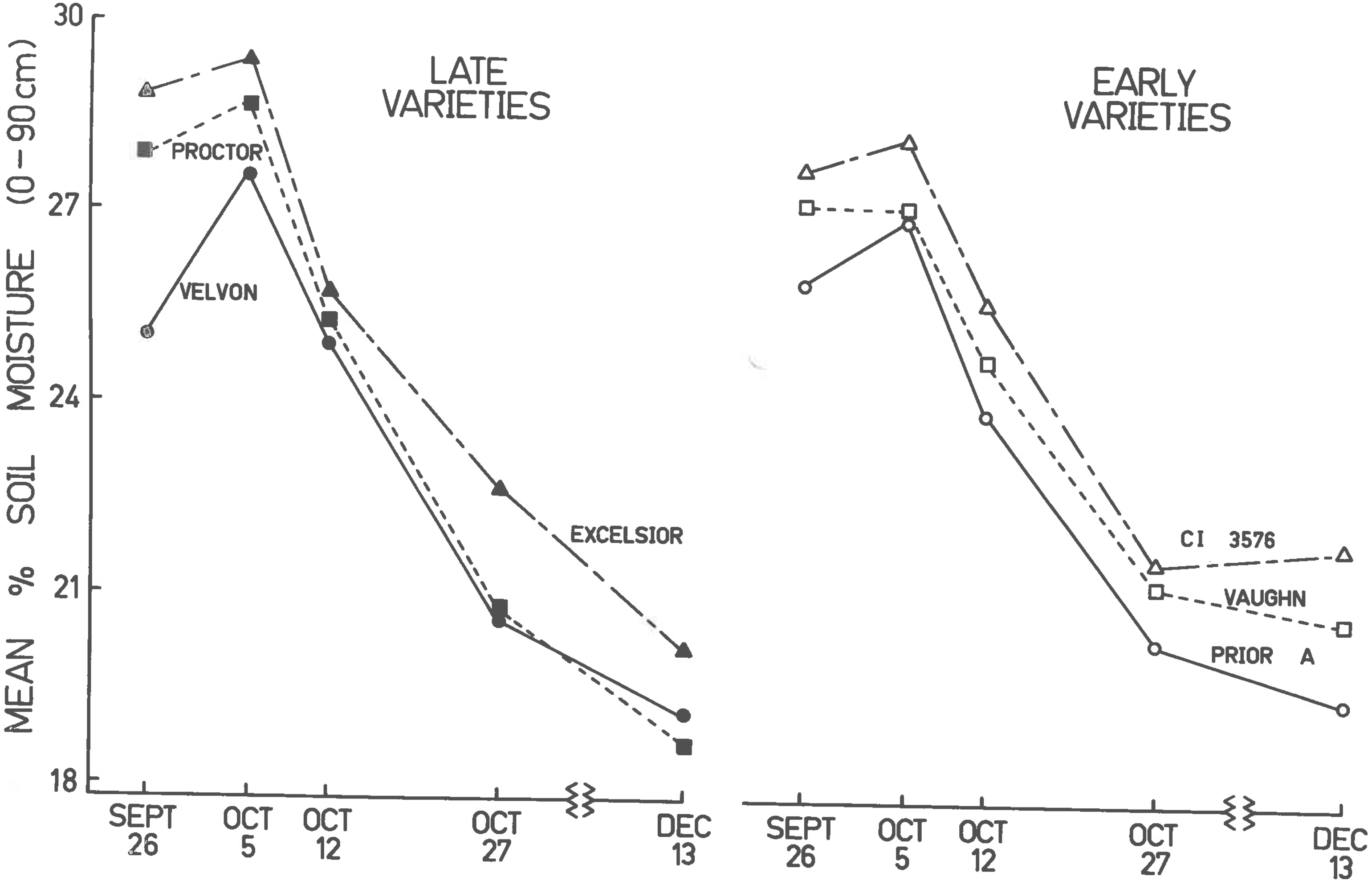
All varieties continued to increase in dry weight until anthesis, which meant that the later varieties had more dry matter by anthesis (Table 40) although a greater percentage of this was senescent.

The increased amount of foliage did not appear to accelerate water loss from the late varieties, but they did remain green after the early varieties senesced, and continued to lose water between October 27 and December 13 at a greater rate than the early varieties (Figure 46, compare CI3576 and Proctor). The three late varieties, Maraini, Excelsior and Proctor therefore used 35 per cent more water than Vaughn, CI3576 and BR1239 between September 26 and December 13.

E. Rate of dry matter accumulation in the grain. Neither density nor nitrogen had any effect on the rate of dry matter accumulation in the grain, although it did continue slightly longer in N_1 than in N_2, and resulted in a slightly higher final weight. Grains in the ears of later varieties gained weight faster than in early varieties (Figure 31, Section VIII), but varieties also varied in their rates at high and low water levels (Figure 47). In some varieties, like Maraini and Proctor, the rates were similar at high and low water levels, but grain filling continued longer at high water. In others, like Velvon and Arivat, the rate was initially much higher at low water.

These results illustrate the value of growing a wide range of varieties, as use of certain pairs of varieties alone would have resulted in very different conclusions. If, for example, the rates of Proctor and Velvon were compared (Figure 47A, B), it would have been easy to conclude that the fewer grains in an ear of Proctor did not compete

Figure 46. Mean percent moisture (v/v) in top 90cm of soil for 3 late and 3 early varieties between September 26 and December 13. Mean over 4 treatments.


MEAN % SOIL MOISTURE (0-90 cm)
30
27
24
21
18
LATE VARIETIES
EARLY VARIETIES
PROCTOR
VELVON
EXCELSIOR
CI 3576
VAUGHN
PRIOR A
SEPT 26
OCT 5
OCT 12
OCT 27
DEC 13
SEPT 26
OCT 5
OCT 12
OCT 27
DEC 13

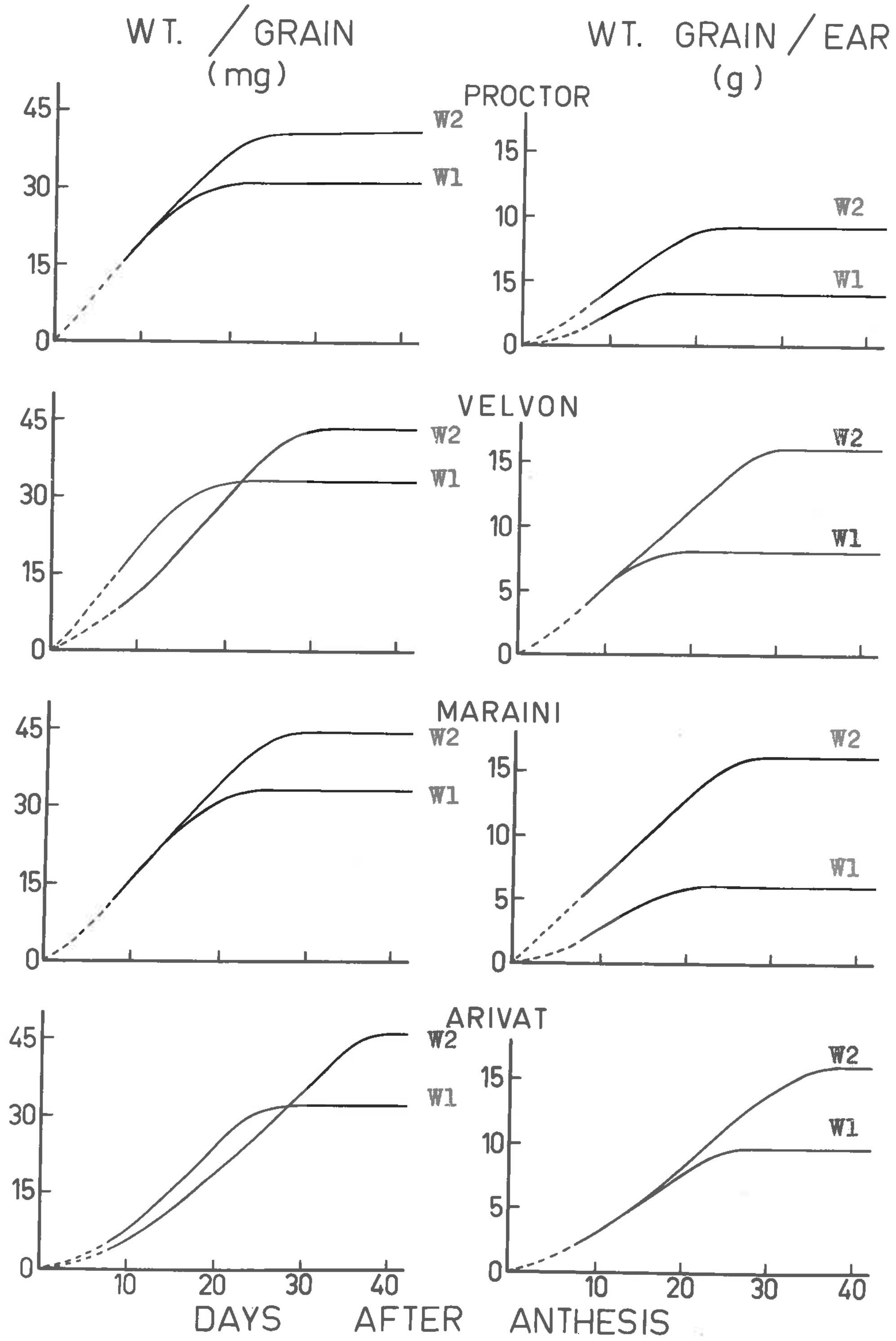


Figure 47. Increase in weight per grain and weight of grain per ear for four varieties at high and low water levels. Curves computer fitted.

with each other even when the number was increased by irrigation from 13.1 to 20.5, but that increasing the number of grains per ear in Velvon from 26.0 to 38.9 was sufficient to induce competition for a limited supply of assimilate and reduce the rate of increase of individual grains. However, the grain number per ear in Maraini was increased from 21.0 to 37.9 by irrigation, but the rate of dry matter accumulation per grain (until the asymptote was approached) was the same at both water levels.

If a comparison were made between one of the early varieties, Arivat, CI3576, Vaughn, or BR1239 (Figure 47), and one of the late varieties, Proctor, Princess or Maraini (Figure 47), it might have been concluded that the later varieties had more soluble carbohydrates available for accumulation in the grain, either from a reduced competition with elongating stems, fewer grains set per m^2 ground, or more reserves available in the stem. However, both Excelsior and Velvon are relatively late, but resemble the early varieties in having different rates at high and low water levels.

Certainly, the early varieties did accumulate more dry matter in the straw after anthesis, while the late varieties had higher yields of total dry matter at anthesis, but afterwards did not increase, and even decreased in straw weight (Table 41). This is however, merely circumstantial proof, and only C^{14} studies could delineate the actual distribution of the dry matter at anthesis and during grain filling. Perhaps both sets of conclusions are true, and are further confounded by the overall differences of varieties in grain yield per unit area.

TABLE 41

The change in non-grain total dry weight between anthesis and maturity for 11 varieties. Varieties listed in order of reaching anthesis.

	At Anthesis TDW, g/m^2	At Maturity TDW minus grain, g/m^2	Difference, Non-grain TDW after anthesis, g/m^2	Increase in TDW after anthesis, g/m^2
CI3576	329	403	+ 74	365
BR1239	349	421	+ 72	293
Arivat	336	450	+114	376
Vaughn	375	443	+ 68	343
Prior A	323	368	+ 45	247
Drake	405	441	+ 36	247
Excelsior	454	461	+ 7	201
Velvon	514	520	+ 6	241
Princess	471	431	- 40	123
Proctor	412	428	+ 16	203
Maraini	526	501	- 25	142

XI. VARIETAL SUSCEPTIBILITY TO MOISTURE STRESS DURING THREE ONTOGENETIC STAGES

XI. VARIETAL SUSCEPTIBILITY TO MOISTURE STRESS DURING THREE ONTOGENETIC STAGES

A moisture stress occurring at a given time during the growing season can effect varieties differentially if their growth stages differ. Stress, during the early vegetative period will reduce the number of ears (Slavik, 1965), during spikelet formation, the florets per ear (Asana and Saini, 1958), during anthesis, the numbers of grains set (Van der Paauw, 1949; Brouwer, 1959; Martin, 1960) and during grain filling, the 1000 grain weight (Asana, 1962; Day and Intalap, 1970). The actual susceptibility of varieties to moisture stress was tested in 1968, by keeping plants at one of two predetermined soil moisture levels for the duration of each of three periods.

Experimental Methods. The plants were grown in non-draining pots in a glasshouse, and the required soil moistures obtained by regularly weighing the pots and adding the requisite amount of water. The plants were therefore relatively immune to the effects of leaf area on water loss; an increased loss just meant more water added to the pot. No competition in the usual sense occurred between plants at the low soil moisture, as although the supply was short, it never diminished.

The soil was a sterilized 50:50 mixture of alluvial medium loam and coarse river washed sand which had the moisture characteristics shown in Figure 48. The high moisture regime was maintained by adding water to the pot whenever the soil moisture content fell to 16.25 per cent (B) (.3 atmosphere - the American field capacity) and raising it to 27.75 per cent (A) (.1 atmosphere - the British field capacity). Likewise, the soil in the pots at the low moisture regime was kept between 4.25 per cent (D) (15 atmospheres -- wilting point) and 6.25 per cent (C). This meant that while all the soil was moist in a pot maintained under the high moisture regime, the surface soil in the pots at the low regime fluctuated between field capacity and wilting point, as the water was poured onto the soil surface. The situation therefore resembled that found in the field when a dry profile receives regular light showers of rain.

The eight varieties selected for the experiment consisted of 2 early six-rows, BR1239 and Arivat, 2 late six-rows, Excelsior and Maraini, 2 early two-rows, Bankuti and CI3576, and 2 late two-rows, Princess and Proctor.

The three ontogenetic periods were defined as:-

1. Seedling emergence to the start of stem elongation.
2. Start of stem elongation to anthesis.
3. Anthesis to maturity.

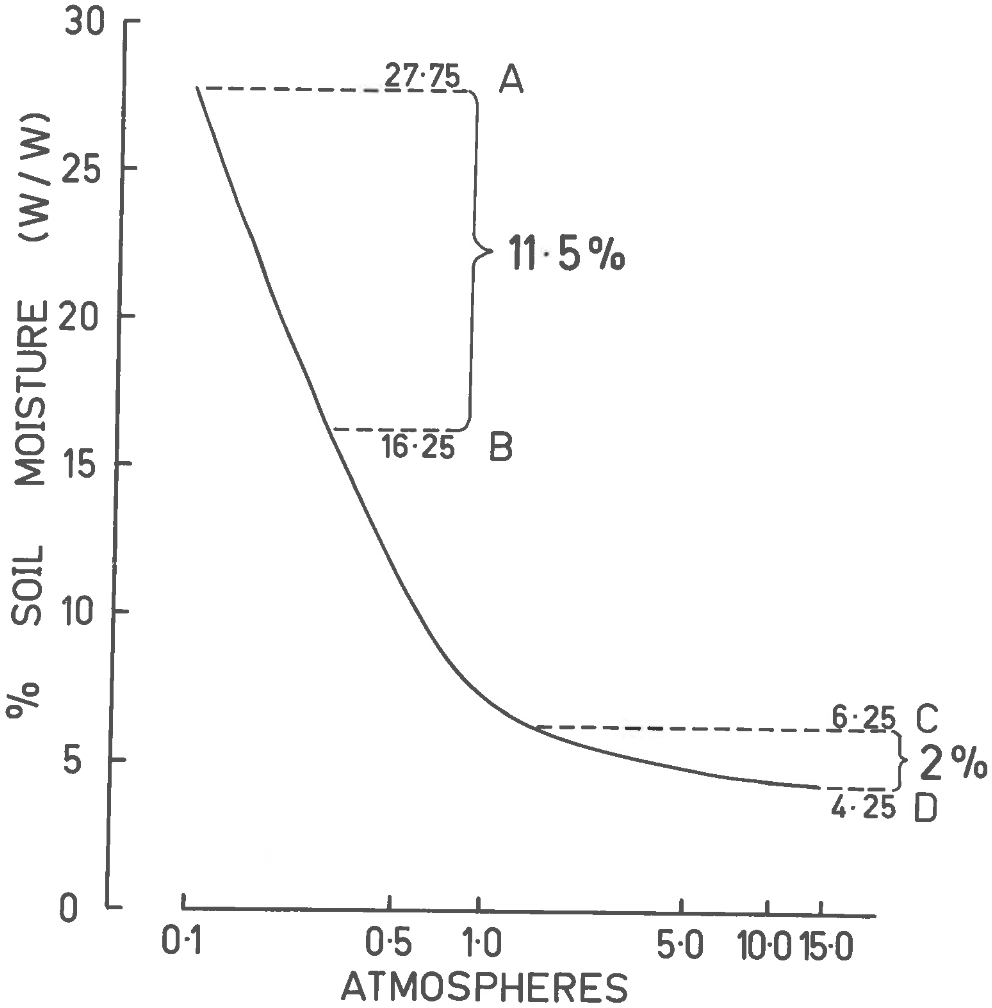


Figure 48. Moisture tension curve for the 50:50 mixture of loam and sand used in the glasshouse experiment.

Moisture stress was applied in none, one, two or all three periods giving a total of eight treatments (Figure 49A). However, the actual length of these periods differed between varieties, and although the same growth processes were subjected to the same stress, Maraini suffered far longer periods of stress than Bankuti (Figure 49B).

The 64 pots (8 treatments x 8 varieties) in each of the three replications were initially randomly arranged in three rows along a bench in the glasshouse, and the order within rows and the order of rows systematically changed every three days. Once differences in height became apparent, the pots were regrouped within a replication according to height, and the systematic rotation continued of both rows and groups.

The cylindrical, white enamel pots were 23cm in diameter and 30.5cm in height, and each contained 13.6 kg of oven dry soil. The nutrient requirements of the crop were met by adding .1 kg phosphorus, .2 kg potassium and .5 kg ground limestone to a ton of soil, and by applying 2.5 g anhydrous $Ca\ (NO_3)_2$ as an aqueous solution to each pot, two days after planting.

Ten plants were grown per pot; five in an inner circle as test plants, and five in an outer circle as border plants (Figure 49C). Each plant occupied an average area of $41.6cm^2$ of soil surface, which was approximately

Figure 49. A. The eight combinations available with moisture stress during three ontogenetic stages.

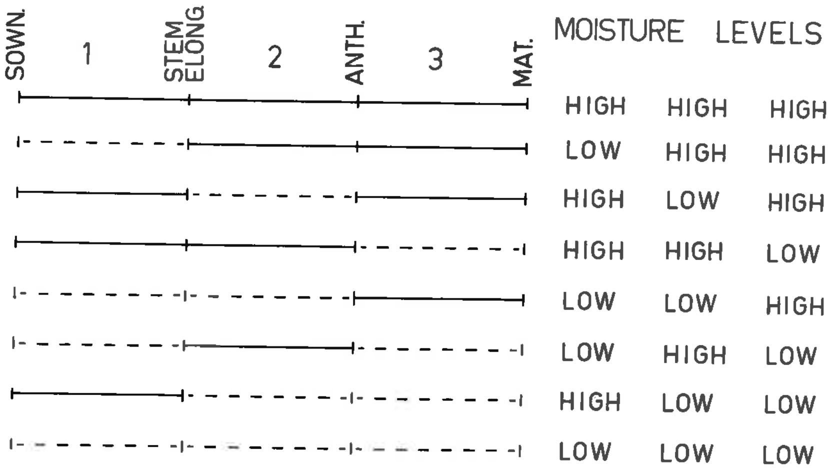
1. Seeding to the start of stem elongation.
2. Start of stem elongation to anthesis.
3. Anthesis to maturity.

(Periods of stress are indicated by broken lines, periods with adequate moisture by solid lines).

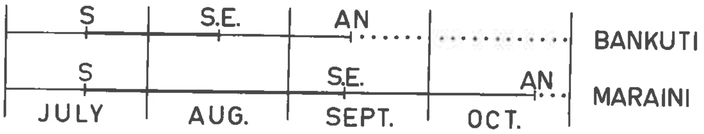
B. Lengths of ontogenetic periods for Bankuti and Maraini.

C. Position of the ten plants in a 23cm diameter pot.

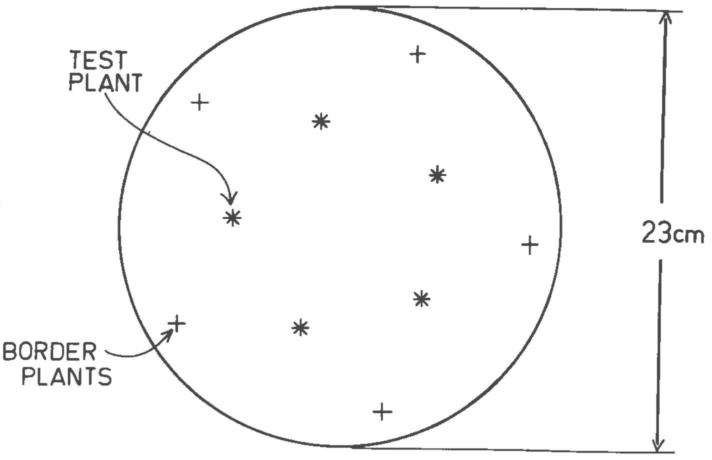
A


SOWN.
1
STEM. ELONG
2
ANTH.
3
MAT.
MOISTURE LEVELS
HIGH HIGH HIGH
LOW HIGH HIGH
HIGH LOW HIGH
HIGH HIGH LOW
LOW LOW HIGH
LOW HIGH LOW
HIGH LOW LOW
LOW LOW LOW

B


S
S.E.
AN
BANKUTI
S
S.E.
AN
MARAINI
JULY
AUG.
SEPT.
OCT.

C


TEST PLANT
BORDER PLANTS
23cm

equal to field density, although the roots were limited to only 30cm depth. The stand of 10 plants was obtained by planting 30 seeds per pot on July 17 and repeatedly excising the surplus during the following weeks. An increasing amount of support was provided as the plants grew.

RESULTS AND DISCUSSION

A. The eight moisture regimes. Most plants tillered profusely when grown in the glasshouse, despite the quite high plant numbers per pot, presumably because of the adequate lateral illumination. Many of these tillers bore ears, and even the plants under continual moisture stress had a mean of 4.5 ears per plant. The mean number of grains per ear, however, was correspondingly low when compared with those under field conditions. The ratio of grain to straw was therefore also low, even in the control, as the ear bearing culms were both tall and leafy when given adequate water. Wilting only occurred when a period of stress followed a period of adequate supply and the continually stressed plants appeared spiky and stunted.

The eight treatments, when arranged in decreasing order of grain yield fell into two distinct groups; those maintained at the high, and those maintained at the low moisture levels between the start of stem elongation and anthesis (Table 42). Moisture stress during this period reduced the number of grains set per ear to approximately one third (Table 42), although the actual number of florets per ear was not affected, as the period of stress only commenced about the time of stamen initiation. Thus, either development was prevented in the floret initials, or there was a specific interference with meiosis in the gametes, similar to that found by Skazkin and Leiman (1952), Novikov (1952), Skazkin and Zavadskaya (1957) and Bingham (1967).

Stress during the first period, from germination to stem elongation, also reduced the numbers of grains per ear, although with far less severity than during the second period. Stress during the two periods also combined to greatly diminish both plant height and the mean length of the rachis internodes. Raising the moisture level in the first period alone resulted in the production of more straw, but no extra grain than when a continual stress was applied.

A lack of stress during the final period, between anthesis and maturity increased the ear number, not from an increased survival of existing ears, but by a sudden flush of late ear-bearing tillers. These could have been stimulated after the temporary inhibition of tillering associated with stem elongation either by water directly, or indirectly by a continued nitrogen availability (Aspinall, 1961). The number of late ears was greatest when adequate moisture followed two periods of stress, and was sufficient to depress the mean weight per grain. However, apart from

TABLE 42

Treatment means for the eight moisture treatments, arranged in decreasing order of grain yield. Measurements per plant.

PERIOD	MOISTURE LEVEL								LSD
Pre-stem elong.	High	Low	High	Low	High	Low	Low	High	
Stem elong.to anthesis	High	High	High	High	Low	Low	Low	Low	
Post-anthesis	High	High	Low	Low	High	High	Low	Low	
Grain Yield, g	3.20	2.29	2.23	1.91	1.07	.92	.51	.47	.37
Weight per grain, mg	37.6	32.9	33.8	30.7	32.7	29.2	33.5	33.0	3.6
Grains/ear	14.5	10.3	14.8	12.3	5.1	3.8	3.2	3.4	2.2
Ears	6.6	6.7	5.0	5.0	6.9	8.1	4.5	5.0	1.1
Ear length, cm	6.3	6.5	6.5	6.3	6.1	5.5	5.8	6.3	.5
Height, cm	113	96	114	97	79	65	64	74	6
Straw, g	10.1	8.2	9.1	7.1	7.6	6.1	4.5	5.9	.6
Total, g	13.3	10.5	11.4	9.0	8.7	7.0	5.0	6.4	.7
Harv. Index	24.8	22.1	21.2	21.0	13.6	13.5	11.5	9.4	4.0

this treatment and the control, the weights per grain of the other six treatments did not differ.

B. Varietal Response

1. Grain yield per plant. The variety x treatment interaction was highly significant for grain yield, and when the data are presented graphically in Figure 50 using a technique similar to that of Finlay and Wilkinson (1963), some of the causes for the interaction become apparent.

Firstly, the two Northern European varieties, Proctor and Princess, adapted to a temperate climate, performed well when always maintained at an adequate moisture level and protected from the arid local climate by a glasshouse.

Secondly, Bankuti had a much higher grain yield than the other seven varieties at the two most severe treatments (3 periods of stress, and stress from stem elongation onwards), but did relatively poorly at the next most severe treatments (stress between stem elongation and anthesis, and before anthesis), as unlike the other varieties, it did not produce late ear-bearing tillers on receiving adequate water during grain filling.

Thirdly, the inflexion in the curves differed between the early and the late varieties. The curves of CI3576, Arivat and BR1239 were convex up as they performed above average at the treatments with medium yields, while

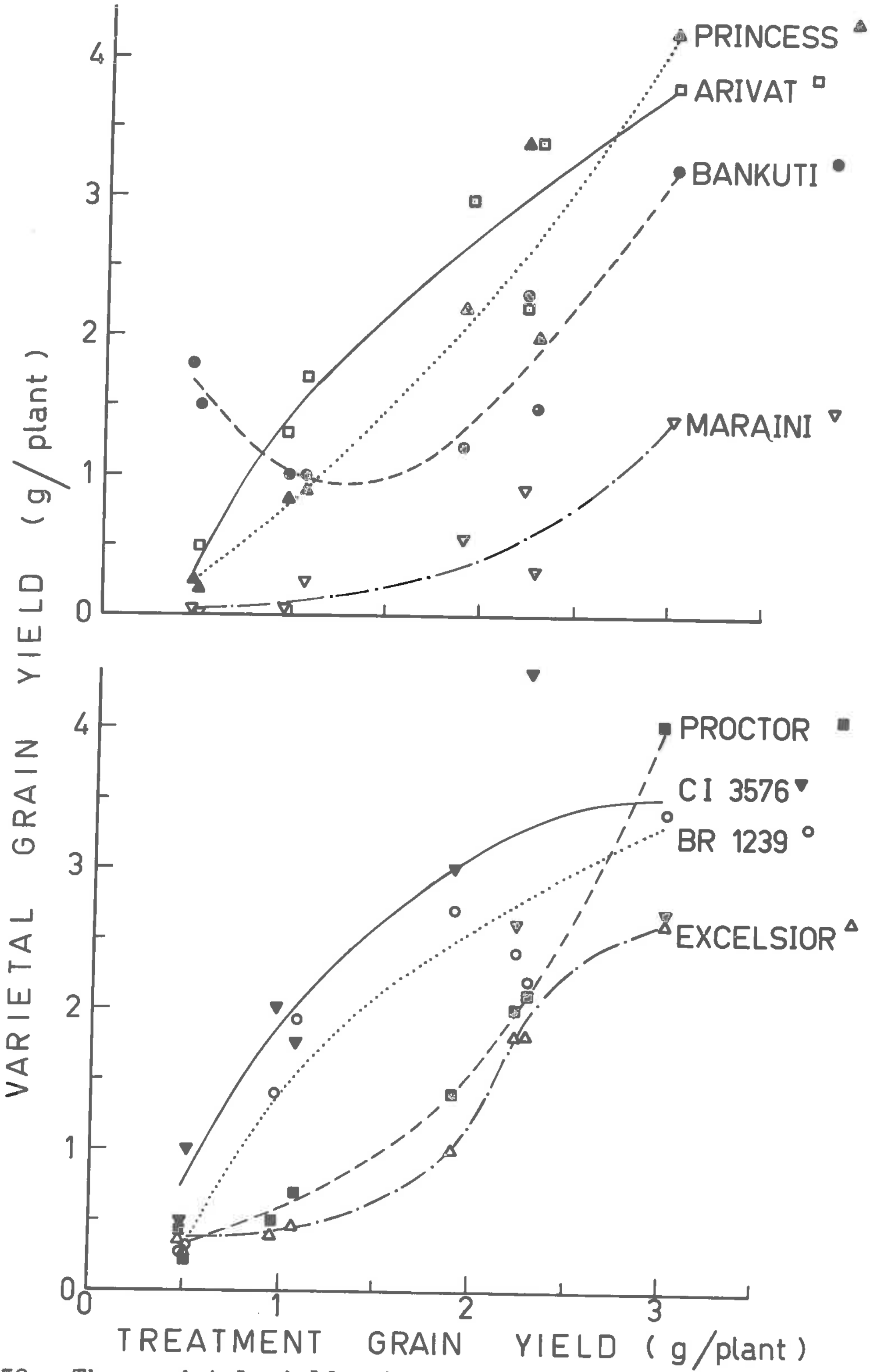


Figure 50. The varietal yields at each treatment plotted against the treatment means over all eight varieties. Curves hand fitted.

the curves of Maraini, Proctor and Princess were concave up since they yielded below average at the same treatments.

Fourthly, the difference between Maraini and other varieties progressively increased as the overall yield level increased; Maraini seems not to be adapted to growth in pots in glasshouses.

The interaction between varieties and treatments in grain yield was solely due to a variation in the number of grains per plant, as the interaction for weight per grain was not significant. The eight varieties are also compared on the basis of percent reduction in grain yield with the non-stressed control equal to 100 per cent (Figure 51), since they obviously greatly differed in yield potential when grown in pots.

2. Percent reduction in yield. Bankuti and CI3576 again appeared most resistant to moisture stress, but apparently not through an increased resistance to loss of activity or to tissue desiccation. Bankuti, for example, developed at an even faster rate in the glasshouse than in the field (Table 43), and consequently suffered moisture stress for much shorter periods of time. This stress was further alleviated by the water content taking longer to fall from the high regime to the low regime, both because of the low leaf area of Bankuti (straw - Table 44), and of the lower evaporative demand earlier in the season.

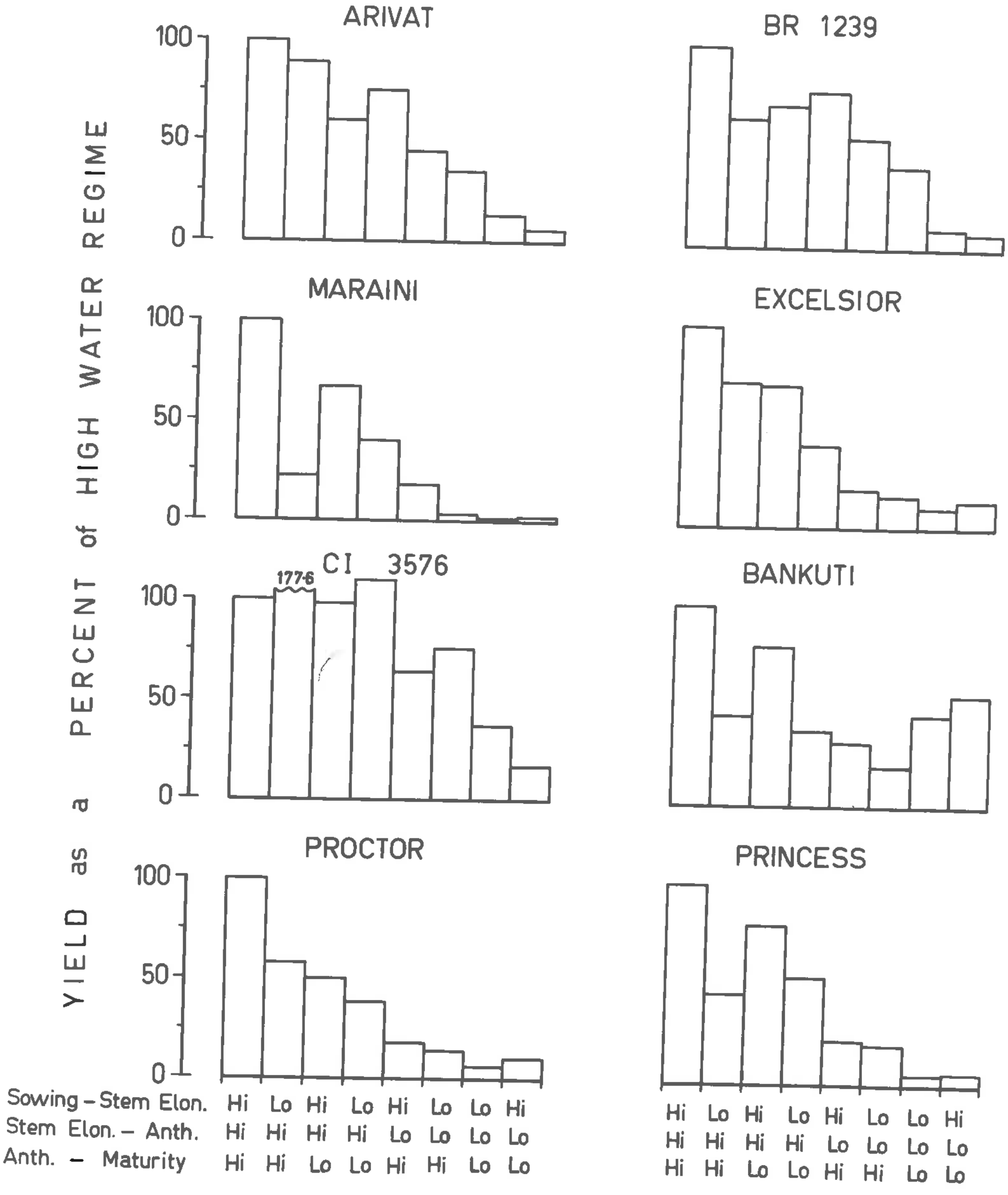


Figure 51. Relative yields of the eight treatments for each of the eight varieties, expressed as a percentage of the control (high level of moisture over all three periods).

The temperatures were often below the glasshouse minimum (20°C) in August and September for most of the day, while in October they usually reached 20°C with attendant lower humidities. It was also probable that the restricted volume of wetted soil at the low water regime was able to supply the requirements of the low evaporative area of Bankuti. Maraini, by comparison, had a greater leaf area at a time of higher evaporative demand for longer periods, and therefore appeared very susceptible to drought, although in Italy, it was released specifically as a drought resistant variety.

TABLE 43

Dates of seeding and anthesis for Bankuti and Maraini in pots and the field in 1968

	1968 pots	1968 field
Date sown	July 17	July 9
Bankuti, anthesis date	September 13	September 26
Mataini, anthesis date	October 24	October 28

CI3576 also developed at a time of lower evaporative demand, but was unique in being able to continue to produce large numbers of ear bearing tillers at any stage of growth (Table 44). The same character enabled CI3576 to have high yields at low densities (Section IX) and to be adapted to growth in the desert depressions in Egypt only occasionally receiving runoff water. The percentage values of CI3576 illustrate the problem of comparing values to a control; if the control by chance happens to be low, then all the other values become inflated. With so many ears, CI3576 also had by far the greatest variability, and the yield in the early stress treatment was sufficiently high to raise the treatment mean for all varieties above that for the late stress treatment (Figure 51).

BR1239 was remarkable in that it did not differ from Arivat in either grain yield or grains per ear, when from its performance in the field, it was expected to become almost completely sterile under severe moisture stress. Perhaps the sexual apparatus of the variety is only susceptible to an arid aerial environment, and can withstand the normal large internal moisture gradients. Arivat appeared slightly more susceptible to a continued moisture stress than Excelsior, and the results supported field observations that Arivat suffered from shrunken grains far more often than did Excelsior.

TABLE 44

Mean grain yields and yield components of the eight varieties over the eight water regimes

	Grain Yield	Number Ears	Grains/ Ear	Weight per grain, mg	Straw, g	Height, cm
Arivat	2.03	6.5	11.1	31.2	7.1	83
Bankuti	1.70	5.7	8.3	37.2	2.9	78
BR1239	1.87	5.6	12.0	29.0	7.9	96
CI3576	2.31	11.0	7.0	37.0	6.7	79
Excelsior	1.10	4.1	8.0	33.6	8.6	101
Maraini	.44	2.2	4.5	33.9	8.5	90
Proctor	1.48	5.8	8.0	29.9	8.5	81
Princess	1.78	6.0	8.4	34.5	8.4	92
LSD	.37	1.1	2.2	3.6	.6	6

XII. GENERAL DISCUSSION AND APPLICATION OF RESULTS

XII. DISCUSSION AND APPLICATION OF RESULTS

Studies involving the agronomic response of a wide range of germplasm can provide information useful to the plant breeder at three stages in a breeding programme. Firstly, the results may reveal suitable parents or parental characteristics to introduce into the programme. Secondly, they may suggest new techniques for screening desirable plants from the large numbers of offspring created by each cross. Thirdly, they may indicate superior methods of assessing the agronomic worth of promising new lines.

A. Identification of useful characters. The following characteristics have been examined in these studies, together with their integration with agronomic practice.

Geographic Origin. At the start of the present investigations, it appeared that varieties derived from North African material probably had a higher intrinsic yield than the other varieties. However, it became evident that most of the other varieties occasionally surpassed or equalled the North African derivatives when favoured by seasonal and agronomic conditions. Maraini, for example, had a high yield at 0 kg nitrogen/ha in a very wet year (Section V), while Bankuti and Drake performed well at high density (Section IX), Excelsior at medium density in 1969 (Section VII) and BR1239 in 1967 without irrigation

(Section X). Only Proctor and Princess had yields consistently below the other varieties, and this was probably a result of their late development rather than their temperate origin.

Conversely, Arivat, Vaughn, and CI3576 performed well in their respective six or two-row groups in all three years. However, the specific characteristics that contributed to this performance did not seem exclusive to North African material. It would have been interesting to include more early varieties from low latitudes (40^oS to 40^oN) for comparison with the North African material (i.e. varieties from China, India, South Korea, Southern Japan and Kenya). Varieties from high Northern latitudes, while having a short, native growing season, have a long photoperiodic requirement and flower too late to have much value in South Australia.

Rate of development. Earliness proved to be the most valuable trait for any variety to be grown successfully in South Australia. The direct effects of early flowering were:-

(1) fewer resources were used during the shorter growth stages (Section IX),

(2) each growth stage was subjected to a shorter period of stress (Section XI),

(3) varieties flowered before the onset of severe

vapour pressure deficits (Section X).

As a result, the earliest variety, Bankuti, had no floret abortion at normal densities (Section VII), and more ears and grains per ear at high densities (Section IX). In northern New South Wales, earliness accounted for 90 per cent of the variation in drought resistance in wheat (Derera et al., 1969).

The relationship between flowering date in the field and photoperiod is not direct (Aspinall 1966b), but all varieties have a quantitative long-day requirement for both floral development and internode elongation (Guitard, 1960). Therefore Bankuti, which appeared insensitive to photoperiod in South Australia, must have a requirement below the 10 hours daylength occurring in Adelaide at mid-winter.

Syme (1968b) suggested that the day length insensitivity of Mexican wheats might be a valuable feature in allowing earlier flowering from late sowing, but this seems erroneous, as all varieties of both wheat and barley developed at a similar rate and nearly flowered together from late sowing (Section IV). The longer photoperiods and the higher temperatures encountered after sowing at the end of July or in early August apparently fulfilled the flowering requirements of all varieties. Full advantage can be taken of the rapid development of varieties like Bankuti only if they are sown in early May, on a dry seed bed prior to the opening rains if necessary, and flower in late August or in early September before any severe moisture stress.

Leaf Number. All varieties had a similar number of leaves per culm after late sowing (Section IV). With early sowing, both the number of leaves per culm and the individual leaf length were greatly increased in the late varieties, and the period before stem elongation was lengthened (Section IV). All three factors contributed to an increased occurrence of juvenile lodging, and grain yields are frequently depressed in a May sowing. Barley ~~sowing~~ is therefore usually sown in June or early July in South Australia, but this discriminates against the very early varieties in field testing, as their advantage in early flowering is partially lost. Similarly, in wheat the early sowing of standard-height varieties led to excessive quantities of straw and caused adult lodging; on the other hand the semi-dwarf varieties benefited from early planting. (Briggle and Vogel, 1968).

Leaf Length. The leaf length increased in all varieties whenever there were abundant supplies of moisture and nitrogen and the light intensity fell to low levels within the canopy. The most responsive variety was Excelsior which increased from 16cm in 1967 to 38cm in 1969 and the least responsive, BR1239, which increased from 16cm to 29cm.

Leaf length was positively associated with the degree of juvenile lodging, and reducing the leaf length by clipping or applying CCC increased the number of surviving ears (Section VI). The leaf length and hence the leaf area per culm did not seem related to either the number of grains per ear (Section VII), which was more strongly influenced by genotype and the severity of induced competition, or the weight per grain, as long as there was approximately 5-6cm^2 of green area per grain at anthesis (Section VIII).

Unfortunately, all the varieties except BR1239 responded excessively in leaf length under moist, fertile conditions, if the critical length is arbitrarily taken as 30cm. However, varietal differences in leaf length are maintained over different environments and seasons (Hamblin, unpubl. data), so rigorous selection is feasible, especially if attempted in a year like 1969 when the differences were greatly accentuated by the environment.

Leaf area/leaf weight ratio. Greater photosynthetic rates per unit leaf area have been found correlated with denser or thicker leaves in temperate grasses (Carlson et al., 1970; Cooper and Wilson, 1970), apparently because of the greater number of small stomates (Miskin and Rasmusson, 1970). However, there were no significant differences in the leaf area/leaf weight ratio between varieties growing in the field either in the drought year

(1967) or the very wet year (1968). The mean in both years was approximately 300cm^2/g. There were differences under the moist, fertile conditions of 1969, but these differences were not related to grain yield, or even to leaf length or juvenile lodging (Section VII) as BR1239, Velvon and Princess had thin or less dense leaves, and Excelsior and Proctor had thick or dense leaves. However within varieties, CCC did reduce leaf length, juvenile lodging and the leaf area/ leaf weight ratio, from 345 to 280cm^2/g, in 1969.

Selection for a low ratio could easily be accomplished through the use of leaf discs, but variation might mask differences if the growth of some members of a cross resembled that of Bankuti, whereby there was a high initial ratio followed by a sudden drop as new tissue became differentiated.

The thin-walled succulent tissue developed under conditions favourable for growth is extremely susceptible to desiccation in an arid climate (Iljin, 1957), but there did not seem to be any varietal differences to'haying off' after the early irrigation in 1967, other than those conferred by differences in the time of development.

Tiller number. Many of the problems in attaining high barley yields emanate from the considerable overproduction of tillers under favourable conditions. Only a small loss of dry weight could be attributed directly to sterile tillers, but the loss of potential yield through juvenile lodging and ear abortion under the changed microclimate was tremendous. For instance, only 190 of the 1500 tillers/m^2 produced by Arivat at high nitrogen in 1969 survived to bear ears, fewer ears than produced during the record drought in 1967. The percentage of tillers surviving in Arivat increased both under higher light intensities (1967) and lower fertilities (1968, low nitrogen 1969) and up to 430 ears/m^2 survived in 1968 (Figure 52).

Uniculm varieties have been produced by Donald (1968a, b) to allow control of leaf area and tiller number, and had sufficient seed been available, they would have provided an interesting comparison with Bankuti, to ascertain if their real advantage lies in the single tiller characteristic or in their extreme earliness. Uniculm derivatives of late or early varieties flowered within a week of each other at the end of September, and suggest that the lack of tiller development can dominate photoperiodic response in determining flowering date. Plants of all varieties became functional uniculms at high densities when the vestigial tillers on each plant died, but at these densities, it made no difference to grain yield per unit area whether the surviving ears were on potentially high tillering plants (CI3576) or on potentially weakly tillering plants (Bankuti).

CI3576 is somewhat unusual in that early varieties

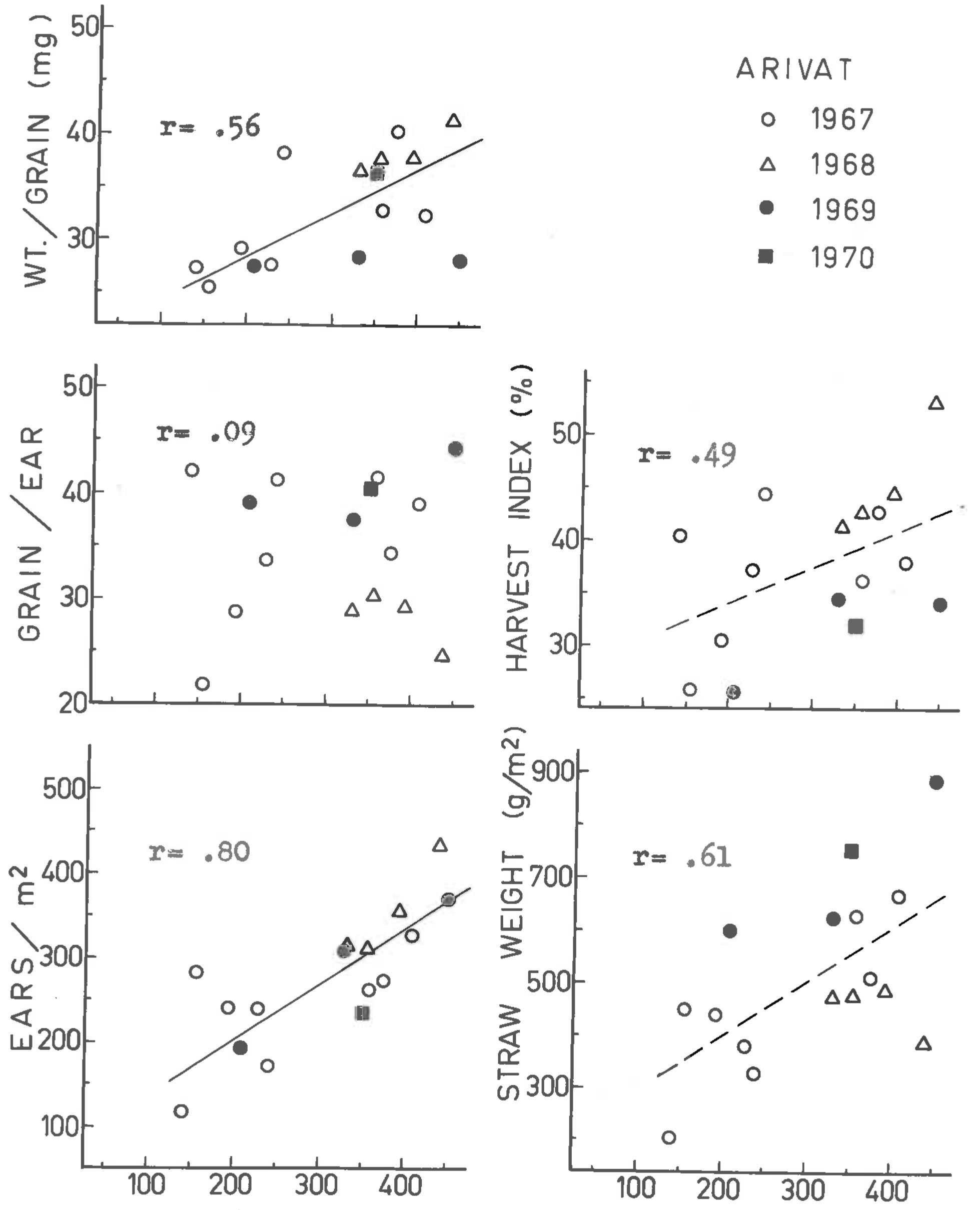


Figure 52. The relationship between grain yield and the three yield components, harvest index, and straw yield for Arivat in 1967, 1968, 1969 and 1970. Arivat, Excelsior and Proctor were selected for Figures 52, 53 and 54 respectively because of the availability of additional values from unreported experiments involving the three varieties.

usually have a reduced tillering potential (Asana, 1963), but as an early and profusely tillering variety, it was able to maintain high yields, relative to other varieties, at both high and low nitrogen levels (Section V) and high and low densities (Section IX) when little lodging occurred. In comparison, Bankuti and BR1239 are weakly tillering and have specific requirements for a high density and a high nitrogen level respectively.

It is clear that Bankuti would have performed considerably better in the trials of Finlay and Wilkinson (1963) had a greater seeding rate been used to compensate for the low tillering rate per plant, especially as this very early variety can tolerate the added competition so effectively. A higher density may also have been able to compensate for the reduced ear number of Arivat at low nitrogen in the systematic nitrogen trial in 1968 (c.f. Montgomery, 1912; Boyd, 1952).

Height. A further reduction in height would be necessary before very early varieties could be commercially planted early at high densities. Lodging only occurred in these experiments after physiologic maturity, and the grain yield remained unaffected, as all the material was harvested by hand. Machine harvesting, however, might have resulted in a considerable loss of grain.

An attempt was made in 1968 to increase the range of height in the group of varieties by including three dwarf varieties developed in England, Sweden and Japan, but the increase blocks vanished under a volunteer crop of barley. The lack of any increase in height with increasing density (i.e. Bankuti and BR1239) in particular seemed a character worth investigating.

Ideally, barley would have the same height characteristics as semi-dwarf wheat varieties, which are of similar height to standard wheat varieties under low moisture or fertility levels, but are considerably shorter under optimum conditions (Krull and Borlaug, 1970). Unfortunately, the dwarfing genes in barley are tightly linked with genes causing shrivelled grain and a reduced grain number per ear (Berbigier, 1968), and a similar linkage required much effort before being broken in wheat.

Pseudostem length. The genes responsible for the short straw characteristic in wheat also cause~~s~~ a shortened coleoptile length that has sometimes hindered seedling emergence (Allan et al., 1962). However, it would seem logical that these genes would also shorten the pseudostem length and might even result in the increased ear number reported in semi-dwarfs (Paquet, 1968; Krull and Borlaug, 1970). Leaf length and height are also related in wheat (Chowdhry and Allan, 1966), but not apparently in barley as BR1239 was tall but had the shortest leaf length.

Erect leaf type. The erect-leaved canopy of BR1239, and the lodged canopy of Excelsior represent the extreme types of the floppy and upright-leaved canopies studied previously in barley (Gardener, 1966) and rice (Hayashi and Ito, 1962). The narrow (.8cm wide) and long (38cm) leaves of Excelsior completely lacked support and bent readily along with the shaded, weak pseudostem. BR1239 had wider (1.4cm) and shorter (29cm) leaves, few tillers, and wide, sturdy pseudostems. The resulting erect canopy proved very resistant to lodging, and seems a necessary prerequisite for high yields under moist fertile conditions. The extreme erectness conferred by the liguleless[1] character, however, again increased the incidence of juvenile lodging, apparently because of the increased shading of the pseudostem by the tube-like leaves.

Disease resistance. An open, erect canopy with thicker differentiated tissue is also of value to the plant breeder in that it seems to bestow a general resistance to disease. In 1967, when the canopy was sparse and well ventilated with no sustained moist conditions for spore germination, no outbreaks of disease were recorded. In 1969, when the canopy became more compact through CCC application, and the leaf length remained long, both mildew and *Rhynchosporium* were greatly encouraged as was *Cercosporella* in wheat (Briggle and Vogel, 1968). The thinner, more

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[1] Noticed during the screening of material for susceptibility of juvenile lodging.

luxuriant foliage developed under moist, fertile conditions was also more susceptible to the spread of mildew (c.f. Howard et al., 1970).

Yield components. Both number of ears/m^2 and number of grains/ear are much more difficult to evaluate than readily discernable morphologic characteristics, and are subject to the variation induced by previous yield determining processes. High nitrogen levels, for example, can reduce the number of florets aborting through nitrogen deficiency, but increase abortion through moisture stress. Ear numbers are greatly affected by variations in the environment and often cause compensatory changes in grain numbers per ear.

However, when the three components are plotted against the grain yields of each variety, obtained in field plots at medium densities (150-300 plants/m^2) over three or four years, grain yield is clearly dependent on the number of ears/m^2 (i.e. Arivat ($r = .80$), Figure 52; Excelsior ($r = .84$), Figure 53; Proctor ($r = .90$), Figure 54). The number of grains/ear was depressed when the late varieties, adapted to temperate regions, were grown under low yielding, drought conditions (i.e. Proctor ($r = .72$), Figure 54) but the other varieties showed little relationship between grains/ear and grain yield (Figures 52 ($r = .08$) and 53 ($r = .12$)), despite a two-fold variation in the number of grains/ear.

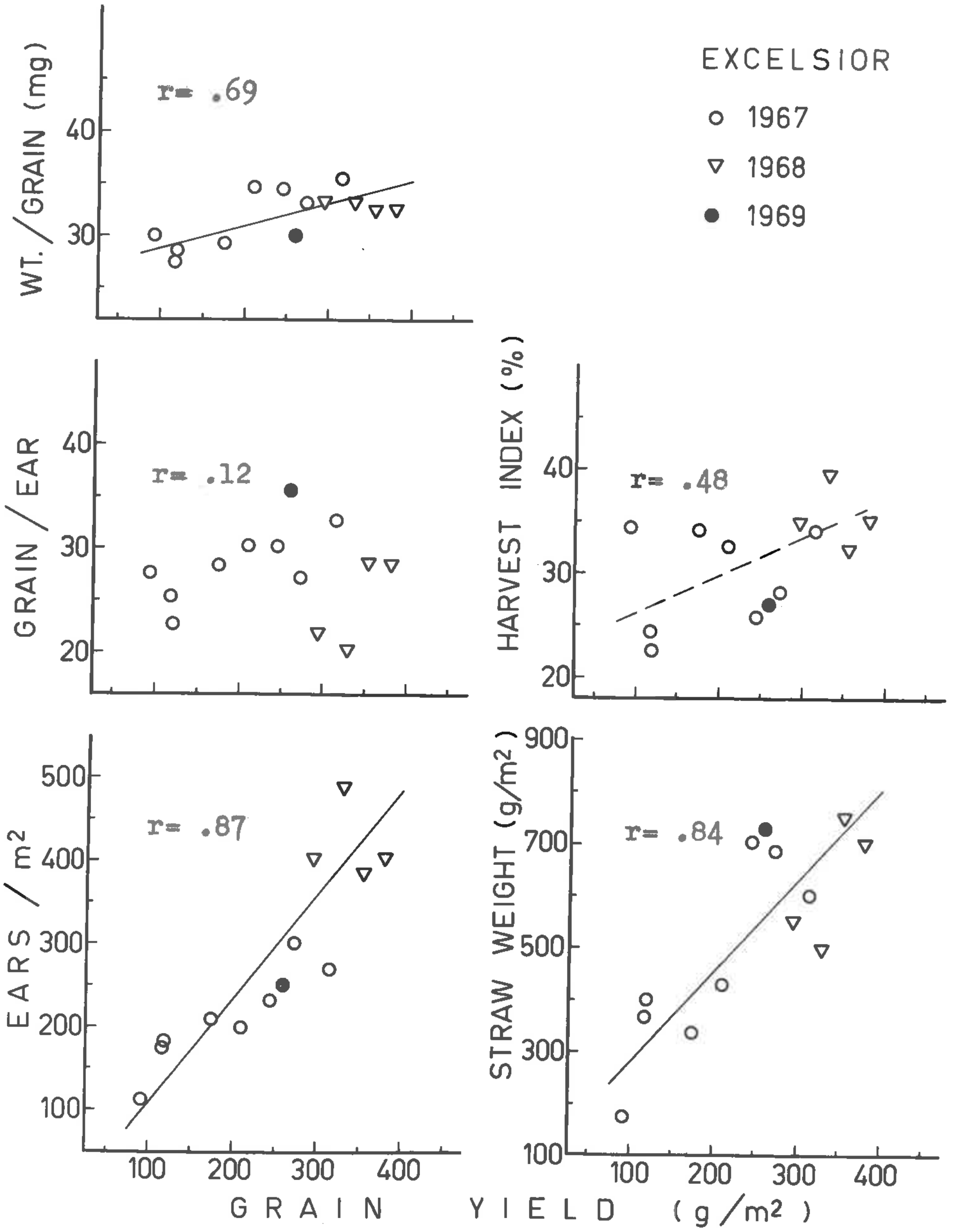


Figure 53. The relationship between grain yield and the three yield components, harvest index, and straw yield for Excelsior in 1967, 1968 and 1969.

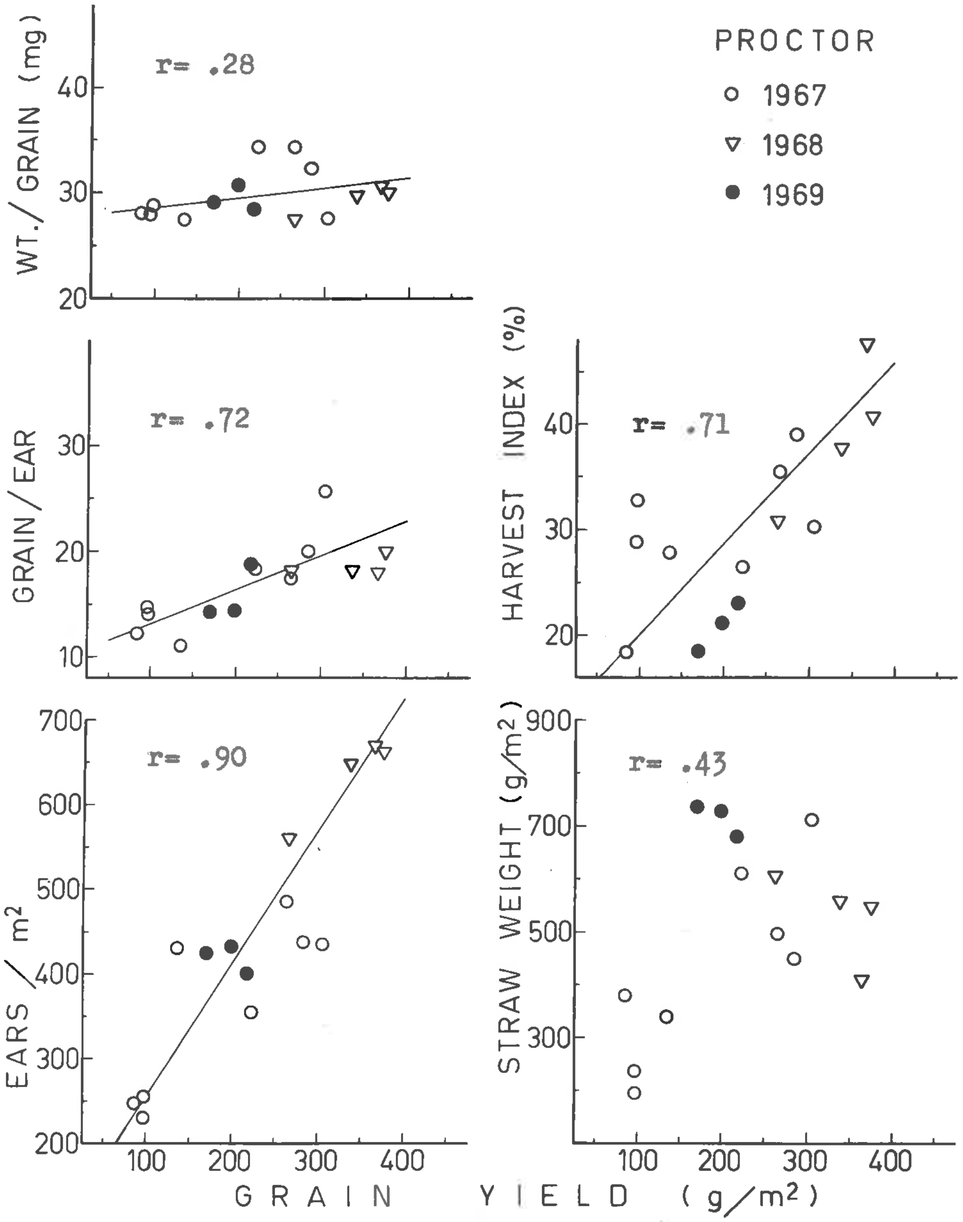


Figure 54. The relationship between grain yield and the three yield components, harvest index, and straw yield for Proctor in 1967, 1968 and 1969.

The weight per grain showed less variability, and also increased with grain yield, but only markedly in the case of Arivat, which failed to fill grains completely under the low yielding environments. Arivat produced a large number of grains/m^2 in these environments, which suggests that the consistently plump grains required for malting, found in Prior and Proctor, are not compatible with consistently high potential yields, even in early varieties.

When comparisons were made between, instead of within varieties, the yield differences no longer depended on ear number (Proctor and CI3576 had a similar number of ears) but instead were related to differneces in the number of grains/m^2. But these are the product of the number of ears/m^2 and the number of grains/ear, so there seems little advantage in measuring the individual components in a breeding programme, over just obtaining grain yield and weight per grain.

When free of juvenile lodging, six-row varieties produced as many ears per m^2 as two-row varieties, but had more grains per ear except when the varieties were grown at high densities (Section IX). At the time of floret initiation, two-and six-row varieties did not differ in leaf area or weight per tiller, and indeed, three floret initials are formed at each rachis node in all varieties.

It is only later that the lateral spikelets cease development in two-row varieties. There was therefore a greater demand for assimilate in six-row ears, less likelihood of the sink being limiting and more chance of the potential grain size not being realised. However, in 1969, the weights per grain of the six-row varieties were not affected more by awn and leaf removal than those of the two-row varieties. Six-row varieties therefore have a greater yield potential than two-row varieties at the seeding rates currently employed in South Australia.

Harvest index. It was expected that the harvest index would show a parabolic response when plotted against total dry matter, similar to that found by Medinets (1967), but the relationship was poor (r =-.08) (Figure 55) despite total dry matter being the denominator in the expression for harvest index. The relationship between harvest index and grain yield (the numerator) was only marginally better (Figure 52, 53, and 54). The poor relationships therefore arose both from variation in the weight of grain in an ear produced by a stem, and from variation in the weight of a reproductive stem.

The harvest indices under low yielding environments were lowest in the late varieties (Proctor and Excelsior) and highest in the early varieties (Arivat). Under high yielding environments, Arivat and Proctor had a higher

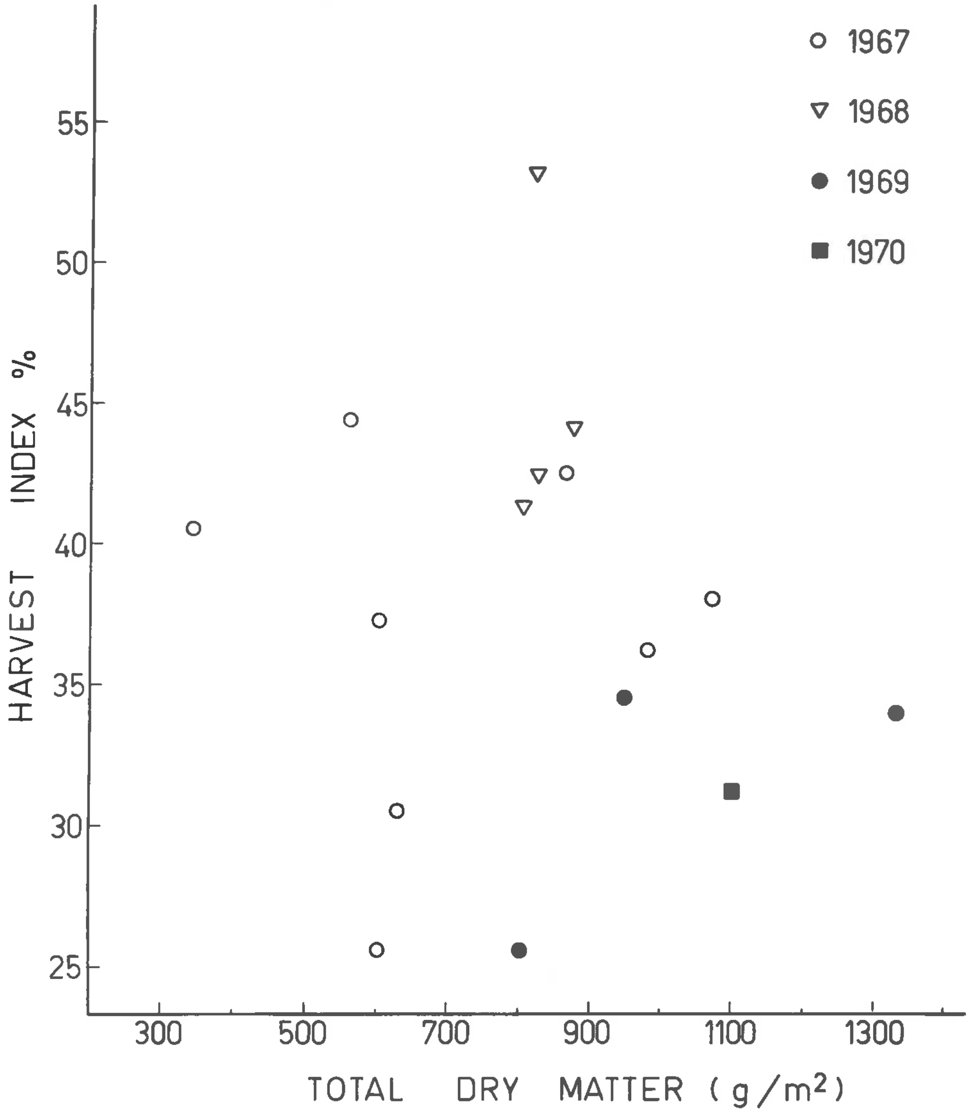


Figure 55. The harvest index for Arivat plotted against the weights of total dry matter recorded in 1967, 1968, 1969 and 1970. r= - 0.078 (r= 0.11 in Excelsior and 0.069 in Proctor).

percentage of grain than a prodigious producer of straw like Excelsior. Proctor and Excelsior both had their highest grain yields under medium fertility in the wet year of 1968. The top yield of Arivat occurred in 1969 under conditions of high natural fertility.

In these experiments, the harvest index has proved useful when assessing the response of varieties to agronomic factors. However, as a selection criterion, the harvest index depends on the complex and variable relationship between straw and grain yield; two variables affected differentially by environmental changes. It is probably more effective to select indirectly for high harvest indices through short height, high grain yield and early flowering (i.e. early varieties in Figure 8), than to measure the yield of both straw and grain.

LAI, LAD and RDMP. The physiologic parameters, while proving valuable in describing the various responses of the varieties, provide characteristics less tangible and useful to a plant breeder than the yield components, of which the product at least equals yield itself. The physiologic parameters always appeared to result from other yield determining characteristics and processes, rather than being directly causal of yield differences.

The RDMP was initially greater in the earlier varieties regardless of the seedling leaf area (Section VII) presumably because of the earlier onset of the reproductive phase (Knight, 1965). The LAI first reflected the differing patterns of tillering and dry matter production between varieties, but high values suddenly became yield depressant with the occurrence of juvenile lodging and the LAIs finally reflected the number of ears surviving.

Both irrigation and nitrogen increased the LAD after anthesis and the LAD per grain; irrigation increased, while nitrogen decreased the weight per grain. Increasing or decreasing the dry weight per tiller had little effect on the number of grains per ear (Section VI, VII) and conversely, varieties formed different numbers of florets from similar leaf areas and dry weights per tiller. Leaf areas and dry weights per tiller or per floret do not appear measurements likely to have much value in a cereal breeding programme.

Ideotype. The preceding discussion can be best summarized by presenting the characteristics considered useful for South Australian conditions in the form of an ideotype or model variety for high yield. The ideotype would have:-

(a) A photoperiodic requirement below 10 hours and early flowering approximately three months after sowing.

(b) A height below 80cm under moist, fertile conditions.

(c) Wide, thick, elastic stems resistant to mature lodging and breakage.

(d) Wide, thick leaves below 30cm in length at high fertility and density.

(e) A short and sturdy pseudostem.

(f) Few tillers per plant.

(g) Maintenance of floret fertility under nitrogen deficiency or moisture stress.

(h) General field resistance to mildew and Rhynchosporium.

(i) Relatively dense ears to prevent shattering.

(j) Firmly attached, non-dehiscent awns.

(k) Six-rowed ears.

To take full advantage of these characteristics, the variety would have to be planted in early May at densities of 450-500 plants/m^2. This rate would compensate for the lack of tillering ability at low fertilities, and the variety should be able to tolerate physiologically the competition apparent at high fertilities. Therefore, while the variety has specific requirements for density and time of sowing, it should be capable of producing high yields over a wide range of environments because of the relative insensitivity to environmental change. In other words, it is proposed that it is advantageous to grow a genotype adapted to a wide range of environmental differences, rather than to grow different genotypes to suit specific environments (Richmond, 1962) or to seek to minimize environmental differences by irrigation and fertilization to suit one genotype (Frankel, 1959).

B. The choice of parents. Relatively few parents are used in a cereal breeding programme compared to the number of progeny tested, so more resources can be devoted to the examination of potential parents than to individual offspring. Conversely, the correct choice is so important that selection of parents is often restricted by caution to lie within a group of locally adapted and highly productive varieties (Allard and Hansche, 1964; Frankel and Bennett, 1970). Unadapted, exotic varieties tend to be used only for highly heritable characters such as disease resistance, that can be incorporated by backcrossing into local varieties. Such conservatism has some justification, as the general use of exotic material could result in the replacement of locally adapted populations, developed over many years, with lower yielding material having little chance of early success. Extensive backcrossing to adapted material may, however, prevent further major improvement of the potential yield of a crop (Krull and Borlaug, 1970); both the successful Mexican wheat and Philippine rice varieties resulted from the introduction of foreign material.

One solution propounded by Suneson (1956) was to make a very large number of crosses between local and exotic varieties, latterly using male sterility (Suneson and Wiebe, 1962), and then let natural selection eliminate the inferior material. The positive relationship between competitive ability and yielding ability has been challenged (i.e. Donald 1968a, b), but an increasing percentage of superior lines do emerge in later generations (Suneson, 1956; Allard and Jain, 1962).

However, several problems remain in using composite crosses. First, outstanding progeny still have to be identified and isolated from the community. Second, the bulk has to be grown under agronomic conditions which result in the survival of plants having a superior performance in pure stands. Third, the extremes in each character are rapidly eliminated leaving a mean not necessarily optimal for the environment (Allard and Jain, 1962). And fourth, the successful utilization of variability requires that the plant breeder have a clear concept both of the trait sought, and its exact function in increasing productivity (Krull and Borlaug, 1970).

Identification of desirable traits can be made through the use of isogenic lines, but their production is time consuming and their worth may be limited by the characteristics and genetic modifiers peculiar to the genotype. Both these objections have been partially overcome by the use of isogenic populations (Jennings and Herrera, 1968), but a much wider inference can be obtained through the study of a wide range of each character, especially if the material is grown under different agronomic conditions. The inferences made in the present investigations might have been further strengthened by the inclusion of at least two varieties carrying the extremes of each characteristic. For example, the value of extremely early varieties could have been more fully tested if a six-row (Stewart) had been included with Bankuti, as the response curves of the two- and six-row varieties quite often differed.

When the value of a particular trait is recognized, it would seem preferable to search first for the trait amongst locally adapted material. Then, if sufficient variability does not exist, it should be transferred into the local material by backcrossing to reduce the risk of also introducing detrimental genes (Sprague, 1969).

Six of the varieties in these investigations have been used as parents. Many crosses have included Prior, the dominant Australian variety for many years. Prior has consistently produced medium yields of malting quality under average conditions when sown in June or July, and farmers soon learned to roll it to prevent neck breakage. In these experiments Prior A was tolerant of crowding, and usually had a low LAI, ear number and total dry weight. It may therefore normally suffer less moisture stress per unit leaf area, as moisture removal from the soil was equal to the other varieties.

Currently, Prior is being replaced by a new variety, Clipper, bred by D.H.B. Sparrow. Clipper is a Proctor x Prior cross with maturity similar to Prior, but having the better malting quality, shorter height and the many small ears of Proctor. Less neck breakage occurs and Clipper seems adapted to slightly more fertile conditions with a higher rainfall and earlier planting in June. Proctor performed constistently poorly in these experiments largely on account of its extreme lateness and slow development.

As a result of these studies, Bankuti and BR1239 have been recently crossed with Clipper as their respective extreme earliness and excellent morphology were ~~was~~ not available in locally adapted material. Excelsior has been crossed with American winter barleys, on the chance that the introduction of its green, long-lived awn characteristics might offset the premature senescence of their foliage, and result in better and more consistant grain filling.

CI3576 has been used more extensively in the local programme, because of its evaluation as the highest yielding two-row variety over a large number of sites. The variety produces many ears with large grains, but the short straw is weak and the malting quality very poor.

C. Screening the progeny. All plant breeders involved in varietal improvement have to make a decision on how and when to impose selection on the potentially infinite number of combinations generated by a cross. Ideally, single plants would be screened for yield in early generations, thus using the minimum of time, effort and space, but so far, this has failed to identify lines that later have a high yield in pure stands (Allard, 1960; Bell, 1963). Four possible causes for this failure have been suggested (Shebeski, 1967).

Firstly, the more heterozygous plants may have higher yields in early generations, but this advantage is lost with the increasing homozygosity of later generations.

Secondly, selection is carried out in an environment different to that in which the progeny are tested for yield. This can be particularly important in South Australia when even the ranking of varieties grown in plots can change between years.

Thirdly, single plants that are successful competitors in a heterogeneous population, may not yield well in a pure stand of like individuals.

Fourthly, no replication of plants exists in early generations, and variations in the microenvironment around individual plants mask their true yield.

However, differences in morphological characters are less affected by competition, microenvironment and the genotype x season interaction than are differences in yield and the former have a high heritability between generations (Hamblin, unpubl. data). Donald (1968a, b) therefore proposed identifying the plants high yielding in later generations indirectly through their morphological characteristics. Further, a quick visual evaluation is of more worth than precise measurement when evaluating large numbers of individuals. Many of the desirable characteristics previously discussed can be easily screened in segregating populations, especially if the character is deliberately accentuated by agronomic or physiologic treatments.

For example, it is necessary to grow plants far enough apart in segregating populations to be easily able to distinguish adult plants, but is also highly desirable to have light conditions similar to those in a normal crop canopy. The easiest solution ~~seems~~ is to grow one or two generations under a large tobacco shade cloth similar to those used by Stinson and Moss (1960) for testing the shade tolerance of maize inbreds. Less moisture stress develops under such shades (Campbell et al., 1969), and under high fertility, any differences in leaf length, pseudostem length and height should become readily apparent. All the plants with long narrow leaves, tall thin stems or excessively etoliated pseudostems could then be removed from the population. The microclimate under the shade cloth should also prove conducive to the growth of fungal spores, and provide satisfactory differentiation of those plants possessing a generalized or broad spectrum of disease resistance.

Similarly, if the population were space planted in May, it would be possible to inspect early in September and rogue out all plants that had not flowered. The number of leaves per culm would be decreased along with the earlier anthesial date.

In essence, this is mass selection against tall, late, narrow and long-leaved, disease and lodging prone plants, similar to the mass selection successfully used by Romero and Frey (1966) in reducing the mean height in oat populations. It does result in many more plants being retained than if just those plants possessing model characteristics are selected, but a low selection pressure may be advantageous in visual selection (Boyce et al., 1947; Hanson et al., 1962; Briggs and Shebeski, 1970).

Long leaves and tall stems have been found to impart a competitive advantage to plants in populations segregating for these characters (Jennings and Aquino, 1968; Jennings and de Jesus, 1968; Jennings and Herrera, 1968). It seems possible that in a population devoid of these types, natural selection might continue in a bulk with great reduction in the usual confounding effects of competition. This might then allow lines to emerge with superior floret fertility and resistance to moisture stress, nutrient deficiency and crowding, according to the conditions imposed.

D. The agronomic testing of lines and varieties. The response curves obtained for varieties in these studies, indicate that different varieties would have been selected for high yield, depending on the nitrogen and density levels employed by the plant breeder (Figures 56 and 57). Varieties like Bankuti and BR1239 have been previously considered low yielding because the current agronomic practices are sub-optimal for yield. Conversely, these current practices are near optimal for Arivat, and this variety has been considered as highest yielding in the collection. Yield is, in fact, highly relative and a general ranking of genotypes is not possible, as each variety has its own pattern of response to particular environmental conditions.

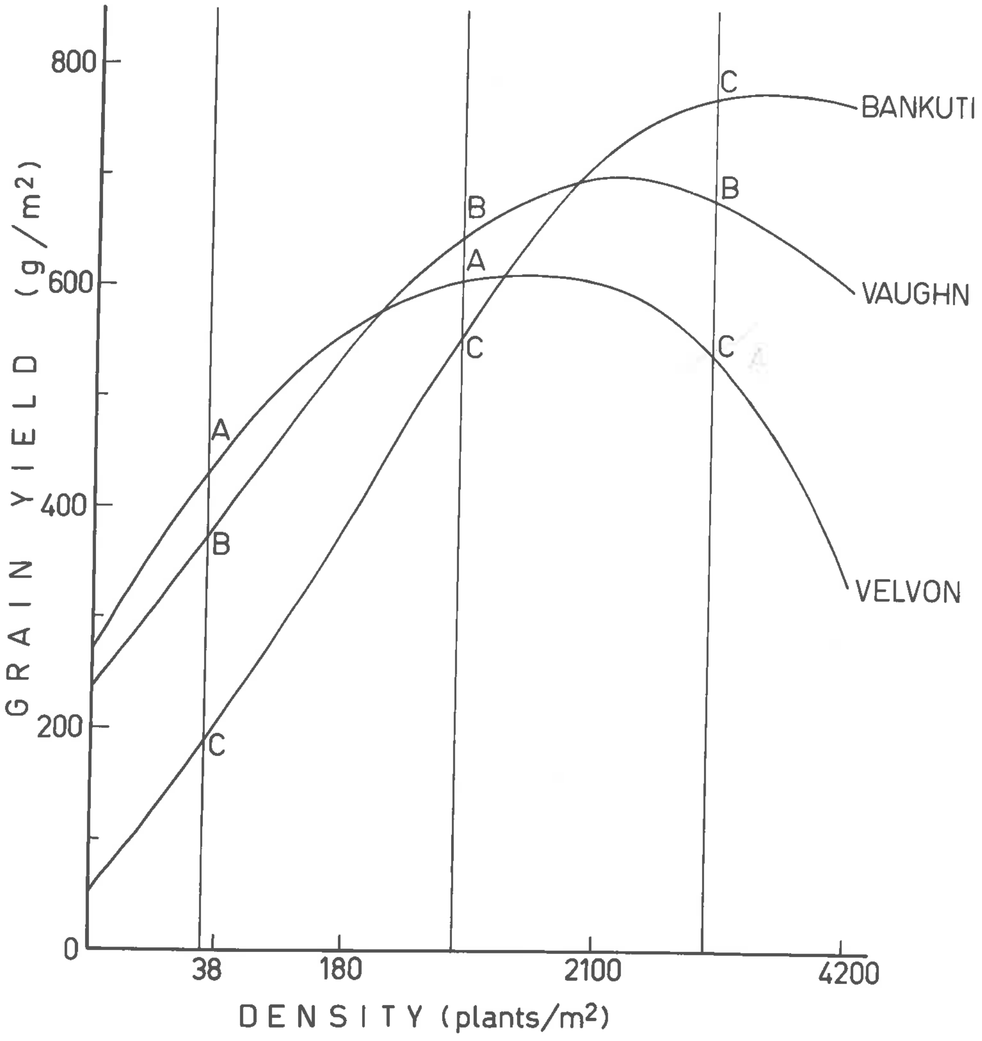
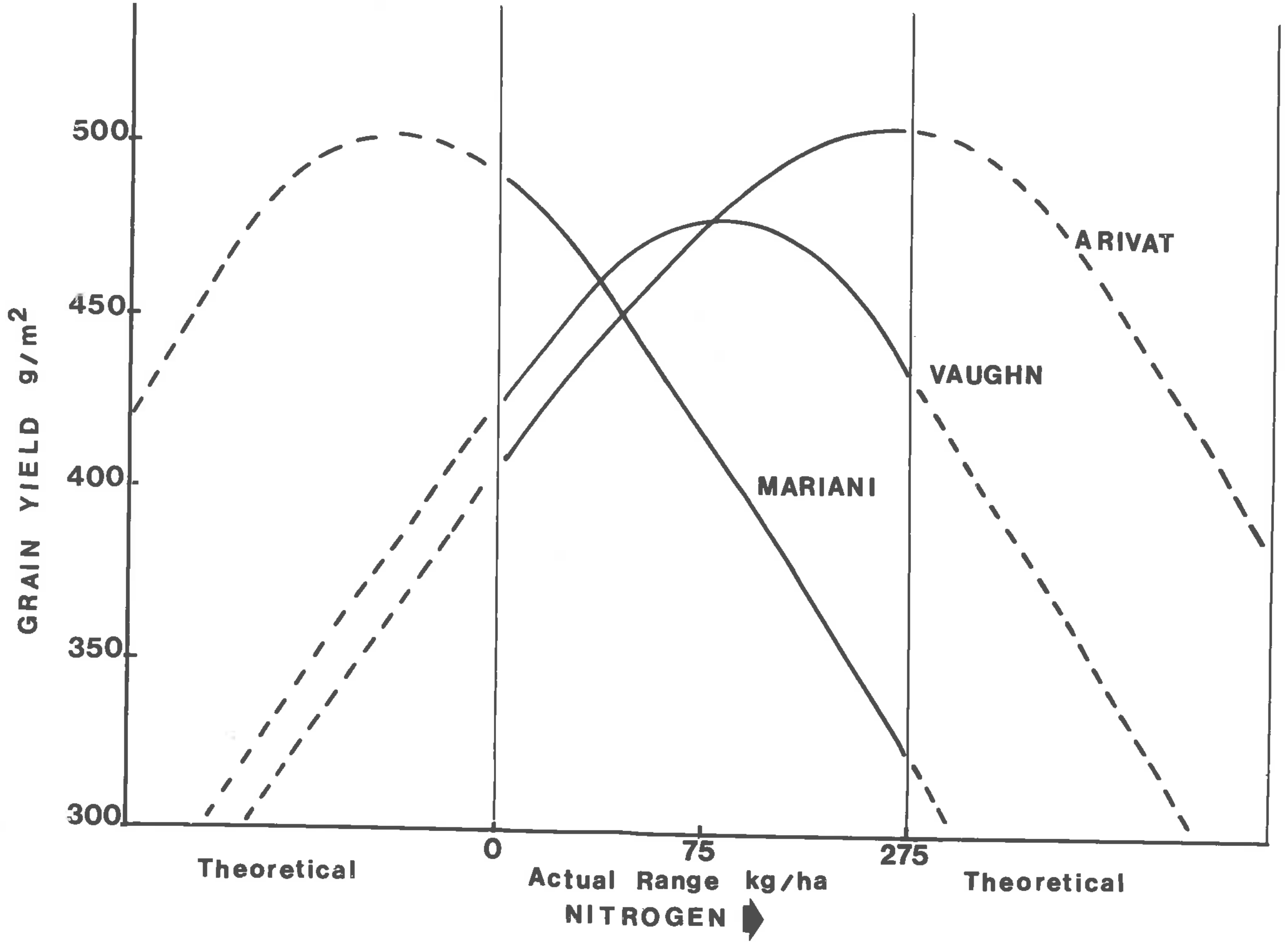


Figure 56. The interaction of the yield of three genotypes with density. Computer fitted curves (Figures 34 and 35).

Figure 57. The interaction of the yield of three 6-row genotypes with the level of nitrogen. Computer fitted curves (Figure 7).


GRAIN YIELD g/m^2
500
450
400
350
300
ARIVAT
VAUGHN
MARIANI
Theoretical
0
75
275
Actual Range kg/ha
Theoretical
NITROGEN

However, the large number of lines that must be tested in advanced generations usually precludes the use of more than one set of conditions. Further, if extra resources are available, most plant breeders in a variable environment would rather increase the number of locations than obtain more information at one site. A possible compromise is to sow additional replications early at high density at two or three sites to assess the most important genotype x methodology interaction.

Duncan (1958) was able to estimate the complete response curve for maize hybrids using only two densities, since the log grain yield per plant fell linearly with density. However, the varieties in the density trial (Section IX) showed a curvilinear relationship (Figure 58), and while narrowing the range of densities increases the linearity, it also rapidly decreases the accuracy of the estimations. Later Duncan (196~~8~~9) and Bleasdale (1967) were respectively able to compare maize and vegetable crops (lettuce and cauliflower) successfully using fan designs, but even these seem unsuited to providing practical recommendations on the correct densities for cereals.

Systematic designs do have a place in plant breeding, however, not to test the advanced lines, but to indicate the correct density or nitrogen level at which to test the material remaining after selection. The limitation

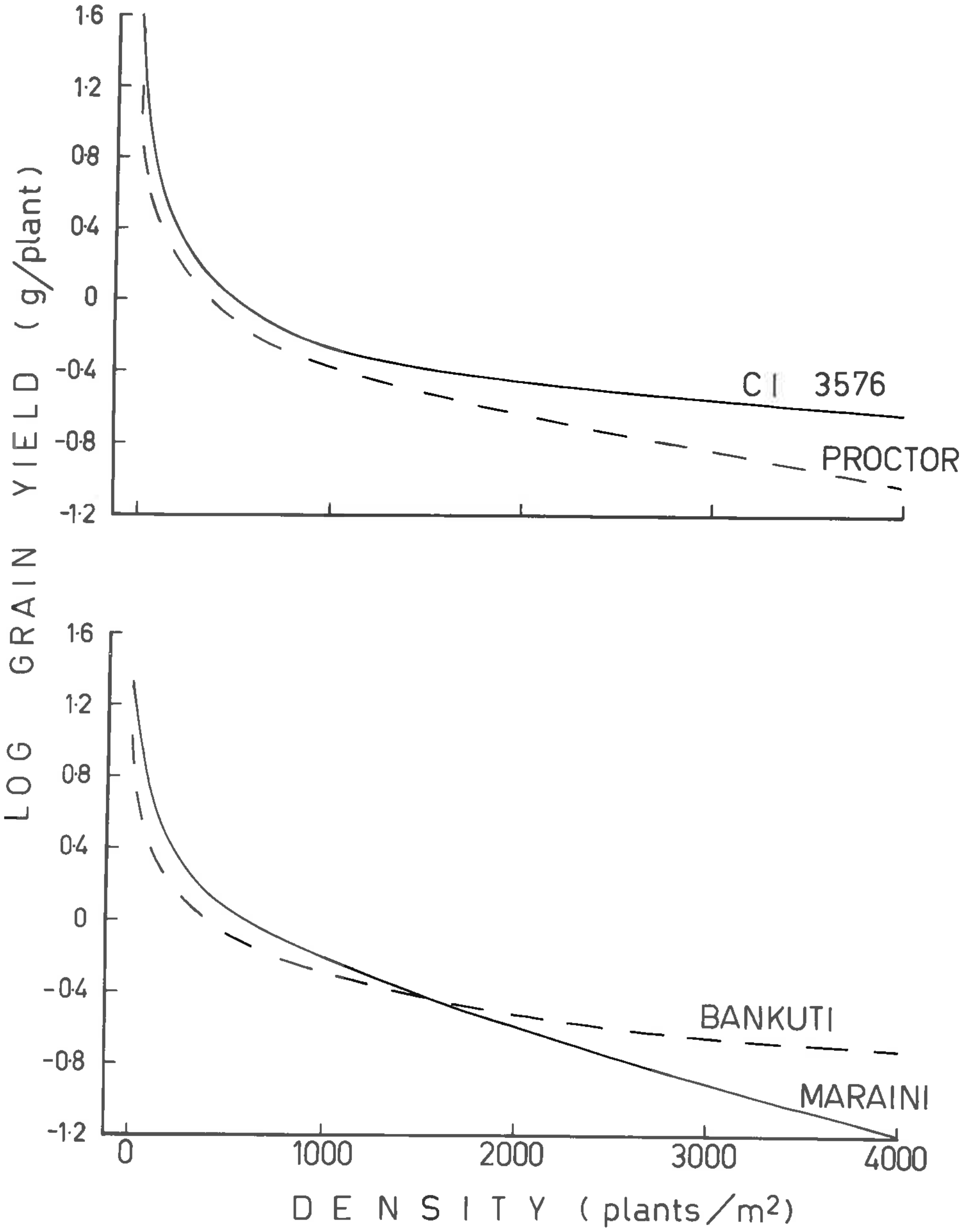


Figure 58. The curvilinear relationship between the log grain weight per plant and density in four varieties.

of the fan design for cereals, is that cereals produce their highest grain yields when the individual plants and the spacings between plants are small. The area per plot then becomes miniscule towards the centre of the cartwheel, and the competition is in fact much below that suffered in a continuous, uniform canopy of the same density.

The present trials indicate that, if juvenile lodging is likely to be encountered, a plot width of at least 2m is desirable with no paths between plots. A rectangular plot, 10m x 2m, could contain ten 1m x 2m subplots of density or nitrogen arranged systematically. Adequate chemical weed control and a 5m spray boom would of course be mandatory. Large numbers of replicates are necessary in systematic designs to overcome the non-random variability, but it might be possible to apply two levels of a second treatment e.g. additional water to each of two replicates and thus gain a tremendous amount of information on the correct agronomic methods for testing and commercially growing the new material. More selection criteria and an increased understanding of the crop would also accrue from such trials, and new concepts develop in the mind of the plant breeder.

XIII. CONCLUSIONS

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The following conclusions from Sections IV to XI are presented here to provide a more integrated account of the results of these studies.

1. The twelve varieties, selected on the basis of origin, maturity and row number produced their maximum grain yields at very different densities and levels of nitrogen. The yields also varied at the specific optima of each variety. Comparisons were misleading if not made at comparable points on the response curve.

2. Systematic designs proved an excellent method of varying each agronomic factor over a range sufficiently wide to meet the optimum but unknown requirements of each variety.

3. The grain yield of the highest yielding variety at 0,80 or 275 kg N/ha was similar. This suggests that it would be more profitable to grow different varieties in areas of naturally low or high nitrogen, than to apply additional nitrogen to varieties adapted to the higher fertility levels.

4. Variation in varietal yields with nitrogen reflected variation in ear members. The grain weight per ear remained relatively constant in eleven varieties, as changes in weight per grain compensated for changes in number of grains per ear. One variety, adapted to fertile Prairie conditions, was extremely susceptible to nitrogen deficiency, showing a large reduction in number of grains per ear.

5. The number of ears per m^2 was greatly reduced when the crop lodged in the juvenile stage prior to stem elongation. Both the leaves and pseudostems became etoliated when the crop was planted early at high densities and grown under high fertility during the winter months of low light intensities and ample moisture.

6. CCC application, defoliation, mechanical support and reduction of available soil nitrogen status by straw incorporation all prevented juvenile lodging and increased ear numbers. However, CCC also resulted in a more compact and poorly ventilated canopy that greatly encouraged <u>Rhynchosporium</u> in a susceptible variety.

7. Varieties with short leaves (below 30cm in length) were relatively immune to juvenile lodging, especially if the leaves were also wide and therefore erect and the pseudo-stems thick. Late varieties with many long narrow leaves per tiller and many tillers were most prone to lodging.

8. In a drought year (326 mm rainfall), an additional 115 mm of water, added early in the growing season, stimulated excessive vegetative growth, and caused shrunken grain and poor fertility in early varieties and failure to emerge from the boot in late varieties. This seemed to be identical with the phenomenom known as 'haying off'.

9. When irrigation was continued throughout the growing season of the drought year, the ranking of varieties remained remarkably constant in the irrigated and non-irrigated blocks. This ranking was similar to that previously obtained over several locations, where moisture was also considered the dominant factor determining yields. Under these conditions, there was a strong negative relationship between the number of grains set per m^2 and the varietal date of anthesis.

10. In years of record high and low rainfall, there were only occasionally significant differences in the uptake of water by varieties. These differences did not seem to be closely related to differences in leaf area or dry matter, although there was a tendency for early varieties to use more water early in the season. In one year, late varieties continued to use water after the early varieties had matured.

11. The application of nitrogen increased moisture use in all instances except one. The exception was when a very high rate (200 kg/ha) increased depletion in the top 30cm of the soil, but resulted in less removal from the next 60 cm in the profile.

12. An extremely early variety (Bankuti Korai) appeared insensitive to photoperiod, and usually flowered in the field approximately two and one half months after sowing. The latest variety (Maraini) always flowered at the end of October regardless of sowing date. The ability of Bankuti to escape the high vapour pressure deficits and moisture stress of the late spring was therefore lost with late sowing. Conversely Maraini did not escape the late stress by early sowing.

13. The characteristics associated with extreme earliness, i.e. short leaves, only seven leaves per culm and very few tillers per plant, resulted in a very sparse canopy and low grain yields at a conventional spacing, but an increase in density depressed the yield per plant relatively little, and these types had high yields at high densities.

14. The ranking of varieties changed with plant density. The late six-row varieties performed well at low densities, the early six-row varieties well at intermediate densities, and the early two-row varieties best at high densities. However one early two-row (CI3576) tillered profusely and also had the highest yield at low density, while a late two-row (Proctor) performed poorly at all densities. The highest grain yields were obtained in varieties with the highest optimum densities.

15. More ears survived in the early varieties, and it seemed that the yield components were subjected to less competition in the shorter growth periods. The distribution of ear size became more skewed with each increase in density and delay in varietal maturity, until the distribution became bimodal with a large class of aborted ears.

16. However, at high densities, ear survival was not always reflected in higher yields, as other varieties gave similar yields from fewer ears containing more, heavier grains.

17. Even when the advantage of the early varieties, in developing before serious competition arose, was nullified by applying a predetermined moisture stress over each ontogenetic period, the early varieties still suffered less, probably because of the shorter duration of the periods rather than a greater intrinsic tolerance to drought. A stress between the start of stem elongation and anthesis reduced the number of florets setting grains to one third over all varieties, and had a far greater effect on yield than stress between seedling emergence and stem elongation, and anthesis and maturity.

18. The dry weight of the seedlings was initially proportional to the weight of the seeds sown, but the early varieties then increased in dry weight and leaf area more rapidly, regardless of whether they had few large tillers or many small tillers. This was associated with a higher leaf area/leaf weight ratio in the wet year. The later flowering varieties continued tillering longer, and had greater total dry weights by anthesis.

19. Shading the crop by the insertion of dowels during ear initiation but after the formation of many small tillers, reduced the weight per tiller but slightly increased the number of florets per ear in all varieties. This was probably due to a longer period for spikelet formation. Generally, lower weights per tiller did not seem related closely to the number of florets per ear.

20. Light interception seemed more a reflection of varietal differences in total dry matter than causal of these differences. The percentage light intercepted per unit leaf area was dependent on the LAI. Some varieties with narrow leaves and many small tillers did intercept less light per unit leaf area, but this had little effect on total or grain yields.

21. The six-row varieties always had a far greater potential yield than the two-row varieties at conventional densities, despite similar light interception, LAIs and total dry matter as they could produce as many ears, and had fertile lateral florets. However, juvenile lodging reduced the ear numbers in the late six-row varieties, and some varieties suffered from reduced floret fertility,so it was usually one of the early six-row varieties derived from North African material that had the highest grain

yield. At very high densities, however, the number of grains per ear in the six-row varieties fell below those of two-row varieties.

22. The late flowering varieties produced more total dry matter by anthesis than the early varieties, but between anthesis and maturity produced less or equal dry matter to that accumulated in the grain. The early varieties produced dry matter well in excess of that stored in the grain after anthesis.

23. Individual grains in the late varieties increased in weight initially after anthesis at a much faster rate than grains in early varieties, and grain weights were little reduced by awn and leaf removal while they were reduced up to 36 percent in early varieties.

24. Over all varieties, the leaf area per grain fell from 11.4 cm^2 to approximately 6 cm^2 without much depression in the weight of individual grains, but a further reduction below 6 cm^2 decreased grain weight considerably.

25. Shading (48 per cent transmission) the crop after anthesis decreased the rate of gain in dry matter of the grains, but grain filling continued longer, either because

of the cooler, more moist microclimate or because of the dictate of sink size, with grains in the shaded crop finishing only 2.5mg lighter than those on plants receiving full light. Shading did not affect varieties differentially.

26. Increasing the amount of light available to a crop at different ontogenetical periods had most effect in increasing total dry matter before and during stem elongation when tiller numbers were greatly increased; during grain filling, increased light did not increase thousand grain weights.

27. Nitrogen increased leaf area and delayed senescence in the drought years, thereby increasing both the LAD after anthesis and the LAD per grain, but the weight per grain was still decreased by nitrogen application. Physiological parameters like LAD can therefore be misleading in an arid climate.

28. The expected relationship between total dry matter (assymptotic) and grain yield (parabolic) with increasing density did not hold over the wide range of densities and varieties used in these experiments.

29. The findings indicate that the differential responses of varieties to agronomic factors are often associated with easily identifiable characteristics, but that incorporation of these characteristics into new varieties to raise yields will only prove successful if agronomic practices are simultaneously changed.

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APPENDIX A

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values from unreported experiments involving the three varieties.

The r values between grain yield and
weight/grain = 0.558*
grains/ear = 0.085
ears/m^2 = 0.795*
harvest index = 0.488
straw yield = 0.611*

53. The relationship between grain yield and the three yield components, harvest index, and straw yield for Excelsior in 1967, 1968 and 1969.

The r values between grain yield and
weight/grain = 0.686*
grains/ear = 0.119
ears/m^2 = 0.874**
harvest index = 0.480
straw yield = 0.836**

54. The relationship between grain yield and the three yield components harvest index and straw yield for Proctor, in 1967, 1968 and 1969.

The r values between grain yield and
weight/grain = 0.278
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ears/m^2 = 0.896**
harvest index = 0.714**
straw yield = 0.426

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APPENDIX C

EQUATIONS FOR COMPUTER FITTED CURVES: RESPONSE OF VARIETIES TO NINE LEVELS OF NITROGEN.

The curves shown in Figures 6, 7 and 8 are fitted by multiple regression equations for the following terms:

Ears/m^2 = Number of ears per m^2
Grain/m^2 = Yield of grain, g per m^2
D.M./m^2 = Yield of total dry matter, g per m^2
H.I. (%) = Harvest Index as a percentage
Weight/grain = Weight per grain, mg
Grain/ear = Weight of grain per ear, g
Grains/ear = Number of grains per ear

when GN (geometric nitrogen) is 1, 2, 3, 4, 5, 6, 7, 8 or 9.

$F_{.05} = 4.46$
$F_{.01} = 8.65$

	EXCELSIOR	R^2(%)	V.R.
Ears/m^2	$= 400.1 + 45.3\ GN - 4.65GN^2$	83.2	14.8
Grain/m^2	$= 295.1 + 46.4\ GN - 4.87GN^2$	66.4	5.9
D.M./m^2	$= 678.9 + 154.3GN - 9.85GN^2$	91.8	3.3
H.I. (%)	$= 41.7 - 1.31\ GN - .059GN^2$	96.4	79.7
Weight/grain	$= 30.3 - .70\ GN + .12\ GN^2$	99.2	122.2
Grain/ear	$= .75 + .015\ GN - .0019GN^2$	60.4	1.5
Grains/ear	$= 24.9 + 1.01\ GN - .15GN^2$	89.0	8.1

	VELVON		
Ears/m^2	$= 386.6 - 10.7\ GN + .11\ GN^2$	60.8	4.7
Grain/m^2	$= 408.3 - 23.7\ GN + 1.12GN^2$	63.2	5.1
D.M./m^2	$= 927.4 - 9.9\ GN - .17\ GN^2$	29.9	1.3
H.I. (%)	$= 43.9 - 2.06\ GN + .11\ GN^2$	78.3	10.8
Weight/grain	$= 35.0 - 1.78\ GN + .14\ GN^2$	95.9	23.6
Grain/ear	$= 1.03 - .018\ GN + .00083GN^2$	92.2	11.8
Grains/ear	$= 29.3 + 1.25\ GN - .12\ GN^2$	97.9	47.4

MARAINI

		R^2(%)	V.R.
Ears/m^2	$= 432.9 - 24.4\ GN + .24\ GN^2$	83.7	15.4
Grain/m^2	$= 506.0 - 24.7\ GN + .31\ GN^2$	76.3	9.6
D.M./m^2	$= 1113.6 - 27.2\ GN + .91\ GN^2$	31.4	1.4
H.I. (%)	$= 46.0 - 1.46\ GN - .00070\ GN^2$	95.4	62.0
Weight/grain	$= 37.6 - 1.18\ GN + .10\ GN^2$	52.0	1.1
Grain/ear	$= 1.25 - .024\ GN + .0037\ GN^2$	97.6	40.3
Grains/ear	$= 33.2 + .55\ GN + .000\ GN^2$	71.4	2.5

BR1239

		R^2(%)	V.R.
Ears/m^2	$= 391.9 - 6.9\ GN + .54\ GN^2$	4.1	.1
Grain/m^2	$= 214.5 + 32.6\ GN - 1.76\ GN^2$	61.0	4.7
D.M./m^2	$= 601.3 + 102.6\ GN - 6.69\ GN^2$	64.5	5.4
H.I. (%)	$= 35.7 - .46\ GN + .069\ GN^2$	33.0	1.5
Weight/grain	$= 31.0 + .54\ GN - .062\ GN^2$	64.5	1.8
Grain/ear	$= .49 + .13\ GN - .0091\ GN^2$	87.7	7.1
Grains/ear	$= 15.8 + 3.70\ GN - .24\ GN^2$	90.6	9.6

ARIVAT

		R^2(%)	V.R.
Ears /m^2	$= 464.1 - 15.5\ GN + 1.93\ GN^2$	15.3	.5
Grain m^2	$= 384.0 + 27.7\ GN - 1.55\ GN^2$	37.0	1.8
D.M./m^2	$= 770.5 + 59.2\ GN - 1.61\ GN^2$	59.7	4.4
H.I.(%)	$= 50.1 - .39\ GN - .040\ GN^2$	92.8	38.0
Weight/grain	$= 40.0 - 2.86\ GN - .194\ GN^2$	44.9	.8
Grain/ear	$= .79 + .11\ GN - .0089\ GN^2$	94.0	15.6
Grains/ear	$= 17.0 + 6.55\ GN - .495\ GN^2$	65.5	1.9

VAUGHN

		R^2(%)	V.R.
Ears/m^2	$= 455.9 + 13.1\ GN - 1.77\ GN^2$	14.1	.4
Grain/m^2	$= 386.7 + 35.0\ GN - 3.28\ GN^2$	18.9	.7
D.M./m^2	$= 763.3 + 86.0\ GN - 5.62\ GN^2$	48.1	2.8
H.I.(%)	$= 50.4 - .81\ GN - .033\ GN^2$	96.9	93.9
Weight/grain	$= 39.2 - .22\ GN + .0022\ GN^2$	99.4	155.1
Grain/ear	$= .86 + .020\ GN + .00008\ GN^2$	82.5	4.7
Grains/ear	$= 22.0 + .63\ GN + .0043\ GN^2$	87.4	6.9

BANKUTI

		R^2(%)	V.R.
Ears/m^2	$= 522.6 + 6.2\ GN - 1.62\ GN^2$	41.8	2.2
Grain/m^2	$= 252.9 + 11.0\ GN - 1.56\ GN^2$	49.8	3.0
D.M./m^2	$= 486.4 + 64.3\ GN - 5.89\ GN^2$	52.3	3.3
H.I.(%)	$= 50.4 - 2.71\ GN + .15\ GN^2$	97.8	131.9
Weight/grain	$= 36.9 - .17\ GN - .0022\ GN^2$	89.4	84.1
Grain/ear	$= .48 + .017\ GN - .0016\ GN^2$	52.2	1.1
Grains/ear	$= 13.0 + .53\ GN - .04\ GN^2$		

CI 3576

Ears/m^2	$= 713.2 - 7.00\ GN + 1.94\ GN^2$	41.3	2.1
Grain/m^2	$= 419.9 - .80\ GN + .30\ GN^2$	9.5	.3
D.M./m^2	$= 875.0 + 2.4\ GN + 2.68\ GN^2$	79.9	11.9
H.I. (%)	$= 48.2 - .47\ GN - .060\ GN^2$	97.5	115.4
Weight/grain	$= 42.9 - .20\ GN - .0096\ GN^2$	85.4	5.9
Grain/ear	$= .62 - .010\ GN + .00019\ GN$	96.9	31.3
Grains/ear	$= 14.3 - .18\ GN + .0069\ GN$	91.8	11.2

PRIOR A

Ears/m^2	$= 546.6 - 9.1\ GN + 2.71\ GN^2$	66.2	5.9
Grain/m^2	$= 357.0 + 22.6\ GN - 1.53\ GN^2$	43.5	2.3
D.M./m^2	$= 748.0 + 52.9\ GN - 2.10\ GN^2$	68.9	6.7
H.I.(%)	$= 47.6 - .26\ GN - .048\ GN^2$	98.8	256.6
Weight/grain	$= 40.6 + .22\ GN - .10\ GN^2$	96.5	27.8
Grain/ear	$= .65 + .048\ GN - .0056\ GN^2$	99.3	149.5
Grains/ear	$= 16.0 + 1.12\ GN - .0941\ GN$	96.5	27.2

DRAKE

Ears/m^2	$= 414.4 + 9.1\ GN + .47\ GN^2$	62.3	5.0
Grain/m^2	$= 325.7 + 21.4\ GN - 1.96\ GN^2$	28.5	1.2
D.M./m^2	$= 732.4 + 57.3\ GN - 3.74\ GN^2$	56.9	4.0
H.I.(%)	$= 44.3 - .39\ GN - .033\ GN^2$	90.7	29.3
Weight/grain	$= 34.0 - .54\ GN - .012\ GN^2$	83.0	4.9
Grain/ear	$= .77 + .039\ GN - .0053\ GN^2$	58.9	1.4
Grains/ear	$= 22.4 + 1.64\ GN - .16\ GN^2$	66.0	1.9

PRINCESS

		R^2(%)	V.R.
Ears/m^2	$= 465.8 + 44.0\ GN - 5.19\ GN^2$	88.5	23.2
Grain/m^2	$= 281.7 + 16.1\ GN - 2.26\ GN^2$	41.2	2.1
D.M./m^2	$= 697.5 + 87.8\ GN - 7.83\ GN^2$	61.7	4.8
H.I.(%)	$= 39.2 - 1.57\ GN + .045\ GN^2$	81.9	13.6
Weight/grain	$= 30.1 + .010\ GN + .0018\ GN^2$	28.8	.03
Grain/ear	$= .53 + .021\ GN - .0026\ GN^2$	55.3	1.2
Grains/ear	$= 17.5 + .67\ GN - .086\ GN^2$	75.3	3.0

PROCTOR

Ears/m^2	$= 785.7 - 23.4\ GN + 2.79\ GN^2$	53.7	3.5
Grain/m^2	$= 404.4 - 12.4\ GN + .68\ GN^2$	42.9	2.2
D.M./m^2	$= 901.6 - 12.5\ GN + 3.67\ GN^2$	68.2	6.4
H.I.(%)	$= 44.9 - .93\ GN - .059\ GN^2$	92.2	35.4
Weight/grain	$= 30.4 - 1.22\ GN + .11\ GN^2$	94.9	18.4
Grain/ear	$= .52 - .00013\ GN - .0013\ GN^2$	95.8	23.0
Grains/ear	$= 17.2 + .79\ GN - .11\ GN^2$	93.0	13.3

APPENDIX D

EQUATIONS FOR COMPUTER FITTED CURVES: RESPONSE OF VARIETIES TO 30 DENSITITIES

The curves in Figures 34 and 35 can be constructed (See Section IX) using the two following multiple regression equations for each term. The arithmetic equations poorly fit the data at low density and the geometric constant is a better indicator of the true intersect. Equations are given for the following variables:-

D.M./m^2 = Yield of total dry matter, g per m^2
Grain/plant = Weight of grain per plant, g
Grain/m^2 = Yield of grain, g per m^2
H.I. (%) = Harvest Index expressed as a percentage
Ears/m^2 = Number of ears per m^2
Grain/ear = Weight of grain per ear, g
Weight/grain = Weight per grain, mg
Grains/ear = Number of grains per ear
Height = Height in cm

Geometric density (GD)	1	2	3	4	5	6	7	8
Arithmetic density (AD)	9	12	14	18	22	27	33	41

GD	9	10	11	12	13	14	15	16	17	18
AD	50	62	77	95	117	145	179	220	272	336

GD	19	20	21	22	23	24	25	26	27
AD	415	512	632	780	963	1189	1468	1812	2237

GD	28	29	30
AD	2762	3413	4202

$F_{.05} = 3.35$
$F_{.01} = 5.49$

EXCELSIOR

		R^2(%)	V.R
D.M./m^2	$= 781.1 + 22.5\,GD + .82\,GD^2$	75.6	41.7
	$= 1018.5 + .83\,AD - .00014AD^2$	74.2	38.7
Grain/plant	$= 27.1 - 2.37\,GD + .51\,GD^2$	97.9	616.4
	$= 11.2 - .013\,AD + .0000026AD^2$	43.5	10.4
Grain/m^2	$= 227.2 + 25.7\,GD - .36GD^2$	59.2	19.6
	$= 400.4 + .30\,AD - .000064AD^2$	49.8	13.4
H.I.(%)	$= 33.3 + 1.07\,GD - .040\,GD^2$	59.5	19.9
	$= 38.6 + .000040AD - .00000080AD^2$	62.1	22.2
Ears/m^2	$= 314.1 - 33.0GD + 2.53\,GD^2$	84.7	44.3
	$= 259.2 + .74\,AD - .00011AD^2$	88.8	63.2
Grain/ear	$= 1.37 + .010GD - .0015\,GD^2$	87.2	54.7
	$= 1.28 - .00057AD + .000000088AD^2$	85.8	48.3
Weight/grain	$= 38.5 - .14GD - .0050\,GD^2$	95.1	39.2
	$= 37.3 - .0062AD + .0000013AD^2$	92.7	25.5
Grains/ear	$= 35.6 + .36GD - .038\,GD^2$	93.0	26.6
	$= 36.5 - .017AD + .0000033AD^2$	98.1	101.6
Height	$= 101.3 + 2.89\,GD - .14GD^2$	94.4	16.8
	$= 111.3 - .0055AD - .0000071$	96.0	24.2

VELVON

D.M./m^2	$= 796.1 + 24.5\,GD + .19GD^2$	80.2	54.7
	$= 1007.2 + .54\,AD - .000097AD^2$	72.3	35.3
Grain/plant	$= 31.1 - 2.78GD + .061\,GD^2$	97.3	480.4
	$= 12.6 - .014\,AD + .0000030AD^2$	42.0	9.8
Grain/m^2	$= 241.6 + 34.9GD - .91\,GD^2$	53.6	15.6
	$= 449.5 + .18\,AD - .000048AD^2$	26.9	5.0
H.I.(%)	$= 34.5 + 1.86\,GD - .071GD^2$	61.9	22.0
	$= 43.9 - .0029AD - .00000080AD^2$	49.7	13.4
Ears/m^2	$= 467.4 - 67.3GD + 3.66GD^2$	93.1	107.3
	$= 263.1 + .55AD - .000039AD^2$	96.1	198.1
Grain/ear	$= 1.58 + .022GD - .0024GD^2$	95.0	152.9
	$= 1.52 - .00080AD + .00000012AD^2$	92.9	104.0
Weight/grain	$= 37.7 + 13\,GD - .016GD^2$	93.2	27.4
	$= 37.0 - .0043AD + .00000035AD^2$	94.0	31.5
Grains/ear	$= 40.5 + .84\,GD - .069GD^2$	95.4	42.0
	$= 42.3 - .024AD + .0000040AD^2$	92.9	26.3
Height	$= 100.1 + 1.86GD - .11GD^2$	91.1	10.3
	$= 108.8 - .043AD + .000015AD^2$	88.3	7.5

MARAINI

		R^2(%)	V.R.
D.M./m^2	$= 589.6 + 62.7GD - .95\ GD^2$	62.9	22.9
	$= 993.0 + .78AD - .00018AD^2$	58.5	19.0
Grain/plant	$= 27.5 - 2.40GD + .052\ GD^2$	97.2	460.5
	$= 11.4 - .013\ AD + .0000026AD^2$	43.3	10.3
Grain/m^2	$= 134.0 + 49.9GD - 1.31GD^2$	45.0	11.1
	$= 418.7 + .32AD - .000092AD^2$	40.8	9.3
H.I.(%)	$= 31.5 + 1.95GD - .072GD^2$	72.4	35.3
	$= 41.3 + .00084AD - .0000016AD^2$	73.8	38.0
Ears/m^2	$= 155.6 - 5.33GD + 1.20\ GD^2$	82.2	37.1
	$= 212.8 + .59\ AD - .00011AD^2$	87.6	56.7
Grain/ear	$= 1.58 + .060GD - .0037GD^2$	92.4	97.9
	$= 1.81 - .00088AD + .00000013AD^2$	91.9	90.3
Weight/grain	$= 38.0 + .15GD - .016GD^2$	85.6	11.9
	$= 37.8 - .0044AD + .00000046AD^2$	91.0	20.1
Grains/ear	$= 38.0 + 2.18GD - .11GD^2$	97.6	83.0
	$= 47.4 - .019AD + .0000024AD^2$	95.9	46.4
Height	$= 92.1 + 2.47GD - .11GD^2$	96.6	28.3
	$= 102.3 - .0082AD - .0000018AD^2$	80.4	4.1

BR 1239

		R^2(%)	V.R.
D.M./m^2	$= 710.9 - 5.25GD + 1.60\ GD^2$	87.8	97.5
	$= 786.4 + 7.39AD - .00011AD^2$	38.0	98.9
Grain/plant	$= 23.5 - 2.16GD + .048GD^2$	94.0	212.8
	$= 9.24 - .010AD + .0000022AD^2$	38.1	8.3
Grain/m^2	$= 229.5 + 9.25GD + .11GD^2$	72.9	36.3
	$= 308.1 + .24\ AD - .000044AD^2$	70.5	32.3
H.I.(%)	$= 35.0 + .77GD - .032GD^2$	70.9	32.9
	$= 38.7 - .0031AD + .00000020AD^2$	59.1	19.5
Ears/m^2	$= 612.9 - 126.5GD + 6.29\ GD^2$	94.2	129.1
	$= 152.7 + .77\ AD - .000034AD^2$	98.3	463.0
Grain/ear	$= 1.42 + .011GD - .0019GD$	92.9	105.3
	$= 1.31 - .00077AD + .00000013AD$	90.9	79.7
Weight/grain	$= 33.6 + .73GD - .039GD^2$	96.8	60.2
	$= 36.8 - .0096\ AD + .0000016AD^2$	96.2	50.2
Grains/ear	$= 39.3 + .117\ GD - .040GD^2$	97.2	69.4
	$= 38.1 - .023AD + .0000044AD^2$	97.8	95.0
Height	$= 105.9 - .57\ GD - .031\ GD^2$	70.8	2.4
	$= 97.8 - .0088AD - .0000054AD^2$	75.0	3.0

ARIVAT

		R^2(%)	V.R.
D.M./m^2	$= 648.0 + 48.3\ GD - .74\ GD^2$	81.7	60.4
	$= 1008.7 + .33\ AD - .000052 AD^2$	50.7	13.9
Grain/plant	$= 33.6 - 2.95\ GD + .064\ GD^2$	98.5	885.7
	$= 13.9 - .016\ AD + .0000033 AD^2$	44.0	10.6
Grain/m^2	$= 283.2 + 35.0\ GD - .51\ GD^2$	67.3	27.8
	$= 512.3 + .13\ AD - .000028 AD^2$	17.8	2.9
H.I.(%)	$= 46.8 + .81\ GD - .035\ GD^2$	64.8	24.8
	$= 50.6 - .0035 AD + .00000010 AD^2$	63.5	23.5
Ears/m^2	$= 860.9 - 169.0\ GD + 8.0\ GD^2$	90.2	73.5
	$= 257.6 + .66 AD + .000039 AD^2$	99.4	1262.5
Grain/ear	$= 1.72 + .018 GD - .0025 GD^2$	96.4	216.5
	$= 1.62 - .00099 AD + .00000016$	96.8	241.8
Weight/grain	$= 37.0 + .54 GD - .034\ GD^2$	89.7	17.4
	$= 39.0 - .0094 AD + .0000015 AD^2$	92.3	23.9
Grains/ear	$= 43.5 + .64\ GD - .067\ GD^2$	96.5	54.8
	$= 44.8 - .029 AD + .0000053 AD^2$	99.5	407.4
Height	$= 87.5 + 3.13 GD - .14\ GD^2$	97.3	35.8
	$= 99.9 - .0044 AD - .0000057 AD^2$	85.8	6.0

VAUGHN

		R^2(%)	V.R.
D.M./m^2	$= 684.1 + 19.0\ GD + .80\ GD^2$	85.0	76.7
	$= 929.0 + .57\ AD - .000068 AD^2$	30.0	54.1
Grain/plant	$= 29.2 - 2.55\ GD + .055\ GD^2$	98.8	1146.2
	$= 12.3 - .014\ AD + .0000029 AD^2$	45.0	11.0
Grain/m^2	$= 289.1 + 21.0\ GD - .27 GD^2$	65.4	25.5
	$= 444.8 + .19 AD - .000031 AD^2$	48.4	12.7
H.I.(%)	$= 46.5 + .46 GD - .030 GD^2$	88.2	100.7
	$= 47.7 - .0065 AD + .00000070 AD^2$	84.0	70.9
Ears/m^2	$= 476.3 - 74.2 GD + 4.30\ GD^2$	92.0	91.2
	$= 236.0 + .86 AD - .000099 AD^2$	95.3	161.9
Grain/ear	$= 1.60 - .012 GD - .0012 GD^2$	94.0	124.9
	$= 1.34 - .00077 AD + .00000013 AD^2$	91.5	85.8
Weight/grain	$= 38.5 + .381 GD - .015 GD^2$	53.1	2.3
	$= 40.3 - .0010 AD - .000000049 AD^2$	54.6	2.4
Grains/ear	$= 41.0 - .66 GD - .018 GD^2$	95.4	41.2
	$= 35.8 - .027 AD + .0000056 AD^2$	95.0	38.0
Height	$= 100.2 + 1.15 GD - .080 GD^2$	99.7	291.6
	$= 103.8 - .026 AD + .0000056 AD^2$	99.8	423.2

BANKUTI

		R^2(%)	V.R.
D.M./m^2	$= 375.1 + 4.58GD + 1.66GD^2$	94.5	232.7
	$= 566.4 + .77AD - .000098AD^2$	91.2	139.1
Grain/plant	$= 11.0 - .80GD + .015GD^2$	98.3	762.5
	$= 5.57 - .0059AD + .0000012AD^2$	57.2	18.1
Grain/m^2	$= 109.1 + 10.7GD + .42GD^2$	93.8	204.0
	$= 235.6 + .35AD - .000052AD^2$	86.1	83.7
H.I.(%).	$= 33.1 + 1.25GD - .035GD^2$	66.4	26.7
	$= 40.6 + .0035AD - .0000010AD^2$	14.6	2.3
Ears/m^2	$= 849.8 - 164GD + 8.6 GD^2$	92.2	94.5
	$= 338.3 + 1.11 AD - .000047AD^2$	97.9	371.0
Grain/ear	$= .57 + .018GD - .0011GD^2$	95.0	151.4
	$= .64 - .00025AD + .000000036AD^2$	94.4	135.9
Weight/grain	$= 36.6 + .48GD - .022GD^2$	93.2	27.4
	$= 38.3 - .0021GD + .0000000030AD^2$	90.7	19.6
Grains/ear	$= 14.3 + .62GD - .030GD^2$	97.1	66.5
	$= 17.0 - .0051AD + .00000068AD^2$	95.0	37.9
Height	$= 96.2 - .020GD - .032GD^2$	54.5	1.2
	$= 92.8 - .0082AD - .0000020AD^2$	54.8	1.2

CI 3576

D.M./m^2	$= 863.1 - 22.7GD + 2.30 GD^2$	90.6	129.7
	$= 878.3 + .64AD - .000065AD^2$	93.5	194.8
Grain/plant	$= 31.9 - 2.92GD + .065 GD^2$	96.6	378.1
	$= 12.5 - .014AD + .0000030AD^2$	39.4	8.8
Grain/m^2	$= 363.0 + 1.17GD + .49GD^2$	85.0	76.7
	$= 417.7 + .22AD - .000026AD^2$	84.6	74.1
H.I.(%)	$= 45.1 + .48GD - .026GD^2$	91.8	151.6
	$= 47.0 - .0053AD + .00000070AD^2$	89.5	114.5
Ears/m^2	$= 1064.9 - 160.3GD + 7.86GD^2$	89.1	47.2
	$= 573.9 + .62AD + .000053AD^2$	99.1	895.4
Grain/ear	$= .75 + .010GD - .00094GD^2$	95.1	155.4
	$= .73 - .00028AD + .000000039AD^2$	90.9	79.5
Weight/grain	$= 51.6 - .58GD - .0028GD^2$	76.4	6.5
	$= 48.3 - .018AD + .0000044AD^2$	88.0	14.6
Grains/ear	$= 13.4 + .73GD - .031GD^2$	82.8	9.6
	$= 16.6 - .0024AD - .000000044AD^2$	78.6	7.4
Height	$= 90.1 + .17GD - .042GD^2$	57.4	1.3
	$= 94.2 - .073AD + .000033AD^2$	85.6	6.0

PRIOR A

		R^2(%)	V.R
D.M./m^2	$= 705.9 + 13.4GD + .73GD^2$	77.2	45.7
	$= 900.3 + .44AD - .000045AD^2$	73.9	38.2
Grain/plant	$= 26.7 - 2.36GD + .051GD^2$	98.1	698.3
	$= 11.0 - .013AD + .0000026AD^2$	43.5	1.0
Grain/m^2	$= 286.8 + 11.2GD + .045GD^2$	63.1	23.1
	$= 391.6 + .16AD - .000018AD^2$	56.3	17.4
H.I.(%)	$= 41.7 + .39GD - .018GD^2$	43.0	10.2
	$= 43.4 - .0030AD + .00000040AD^2$	36.8	7.9
Ears/m^2	$= 664.5 - 89.7GD + 4.86GD^2$	76.9	26.7
	$= 383.8 + .73AD - .000049AD^2$	82.3	37.1
Grain/ear	$= .89 + .010GD - .0011GD^2$	93.5	115.0
	$= .87 - .00038AD + .000000061AD^2$	92.4	96.9
Weight/grain	$= 29.9 + 1.77GD - .064GD^2$	97.4	74.6
	$= 38.8 - .0019AD - .00000045AD^2$	65.7	3.8
Grains/ear	$= 27.2 - .48GD - .0049GD^2$	97.9	94.9
	$= 23.4 - .012AD + .0000024AD^2$	90.7	2.0
Height	$= 94.5 + .52GD - .056GD^2$	56.1	1.3
	$= 91.6 + .01AD - .000014AD^2$	79.4	3.8

DRAKE

		R^2(%)	V.R
D.M./m^2	$= 622.1 + 17.2GD + 1.06GD^2$	88.6	104.4
	$= 863.1 + .74AD - .00011AD^2$	1.5	59.6
Grain/plant	$= 21.2 - 1.76GD + .037GD^2$	98.6	919.5
	$= 9.36 - .010AD + .0000021AD^2$	47.9	12.4
Grain/m^2	$= 207.5 + 15.5GD + .19GD^2$	86.8	88.6
	$= 356.4 + .32AD - .000049AD^2$	75.4	41.3
H.I.(%)	$= 34.5 + 1.01GD - .029GD^2$	73.8	37.9
	$= 40.7 + .0016AD - .00000050AD^2$	5.3	.7
Ears/m^2	$= 637.3 - 98.7GD + 5.38GD^2$	93.0	105.6
	$= 352.9 + .78AD - .000048AD^2$	96.4	215.5
Grain/ear	$= .86 + .027GD - .0016GD^2$	91.4	84.5
	$= .97 - .00039AD + .000000059AD^2$	91.4	85.0
Weight/gain	$= 37.4 + .47GD - .033GD^2$	99.8	961.1
	$= 38.8 - .0096AD + .0000015AD^2$	98.9	178.4
Grains/ear	$= 22.5 + .53GD - .028GD^2$	98.7	152.5
	$= 24.6 - .0052AD + .00000068AD^2$	94.9	36.9
Height	$= 103.0 + .73GD - .062GD^2$	99.0	98.1
	$= 105.4 - .03AD + .0000094AD^2$	99.4	180.8

PRINCESS

							R^2(%)	V.R.
D.M./m^2	=	617.1	+	35.0GD	+	.18GD^2	77.0	45.1
	=	913.4	+	.68AD	−	.00012AD^2	70.7	32.6
Grain/plant	=	19.5	−	1.57GD	+	.032GD^2	98.7	1059.2
	=	8.82	−	.0098AD	+	.0000020AD^2	50.5	13.8
Grain/m^2	=	180.6	+	21.7GD	−	.26GD^2	64.2	24.2
	=	336.2	+	.24AD	−	.000044AD^2	51.5	14.4
H.I.(%)	=	30.8	+	.92GD	−	.030GD^2	42.7	10.0
	=	36.1	−	.00025AD	−	.00000020AD^2	10.8	1.6
Ear/m^2	=	413.5	−	24.8GD	+	2.23GD^2	89.3	66.6
	=	467.9	+	.56AD	−	.000063AD^2	89.3	67.8
Grain/ear	=	.79	+	.0081GD	−	.00079GD^2	76.0	25.4
	=	.77	−	.00025AD	+	.000000038AD^2	70.4	19.1
Weight/grain	=	36.4	+	.080GD	−	.010GD^2	84.1	10.6
	=	36.0	−	.0030AD	+	.00000037AD^2	77.2	6.8
Grains/ear	=	22.4	−	.16GD	−	.0058GD^2	79.9	7.9
	=	21.3	−	.0089AD	+	.0000021AD^2	87.9	14.5
Height	=	93.7	+	.79GD	−	.049GD^2	63.4	1.7
	=	98.8	−	.037AD	+	.000016AD^2	75.0	3.0

PROCTOR

D.M./m^2	=	562.0	+	37.3GD	−	.088GD^2	89.2	111.7
	=	866.6	+	.55AD	−	.000094AD^2	74.6	39.5
Grain/plant	=	18.4	−	1.47GD	+	.030GD^2	98.7	1024.1
	=	8.39	−	.0093AD	+	.0000019AD^2	51.1	14.1
Grain/m^2	=	109.4	+	36.4GD	−	.88GD^2	85.6	80.6
	=	336.3	+	.20AD	−	.000049AD^2	40.6	9.2
H.I.(%)	=	26.5	+	2.07GD	−	.071GD^2	94.6	235.7
	=	37.7	+	.00048GD	−	.0000011	57.4	18.2
Ears/m^2	=	237.7	+	17.6GD	+	1.02GD^2	93.3	111.9
	=	606.9	+	.59AD	−	.000081AD^2	86.6	51.6
Grain/ear	=	.97	−	.026GD	+	.000077GD^2	95.5	168.2
	=	.66	−	.00025AD	+	.000000037AD^2	74.1	22.9
Weight/grain	=	38.2	−	.241GD	−	.0052GD^2	87.0	13.4
	=	35.6	−	.0055AD	+	.00000080AD^2	73.7	5.6
Grains/ear	=	26.3	−	.75GD	+	.0084GD^2	95.2	39.8
	=	21.1	−	.0086AD	+	.0000017AD^2	74.7	5.9
Height	=	85.1	+	1.20GD	−	.071GD^2	98.3	57.3
	=	89.6	−	.020AD	+	.0000046AD^2	94.2	16.2

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