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INFLUENCE OF NODAL ROOT PRODUCTION ON WHEAT YIELDS UNDER CONDITIONS OF LIMITED SOIL WATER AND PHOSPHORUS SUPPLY

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SUMMARY

A number of field and pot experiments was conducted in an attempt to quantify the effects of nodal root production on tillering and phosphorus uptake from various soils.

The nodal root number produced per plant was found to be highly correlated with tiller number where the soil water was frequently recharged but not where such recharge was limited in frequency.

Delaying nodal root establishment beyond mid tillering led to either a reduced production of tillers and/or to reduced survival of these tillers. This effect was more marked under conditions of low soil phosphorus with fertilizer phosphate banded in the surface soil, suggesting an improved P uptake efficiency of nodal roots over seminal roots alone. This increased tillering and growth of plants with both nodal and seminal roots also occurred on P deficient soils with no added fertilizer.

The effects of the increased tillering and growth of plants with both nodal and seminal roots on grain yield depended on the interaction of the increased water use of such plants and the rainfall or watering pattern from anthesis onwards.

I. INTRODUCTION

Because of the paucity and high variability of growing season rainfall, the time of production of nodal roots by wheat crops in Queensland shows wide variation between years. It is relatively common for such roots not to be successfully established for 8 weeks or more after sowing.

The influence of nodal roots on water use and yield has been studied both directly and indirectly in recent years. Pinthus (1969) showed that the number of nodal roots produced per plant was positively correlated with the tiller number and hence with any factor, including genotypes, which influenced tillering. This work was conducted in the field where ample soil water was maintained by frequent rainfall or irrigation. However, Derera *et al.* (1969) found that wheat growing in pots under soil water stress showed a positive association between grain yield and nodal root number which was not associated with tiller number.

The interaction between soil phosphorus status and the presence or absence of nodal roots was studied by Boatwright and Ferguson (1967) in pots. They found that with low phosphorus, early tillering was enhanced where both nodal and seminal roots were present. The absence of nodal roots was found to reduce water use, presumably by the lower tillering, and hence plant top growth and transpiration potential were reduced.

This paper reports the results of experiments conducted on the influence of nodal root number on wheat performance in Queensland, where delayed nodal root development, water stress and soil P deficiency are all relatively common.

II. EXPERIMENTAL METHODS

Experiments 1 and 2 were conducted in the field to provide information on the influence of the timing of nodal root establishment on wheat yields and associated characters. Experiment 1 was conducted on a Krasnozem soil, deficient in P, at Toowoomba, Queensland. Main treatments consisted of two wheat cultivars, Gamut and Festiguay, sown during late May at the rate of 35 kg ha^{-1} in rows 18 cm apart in plots 20 m x 4 m. Single superphosphate at the rate of 35 kg P ha^{-1} was drilled in with the seed. There were four replicates. Within each cultivar plot four 2-m^2 subplots were selected. Each subplot had a small levy bank formed around it and if rain appeared likely, it was covered by a 2·5 m^2 plastic shelter. The subplots were each assigned one of the watering subtreatments, viz. 15 mm of water added each fortnight, or a single 15-mm watering at 4 weeks, at 8 weeks, or at 12 weeks after sowing. All subplots were watered to field capacity at 15 weeks (with Gamut at the boot stage and Festiguay at late stem elongation) and fortnightly thereafter.

Ten plants from each subplot were harvested for tiller and root counts 14 weeks after sowing. At maturity, quadrats (1 m^2) harvested from the centre of each subplot supplied data on grain yield and yield components. Leaf relative water content was measured at 8, 12 and 15 weeks after sowing on 4 leaves from each subplot, using the technique of Barrs and Weatherley (1962).

Experiment 2 was similar to Experiment 1 except that it was conducted on a fertile Waco Black Earth with no added fertilizers and two additional cultivars, Spica and Timgalen, were incorporated as main plots and the replications were reduced to three. Soil water content was measured gravimetrically to 120-cm depth at planting and at boot stage, and these soil cores were also used to measure root density by the technique of Newman (1966). Otherwise all subplot treatments and harvest details were as in experiment 1.

Experiment 3 was conducted in the glasshouse at the Queensland Wheat Research Institute, Toowoomba, during the winter months using PVC tubes 15 cm in diameter and 90 cm long. Each tube was filled to within 18 cm of the top with either a fertile Waco Black Earth or a P deficient sandy loam. The latter soil either received no fertilizer, or superphosphate was added at a rate equivalent to 40 kg P ha^{-1} and either mixed throughout the soil or banded at this 18-cm level. All pots were watered to their pre-determined field capacity and then four pre-germinated seeds of cv. Gamut, Spica, WW15 or Timgalen were planted in each pot and covered by 2 cm of soil which was also watered to field capacity. Each pot was then topped with 12 cm of polystyrene beads restricted inside a 10 x 15-cm PVC tube and covered with black plastic to induce the crown node to form well up in these beads. When the seedling leaves had emerged this black plastic was removed. When nodal root development was required the polystyrene beads at and below the plant crown were replaced with a coarse sand and all pots were top watered to field capacity. At other times the pots could be watered at seed depth around the side of the smaller PVC tube.

Two experiments were conducted with these pots. The first (experiment 3) compared plants with and without nodal roots established in the fourth and fifth weeks after planting in the black earth soil and in the sandy loam with banded phosphate. There was no water added between the fifth week and boot stage, when a harvest was taken and all pots were rewatered to field capacity. The second experiment (experiment 4) compared genotypes with and without nodal roots, grown in the sandy loam soil. Treatments were: with no added phosphate; with phosphate banded at the 6-cm soil depth; phosphate mixed throughout the soil. No water was added to the pots after nodal roots were established between the fourth and sixth week.

In both these pot experiments there were four replications of two harvests. The first harvest was taken at the boot stage, and the soil water content, and the weight, tiller number and N and P concentrations of plant tops were measured. The roots were recovered from the soil in 30-cm layers by a flotation and sieving technique. The relative water content of leaves was measured by the technique of Barrs and Weatherley. The maturity harvest gave data on the yield and yield components.

III. RESULTS

Number of tillers and nodal roots per plant, as measured in the field experiments (experiment 1 and 2) are presented in tables 1 and 2. This shows that where there was frequent soil water recharge, the nodal root number was positively correlated with the tiller number. Measurement of this character for a range of genotypes, under irrigation, has produced the relationship: no. nodal roots $= -6\cdot7 + 6\cdot2$ no. tillers; $r = 0\cdot92$.

Where there was only a single soil water recharge the nodal root number was relatively constant (mean 8·6) irrespective of variation in tiller numbers, wheat cultivars or time of initiation. In all experiments the seminal root number per plant was also relatively constant (mean 5·9) and no significant differences due to cultivar were apparent.

The influence of the time of nodal root establishment on tiller and ear number is shown in table 1 for the experiment conducted on the Krasnozem and in table 2 for that conducted on the Black Earth. These tables show that on the Krasnozem, delaying nodal root establishment to late tillering or beyond reduced the final number of ears per plant for both cultivars, either by reducing the maximum tiller number and/or by increasing tiller mortality. On the Black Earth this effect was restricted to the treatment where nodal root production was delayed to mid-elongation and then only occurred in the higher tillering cultivars Timgalen and Festiguay. The reduced ear number in the trial on the Krasnozem was reflected in grain yield. The influence of this factor on grain yield in the Black Earth trial was, however, strongly affected by frosting at anthesis and the yield results are not presented; however in both Timgalen and Festiguay, which were least affected by the frost, there were no significant yield differences between treatments.

Table 3 presents data on the plant and soil water status at the boot stage just before full irrigation of all treatments was begun. The data presented are the mean of four wheat cultivars which did not differ significantly in the characters presented. This table indicates that frequent soil water recharge increased leaf relative water content (R.W.C.) but that there were no significant differences in leaf R.W.C. between differing timings of a single soil water recharge.

TABLE 1

Influence of the Time of Nodal Root Establishment on Tiller, Ear and Grain Production—Krasnozem Soil—P Fertilizer Banded with the Seed (Experiment 1)

Time of Watering to Produce Nodal Roots	Cultivar								Min. leaf R.W.C. (6 a.m.) (%)
	Festiguay				Gamut				
	Yield ($g\ m^{-2}$)	Max. Tiller no. per Plant	No. Ears per Plant	No. Nodal Roots per Plant	Yield ($g\ m^{-2}$)	Max. Tiller no. per Plant	No. Ears per Plant	No. Nodal Roots per Plant	
Fortnightly ..	212	8·0	4·3	44	187	4·9	3·7	24	91
At early tiller ..	175	8·3	4·0	9	162	5·1	3·1	11	70
At late tiller ..	137	7·1	2·9	8	137	4·0	2·8	7	74
At mid elongation	140	6·0	2·5	6	120	4·2	2·4	9	72
L.S.D. $P = 0{\cdot}05$	32	1·3	0·8	5	32	1·3	0·8	5	4·5

Note: No. of nodal roots was measured at the boot stage.

TABLE 2

INFLUENCE OF THE TIME OF NODAL ROOT ESTABLISHMENT ON TILLER, EAR AND GRAIN PRODUCTION—BLACK EARTH—NO FERTILIZER, NATURALLY P SUFFICIENT (EXPERIMENT 2)

Time of Watering to Produce Nodal Roots	Cultivar											
	Timgalen			Festiguay			Gamut			Spica		
	Max. Tiller No.	No. Ears	No. Nodal Roots	Max. Tiller No.	No. Ears	No. Nodal Roots	Max. Tiller No.	No. Ears	No. Nodal Roots	Max. Tiller No.	No. Ears	No. Nodal Roots
Fortnightly	7·5	4·8	41	6·9	4·7	37	4·5	3·4	21	4·8	3·3	22
At early tillering	7·1	4·5	7	7·1	4·1	8	4·7	3·5	8	4·7	3·3	6
At late tillering	7·7	4·3	8	7·2	4·1	10	4·3	3·1	7	4·7	3·1	8
At mid elongation	6·2	4·0	8	5·8	4·0	9	4·2	3·1	7	4·4	3·3	10
L.S.D. P = 0·05	1·0	0·8	4	1·0	0·8	4	1·0	0·8	4	1·0	0·8	4

NOTE: 1. All data in Table 2 are presented on a per plant basis.
2. No. of nodal roots was measured at the boot stage.

TABLE 3

SOIL WATER AND ROOT MEASUREMENTS UNDER DIFFERENT TIMES OF NODAL ROOT ESTABLISHMENT ON A FERTILE BLACK EARTH AT THE BOOT STAGE (MEAN OF 4 WHEAT CULTIVARS)

Time of Watering to Produce Nodal Roots	Avail. Soil Water at Planting (0–120 cm) (mm)	Avail. Soil Water at Boot Stage (0–120 cm) (mm)	Rain Plus Irrigation (mm)	Minimum Leaf R.W.C. (6 a.m.) (%)	Root Density ($cm\ g^{-1}$) at Boot Stage in Depth Intervals		
					0 to 10 (cm)	10 to 60 (cm)	60 to 120 (cm)
Fortnightly	210	88	110	90·2	5·87	0·54	0·38
At early tiller	214	78	15	80·0	3·01	0·77	0·31
At late tiller	207	71	15	81·6	2·54	0·74	0·27
At mid elongation	209	64	15	78·4	3·41	0·64	0·38
L.S.D. $P = 0{\cdot}05$	NSD	15	..	3·4	1·33	0·21	0·20

A similar result was found on the Krasnozem (table 1) although the stress here was more marked than on the Black Earth. Total water use, estimated as the change in soil water status plus rainfall over the period from planting to the boot stage, showed exactly the same trend as leaf R.W.C. The root density data showed no significant differences between treatments below a soil depth of 10 cm. Above this the frequent watering produced a higher root density than the other treatments.

The results of the pot trials (experiments 3 and 4) conducted to seek genotypic differences in response to the presence or absence of nodal roots under various soil phosphate levels and placements are presented in table 4. In no trial was there significant genotypic variation in response to nodal roots and hence the data for cv. Timgalen only are presented.

TABLE 4

INFLUENCE OF NODAL ROOTS AND APPLIED PHOSPHORUS ON THE GRAIN YIELD AND ASSOCIATED CHARACTERS OF WHEAT (CV TIMGALEN) UNDER SIMULATED DROUGHT IN POTS (EXPERIMENTS 3 AND 4)

Water Treatment	Drought Relieved at Boot (Expt. 3)		Drought Unrelieved (Expt. 4)		
Soil	Fertile Black Earth	Infertile Sandy Loam	Infertile Sandy Loam		
P Treatment	No P	+ P in Band 6 cm in Soil	+ P in Band 6 cm in Soil	No P	+ P throughout Soil
RELATIVE † DATA					
At maturity					
Grain yield	1·06	1·18*	0·78	1·14	Nil
No. grains per ear	1·04	1·08	0·79	0·97	Nil
No. ears per plant	1·07	1·08	0·98	1·29*	0·87
1,000 grain weight	0·96	1·09	0·92	0·90	Nil
At boot					
Plant dry wt.	1·03	1·11	1·14	1·28*	1·11
Root dry wt.	0·92	1·20*	1·19	1·10	1·10
Plant N yield	0·98	1·08	1·11	1·10	0·92
Plant P yield	1·00	1·11	1·20*	1·01	1·04
Tillers (No. per plant)	1·11	1·23*	1·17*	1·40*	1·09
Water use	1·02	1·14*	1·20*	1·04	0·96
ACTUAL DATA					
Plant plus nodals					
Grain	2·49	1·51	0·33	0·65	Nil
Max. Tiller no.	4·1	3·7	4·0	1·8	4·1
Minimum R.W.C.					
Plus nodals	68·5	58·0	50·8	81·0	leaf dead
Without nodals	66·2	64·1*	61·6*	84·0	leaf dead
Nodal root no.					
Plus nodals	17·0	13·0	19·5	6·2	15·0
Minus nodals	1·1*	0·70*	1·2*	0·5*	0·3*

* Significant influence of nodal roots at P = 0·05.

† Relative data are result of expressing the measurement of a character as that from plants with nodal roots divided by that from plants without nodal roots.

The only consistent feature of all these trials was the success of the treatment in gaining high and low numbers of nodal roots, and also the higher tiller number at boot stage from plants with the larger number of nodal roots. This increase in tiller number, associated with a greater production of nodal roots, was larger where phosphate was applied in a band rather than mixed throughout the soil core, irrespective of whether the drought was relieved at boot or not.

In the trials where no water was added after nodal root initiation at early tillering, the response in tillering to nodal root number varied with phosphate addition and placement. Where the whole soil core was fertilized plants under both root treatments had used the available water by boot stage and as a result no grain yield occurred. Where no phosphate was added the plants produced were depauperate and water use was low: the higher tiller number produced by the plants with nodal roots was carried over to final ear number. The treatment with phosphate banded at seed depth produced larger plants when nodal roots were present, with a higher water use. This was reflected in the phosphate yield of the tops, the tiller number, the leaf relative water content and the very low grain yields.

When plants were grown on the fertile Black Earth there were no significant differences in any of the measured characters between plants with and without nodal roots when drought was relieved at the boot stage. When grown in the infertile soil, with banded phosphate, however, the plants without nodal roots had a significantly lower grain yield. This was due to their lower plant growth as reflected by tiller and root measurements at the boot stage and in spite of their better water status as measured by water use and leaf R.W.C. water use.

IV. DISCUSSION

The positive correlation between tiller number and nodal root number when the soil was frequently rewetted is in accord with the results of Pinthus (1969). The relative constancy of nodal root number, irrespective of tiller number, when soil water was recharged only once was presumably due to the short duration of the period when the soil surrounding the plant crown was sufficiently moist to support nodal root growth. Salim *et al.* (1965) have shown that nodal root growth in wheat is reduced above a soil water tension of 10 bars and ceases altogether at 15 bars. Genotype differences in nodal root number occurred only under frequent soil water recharge and then were associated primarily with differences in tiller numbers per plant.

Low nodal root production reduced grain yield on the lighter soils with phosphate banded in the surface in both the pot and field experiments, providing the plants were adequately watered from boot stage onwards. This reduced grain yield was associated with a lower production of tillers and/or a reduced proportion of these tillers becoming fertile. A quantitative relationship between nodal root number with fertile tiller number and grain yield has been shown by Black (1970b). The similar experiment with the fertile Black Earth showed similar tiller effects, although in the field experiment there was a suggestion that these were confined to cultivars with a high tillering capacity. This was not supported by the pot experiments where there was no genotype interaction with tiller number. In these experiments, however, the tiller numbers of all cultivars were very low, due presumably to the faster development in the glasshouse.

The experiments reported in this paper support those of Black (1970a and b) in showing a positive correlation between nodal root number, fertile tiller number and grain yield, although where infrequent soil water recharge takes place the correlation between tiller and nodal root number breaks down. Also it appears that high tillering cultivars show greater tiller instability under low nodal root numbers. These factors together suggest that cultivars whose yield performance depends on a relatively high fertile tiller number to counteract an inherent low grain number per ear or low weight per grain, i.e. Timgalen, should be avoided in regions where there are few and variable periods of rain recharge, especially if these regions also have a marginal nutrient status.

In field studies the timing of nodal root establishment is strongly confounded with the timing of the water recharge of the soil and hence wetting of the fertilizer zone. Boatwright and Ferguson (1967) separated these effects and concluded that tiller production was enhanced where both seminal and nodal roots were present. The field and pot experiments presented here generally support this view but also show a strong effect of soil fertility. Thus with a highly P-fertile soil whilst there was an increase in tiller number with the early presence of nodal roots, there was no increase in root density below 10 cm, or P uptake and little effect on soil water use.

In the infertile soils, with P banded at seed depth, the presence of nodal roots increased P uptake and plant top and root growth. This supports the results of Boatwright and Ferguson (1967) who found improved P uptake efficiency when both seminal and nodal roots were present. The data from both the fertile soil and the infertile soil with no added fertilizer shows that the improved tillering of plants with nodal roots was however not dependent upon increased P uptake.

The relative yield performance of plants with and without nodal roots depended upon the interaction between the increased water use of the plants with nodal roots consequent on their improved top growth and the future water environment. Where the water environment after the 'boot' stage was good, increased top growth was shown in increased grain yield; whereas when drought continued after the 'boot' stage the grain yields fell to similar levels irrespective of the presence of nodal roots.

V. CONCLUSION

Nodal root production in the field is dependent upon rainfall. Early rainfall, whilst inefficient in recharging soil water reserves due to a high soil evaporation loss, does produce nodal roots and hence allows both higher tiller numbers to develop, and more efficient use of applied P fertilizer. The consequent increase in water use potential of these plants with nodal roots would prove disadvantageous only at extremely low and non-economic yield levels.

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