MISCELLANEOUS SERIES

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THE CONTRIBUTION OF SOME PHOTOSYNTHESISING PLANT ORGANS TO GRAIN YIELD IN WHEAT

7. 0. 0.

INTRODUCTION

The grain yield of any cereal crop is determined by at least two sets of factors. The first consists of those factors which result in the net gain between photosynthesis and respiration. The second consists of those factors which determine the relative distribution of the assimilates formed. Archbold and Mukergee (1942) and Thorne (1962, 1965) have each demonstrated that photosynthesis and translocation after emergence of the inflorescence are key factors in determining grain yield in cereals. At this stage of plant development the youngest and most actively photosynthesising tissue is the last formed or flag leaf and its sheath; the peduncle or top internode of the inflorescence and the tissue of the floral parts of the inflorescence, each of which, including the young grain, is photosynthetically active. Blake (1967) considered, on the basis of available literature, that up to 90% of the dry matter in the grain at maturity is the result of photosynthesis in the flag leaf, the peduncle and the tissue of the inflorescence.

The relative contribution to grain yield of each of these organs individually has been the subject of extensive research, and has been shown to vary with the technique used for determination, and/or with seasonal conditions (Kriedemann 1965), with light intensity (Carr and Wardlaw 1965), with temperature (Hsia, Wan and Wang 1963), and with

cultivar (Chester 1945). In the literature three major experimental techniques have been used by research workers to determine the relative contribution of individual plant organs to grain yield. These are shading, clipping of components and the use of carbon isotopes to determine the pattern and/or rate of distribution of assimilates. Each technique has its critics, the most common criticisms being excessive alteration of the micro-environment of the plant tissue during treatment, and compensation by remaining photosynthetic tissue for shaded or removed organs (Puckridge 1968).

In view of substantial differences in arrangement in depth of plant organs down the plant profile, hereafter referred to as spatial arrangement of organs and the dimension of some components, e.g., the peduncle, (Plate 12) between short stature and standard height cultivars, an experiment was designed to determine if significant differences exist in the supply of assimilates from the various organs of the plant culm between cultivars of different stature.

PLATE 12

A full dwarf at anthesis showing the extreme abbreviation of the peduncle.

EXPERIMENTAL METHODS

7. 1. 0.

Two cultivars, Gamut and Mexico 120, a standard height and dwarf type respectively, were grown in the field in 30 cm. diameter pots (3 plants per pot and 40 pots per cultivar arranged in 4 rows of 10 pots for each cultivar) containing sand with a full nutrient solution (Long Ashton Solution B, described previously in the text) applied twice weekly. The same cultivars were also grown in adjoining field blocks of ten rows 18 cm. apart by 15 m. in length for each cultivar. In both field plots and pots, nine days after first visible anthesis had occurred for each cultivar, treatments were applied to all organs on a "per plant" basis as follows.

Treatments

1. Ears of the awned cultivar Mexico 120 were clipped to remove all awns.
2. Ears of both cultivars were shaded by enclosing in glassine paper envelopes which had been previously spray-painted with grey lacquer and tested for light exclusion, so that less than 900 f.c. could be recorded by a lightmeter inside the envelope when outside intensity was in excess of 10,000 f.c. The envelopes were attached over the wheat ears to the top of the peduncle with paper clips to provide some ventilation, whilst at the same time preventing entry of light.
3. Flag leaves were removed at the ligule.
4. Peduncles were wrapped in aluminium foil.
5. All leaves below the flag leaf were removed by clipping at the ligule.
6. Controls, selected at random and tagged for identification at maturity.

These treatments were applied at random amongst pots and plants in the field. As the number of tillers on the two cultivars in the field and in pots differed, and individual plants were difficult to identify, tiller numbers rather than plants were counted for each treatment and are recorded in Table 41.

At the time treatments were imposed green leaf area (excluding flag) and flag leaf area on a "per plant" basis was measured on ten plants randomly selected from each site and from each cultivar. Ten days and fifteen days after the treatments were imposed light values over the depth of the plant profile for each cultivar at both sites was determined with a Megatron type light meter (model E1) in the following manner. Recordings on both days were made between 10.00 a.m. and 10.30 a.m. and 2.00 p.m. and 2.30 p.m. by randomly selecting plants and placing the probe at the middle of the peduncle, on the leaf blade immediately below the flag leaf, (approximately 1/3 down the plant profile) and at the first distinct node which could be felt above soil level (approximately 2/3 down the plant profile). Twelve readings for each position at each sampling were recorded (on both days light flux was in excess of 10,000 f.c.).

At maturity ears were harvested individually, threshed singly on a rubbing board and hand winnowed. The grain from each ear was finally hand cleaned and after drying for 24 hours at 110°F was weighed and counted.

RESULTS

7. 1. 1.

The mean green leaf, flag leaf and total leaf areas for each cultivar and site at anthesis are recorded in Table 39.

TABLE 39

LEAF AREAS PER PLANT AT ANTHESIS (MEAN OF TEN PLANTS)

Site	Cultivar	Leaf Area (cm^2)		
		Green	Flag	Total
Field	Gamut	113	47	160
"	Mexico 120	109	72	181
Pots	Gamut	85	40	125
"	Mexico 120	90	47	137
5% Studentized Range for cultivars and sites (Appendix 65)		15.7	7.5	19.4

To examine the question of the different percentages of flag leaf to total leaf area in the two cultivars the percentages were subjected to an arc sine $\sqrt{\text{percentage}}$ transformation (Snedecor & Cochran 1967). The resulting "t" - test performed on the differences between means was non significant in the pots but under field conditions the percentage of flag leaf was significantly greater ($P < 0.01$) in Mexico 120 than in Gamut.

The overall site effect on total leaf area was significant ($P < 0.001$). The cultivar x sites interaction was non significant and this is borne out by separate tests for each cultivar where the total leaf area under field conditions was significantly greater, ($P < 0.05$ in both cases) for each cultivar than that under pot conditions. If each site is examined separately the differences between cultivars at each site was non-significant.

In Table 40 the light values measured at three levels down the plant profile are listed. These values are the arithmetic means of all recordings, i.e., twelve measurements per cultivar per site at two sun inclinations over two days. The variability between readings of this nature is considerable as consecutive readings may range from one in direct sunlight to one which is heavily shaded by leaves higher in the profile.

TABLE 40

MEAN LIGHT VALUES RECORDED ON PLANTS IN POTS AND IN THE FIELD (f.c.)

Cultivar	Position of Recording in Canopy Profile	Light Value Field	Pots
Gamut	Against the top of the peduncle. (Top Profile)	10,000	10,000
	At the leaf blade immediately below the flag leaf. (Mid Profile)	2,830	7,435
	At the first distinct node above soil level. (Lower Profile)	850	7,165
Mexico 120	Against the top of the peduncle. (Top Profile)	10,000	10,000
	At the leaf blade immediately below the flag leaf. (Mid Profile)	2,300	7,640
	At the first distinct node above soil level. (Lower Profile)	1,425	5,460

5% Studentized Range in Lower Profile (Cultivars) = 587

(Sites) = 584

5% Studentized Range in Mid Profile (Cultivars) = 625

(Sites) = 625

Analysis of variance for all data from the mid and lower profiles demonstrated that sites and profiles were both statistically significant ($P < 0.001$) (Appendix 66). Because of the interest in the significant site x cultivar interaction ($P < 0.05$), and the presence of a significant ($P < 0.001$) three factor interaction (sites x cultivars x

profiles) in the overall analysis, the data were analysed separately at each of the two profiles (mid and lower) and the interpretations made of the cultivar x site interaction will thus be pertinent only to that particular profile.

In the two separate profile analyses differences in light values between plants in the field and in pots were highly significant ($P < 0.001$) (Appendices 67 and 68). In the lower profile (Appendix 68) examination of the significant ($P < 0.001$) site x cultivar interaction table indicated that in the field available light was greater in Mexico 120 than in Gamut although the difference was not significant. In the pots light values in Gamut were significantly ($P < 0.01$) greater than in Mexico 120. Thus the significant interaction indicates that the increase in available light between field and pots is less in the lower profile for Mexico 120 than for Gamut and that in a crop community the higher leaves of Gamut are more effective in shading the lower profile than those of Mexico 120. In the mid profile, analysis of variance failed to establish significant statistical differences between cultivars or significant cultivar x site interactions (Appendix 67).

Average grain weight and grain number per ear for each treatment is recorded in Table 41.

TABLE 41

GRAIN WEIGHT AND NUMBER PER EAR AND NUMBER OF TILLERS TREATED

(% REDUCTION IN PARENTHESIS)

Site	Cultivar	Treatment	Tillers Treated	Grain Wt. (g)		Grain No.	
Field	Gamut[1]	Control	39	1.73		37.4	
		Flag Clipped	27	1.26	(27.2)	38.0	
		Clipped Below Flag	22	1.40	(19.1)	36.8	(1.6)
		Ears Bagged	20	1.37	(20.8)	36.7	(1.8)
		Top Internode Wrapped	44	1.60	(7.5)	39.8	
"	Mexico 120	Control	39	1.53		36.8	
		Flag Clipped	33	1.44	(5.9)	38.4	
		Clipped Below Flag	35	1.18	(22.9)	34.7	(5.7)
		Ears Bagged	22	1.35	(11.8)	37.4	
		Top Internode Wrapped	27	1.55		38.1	
		Awns Clipped	41	1.42	(7.2)	37.9	
Pots	Gamut	Control	14	1.49		35.7	
		Flag Clipped	60	1.30	(12.8)	34.6	(3.1)
		Clipped Below Flag	34	1.35	(29.5)	33.3	(6.7)
		Ears Bagged	31	1.12	(24.8)	35.7	
		Top Internode Wrapped	50	1.20	(19.5)	36.0	
"	Mexico 120	Control	35	1.23		34.6	
		Flag Clipped	66	1.32		33.5	(5.2)
		Clipped Below Flag	35	1.08	(12.2)	30.2	(12.7)
		Ears Bagged	35	1.10	(10.6)	34.0	(1.7)
		Top Internode Wrapped	80	1.37		35.9	
		Awns Clipped	50	1.20	(2.4)	31.4	(9.2)

1. Gamut Ears are Tip-awned only

5% Studentized Range	Treatments	0.07	1.08
"	" Cultivars	0.03	0.49
"	" Sites	0.03	0.49

As the number of organs treated was variable, analyses of variance were conducted on a sample of ten ears randomly drawn from each cultivar x site x treatment combination (Appendix 69a and b). If multiple range tests are carried out on the means of the five treatments within the Gamut field trial (Appendix 70), the reduction in grain weight divides the five treatments into four groups which are all significantly different at the 5% level, viz., [flag leaf clipped (1.25)], [ear bagged (1.37) and clipped below the flag leaf (1.40)], [top internode wrapped (1.60)], and [control (1.72)]. Thus the largest reduction in grain weight for the cultivar Gamut results from the removal of the flag leaf. This is a smaller flag leaf than that of Mexico 120 (Table 39) but is very advantageously positioned in a crop to intercept light during a long period of the day. Covering of Gamut ears which are particularly well situated for light interception because of characteristically long peduncles resulted in substantial loss in grain weight, and it appeared that in this cultivar the ears made a major contribution towards final grain dry weight. The contribution of the top internode in Gamut in these data is less than the other treatments which is surprising in view of the extreme length of the internode (approximately 30 cm.) and its favourable position for light interception. Removal of the leaves below the flag leaf also resulted in substantial loss in grain weight. In the poor light regime (850 f.c.) available to these lower leaves this result is difficult to explain and suggests that under normal circumstances there may occur some redistribution of assimilates from the older leaves during senescence.

Multiple range tests carried out on the means of the six

treatments within the Mexico field trial (Appendix 71) divided the treatments on the basis of grain weight reduction into five groups all of which were significantly different, viz., [clipped below the flag leaf (1.18)],[ears bagged (1.36)], [awn clipped (1.41)], [flag leaf clipped (1.44)] and finally [control (1.52) and top internode wrapped (1.54)]. The largest reduction in grain weight resulted from removal of leaf tissue below the flag leaf. Removal of the flag leaf or awns, bagging of ears, or wrapping of the top internode had a minor effect on grain weight relative to the effect of clipping below the flag. Thus the relative contribution by the plant components of the cultivar Mexico 120 differed from Gamut particularly in the role played by the lower leaves, which in the short stature wheat remained functional longer and experienced a slightly better light regime (1425 f.c.).

In pots where the light regime available to the lower plant profile is superior to the field situation the relative contribution by organs changed. For the Gamut pot trial (Appendix 72) multiple range tests divided the five treatments into three groups, viz., [ears bagged (1.13) and top internode wrapped (1.13)], [flag leaf clipped (1.29) and clipped below the flag leaf (1.35)], and [control (1.45)]. In pots the ear and top internode of Gamut made major contribution towards grain weight and the dependence on the flag leaf for grain photosynthates, which was demonstrated in the field decreased, indicating a "compensatory ability", as suggested by Wardlaw, Carr and Anderson (1965) on the part of the organs to fill the deficit caused by loss of the flag leaf. The relatively insignificant contribution by the top internode under field conditions and its apparent significance under pot

conditions may be the result of smaller leaf areas of plants in the pots and an observed faster rate of leaf senescence than in the field.

For the cultivar Mexico 120 in pots (Appendix 73) no statistically significant treatment effects could be demonstrated.

In terms of grain number per ear no significant statistical differences could be demonstrated between treatments for the cultivar Gamut under field conditions (Appendix 74). For the short stature cultivar Mexico 120 under field conditions multiple range testing of the means of the six treatments (Appendix 75) established a reduction in grain number, resulting from the clipping bleow the flag leaf treatment which was statistically significant at the 5% level from all other treatments. Under pot conditions reduction in grain number per ear as a result of clipping below the flag leaf was similarly established for Gamut, viz., [clipping below the flag leaf (33.12)], [flag leaf clipped (35.66), control (35.79), ears bagged (35.81), and top internode wrapped (36.16)] (Appendix 75). This inference, however, must be viewed with a degree of caution since [clipped below the flag, flag leaf clipped, control and ear bagged] also form one group which is significantly less (at the 5% level) than [top internode wrapped].

For Mexico 120 in pots multiple range testing of the means of the six treatments divided these into two distinct groups which were significant at the 5% level, viz., [clipped below the flag leaf (31.08) and awns clipped (32.88)], and [ears bagged (34.11), control (34.22), flag leaf clipped (34.37, and top internode wrapped (34.67)], (Appendix 77). The mechanism for such reduction in grain number per ear resulting

from clipping below the flag leaf is difficult to explain, as it implies either early abortion or cessation of grain development shortly after application of treatments. Although both phenomena are common in legumes, neither has been previously reported to the knowledge of the author in temperate cereals.

7. 1. 2.

In the literature most research workers have studied the contribution by various plant organs to grain development in clipping or shading experiments with a single cultivar in one environment. Most commonly the environment chosen has been a pot trial under greenhouse conditions and the cultivar has been of normal stature. The present data indicate the importance of the environment x cultivar x relative contribution interaction, as evidenced by different results between field and pot conditions and between cultivars.

Under field conditions, Gamut responded to removal of various photosynthesising tissues in accordance with the general findings of other research workers. Major dependence on flag leaf and inflorescence tissue was indicated. The apparent role of the top internode however, was surprisingly small in these data, particularly in view of its exaggerated length in this cultivar. The data also indicated a significant contribution to grain development by leaf tissue below the flag leaf. Under pot conditions grain filling in Gamut was dependent on the inflorescence tissue and, in contrast to the field, on the top internode. The order of importance of organs in contribution under pot conditions was that commonly recorded in the literature, i.e., inflorescence tissue, top internode and flag leaf.

In the field the contribution pattern of the short stature wheat, Mexico 120 differed from that of Gamut. The importance of leaf tissue below the flag leaf and top internode was demonstrated. Under

pot conditions no significant differences between treatments could be demonstrated for this cultivar suggesting that complete compensation is possible in this cultivar when the canopy is adequately illuminated.

The difference in the pattern of the contribution of both cultivars to clipping and shading under field and pot conditions indicates the importance, in terms of grain development, of light distribution over the full plant canopy. Examination of the distribution of light in the field suggest that the taller cultivar is more efficient in intercepting light in the upper leaves, the result of which is a lower light intensity on the older leaves. For a plant in isolation such an arrangement for light interception could be regarded as efficient, as it concentrates solar energy in most active photosynthesising tissue. As such it indicates strong competitive ability for that cultivar. In a community however, it results in encroachment into the environment of its neighbours, or "intra-genotypic" competition for light (Donald 1968).

In the short stature cultivar under field conditions more light is able to penetrate to the lower leaves. As a consequence the short stature wheat, although possessing a lower shading ability than the taller wheat, for a comparable leaf area, may exert a lower degree of "mutual interference" in a community. The result of this reduced interference may be a higher grain yield under conditions when other components of the environment are not limited.

These data indicate several important physiological phenomena. Firstly they suggest the strong "compensatory ability" of organs from

the one plant to increase production or distribution of photosynthates if the photosynthesis of any one organ is limited by an external factor. This would tend to support the contention of Wardlaw (1971) that the cereal plant may be "over-endowed" with photosynthetic capacity in many environments where ultimate yield is restricted by a deficiency of one or more other factors. Secondly, these data indicate the possibility of a more significant role for those leaves below the flag leaf in grain development in the case of some cultivars than that generally accredited to them, and the varietal nature of dependence on any one organ or group of organs. Finally, the data emphasise substantial differences in light availability in the lower leaf canopy between pot and field conditions. As much of the research data in the literature is the result of pot trials this last factor was influential in conducting a field trial to determine the contributory role of awns which is described in the following section.

THE CONTRIBUTION OF AWNS TO GRAIN DEVELOPMENT

7. 2. 0.

The majority of research papers indicate a slight advantage in grain weight for awned as opposed to awnless wheat spikes; however, the contribution of the awn to grain filling has remained a matter of some contention between research workers, particularly in more arid environments. Vogel et al. (1963) and Krause (1966) have stressed the important role of awns in regard to short stature wheats although neither author has quoted any supporting quantitative data.

Awns are reduced leaf blades of which little more than the midveins remains. As a result of their structure they have been credited with marked xero-morphic characteristics (Van de Sande Bakhuyzen 1937). The surface area of awns on any awned cultivar is considerable although length of awns is a varietal characteristic. In relation to other photosynthetic activity during the period of grain development, and coupled with its favourable location to intercept solar radiation, it might be expected that awns play a major contributory role in the development of the grain. Lamb (1967), in fact, when reviewing the role of awns in wheat, concluded that the contribution to total grain weight made by the awns was in the order of 41% of that of the entire spike. To obtain more definite information on this question a range of short stature and standard height cultivars was selected to determine (1) if loss of awns by clipping at anthesis caused significant reduction of yield either as a result of lower final grain weight or grain numbers in awned wheats generally, under simulated crop conditions, and (2) if short stature wheats responded to a different degree to standard height cultivars, as a result of this treatment.

7. 2. 1.

Plots of the cultivars listed in Table 42 were sown in a randomised block design with four replications on 12. June 1968.

TABLE 42

CULTIVARS USED IN AWN CLIPPING EXPERIMENT

Cultivar	Classification
Mexico 120	Mexican Dwarf — *T. Aestivum*
Pitic 62	Mexican Semi-Dwarf — "
Chile 1B	" " " — "
Funello	Italian " " — "
Timgalen	Australian Standard Height — "
Spica	" " " — "
Dural	" " " — (*T. durum*)

Each plot consisted of a small block, four rows wide, each 18 cm. apart x 15.0 m. in length, with an interplot space between cultivars of 53 cm. A compound fertilizer (20-11-0) was applied at sowing at the rate of 250 Kg/ha. The trial was spray irrigated on 15. August and 21. September when the plants were actively tillering and "ear-peeping" respectively.

At the stage of early anthesis for each cultivar in each replication one hundred spikes were randomly selected from the two

inner rows of each plot and labelled. The awns on these spikes were removed at the top of each spikelet with surgical scissors. At the same time an equal number of spikes of each cultivar was labelled for subsequent identification to serve as controls.

At maturity treated spikes and untreated controls were harvested and oven dried at 110°F for 24 hours. Subsequently, for each plot, spikes were randomly placed into groups of ten, each of which was carefully hand threshed and weighed. The sum of the ten groups was used to provide the recorded weight of grain per 100 spikes for each replication. Seed counts on twenty spikes were made for each cultivar in each replication.

During the Seed phase of development it was observed that from the time of anthesis a major difference appeared in the growth of the awns on the cultivar Dural, and those on the other cultivars. In the case of Dural, elongation of the awns appeared to continue well into the Seed phase, whereas in the cultivar Mexico 120 there appeared to be no elongation of awns after early anthesis. In an endeavour to quantify this difference between these cultivars, four ears of near equal length were selected at the stage of ear emergence from each cultivar in an adjoining, but later, sowing. The awns were clipped from each of the heads and total linear length of awn per ear was determined. This was repeated at 5 day intervals over a further 6 harvests.

7. 2. 2.

The mean grain weight and grain number per ear are listed in Table 43.

TABLE 43

MEAN GRAIN WEIGHT AND NUMBER PER EAR FOR AWNED AND DE-AWNED TREATMENTS

Cultivar	Awn Clipped		Control	
	Grain Wt.(g.)	Grain No.	Grain Wt.(g.)	Grain No.
Pitic 62	1.66	38.2	1.79	42.9
Funello	1.59	35.0	1.36	33.1
Spica	1.82	37.2	1.53	34.0
Dural	2.56	42.6	2.36	39.8
Mexico 120	1.59	41.9	1.62	40.3
Chile 1B	1.20	35.4	1.28	33.7
Timgalen	1.07	29.0	1.18	31.9
5% Studentized Range (cultivars)		0.22		0.69
" " (treatments)		0.08		2.33

Analysis of variance demonstrated a significant ($P < 0.05$) treatment x cultivar interaction for grain weight (Appendix 78). Examination of the two-way table of means indicated that the 5% Studentized Range between treatments (i.e., clipped - awned) within cultivars was exceeded only by Funello, Spica and Dural, denoting

statistically significant increase in grain weight as a result of de-awning. It was noted that all remaining clipped v awned comparisons were negative. Although not statistically significant these other cultivars tended to a small but consistent reduction in grain weight as a consequence of de-awning.

Analysis of variance for grain number indicated no significant treatment effect but a significant ($P < 0.001$) effect of cultivars (Appendix 79). When the Student - Neumann Kerls' Test (Steel and Torrie 1960) for multiple range was applied, the group [Timgalen, Funello and Chile 1B] was significantly less than the group [Spica, Pitic, Mexico 120, and Dural]. However, [Funello, Spica, Chile 1B and Dural] were also considered as a group at the 5% level.

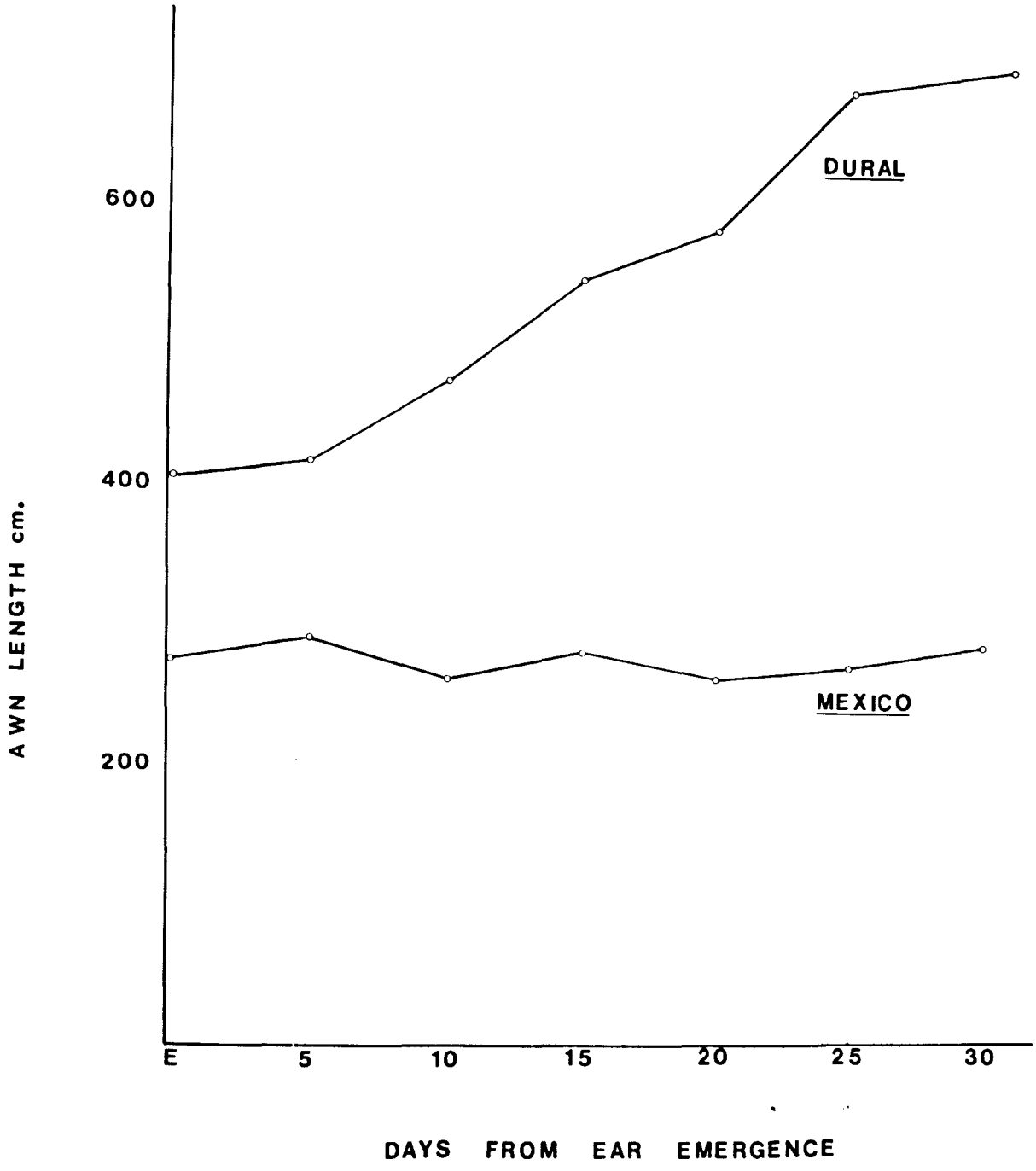
Attempts to establish statistically significant reduction in grain weight as a consequence for de-awning for the cultivars Chile 1B, Mexico 120, Pitic 62 and Timgalen were made by partitioning the data on the basis of a common factor in pedigrees for Dural, Spica and Funello, i.e., Triticum durum. These were not successful (Appendix 80). Further, partitioning the between treatment within pedigree sum of squares (4018.57 on 2 df) with single degrees of freedom given by between treatments with durum (3432.04 on 1 df) plus between treatments within aestivum (586.53 on 1 df) indicated that between treatments in durum is significant ($P < 0.001$) and the between treatments in aestivum is not significant.

The results of measurement of awn length development for Mexico 120 and Dural in the adjoining plots are illustrated on the basis of total

linear length per ear at each harvest in Figure 14 and recorded in Appendix 81. If simple linear regression of total awn length on harvest number is applied to both cultivars separately the slope of Dural is significantly ($P < 0.001$) greater than zero, and the slope of Mexico 120 is not significantly different from zero. This was confirmed by a test of difference between the slopes which was significant ($P < 0.001$). Thus the data indicated a pronounced difference in the pattern of awn elongation between the two cultivars. Awn elongation for Mexico 120 had ceased by the time of ear emergence from the flag leaf. The awns of Dural however continued to elongate until more than twenty five days after emergence from the flag leaf.

FIGURE 14

Linear growth of awns after ear emergence - Mexico 120 and Dural.


AWN LENGTH cm.
600
400
200
DURAL
MEXICO
E
5
10
15
20
25
30
DAYS FROM EAR EMERGENCE

7. 2. 3.

Although no statistically significant differences were found as a result of removing awn tissue from the cultivars Pitic 62, Mexico 120, Chile 1B or Timgalen there appears in the data for these cultivars a consistent (but not significant) trend to a small reduction in grain weight resulting from the loss of the awns as a photosynthesising organ over the major portion of the period for grain development. The magnitude of the reduction however is small despite a comparatively large sample size for each cultivar treated, and emphasises the basis of contention between research findings reported in the literature on the role of awns in grain development. In this experiment supplementary irrigation was used intermittently and at no stage during the life cycle of the plants was moisture stress obvious. In the literature a positive advantage for awns has frequently been associated with semi-arid environments (Leonard and Martin 1963). Thus it is interesting to speculate whether the trend to a reduction in grain weight resulting from loss of awns for these cultivars may have in fact become a significant reduction under conditions of moisture stress. Results for the other cultivars examined, i.e., Dural, Spica and Funello are in marked contrast and demonstrate statistically significant increase in grain weight as an effect of de-awning. Each of these cultivars may possibly have a common factor in its pedigree. Dural is a Triticum durum, whereas both Funello and Spica although specificially Triticum aestivum are each reputed to have a durum wheat in their pedigree. However, considerable caution must be associated with this inference, as on the basis of data derived from

seedling reaction to stem rust, Watson (pers. comm.) queries the validity of the written pedigrees for both cultivars. The inference that there may be a differential response behaviour to de-awning between Triticum durum and Triticum aestivum however warrants further investigation and, in view of the inclusion of a durum parent in the pedigrees of a number of Australian bread wheats (Macindoe and Walkden - Brown 1968), may explain the classification of Derera (pers. comm.) of awns into "positive", "neutral" and "negative" contributors to grain filling.

A mechanism for differential response pattern to de-awning is suggested by the data for comparative development of awn length after ear emergence for the bread wheat Mexico 120 and the durum Dural. It must however, be emphasised that in the interpretation of these data due cognisance be taken of the fact that, despite the same sowing date for both cultivars, there is a difference in time of 24 days in ear emergence. Such a difference means that the earlier parts of the Seed phase were undertaken in different environments for each cultivar, a factor which could be of greater significance in contribution than possible varietal or specific differences.

Blake (1967) suggests that "two critical periods in the life of the wheat plant may be defined when it is most susceptible to water and nutrient stresses". The first is - "immediately before the ear emerges. It is at this stage that the number of fertile florets per spikelet is determined". The magnitude of the awns, as measured by linear length in these data for the cultivar Dural is 2-3 times that of the cultivar Mexico 120. Further, in Dural active growth of the

awns is proceeding from before ear emergence to well after anthesis. Conversely in the cultivar Mexico 120 growth of awn appears to have largely ceased at the time of ear emergence. It may then be inferred from these data that in Dural the awn is a major competitor with the grain for assimilates in the early stages of the Seed phase and may well have a sink capacity of sufficient magnitude to rival the developing grain. Further, competition in the late Reproductive phase between the awn and the developing floret may be part of the explanation for the partial sterility in durum heads which is commonly observed. As a result, when the ear of Dural is de-awned the competition is removed, and more photosynthates are available for grain development.

7. 2. 4.

From the data derived from these experiments, several features are noteworthy. The contribution to grain filling by the leaves below the flag leaf is greater in the case of Mexico 120 than in the standard height cultivar Gamut, which appears to be more dependent on ear tissue for this purpose.

The significance of the contribution to grain filling by the top internode is of very minor consequence in all short stature wheats where its dimension is severely abbreviated. In the standard height type Gamut its significance is variable and it may well be the principal "compensatory tissue" when other photosynthetic area is restricted either by mechanical or environmental means.

The role of awns in grain filling appears to be a varietal characteristic. The contribution of awn tissue may be dependent on the extent of competition which exists between the awns and the developing grains. As a generalisation however, de-awning at anthesis or shortly after results in minor reduction of grain weight.

In the cultivars examined there appears to be a compensatory ability between various photosynthetic tissues to rectify a deficiency in the production of assimilates by one or more organs.

Parts of these data are believed to be of sufficient interest to warrant substantiation on a broader varietal base and subsequent investigation, particularly the relative growth behaviour of awns, between different cultivars after ear emergence.

VARIETAL DIFFERENCES IN ROOT DEVELOPMENT

7. 3. 0.

From the earlier stages of the Growth Analysis experiment described previously it was apparent, that differences existed between the structure of the roots of the short stature wheat Mexico 120 and the standard height Gamut. The roots of the former appeared to be finer in texture, to be much more branched, shallower and to be horizontally rather than vertically distributed in the pots. Conversely, the roots of Gamut appeared to be coarse in texture, to be sparsely branched, deeper, and to be vertically rather than horizontally distributed. This appeared to be a consistent difference between the majority of plants and between harvests of these two cultivars. This is illustrated in Plate 13 which was photographed from flotation tanks out of which the water had been syphoned.

It was also observed, when coleoptile lengths were being studied, that root differences existed between these two cultivars from the earliest stages after germination. By the time of emergence of the first leaf the seminal roots of Gamut were approximately 2 cm. longer, and showed no indication of the development of any laterally oriented roots. At the same stage of development Mexico 120 was beginning to show signs of roots which were markedly orientated in a lateral direction. These differences are illustrated in Plate 14.

Because of these apparent differences in the pattern of root development between the two cultivars an experiment was designed to quantify this difference and to measure the extent to which it was under varietal control.

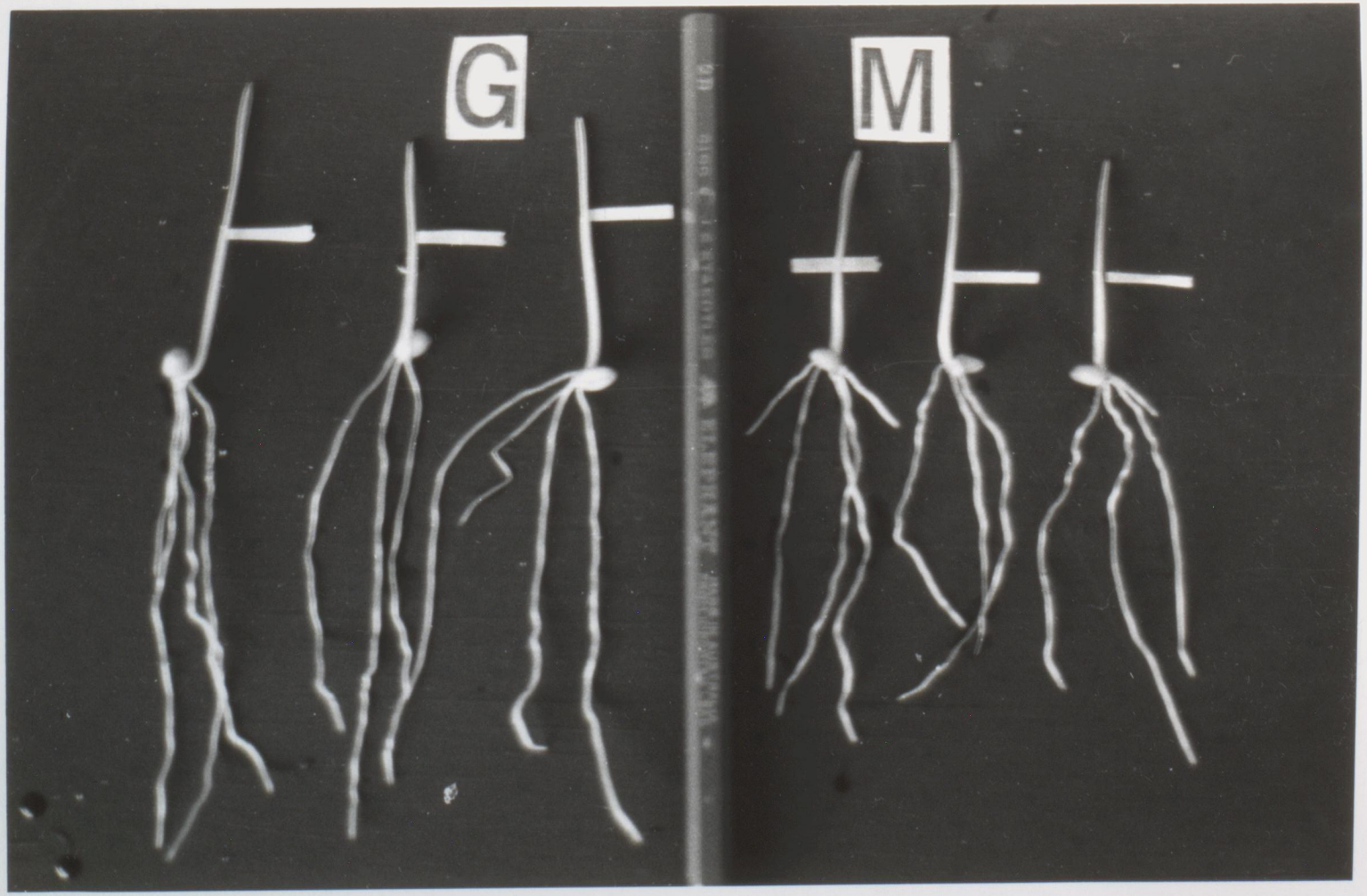
PLATE 13

Roots of wheat plants grown in sand and photographed after washing in a flotation tray.

(Gamut at left - Mexico 120 at right)

PLATE 14

Seedling roots of short (M = Mexico) and tall (G = Gamut) cultivars beginning to show differences in root pattern.


G
M

7. 3. 1.

Troughton and Whittington (1969) state that "lateral root development is genetically controlled and it is possible to recognise specific and varietal differences. Such differences may be exaggerated in cultured roots, or differences in lateral frequency and growth not apparent in whole plants may be revealed in culture." In the absence of facilities and techniques for culture of excised roots an attempt was made to differentiate between the two root systems by growing plants in nutrient solution. Large glass containers were filled with diluted nutrient solution (Long Ashton B) and germinated seedlings were suspended over the solution which was aerated with a fish-tank aerator. The containers were covered in heavy black paper and taped to exclude entry of light through either top or sides. The solution was changed at 7 day intervals under conditions of very low light intensity, after which the containers were resealed.

Excellent plants were produced by this technique but no root differences of any type could be established between the cultivars Mexico 120 and Gamut at any stage of development. An example of the cultivars, at a stage shortly after anthesis is illustrated in Plate 15.

Goedewaagen (1955) reported the results of root investigations which had been conducted in wooden boxes in which one vertical wall was replaced by a glass panel, sloped towards the middle of the base, which allowed visual examination of the root structure against the glass. On the basis of his paper a series of twelve boxes, each divided in half by a steel partition, was positioned in the field, filled with

PLATE 15

Typical root growth of all wheat cultivars when cultured in nutrient solution.

coarse sand and sown 10. September 1969. Three seeds of each cultivar were sown in one half of every box, and after seedling emergence, these were reduced to one plant per half box. Nutrient solution (Long Ashton B) was applied twice weekly at the rate of 400 ml. per plant and measured volumes of water were applied uniformly over each box at two day intervals. These boxes (Plate 16) were 80 cm. long, 30 cm. wide and 70 cm. deep.

The boxes were carefully opened for examination on the last day of each month throughout the life cycle of the plants and then resealed against light entry.

Lack of colour contrast between roots and sand made observation difficult, particularly as the glass stained over time and prevented any photographic record being kept. No difference in pattern of distribution of roots between cultivars could be distinguished by this method in the experiment.

The trial was repeated with freshly sieved, washed sand in the boxes which were modified in the following manner. The divisions were removed and the false glass wall was replaced by a pin-board as described by Schuurman and Goedewaagen (1965). The pin-board was made by inserting 16 cm. steel nails through peg-board on a 5 x 5 cm. grid and subsequently coating nails and boards with fibreglass to retard rusting. Seed of both cultivars was sown on 3. April 1970 and one plant per box was grown to the stage of early anthesis.

A harvest of three boxes of each cultivar was made when the

PLATE 16

Root boxes used to examine differential root distribution.


3
2

plants were in the early tillering stages. The remaining boxes were harvested at the point of "ear peep". The harvests consisted of dismantling the boxes and washing away sand from the pin-board, care being taken not to disturb the pattern of roots in the process. The results from both harvests are illustrated in Plates 17-20 and indicate the tendency towards a superficial root distribution on the part of Mexico 120 as opposed to the deeper root distribution of Gamut.

Finally, an attempt to differentiate the root systems of Gamut and Mexico 120 was made using a modification of the auger method described by Schuurman and Goedewaagen (1965). The technique used was as follows.

At the stage of anthesis 40.0 x 7.6 cm. diameter soil cores were taken from field blocks of each cultivar, Gamut and Mexico 120, at 3 sites, Armidale, Gunnedah and Tamworth. An electric soil-coring hammer was used and in each case the core was positioned as near as possible to 8 cm. from the crown of a wheat plant. At both Armidale and Gunnedah sites the soil was a heavy black clay, whereas at Tamworth it was a red-brown earth also of high clay content. At each site it was found necessary to pre-water soil 48 hours before the removal of cores to allow penetration of the cylinders and removal of the samples, without fracture.

Five cores of both cultivars were taken randomly from each site. On extraction of the core it was layed in longitudinally-halved, terra-cotta pipes and trimmed to a length of 38.0 cm. from the soil surface. Thereafter it was divided into three portions 12.0 cm., 12.0-25.0 cm. and 25.0-38.0 cm.; these were appropriately labelled and dried at 212°F.

PLATE 17

Roots on a pin-board showing a typical distribution pattern for the cultivar Gamut at the stage of early tillering.

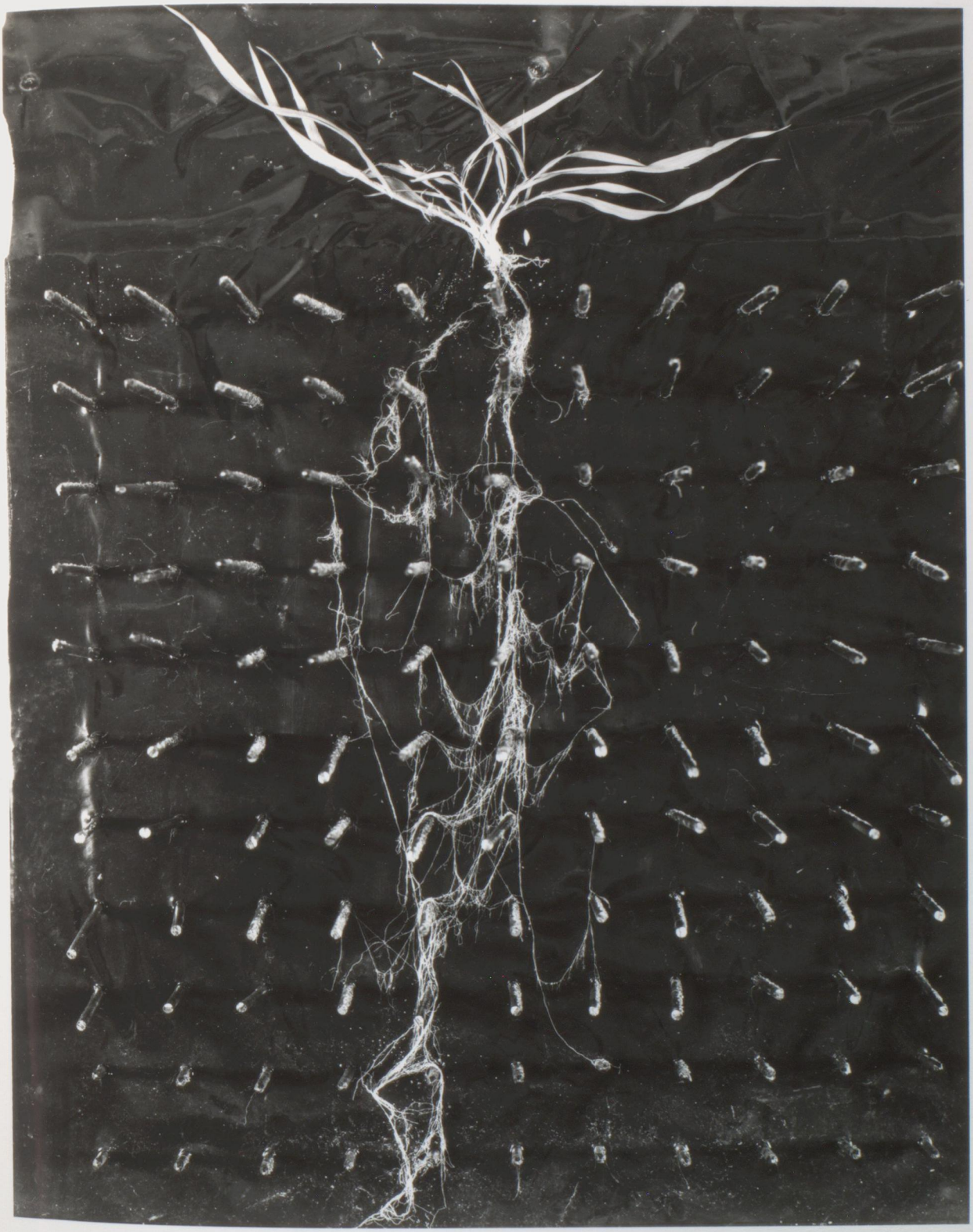


PLATE 18

Roots on a pin-board showing a typical distribution pattern for the cultivar Mexico 120 at the stage of early tillering.

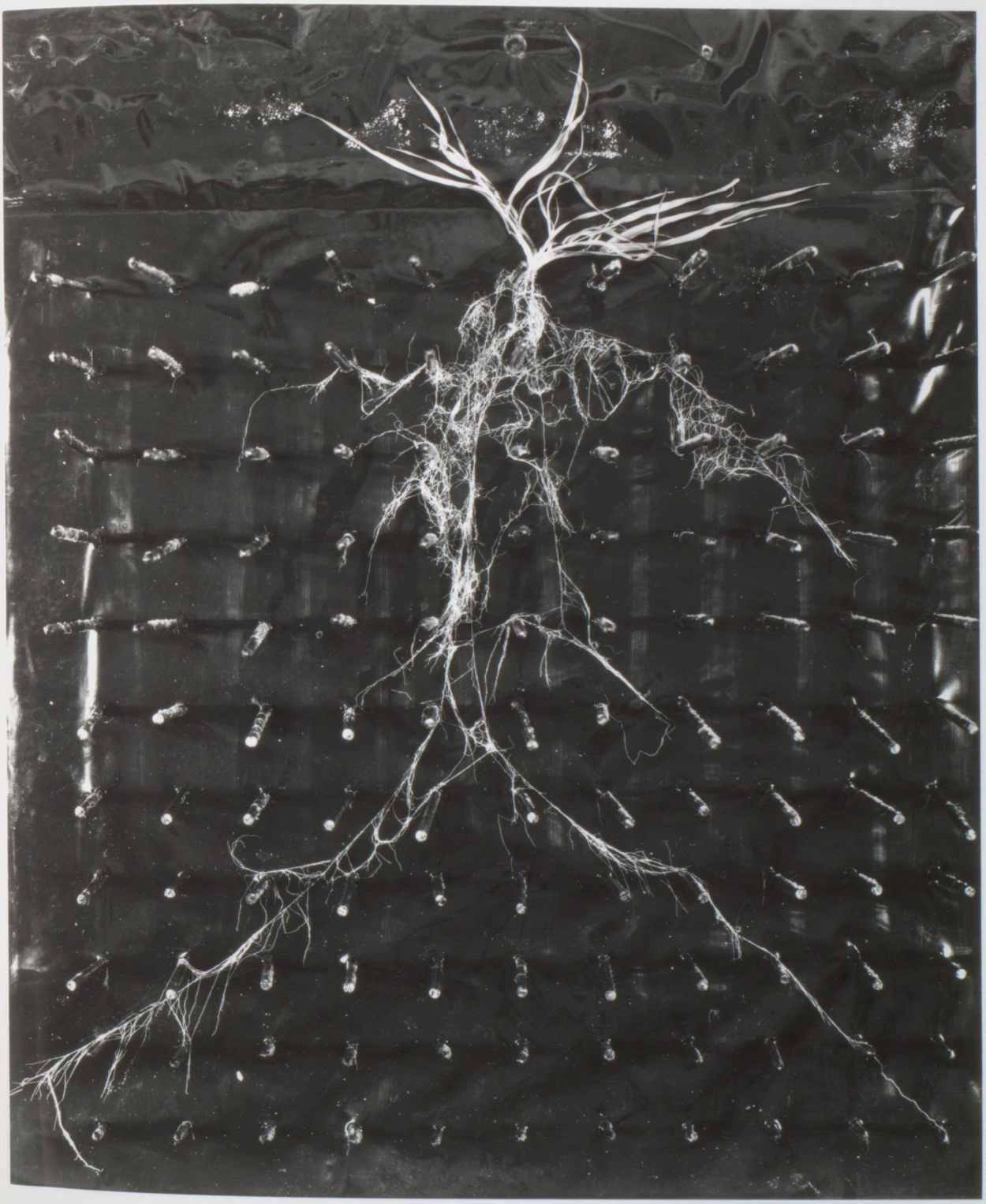
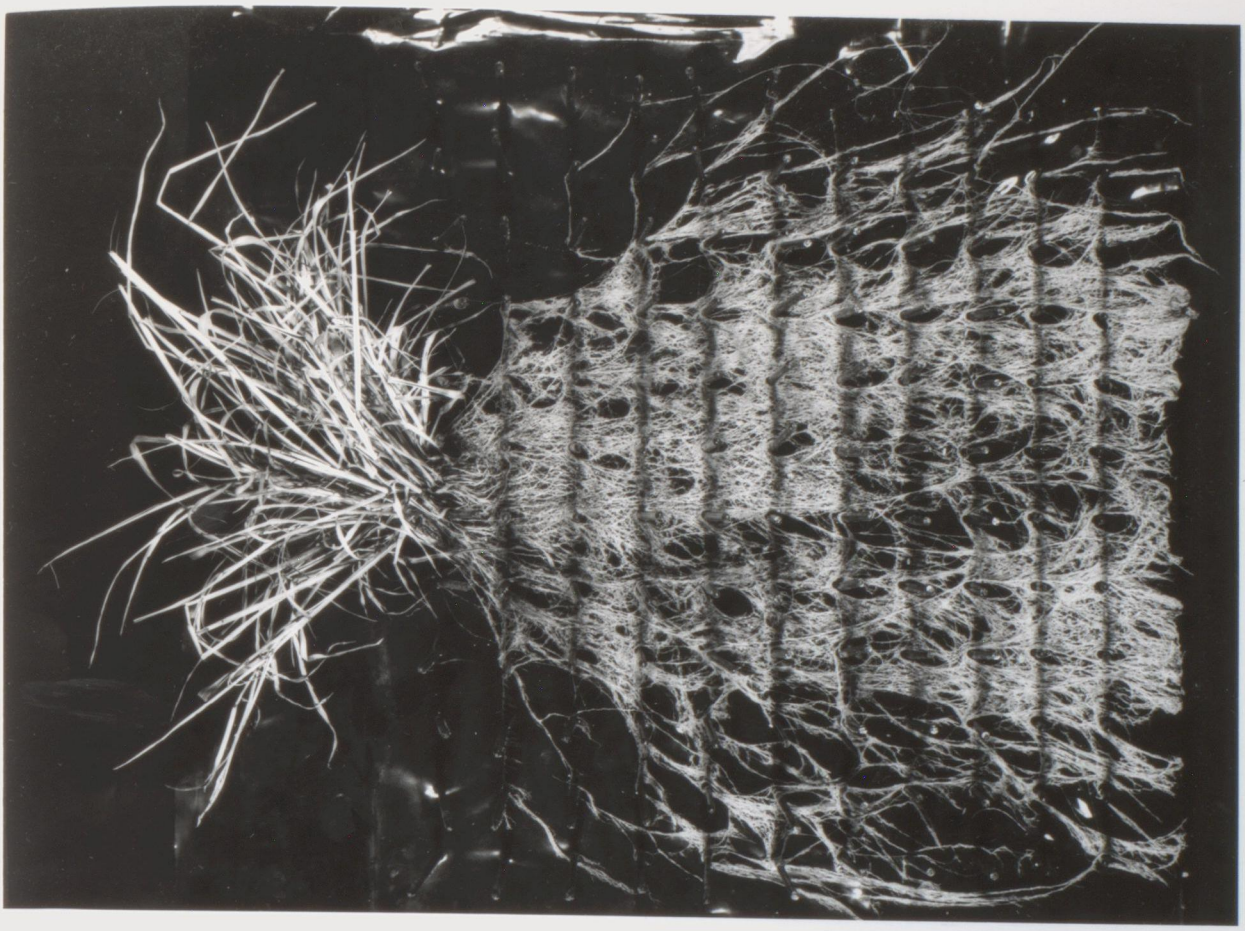


PLATE 19

Roots on pin-boards showing different distribution patterns at the stage of ear peeping.

(Mexico 120 at Top - Gamut Below)

Note - the Gamut ears were broken off by hail.



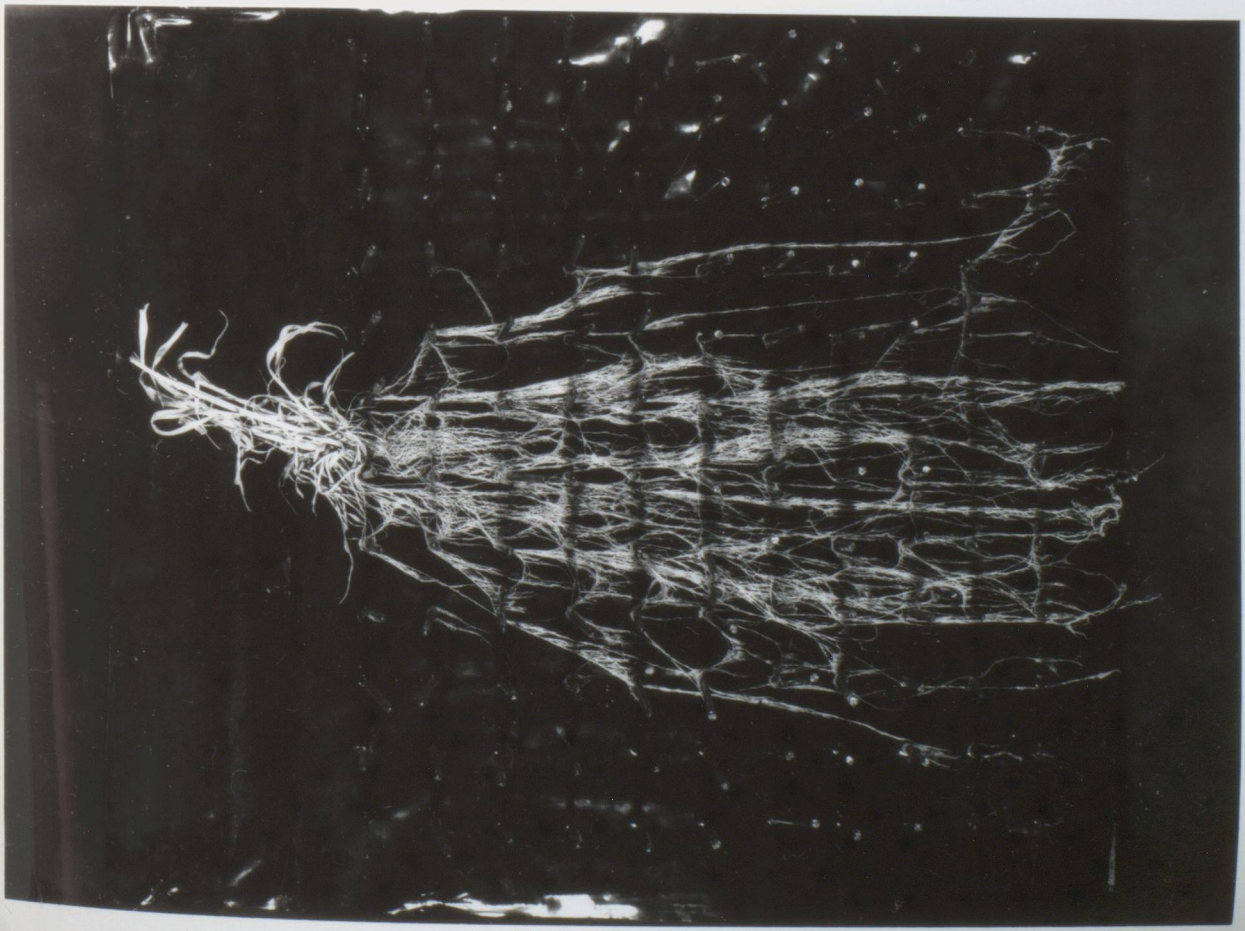
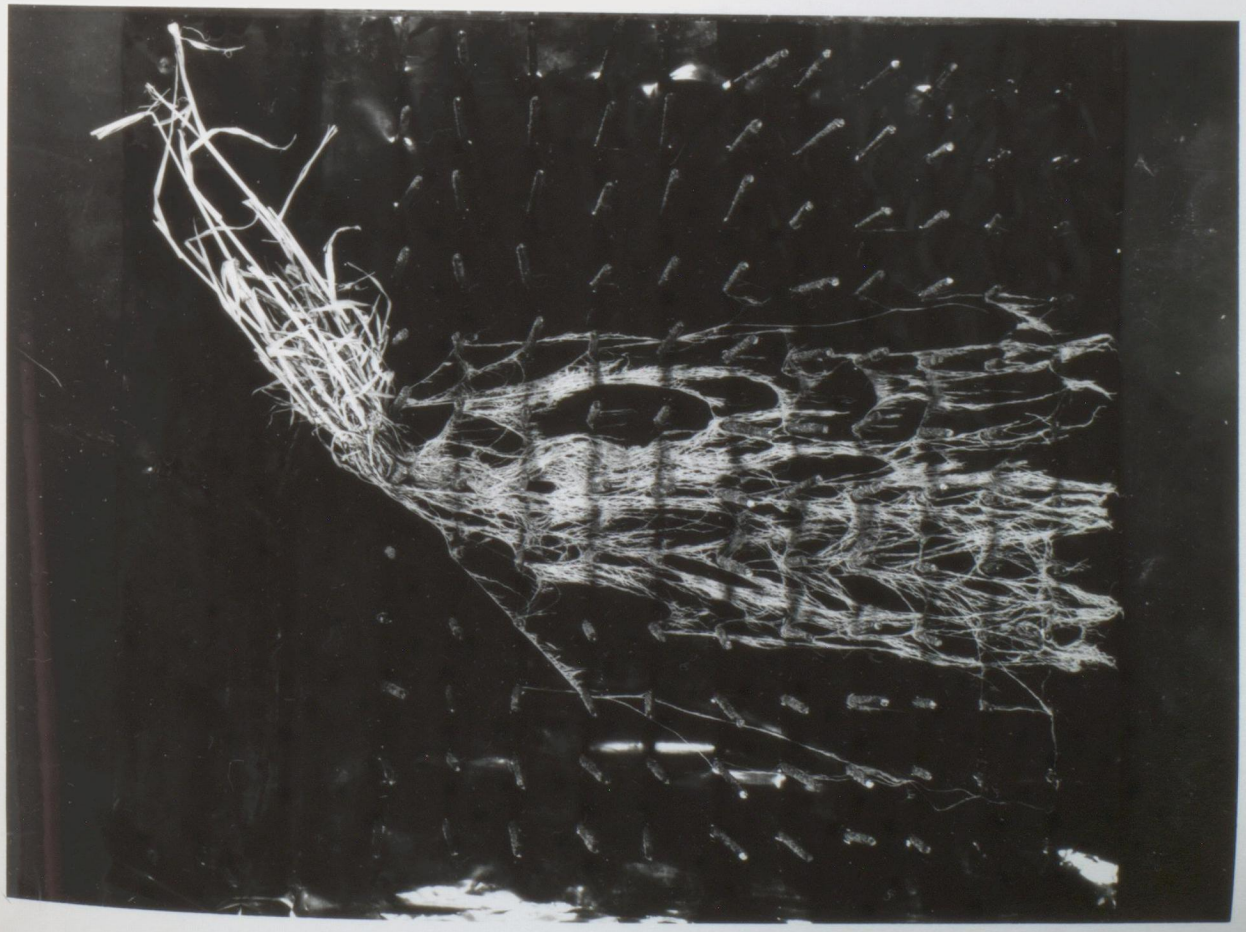


PLATE 20

Roots on pin-boards showing different distribution patterns at the stage of ear peeping.

(Mexico 120 at Top - Gamut Below)

Note - The Gamut ears were broken off by hail.



For analysis the samples were re-wet, clay being dispersed in sodium pyrophosphate solution, then washed, sieved and hand picked, in the manner described by Schuurman and Goedewaagen (1965). No distinction was made during hand-picking between "live" and "dead" root tissue and no ash determinations were attempted. The results are recorded in Table 44.

TABLE 44

ROOT MASS (mgm) FROM SOIL CORES AT THREE DEPTHS

Core Depth	Armidale		Tamworth		Gunnedah	
	Gamut	Mexico	Gamut	Mexico	Gamut	Mexico
0 - 12 cm.	25.5	97.4	66.8	74.0	23.9	33.0
12 - 25	17.3	48.9	96.9	43.1	23.3	34.7
25 - 38	64.0	17.7	53.6	32.6	36.0	31.4
5% Studentized Range						
Cultivars	11.8		18.0		23.5	
Depths	17.7		26.9		35.1	

Analysis of variance for the three sites (Appendix 82) indicated signficance for sites ($P < 0.001$), for cultivar x depth ($P < 0.001$), for cultivar x site ($P < 0.01$), for depth x site ($P < 0.05$) and for cultivar x depth x site ($P < 0.01$) interactions. The cultivar x site interaction table indicated that the cultivars reacted differently at the three sites. At Armidale the root mass of Mexico 120 was significantly greater ($P < 0.05$) than that of Gamut; - at Tamworth it was significantly

inferior ($P < 0.05$) to Gamut; and was not significantly different from Gamut at Gunnedah. The pattern of distribution for both cultivars, (depth x site interaction) was also found to vary between sites. At Armidale root mass in the top profile was significantly greater ($P < 0.05$) than in the mid profile. At Tamworth there was no significant difference between the top and mid profiles both of which were significantly greater ($P < 0.05$) that the lowest profile. At Gunnedah there were no statistically significant differences between profiles.

The three way interaction table for cultivar x depth x site indicated the superiority of root mass for Mexico 120 ($P < 0.05$) in the top profile and inferiority ($P < 0.05$) in the lowest profile at the Armidale site. At Tamworth Mexico 120 was superior ($P < 0.05$) in root mass in the mid profile but inferior ($P < 0.05$) in the lower profile; - in the top profile there was no significant difference between cultivars. At the Gunnedah site Mexico 120 was superior ($P < 0.05$) to Gamut in the mid profile only; in other profiles no significant differences could be demonstrated. Because of the significance of the three way interaction in the overall analysis the data were analysed separately at each site and the interpretations made of the cultivar x depth interactions will thus be pertinent only to that particular site. Further partitioning of the cultivar x site x depth interaction in the above analysis did not seem to be warranted.

At the Armidale site significant varietal differences down the root profile were established by analysis of variance (Appendix 83). Examination of the cultivar x depth interaction indicated that at each

depth the difference in root mass between cultivars was statistically significant. For Mexico 120 there was a decline down the profile from a high root mass in the top 12.0 cm. of the soil to a relatively small root mass in the deepest core. Conversely Gamut increased root mass substantially between the second and third cores suggesting that the major root mass was located in the deepest core of the profile which was examined.

At the Tamworth site there were some similarities in profile root distribution to the Armidale site. For Mexico 120 there was again the greatest root mass per core at the top of the soil profile and a decline to the mid profile, but no statistically significant difference was established between the mid and lowest core (Appendix 84). Gamut produced a root mass in the highest core equal to that of Mexico 120 and increased root mass significantly between the top and mid profile cores. In the lowest core however, root mass had decreased to a mass similar to Mexico 120. Only in the mid profile was there a significant difference ($P < 0.001$) between profiles with root weights for Mexico 120 (43.1) and Gamut (96.9) respectively.

At Gunnedah analysis of variance of the data failed to establish statistically significant effects between cultivars, between depths in the profile or in the depth x cultivar interaction (Appendix 85).

7. 3. 2.

The difficulties associated with the investigation of plant roots are formidable and it is not surprising that there is a dirth of information on such an important plant component. The more traditional techniques of root investigation such as monoliths, root containers, water culture, pin-boards, etc., have each provided somewhat fragmentary contributions to an overall appreciation of the role and response pattern of plant roots. Each technique is, however, subject to various levels of criticism. More recent techniques such as tracing root patterns with ^{35}P., in vitro culture of excised roots, the use of mist chambers and observation laboratories, and the use of moisture probes at different depths in the soil profile as used in plant density studies (Lovett pers. comm.), already appear to be making significant contributions to the overall knowledge.

Perhaps the greatest difficulty associated with the study of plant roots stems from the fact that both root growth and root function are affected by a large number of factors, some of which are known and many of which are not. Further, the interactions between root response and many of the components of the environment are not understood, which makes reproduction of results difficult. A further difficulty lies in the fact that although there appears to be considerable evidence that genetic variation exists for a large number of root characteristics very few estimates exist for the heritability of these. Troughton and Whittington (1969) suggest that selection techniques can lead to the development of plants with many different patterns of root growth. They

point out, however, that the best type of pattern for a particular environment is unknown.

In assessing the implications of the foregoing results some comments on techniques used appears to be warranted. The failure of glass sided boxes, (apart from inability of distinguish clearly between the sand and the roots) to establish different patterns of root development between the two cultivars may have been attributed to the watering technique used. In sand the watering regime consisted of an alternating abundance and shortage of water in rapid and regular succession. On the basis of the data presented by Heydecker and Sivanayagam (1969) the effects of the dry cycle would be more important than the shorter wet cycle and result in the concentration of growth in the primary and lateral roots. Further, in the design of these boxes the glass extended to approximately 1 cm. below soil surface and would result in temperature fluctuation occurring in the glass. This would establish a net flux of moisture and consequent hydrotropic response by the roots. Both these factors may well have over-ridden varietal differences.

When the experiment was repeated, the glass was replaced with peg-board which besides being positioned lower from the soil surface would not have the conductivity to establish temperature fluctuations. In addition the experiment was undertaken at a cooler time of the year when the watering regime could be expected to be more efficient and impose less emphasis on the dry cycle.

Heydecker and Sivanayagam (1969) have in fact reported that soil moisture makes a considerable difference to branching pattern of

roots. The pin-board technique in root boxes in this experiment indicates that, at least under these conditions, varietal differences in root development do exist between the cultivars Mexico 120 and Gamut. In the former, the root system tends to be relatively shallow, to have a high surface area by virtue of profuse branching and smaller diameter roots, and to be laterally rather than vertically distributed. Conversely Gamut appears to have a deeper root system with less branching and coarser diameter components and its distribution appears vertically orientated. It was of interest to note that in the final harvest two of the Mexico 120 replicates conformed to the above pattern. The third replicate produced a pattern quite different to that of either cultivar. No explanation can be suggested for this variation. It does, however, emphasise the need for replication if this method of root classification is used by plant breeders as a selection technique.

The failure to establish differences between varietal forms of root systems in water culture is not surprising as Heydecker and Sivanayagam (1969) report that major differences of root form are observed when root development for a single cultivar in soil and in water culture is compared.

The data presented (Table 44) for the results of root coring analysis demonstrated that at the Armidale and Tamworth sites there existed between the two cultivars examined a difference in root distribution pattern. The data tended to substantiate the findings for the pin-board experiment of a superficial distribution for Mexico 120 with a higher degree of penetration for the major root mass of Gamut. The

Gunnedah site failed to support the distribution pattern of the other sites. However, it is feasible that at this site the natural distribution pattern for both or either cultivar may have been affected by the heavy ripping and pre-seeding irrigation which is practised in this area, and which may result in changes to the edaphic environment that over-ride genetic influence on root distribution.

Support for the Armidale results by data from the Tamworth site which was on a markedly different soil type is of interest, in that it suggests that soil type alone does not necessarily determine root distribution pattern. This was further emphasised by the failure at Gunnedah on a somewhat similar soil type to that of Armidale to demonstrate a similar pattern of root distribution.

The statistical inferences made from soil core analysis together with observations made from pin-boards, from Growth Analysis and from coleoptile measurement indicate that under some conditions a varietal difference in root distribution between Mexico 120 and Gamut does exist. The implications of such differences would be considerable if these cultivars were truly representative of the Norin derivative short stature wheats and Australian standard height cultivars.

The possession of a characteristically shallow, horizontally orientated, multi-branched root system by some short stature wheats may be part of the explanation for the disappointing yield of these wheats under more arid environments. In such environments available moisture is normally expected to be at a lower depth in the profile, and when moisture is available at shallow depths, the concentration of the root mass and

its higher surface area would be responsible for very rapid depletion of these reserves, as reported for some grass cultivars by Hudson (1969). Also a root system of this type may explain the reputed ability of semi-dwarfs to respond vigorously to applied nitrogen.

FINAL DISCUSSION

FINAL DISCUSSION

8. 0. 0.

The experiments reported in this study attempted to provide an understanding of the physiological basis for the superior grain yield potential of selected Norin 10 derivative short stature wheats. The results emphasised the extreme complexity of the yield phenomenon and accented the importance of a favourable combination of many diverse characters rather than of individual characteristics.

The original parental material distributed by O.A. Vogel, which provided the modern germplasm source for short stature wheats was the product of the combination of two very diverse winter wheats, Norin 10 and Brevor 14. On a global basis the strong winter habit of this material limited its adaptability and one of the earliest transformations of the germplasm undertaken by plant breeders was towards a spring habit. In consequence, the earlier releases from the Mexican programme represent a transitional stage in this development as indicated in these data by the cultivars Mexico 120 and Chile 1B, both of which perpetuated part of the original vernalization response of the parental material. The modern techniques of continuous recycling of early generation hybrids over all seasons which are now used in plant breeding programmes have rapidly produced semi-dwarf wheats of total spring habit.

The cultivars Mexico 120 and Chile 1B were found in the course of these experiments to have a combination of characteristics which differed from the Australian standard height cultivar Gamut, and from certain other short stature wheats which were examined. These

characteristics were considered as being of significance in contributing to a higher yield capability in favourable environments and included the following :

In the short stature wheats generally the Seed phase of development was of longer duration than for the Australian spring cultivars examined. For Mexico 120 and Chile 1B the developmental model consisted of a short Juvenile phase coupled with a long Seed phase. Two factors of importance could be associated with such a developmental model. Firstly, the early onset of the Seed phase would permit longer experience of near optimum growth conditions of the environment, before rising temperatures and moisture stress became severely limiting factors. Secondly, the longer Seed phase was associated with a propensity to tiller profusely in the Seed phase but in the experiments this was not unique to the short stature types. Tillering was facilitated by adequate moisture and nitrogen and provided the structure for superior grain yield.

Growth Analysis was unable to demonstrate a superior photosynthetic efficiency in the short stature wheats examined. The technique did, however, demonstrate several growth characteristics which may have important physiological implications on grain yield. For both Mexico 120 and Chile 1B at high levels of nitrogen, photosynthetic area and root mass were maintained at a higher level for a longer period into the Seed phase. Analysis of growth also indicated a horizontally orientated root distribution pattern for these cultivars as opposed to the more vertical distribution of the cultivar Gamut. This was further indicated in subsequent experiments utilising root boxes and soil coring

techniques. The physiological implications of a longer lasting but shallow distribution root system towards grain yield are important. Such a root pattern denotes a more efficient orientation in favourable edaphic environments. It is however, likely to be less drought tolerant in lacking the ability to utilise deeper reserves of moisture or nitrogen during the period of grain development.

Analysis of the contribution of some plant components to grain production indicated relative differences in importance between organs of the short and standard height cultivars. Gamut appeared to follow more closely the classical pattern of major dependence on the photosynthetic tissue of the flag leaf, peduncle and inflorescence. In the short stature wheats, however, those leaves below the flag leaf appeared to more important in contributing to grain development, than in tall wheats.

The spatial arrangement of inflorescences and leaves for the short stature wheats resulted in an altered light regime in the plant profile relative to the standard height cultivar. The net effect of this appeared from measurements of light penetration into the leaf canopy to be a lower degree of mutual interference or competition within and between neighbouring plants in a crop of the low stature cultivar.

The extent of response to nitrogen fertilizer in terms of grain yield was disappointing in field trials where a neutral or negative response was commonly encountered. Perhaps a more significant result was that yield depression at high levels of nitrogen fertilizer could follow positive response in vegetative plant parameters and be associated with deleterious effects on grain weight.

Finally, some doubt must be expressed regarding the suitability of the standard techniques used by plant physiologists in measuring the general plant parameters for modern wheat cultivars of the type studied in this work. The acceleration techniques of plant breeding used in the synthesis of modern cultivars results in fixation of readily measured characters such as disease resistance and quality, but retention of a large degree of genetic variation for less readily discernible characters, which are in many instances those parameters of particular interest to the physiologist. The result is commonly that inherent variability in these characters is high and tends to mask physiological differences.

CONCLUSION

9. 0. 0.

The early Norin 10 derivative germplasm source constituted a fortuitous combination of favourable physiological characters for grain production within a relatively narrow range of climatic environment. The dramatic success of these early derivatives resulted in a widespread distribution into less favourable environments where plant breeders have attempted their adaptation. The complexity of the physiological factors contributing towards the improved yield capabilities, its collective polygenic nature, and the necessary transformation of phenotype associated with local adaptation may have severely diluted the original germplasm in many modern short stature wheats.

The physiological characteristics of early anthesis and long Seed phase, low apical dominance, lesser plant interference and longer enduring root and photosynthetic systems were characteristics of the earlier Norin 10 derivative wheats examined in this study. They are considered by the author to contribute to the high yield capability of the short stature wheats from this source. The majority of these characteristics are relatively simply inherited as single characters and can be selected in segregating populations generally without great difficulty. The incorporation of these characters into a new plant model for improved grain yield in Australian cultivars appears warranted for more favourable environmental situations.