THE DEVELOPMENT OF ROOT MASS OF SUNFLOWER, AND EFFECTS OF ROOT PRUNING ON FLORET INITIATION

Barrie T Steer
Tropical Crops Research Group, School of Agriculture, The University of Western Australia, Nedlands, Western Australia, 6009.

SUMMARY

The aim was to confirm previous findings that the root mass at maturity was determined by N supply rates during, but not after, floret initiation. This contrasted with leaf and stem mass which responded to N supplies in all phases of plant development. Contrary to previous findings N supply after floret initiation did affect root mass but the effect was less than that during floret initiation. Some characteristics of the third lateral root were measured in order to relate them to total root mass. Diameter of the third lateral root was affected by N supply only during floret initiation but its length was affected afterwards. The stele radius was affected by N supply during and after floret initiation, cortex radius was not affected in any phase. Despite root mass being limited by low N supply rates early in plant development, later root functions could compensate for a small mass by an increase in N and water uptake per unit root weight. The large influence of N supply on later root mass suggested an interaction of root and floral meristems during the period when florets were being initiated. Pruning of lateral roots, similar to root loss that could occur due to mechanical or pest damage, just before floral initiation (at plastochron index 8), lowered the number of florets initiated, affecting both the apparent size of the floral generative area and the expansion of the receptacle disc during initiation. A second root pruning at the end of floret initiation had no additional effect on plants root-pruned earlier.

INTRODUCTION

Previous experiments (Steer and Hocking, 1984) demonstrated that the root mass of a mature sunflower plant was determined by N supply rates before but not after floret initiation. By contrast leaf and stem dry matter responded to N supplies after as well as before floret initiation.

Glasshouse experiments have been done to confirm the phasic development of root mass, and other root characters. Root damage early in crop development could have a long-term effect on crop growth and yield so the effects of partial root pruning have been assessed, particularly on the initiation of florets which occurs at the same time as root mass is most affected by N supply rates.

MATERIALS AND METHODS

Seeds were obtained from Pacific Seeds Co. except for those of Sirosun 892952 a 3-way cross from a CSIRO breeding program (Mr. A. Low). All plants were grown in sand culture. The floral stages were assessed after Marc and Palmer (1981) and total floret numbers were calculated using the formula of Palmer and Steer (1985).

Procedures for experiment 1 and nutrient composition for all experiments are given in Steer and Hocking (1983,1984). Protein was extracted from the residue, remaining after ethanol and water extraction of root material, with 0.1 N NaOH + 2.5% sodium dodecyl sulphate.

In experiment 2, two N supply rates were used and changed at one of 3 developmental stages. The third first-order lateral root was removed at anthesis for anatomical examination. It was fixed in 8 per cent glutaraldehyde in phosphate buffer at pH 6.8, then stored in 2-methoxyethanol. Transverse sections were cut within 5 mm of the point of insertion on the tap root and stained with 0.1% aqueous toluidine blue. Root diameters and cell counts were made on these sections.

In experiment 3, N supply rates were changed at the end of floral initiation. Water was witheld for 3 days at full anthesis. After that period the midday water status of leaves was measured.

In experiment 4 the N supply rate was constant at 21 mg N day^{-1} per plant.

RESULTS

Effects of rates of nitrogen supply
The concentrations of P (4.2 mg g^{-1} DW), glucose (80 mg g^{-1} DW) and fructose (16.3 mg g^{-1} DW) in roots of plants at physiological maturity did not respond to N supply rates before or after floret initiation (FI). Sucrose and fructans were present in roots up to anthesis but were absent from mature roots.

Total leaf dry weight and root dry matter, after extraction of ethanol-soluble material and proteins are plotted against the N supply rates after FI (Fig. 1). There was no significant effect of N supply after FI on root cell-wall material, but there was on leaf DW.
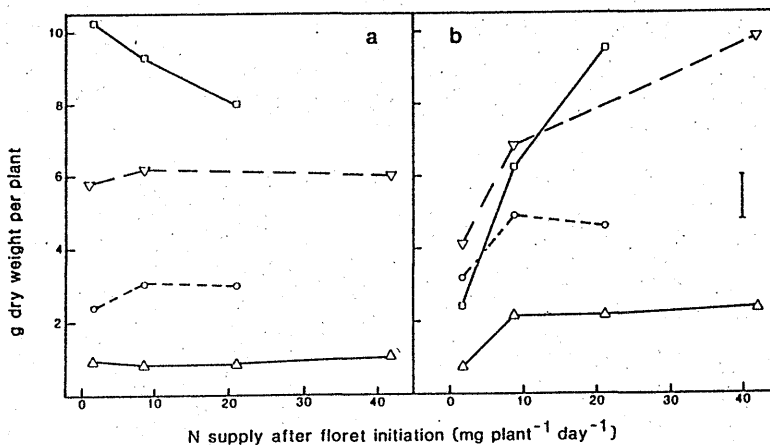

Fig. 1 Protein free, ethanol-insoluble dry matter of roots (a) and leaf total DW as a function of N supply before ($\triangle$ 17; $\bigcirc$ 8.7; $\square$ 21; $\triangledown$ 42 mg N d^{-1} per plant) and after floret initiation. Experiment 1.

In experiment 2, N supply rates during four phases of plant development were tested on the root DW at full anthesis (Table 1). Some characters of the 3rd lateral root were also measured in the hope that they might help explain the early determination of mass of the whole root system. The previous finding that root mass is affected by N supply rates only during floret initiation was not confirmed: root mass was affected by N supply before

Table 1. The response of some root characters of Hysun 30 at full anthesis to two N supply rates in four developmental phases. Only data from significant responses are shown. Experiment 2.

	Before plastochron index 5		Before floral stage 1		Before floral stage 8		After floral stage 8	
	mg N day^{-1} per plant							
	1.7	10.5	1.7	10.5	1.7	10.5	1.7	10.5
g PLANT DW	37.0 *** 49.3	a[1]	25.2 *** 61.1	a	25.8 *** 60.5		29.9 *** 56.4	
g ROOT DW	nse	a	6.28 * 9.15[2]	a	3.63 *** 10.6		5.38 ** 8.86	
LEAF NUMBER	25.0 ** 29.4	a	22.4 *** 34.6	-	nse		nse	
FLORET NUMBER	nse	a	nse	a	480 *** 1489		nse	

3rd LATERAL ROOT, within 5 mm of insertion on tap root

mm diameter	nse	a	nse	a	1.84 * 2.54		nse	
mm stele diameter	nse	a	nse		1.06 * 1.53		1.06 * 1.52	
number stelar parenchyma cells in radius	nse	a	nse	a	24.8 * 34.8		24.9 * 34.6	
cm length	nse	a	nse	a	nse		171 * 262	

[1] a significant effect recorded of N supply after plastochron index 5 or floral stage 1.
[2] the level of significance is shown as: * P<0.05; ** P<0.01; *** P<0.001.
nse = no significant effect

Table 2. Effect of N supply rates before and after floret initiation on root mass at physiological maturity and N uptake efficiency per unit weight, for three cultivars.

mg N day^{-1} per plant before/after FI	Hysun 30 root mass at maturity[1]	N uptake after FI[2]	Sunfola 68.3 root mass at maturity[1]	N uptake after FI[2]	Sirosun 892952 root mass at maturity[1]	N uptake after FI[2]
1.2 / 1.2	1.26[a3]	71	8.0[a]	39	2.5[a]	85
42 / 1.2	6.73[b]	30	18.0[b]	23	8.5[bc]	59
1.2 / 42	1.63[a]	374	9.9[a]	85	5.8[ab]	187
42 / 42	8.92[b]	165	21.7[b]	49	12.7[c]	74

[1] g dry weight per plant
[2] mg N g^{-1} root DW
[3] within a cultivar, values with the same appended letter do not differ at P = 0.05

and after FI, but differences between the responses to the two supply rates were greatest during FI. The diameter of the 3rd lateral root was only affected during FI but its stelar diameter was affected after FI also; although the cross-sectional area of stelar parenchyma cells and the number of xylem poles were not affected in any phase. Root length was only affected after FI. However, cortical diameter and the number of cortical cells in a root radius were not significantly affected by N supply rates in any phase (grand means were 0.92 mm and 10.8, respectively). Variance in the length and stelar diameter of the 3rd lateral root could account for 46% of the variance in the mass of the total root system.

The small root mass caused by a low N supply before FI was compensated by a high N acquisition rate per unit root weight when the N supply was increased after FI (Table 2). A similar compensatory mechanism appeared to function for water uptake. The small root mass but large leaf area (Steer and Hocking, 1983) of plants moved from a low to high N supply rate at FI might be expected to hasten water stress when the plants were droughted at full anthesis but the decrease in relative water contents and water potential of leaves (Table 3) were not as great as in plants grown continuously on a high N supply rate.

Table 3. Effect of withholding water for 3 days after full anthesis on the leaf water status of plants of Hysun 33 raised on different N supply rates. Experiment 3.

mg N day^{-1} per plant before/ after FI	Decrease in % relative water content over 3 days		Decrease in leaf water potential (MPa)	
	Control	-H_2O	Control	-H_2O
1.7 / 1.7	-2.1^a	0.9^a	0.13^a	0.22^{ab}
21 / 1.7	3.2^a	14.1^b	0.32^{bc}	0.42^c
1.7 / 21	-0.2^a	19.7^b	0.12^a	1.07^d
21 / 21	3.1^a	38.1^c	0.31^{bc}	1.69^e
Initial value	85.6% RWC		-0.73 MPa	

Within a character values with the same appended letter do not differ at $P = 0.05$.

Root pruning, experiment 4

Floret numbers are determined by N supply rates early in plant development and mature root mass is particularly affected during floret initiation. Can the pruning of roots limit the number of florets initiated? The 10 uppermost 1st order lateral roots were pruned from the tap root at the 8-leaf stage, removing 9 to 29 mg dry weight from a root system with a mean dry weight of 77 mg. The effects were proportional to the amount of root removed, so that plant (Table 4), stem, leaf and root dry weights at anthesis were depressed. Although some unbranched adventitious roots had grown out from the pruned area by the end of floret initiation they were not sufficient to allow a recovery of total root dry weight to the unpruned values. Leaf and floret numbers were both decreased by root pruning. The number of florets in a long parastichy row was depressed in both cultivars, Hysun 30 and Sunfola 68.3, but only in the latter was the number of long parastichy rows decreased by root pruning.

Another root pruning at the end of floret initiation of previously pruned or intact plants, had less effect that the earlier pruning. Removing 90 to 230 mg dry weight from plants with a mean root dry weight of 850 mg had no effect upon leaf and floret numbers because

Table 4. Reduction in plant dry weight, leaf and floret numbers in two cultivars of *Helianthus annuus* by partial root pruning at plant plastochron index 8. Experiment 4.

Plant dry weight (g) at anthesis[1] $\qquad$ = 42.9 - 1.07 RW; v = 22.8;

Leaf number per plant: Hysun 30 = 34.6 - 0.574 RW
Sunfola 68.3 = 28.1 - 0.201 RW; v = 53.0;

Floret number per plant: Hysun 30 = 1009 - 15.2 RW
Sunfola 68.3 = 769 - 15.2 RW; v = 60.0;

Number of florets in long parastichy row
Hysun 30 = 31.2 - 0.300 RW
Sunfola 68.3 = 25.5 - 0.300 RW; v = 52.4;

Number of long parastichy rows[2]
No significant effect in Hysun 30
Sunfola 68.3 = 8.06 - 0.314 RW; v = 44.2;

where RW is mg root dry weight removed, v is percentage variance in Y accounted for by variance in RW.

[1] no significant difference between genotypes
[2] the number of parastichy rows increases in the Fibonacci series. For the purpose of regression analysis they have been given formal levels so that 21 rows = 7, 34 = 8, 55 = 9

they had been initiated by that stage. In Sunfola 68.3 plant height at anthesis was decreased by 24% by root pruning of previously untreated plants, and it reduced the shoot weight more than root weight so that the shoot/root ratio at anthesis decreased by 28%. Other characters, except plant dry weight, plant height, stem and leaf dry weight, were not depressed by the pruning of previously untreated plants. A second root pruning of previously pruned plants had no effect on any character.

DISCUSSION

In species such as *Capsicum annuum* (unpublished results) and safflower (Steer and Harrigan, 1986), which flower indeterminately, root dry weight responded to N supply rates in all developmental phases, in the same manner as total plant dry weight. The root mass of determinate sunflower, on the other hand, responded preferentially to the N rates supplied before floret initiation was complete (Steer and Hocking, 1984; and Table 1). This contrasts with whole plant dry weight which responds to N supply equally in all phases.

When the shoot apical meristem has stopped initiating leaves and florets in sunflower the mass of the root system responds only in a small way to changes in N supply rates. A similar observation was made by Paterson (1984) in shoot-tip cultures of inbred sunflower lines: rooting could not be induced after florets were initiated. In the open-pollinated cultivar Sunfola 68.3, the phase before floret initiation was of greatest significance (P<0.01) in determining root mass at maturity (Table 2). However, there may be some cultivar differences in the control of root production and dry matter accumulation because the primitive, open-pollinated line 'Hopi' produced many adventitious root buds on the lower stem in response to some treatments but hybrid lines did not (Rogers, Unger and

Kreitner, 1984). These root buds became most evident after floret initiation was complete.

It is not yet clear whether one root character is mainly determined during FI and so sets the root mass to be attained at anthesis or maturity, although it is the root stele mass and not cortical mass that responds to N supply. Root functions such as N and water acquisition can compensate for a small root mass but there is no compensation in the relationship between root mass and leaf and floret initiation. Root pruning of sunflower just before the start of floret initiation caused decreases in the number of leaves and florets produced (Table 4). Thus root removal must have taken effect immediately in order to depress the production of leaf primordia. Other characters, such as plant and leaf dry weight at anthesis, could have responded to root loss more slowly, during the rapid accumulation of plant dry matter between floret initiation and anthesis.

The number of long parastichy rows of disc florets evident at the outer edge of the sunflower capitulum is related to the size of the generative area of the floral meristem during floret initiation (Palmer and Steer, 1985). In Sunfola 68.3, but not in Hysun 30, root pruning apparently decreased the circumference of the generative area. In both cultivars, root pruning decreased the number of florets in a long parastichy row from the edge to the centre of the capitulum. This implies that expansion of the meristematic disc during floret initiation (Palmer and Steer, 1985) was depressed by loss of roots.

Pruning, rather than being effective through the removal of root biomass, may function solely through the removal of root apices and their production of plant growth regulators. This could be important before floret initiation, when the shoot apical meristem is still active, but less so afterwards, at which time only the removal of critical root biomass and related root functions might be effective. There was no effect of a second root pruning, after floret initiation, on plants that had already been pruned before floret initiation.

Root loss in sunflower crops, similar to the partial root pruning in experiment 3, can be caused by pest predation on the roots or by damage to roots high in the soil profile during mechanical control of weeds. If this damage occurs before floret initiation then the number of florets and seeds per plant will be decreased and crop yields reduced.

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