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JA1518

PLSO 3301

The effect of root damage caused by simulated white grub attack on the growth, yield and water-use of groundnut plants

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Abstract

White grubs (larval scarabaeids) are now recognized as being important pests of groundnut (peanut) in many parts of the world because of their ability to damage roots. A method of simulating white grub damage to groundnut plants was developed to obtain an indication of how the feeding activity of these insects influences plant growth. The effect of root cutting and drought stress on water uptake and biomass production was evaluated, with roots being cut at three depths in the late vegetative and early podfilling stages. As groundnut plants are often grown under conditions of drought stress, the effects of which would be accentuated by root damage, this factor was introduced into the experiment. Plant water-use measurements indicated that the root systems of plants cut 30 days after emergence (DAE) and watered twice a week became fully functional again after 40 days. Pod and total biomass production were however significantly less than those of the uncut control plants, with drought stress reducing yields below the well-watered controls, particularly when cut at 10 cm below the soil surface. The root systems of plants cut 51 DAE did not regrow to any appreciable extent, and rates of plant water-use remained less than half of the uncut control plants. Over all treatments, there was a strong positive correlation between total (and pod) biomass and plant water-use. It was concluded that the phenological stage of the plant at which root damage occurred had a profound influence on the subsequent recovery in root growth and function, and ultimately on pod yield.

Introduction

It has recently become apparent that white grubs (scarabaeid larvae) can be serious pests of groundnut in southern Africa, most of Asia and in Australia (Bakhetia, 1982; Wightman, 1989; Xu Zeyong, 1991). The densities of up to one per plant detected in farmers fields in Africa far exceed experimentally established damage thresholds (Wightman and Ranga Rao, unpublished). As such, white grubs contribute to the large yield gap characteristic of the resource poor ground-nut farmers of this continent. Farmers of the light soils of India's gangetic plain suffer lost opportunity because of these insects. They sow pearl millet, for instance, instead of the more profitable groundnut, because they know that the dense fibrous root system of the cereal crop renders it less susceptible to the attentions of the root feeders. They know that pearl millet crops can produce a profit in white grub endemic areas whereas the heavy investment in groundnut seed is likely to be completely wasted because of these insects.

These insects usually damage groundnut plants by eating the peripheral roots and severing the tap root. This activity causes seedling death and stunts the growth of older plants (Wightman et al. 1990). Some species also destroy the pods. The Australian species *Heteronyx piceus* Blanchard limits itself to this activity but can be equally damaging (Rogers and Brier, 1992).

Reports of crop yield losses attributable to white grubs are usually generated from insecticide field trials. They frequently indicate that if white grubs had not been present, crop yields would have been more than double those achieved (Bakhetia, 1982; Kumawat and Yadava, 1990; Xu Zeyong, 1991). There are, however, no quantitative accounts of the relationships between the damage they cause to roots and the interaction with above ground biomass production.

Thus, there is a need for more information on the relationships between white grub activity (and density) and crop loss. For instance it is not known if or at what growth stage a plant can recover from root damage. The lack of information in this area is, no doubt linked with the difficulties of obtaining quantitative data associated with soil insects and plant roots. One of the reasons for initiating the research described below was to develop techniques that permit the manipulation and recovery of roots in simulated field conditions.

The experiment described here investigated the effect of root severing treatments applied at three depths and at two growth stages to simulate the root feeding activity of white grubs. As groundnut crops frequently grow under conditions of uncertain rainfall, drought stress was included as a treatment, as the plants' natural tolerance to this constraint is likely to be influenced by damage to the root system. The effect of these treatments on water uptake, biomass production and components of yield were assessed.

Methods

Germinated seeds (variety White Spanish) were sown on 4 February 1992 in soil that had been saturated for a week and allowed to drain for 4 days (i.e. it was at field capacity). The light, red loam soil, a Krasnozem, was typical of that of groundnut farms of SE Queensland. The containers (hereafter referred to as 'pots') were PVC tubes, 75 cm long and 11 cm in diameter. The ends were covered with sheets of perforated plastic.

There were five replicate pots per treatment. The treatments were roots cut at 30 or 51 days after emergence (DAE) 10, 15 or 20 cm below the soil surface, with or without drought stress from 30 DAE (Table 1). Control pots had uncut plants and were either drought stressed or were not drought stressed.

Table 1. Mean weight of water used by plants in all treatments between root cutting and harvest

Drought stress	DAE	Cutting depth	Identifier[a]	Total water used since cutting (kg)
Yes	30	10	30 Y 10	5.36 ± 0.18
		15	30 Y 15	6.37 ± 0.17
	(Control)	0	30 Y 0	8.32 ± 0.27
No	30	10	30 N 10	9.23 ± 0.34
		15	30 N 15	8.34 ± 0.15
		20	30 N 20	10.94 ± 0.19
	(Control)	0	30 N 0	14.76 ± 0.58
Yes	51	10	51 Y 10	1.48 ± 0.11
		15	51 Y 15	2.16 ± 0.30
	(Control)	0	51 Y 0	4.58 ± 0.18
No	51	10	51 N 10	2.33 ± 0.19
		15	51 N 15	3.22 ± 0.11
		20	51 N 20	3.22 ± 0.12
	(Control)	0	51 N 0	8.50 ± 0.43

[a]Adopted to indicate treatments in subsequent tables and Figures.

A key feature of this experiment was the determination the way root cutting and drought stress influenced water uptake by plants. The weight of each pot on the sowing date and after 7 days (by which time the seeds had germinated) was determined. The small amount of weight loss during this period was used as a correction factor for soil evaporation during subsequent measurements. Each week, water removed by the plants from the soil in transpiration was replaced by returning the weight of a pot to its original weight by adding water. The weight of the plant was negligible and was not taken into account. This process was repeated for all pots up to 30 DAE. After this time, when the plants were taking up about 1 L of water per week, half the pots were maintained on this schedule and subsequently suffered drought stress. The soil water content of the remainder was adjusted twice a week in this way: they did not experience drought stress.

The experiment took place in a glasshouse maintained at 34 °C day and 19 °C night (12/12). Every effort was made to ensure that the pots were allocated to treatments with no bias. The position of the pots in the space allocated to this experiment was changed twice a week.

Roots were severed 30 or 51 DAE at a depth of 10, 15 or 20 cm below the soil surface. Water had been added on the day before they were cut. The pipes were held horizontally whilst the walls were cut around their perimeter at the appropriate 'depth' (10, 15 or 20 cm below the soil surface) with a hand saw. A 1–2 cm uncut section of the perimeter acted as a 'hinge'. The pipe was then brought to a vertical position. The roots (and soil column) were cut through by gently opening the pot at the cut to a maximum of 2 cm and passing a knife blade across the resultant gap.

The pipe was closed and resealed with plastic tape. Collars, made from 11.5 cm lengths of pipe that had been slit along their length, were slid over the cut onto a bed of PVC adhesive. They were positioned so that the 2 cm gap in the collar exposed the 'hinge'. This procedure ensured that the structural integrity of the pipe was maintained with no subsequent loss of soil or water from the cut. It was apparent at the end of the experiment that there was no break in the soil column in the cut pipes indicating that the regeneration of roots was not influenced by an air space. The weight of the collar and tape was added to the initial weight of the pot to give a new base weight for subsequent calculations.

The plants were removed from the pot at maturity. Two parallel cuts were made with a handheld, electric saw along the length of the pipe so that it was possible to remove about 25–33% of the pipe wall. The pods were gently washed free of the soil so that the above-ground part of the plant could be removed. The cut pipes were placed on a sloping bench with the exposed soil uppermost. A jet of water from a hose was sufficient to wash away the soil and the remains of the dead roots to expose the (living) root structure without damage to the delicate terminal roots. The process was hastened by soaking the cut pipe in water for a minimum of 10 minutes. Two people processed six to eight pots per hour with this technique.

The total leaf area was estimated by measuring the area of a representative sample of 30 leaflets and multiplying the mean by the total number of leaflets. Stems + leaves, roots and pods were then dried at 80°C to constant weight and weighed. Harvest index was calculated as the ratio of pod biomass to total biomass, expressed as a percentage.

Results

General observations

The empty pots weighed 1.23 kg. The soil at field capacity added a further 9.0 kg (of which 2.5 kg was water) to make the base weight of about 10.2 kg. Soil evaporation averaged 180 g per week. Individual plants were able to extract about 2 L of water from the soil per week by the end of the vegetative stage.

The technique developed during this experiment proved satisfactory, primarily because the plants grew well under the conditions of the experiment. The undamaged, unstressed plants produced, on average, 23 g of pods, equivalent to >4 t ha^{-1} if there are 200 000 plants ha^{-1}. Secondly, we were able to impose a unique set of experimental conditions on the plants that simu-

lated the root cutting activity of white grubs in the field. The important point is that we cut through the roots without disturbing the soil and subsequently separated the roots from the soil without significant root loss.

The plants had begun to flower by 30 DAE, while pod swelling had commenced by 51 DAE. Plants cut at 51 DAE experienced a greater degree of water deficit (i.e. they became severely wilted) than plants cut at 30 DAE. As the plants cut on the later date became fully turgid within an hour of watering, it was concluded that the remainder of their root systems was operating effectively. The roots in these treatments were considerably reduced in size and did not regrow after being cut. This meant that they had a smaller volume of soil from which to extract water compared to the plants in the 30 DAE treatment that were able to regenerate root tissue.

The 51 DAE treatment plants were also extremely chlorotic by the end of the experiment. This is presumably because the leaves were isolated from their source of nitrogen (i.e. root nodules), and other nutrients, when the roots were severed.

The roots of the uncut (control) plants consisted of a single tap root of 3–4 mm diameter that, with the many lateral roots, extended to the bottom of the pot. There was no bunching of roots at the base. Plants cut 30 DAE also had complete root systems extending to the bottom of the pot. However, they usually consisted of four 'tap' roots (+laterals) that emerged from the primary root, just above the level of the cut.

The same degree of recovery was not apparent for plants cut 51 DAE. Compensatory root growth resulted in no more than a covering of new rootlets growing at the cut tap root stump.

Water uptake

The cumulative water use data indicate that the non-drought stressed plants used 50 to 100% more water than their drought stressed counterparts (Fig. 1). The effect of root cutting on water uptake is further illustrated in Table 1, which includes the total weight of water added to each treatment between cutting and the end of the experiment. Analysis of variance showed that
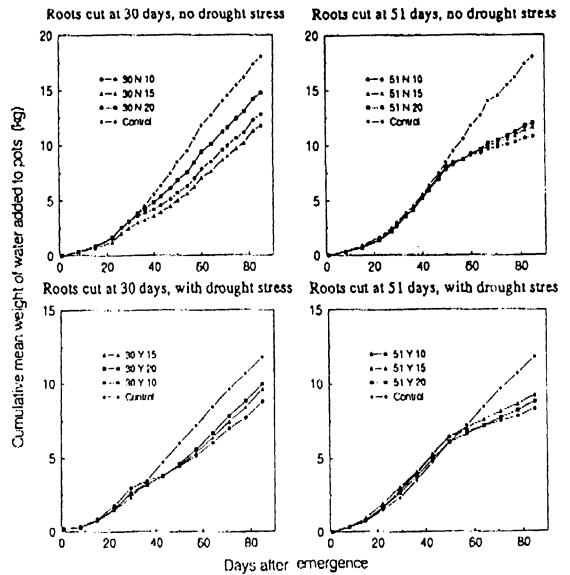

Fig. 1. The cumulative weight of water used by groundnut plants subjected to root cutting at 10, 15 or 20 cm depth, at 30 or 51 days, with or without drought stress.

treatment effects were significant throughout. There were interactions between all factors by the time plants were harvested.

Plants cut at 30 DAE regained the ability to absorb almost as much water per week as the controls after a 40 day recovery period, as indicated by the recovery in relative plant water uptake (ratio of water uptake in cut to control plants) shown in Figure 2. Plants cut at 20 cm suffered less of a set back than those cut closer to the crown (10 and 15 cm).

These data contrast markedly with those for plants cut 51 DAE. Relative plant water uptake dropped sharply at 51 DAE and recovered slowly or not at all (Figures 1 and 2 and in Table 1). Plants cut at 10 cm after 51 DAE, both with and without drought stress, appeared close to death at the time of harvest.

Effect of root cutting on biomass

Roots

The root biomass data in Table 2 confirm that roots of plants cut 51 DAE showed little regrowth compared to uncut control plants. This is in contrast to the roots of plants that were cut
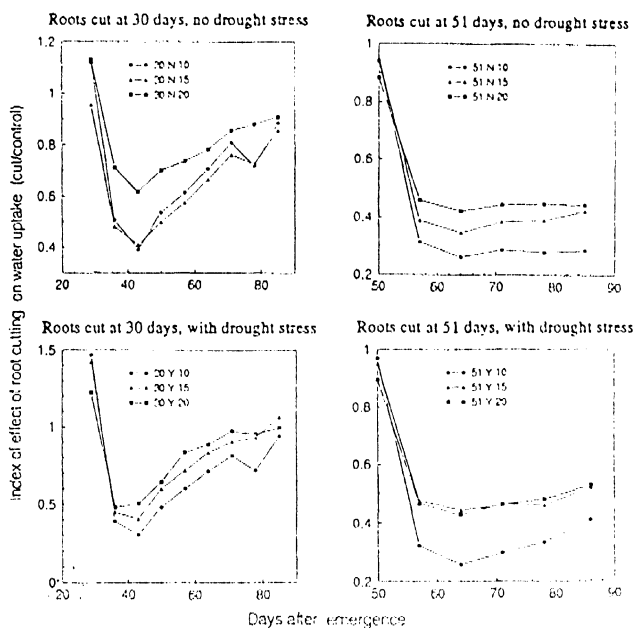
Fig. 2. An index (data from cut plants/data from uncut controls) of the effect of root cutting and drought stress after 30 or 51 days on water use by groundnut plants.

30 DAE. The 0.7–0.9 g of root remaining in the 51 Y 10 and 51 N 10 treatments represented the weight of the 10 cm of root immediately below the crown. This short section of the root system represented approximately 25–30% of the total root biomass. The data also indicate that the compensatory growth initiated after cutting at 30 DAE resulted in root systems slightly larger than those of the uncut control plants.

Root biomass of drought stressed and unstressed plants were not significantly different. As the unstressed plants absorbed considerably more water than the stressed ones, these data provide evidence that the quantity of water taken up by a plant is not necessarily a direct function of root biomass.

Vegetative growth
Although there were significant differences in vegetative growth, it was of a relatively small magnitude (i.e. only 4 g difference between treatments). Weekly observations indicated that most of the vegetative growth was complete within 30–40 days of emergence.

Total biomass
There were marked differences in total biomass between treatments and in particular between the control and cut plants under each watering treatment. This data set indicates that the date of cutting was of greater importance on plant production than was the depth of cutting (Table 2).

Leaf area
Drought stress had a significant effect on leaf area (Table 2). Qualitative observation indicated that the leaves were established by 30 DAE so that subsequent treatments had little effect on this parameter. The importance of leaf area as a regulator of transpiration rate and therefore of water uptake indicate that there is scope for a quantitative study of this factor.

Pods
All three factors had significant effects on the mean number of pods per plant and the total pod weight (Table 3). Differences in pod biomass were strongly related to the severity of plant water deficits. Plants grown under the drought stress treatment (without cutting) produced

Table 2. Mean root, vegetative, and total biomass (including pods) and the leaf area, at maturity

Treatment	Root biomass	Vegetative biomass[a]	Total biomass[b]	Leaf area (cm^2)
	(g)			
30 Y 10	2.95	11.1	23.8	2552
30 Y 15	3.15	10.0	25.2	2514
30 Y 20	2.57	11.2	25.8	2405
51 Y 10	0.92	12.1	20.8	2240
51 Y 15	1.78	11.9	23.0	2632
51 Y 20	1.13	11.3	21.4	2318
Control				
– Y 0	2.32	13.8	28.6	2902
30 N 10	3.17	16.2	33.6	3217
30 N 15	2.74	12.0	29.9	2485
30 N 20	3.12	16.9	33.8	2793
51 N 10	0.70	12.7	24.4	2513
51 N 15	1.28	13.6	28.9	2606
51 N 20	1.09	13.4	28.7	2448
– N 0	2.67	17.7	43.3	3164
Analysis of variance summary:				
Cutting date (T)	* *	* *	* *	–
Drought stress (W)	–	–	* *	*
Cutting depth (C)	–	–	* *	–
T × W	–	–		
T × C	* *	–	–	–
W × C	–	–	*	–
T × W × C	–	–	–	–
LSD 5%				
T and C	0.40	1.86	2.19	271
C	–	–	3.1	–

[a]Weight of (stems + leaves + pegs).
[b]Includes pod biomass.

about half the yield of the unstressed treatment 13 v's 23 g/plant). There was a significant effect of cutting on pod biomass, particularly under the unstressed treatment, where yields were reduced by between 30–50% of the control. Pod yields were reduced more severely as the depth of cutting decreased from 20 to 10 cm. All yield reductions were strongly associated with reduced pod numbers per plant compared to control plants.

Harvest index
As for pod biomass, harvest index (HI) was strongly influenced by watering and cutting treatments (Table 3). Lower harvest indices were associated with higher levels of plant water deficit induced by either the drought stress and/

or cutting treatments. While HI of 15 and 20 cm cut plants was not significantly different to the respective well-watered and droughted controls, it was significantly reduced in the 10 cm cut plants at both harvest intervals.

Root to shoot biomass ratio
Plant water deficits associated with both watering and cutting treatments strongly influenced the relative partitioning of biomass to roots relative to shoots (including pods) (Table 3). The effect was markedly different at the two cutting dates. At 30 DAE, plants under each cutting depth treatment partitioned significantly greater amounts of biomass to roots compared to control (uncut) plants. This response indicates that the cutting treatment caused a preferential allocation

Table 3. Mean number of pods per plant, their biomass and the harvest index (pod biomass/total biomass), and the root to shoot[a] biomass ratio

Treatment	Pod (number plant[-1])	Pod biomass (g)	Harvest index (%)	Root/shoot biomass ratio (%)
30 Y 10	20.2	9.81	41.3	14.1
30 Y 15	23.2	11.17	44.4	14.9
30 Y 20	22.2	12.02	46.9	11.1
51 Y 10	16.2	7.73	36.8	4.6
51 Y 15	20.4	9.36	40.1	8.4
51 Y 20	22.0	8.99	42.1	5.6
Control				
– Y 0	25.0	12.92	44.7	8.7
30 N 10	25.4	14.19	43.4	10.4
30 N 15	25.2	15.11	50.5	10.1
30 N 20	28.6	15.91	50.2	10.9
51 N 10	20.2	10.98	44.8	2.9
51 N 15	22.5	13.93	49.0	4.6
51 N 20	25.2	14.18	49.3	4.0
Control				
– N 0	37.0	22.96	53.2	6.6
Analysis of variance summary:				
Cutting date (T)	*	* *	–	* *
Drought stress (W)	* *	* *	* *	* *
Cutting depth (C)	* *	* *	*	–
T × W	–	–	...	...
T × C	–	–	...	* *
W × C	*	* *	...	–
T × W × C	–	–	...	–
LSD 5%				
T and W	2.18	1.08	2.1	0.5
C	3.08	1.52	3.6	0.7

[a] Vegetative + pod biomass.

of biomass to roots, compared to that in control plants. At 51 DAE, the reverse trend occurred, with root cutting causing a decreased allocation of biomass to roots compared to control plants.

Discussion and conclusions

The results from this experiment clearly show that root cutting strongly influenced growth and yield of groundnut plants. Root cutting clearly reduced subsequent water uptake and use, as evidenced by the dramatic decline in the rate of relative plant water uptake (Fig. 2), and hence total water use following cutting (Table 1, Fig. 1). The reduction in total water use which accompanied root cutting was strongly and nega-

tively related to both total and pod biomass (Fig. 3), such that total and pod biomass declined by 2.4 and 1.6 g per kg of reduction in water use, respectively. The close linear relationship between plant water use (or transpiration) and biomass accumulation is well established for many crops (De Wit, 1958; Tanner and Sinclair, 1983), including groundnut (Hammond et al., 1978).

The timing of root cutting had an important impact on the subsequent recovery in root growth and function. Plants cut during the vegetative to early flowering period (30 DAE) were able to regrow roots and resume rates of water use equivalent to uncut control plants by maturity (Fig. 2). The depth of root cutting had some influence on this recovery, with plants cut at
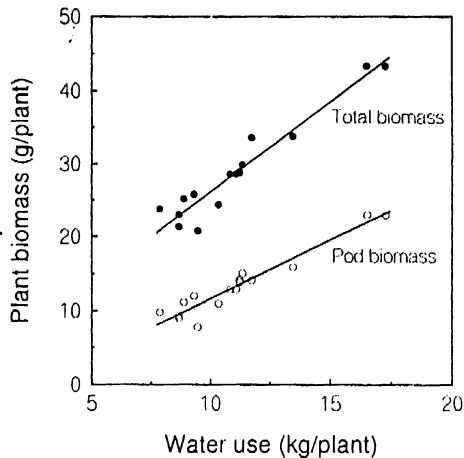
Fig. 3. The relationship between total water use from planting to maturity and pod and total biomass production at maturity for all cutting and drought stress treatments.

10 cm being slower to recover than 15 or 20 cm cut plants. The recovery response at 30 DAE was in marked contrast to that at 51 DAE, where there was no apparent recovery in root growth (Table 2) and plant water use (Fig. 2) compared to uncut control plants.

The differing recovery response to root cutting during either vegetative (30 DAE) or early reproductive (51 DAE) stages could be associated with changes in the partitioning of biomass which accompany the transition from vegetative to reproductive growth. The distribution of biomass has been shown to change as plants develop (Brouwer, 1965; Russell, 1977). During vegetative growth there is a fairly constant relationship between shoot (leaf plus stem) and root biomass. In contrast, the proportion of biomass partitioned to roots during reproductive growth declines substantially, as pods represent a more competitive sink for the available assimilate than do roots. It could therefore be hypothesised that "sink" strength in the root system following cutting at 51 DAE was substantially lower than at 30 DAE, with biomass being preferentially allocated to the stronger pod "sink". The fact that root to shoot ratios were significantly lower following cutting at 51 DAE supports this hypothesis (Table 3).

The chlorotic appearance of the 51 DAE cut plants at maturity indicates that the effect of root damage on nitrogen supply to the shoots is a

factor needing further investigation. Clearly, the shoots were isolated form the bulk of the nitrogen fixation system (i.e. nodules) following cutting. Presumably, available assimilates to re-develop the nodule system in the roots may have been limited as shown previously in groundnut (Venkateswarlu et al. 1989), in a similar manner to that described above for roots.

Damage to the root system during vegetative growth (30 DAE) was followed by active recovery in root growth, such that root biomass (and root to shoot ratios) were greater than uncut control plants (Table 2). This recovery was also associated with altered morphology of the new root system, such that multiple branches developed from the remaining tap root. This recovery pattern may represent an adaptation by the root system to enable tolerance to further cutting (or insect attack). Plants with more than one tap root will obviously be less susceptible to further attack by white grubs. The branching response may also have facilitated plant water uptake, as highly branched root systems have been shown to allow more efficient nutrient and water uptake (Jordan et al., 1979; Nye, 1966).

The roots are also the source of endogenous plant growth substances especially cytokinins, gibberellins and abscisic acid (Russell, 1977). The implication is that damage to the root system by white grubs not only impairs the plant's ability to absorb water and nutrients from the soil but also removes or reduces the supply of the substances that control apical bud dominance, stomatal opening and leaf senescence etc. This is a further potential area of investigation relevant to the topic introduced here.

The actual depth of cutting (or at least the range tested in this experiment) had a relatively small effect on the yield components. The implication of this finding is that, as white grubs are usually active in the 10–20 cm root zone, variations in their depth of feeding caused by fluctuations in soil moisture and temperature are likely to have little influence on plant production. However, the distinct reduction in growth, yield and water use following root cutting are a clear indication that interference with groundnut root systems by insects (as well as tunnelling mammals, millipedes, pathogens etc.) can reduce the yield potential of a groundnut crop.

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Section editor: G R Stewart