Root Volume Effects on Nitrogen Uptake and Partitioning in Peach Trees

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ABSTRACT

Although soil root volume can be modified under field conditions by adjusting irrigation frequency and emitter geometry, little is known about the effect of root volume on tree growth, uptake, and yield. The objective of this work was to investigate effects of physical restriction of root systems on N absorption by peach trees [*Prunus persica* (L.) Batsch.] and N partitioning among tree organs, and to compare experimental data with simulated results. Cumulative NO_3 uptake by 3- and 3.5-yr-old trees grown in containers increased linearly with increasing root volumes from 5 to 10, 20, 40, and 80 L tree⁻¹. This effect was simulated better when assuming a constant ratio of N to dry matter weight in the tree than when assuming a Michaelis-Menten uptake mechanism. Nitrogen partitioning among leaves, branches, fruits, trunk, and roots differed at fruit harvest and at the end of the season. Despite considerable differences in tree organ weights, N concentration in the tree parts was quite similar in the various root volumes and along the growing season. Simulation of N concentration in annual tree parts was less satisfactory than in perennial organs, where initial conditions could be defined accurately. It is suggested that the physical restriction of root growth reduced N uptake, root hormone synthesis rate, and N accumulation in the canopy. The trees have a N-concentration-stat mechanism, which maintains a constant N percentage in the tops by adjusting photosynthesis and growth in direct proportion to the N and cytokinin accumulations in the canopy.

THE ROOT SYSTEM has been shown to play a major role in controlling plant top development, due to its importance in absorbing water (Black and West, 1974) and minerals (Frith and Nicholas, 1974), and as a supplier of growth regulators (Skene, 1975). Restriction of the root volume should, therefore, reduce tree N uptake, growth, and yield, as was observed in apple trees by Levin et al. (1979) under field conditions and by Bar-Yosef et al. (1988) in a container experiment.

Soil root volume effects on tree performance are important because of the widespread use of trickle and microjet irrigation techniques, which allow adjustment and control of tree root volumes under dry summer growing conditions (Dasberg et al., 1981). In an initially dry soil, a sharp wetting front is formed between the wetted hemisphere below the emitter and the surrounding soil. Soil resistance to root penetration strongly increases as soil water content decreases (Gerard et al., 1982), hence root growth from the wetted domain into the dry soil is negligible. This mechanism resembles root growth limitation in containers, where the walls replace the sharp wetting front effect under field conditions.

Our objectives were to investigate the effects of fruiting peach tree root volumes on cumulative NO_3 uptake and N partitioning among roots, trunk, branches, leaves, and fruits, and to use Habib's N-partitioning model (Habib and Mon-

estiez, 1987; Habib et al., 1989) to simulate these effects. Since Habib's model was developed for nonfruiting peach trees, it was modified to include the fruit sink as well.

MATERIALS AND METHODS

Experimental Set-Up

Three groups of 25 Springcrest peach hardwood cuttings (five container volumes [5, 10, 20, 40, and 80 L] at five replicates per volume) were planted in April 1985 in quartz sand and grown until 1988. The experimental design was a randomized block. Water and N (supplied as $6.0 \pm 1.0 \text{ mM NO}_3^-$) were applied in excess relative to plant demand. The concentration of P, K, Ca, Mg, SO_4 , B, Fe, Mn, and Zn in the irrigation solution of all treatments was 0.5, 3.3, 3.0, 3.0, 0.5, 0.01, 0.02, 0.001, and 0.0015 mM, respectively. Iron was supplied as Fe-EDDHA and Fe-EDTA at equal molar concentrations. Fertigation started daily at 0700 h and terminated at 1800 h. Daily transpiration was determined as differences between known inflow and measured outflow. Outflow was collected from one to two containers in each replicate. The trees were destructively sampled on 15 Sept. 1987, 6 June 1988 (Day 163), and 5 Sept. 1988 (Day 253) and separated into leaves, branches, trunk, root collar, and roots (<1 mm, 1 to 3 mm, and >3 mm). Each organ was weighed fresh and dry, ground, and subsampled for chemical analysis. Reduced N-content was determined after digestion in $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ using a Technicon autoanalyzer. Pruned branches and leaves were collected and analyzed as described above.

Dry matter (DM) production and N uptake during the 1988 season were calculated based on DM and N content in trees on 15 Sept. 1987. Nitrogen and DM content in tree organs on that date were assumed to represent N and DM on 18 Apr. 1988 (Day 114), when trees had just started to bloom and fertigation was begun. A preliminary test confirmed that this assumption was reasonable.

Model

The NO_3^- uptake rate per unit root weight (F , $\text{g N g}^{-1} \text{ root d}^{-1}$) was calculated using the Michaelis-Menten equation:

$$F = F_{\max} C / (K_m + C) \quad [1]$$

where C denotes the $\text{NO}_3\text{-N}$ concentration in the irrigation solution (assumed to equal the bulk soil solution concentration, mg L^{-1}), $F_{\max}$ is the maximum F , and K_m is an uptake efficiency term (mg L^{-1}).

The rate of N uptake per plant at a given time t (U_t , g s^{-1}) is a function of F at time t (F_t) and root weight active in uptake (R_t , $\text{g}^{-1} \text{ dry root plant}^{-1}$):

$$U_t = R_t F_t \quad [2]$$

It was assumed that R in Eq. [2] consisted of roots <1 mm in diameter (thin roots: TR). The ratio of TR to total root dry weight throughout the growing season was obtained by interpolation among the three sampling dates mentioned above.

An alternative approach for estimating U_t was by assuming that the total N (Q_N) to total DM ratio (= NF) in trees throughout the growing season is constant (Habib and Monestiez, 1987). According to this assumption, any incremental increase in DM ($\Delta \text{DM} / \Delta t$) will result in $U_t = \text{NF} (\Delta \text{DM} / \Delta t)$.

Abbreviations: DM, dry matter; TR, thin roots; TRR, thin root to total root ratio.

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The N partitioning submodel described the net N outflow (OF_i , g N d⁻¹, Eq. [3]) at any time t from source organ i ($i = 1, 2, 3, 4$) to sink organ j ($j = 1, 5$).

$$OF_i(t) = K_i N_i(t) \sum_{j=1}^5 (a_{ij} \Delta DM_j / \Delta t) \quad [3]$$

Here, K_i is a dimensionless organ-specific transport coefficient, N_i is total N content in organ i (g N g⁻¹ DM), and a is an operator that equals 0 when flow from a given source organ i to sink organ j is precluded, and equals 1 when flow takes place (Fig. 1). Mass conservation (Eq. [4]) enables calculation of the change in total N in plant organ i (Q_{Ni} , g N) throughout the growing season:

$$\Delta Q_{Ni} / \Delta t = [\sum_{j=0}^4 a_{ij} OF_j \sum_{i=0}^4 \Delta DM_i / (a_{ji} \Delta DM_i)] - OF_i \quad [4]$$

Here $j = 0$ indicates N uptake from the soil solution. This equation states that N outflow from any source compartment is divided among the sink compartments according to their relative DM addition rate. Equation [4] differs from that used in the original model (Habib et al., 1989) in two respects. First, Eq. [4] considers N uptake by the roots and then the distribution of N from the roots to other organs (Fig. 1); originally, this was a single-step process. Second, Eq. [4] includes the fruit compartment (Fig. 1).

To solve Eq. [3] and [4], the DM weight of the first to fifth organs (Fig. 1) must be known. The DM data could be obtained from a peach tree photosynthesis and partitioning model, but we did not have such a model. Hence, the total daily DM production ($\Delta DM / \Delta t$) as a function of time was estimated from measured daily transpiration rates ($\Delta Q_w / \Delta t$, L plant⁻¹ d⁻¹) throughout the growing season:

$$\Delta DM / \Delta t = P \Delta Q_w / \Delta t \quad [5]$$

The crop coefficient P (g L⁻¹) was estimated as the total DM production from Day 114 to 163 and Day 164 to 253, divided by the cumulative transpiration during these two time intervals.

Daily DM partitioning among tree organs was calculated according to the known ratios between organ weights and total tree DM on Day 114, 163, and 253. To obtain a smooth function, the daily partitioning factor for each organ was approximated by linear interpolation among the three experimental values.

Model Calibration and Validation

Model partitioning and N uptake parameters were estimated separately using the Michaelis-Menten and the constant Q_N /DM approaches. Parameter fitting was performed according to the numerical procedure described by Habib et al. (1989). In the first case, the best fitting of K_i , F_{max} , and K_m was made according to data on the N quantity in various tree organs in the 20-L treatment. In the second case, the constant Q_N /DM was determined by correlating total tree DM and total N quantity for all container volume treatments on Day 163 and Day 253. The obtained correlation ($n = 10$ observations) was $Q_N = 0.020$ DM ($r^2 = 0.95$). The obtained NF (0.020) was used to calculate N uptake and then to estimate K_i from the N quantity in

Fig. 1. Structure of the partitioning model among roots (R), trunk + root collar (T), branches (B), leaves (L), and fruits (F). OF_i and K_i are as defined in Eq. [3].

Table 1. Parameter values for the N-partitioning model as used to simulate effects of fruiting peach tree root volumes on cumulative NO₃ uptake and N partitioning.[†]

Michaelis-Menten constants		N transport coefficients in tree [‡]	
Variable	Value	Variable	Value
F_{max}	2.83 mg N g ⁻¹ fine root dry wt. d ⁻¹	K_1	1.538
K_m	1.93 mM N	K_2	0.086
		K_3	0.861
		K_4	0.194

[†] Values are best fitted to 20-L root volume experimental results.

[‡] See Eq. [3] and Fig. 1.

tree organ data in the 20-L treatment. The K_i values obtained in the two approaches deviated by <5%.

The estimated parameters (Table 1) were used to compute N uptake, partitioning, and concentration in tree organs in the other volume treatments.

RESULTS AND DISCUSSION

Dry Matter Input Functions

The ratio of total DM production to accumulated transpiration (P , Eq. [5]) for the five container volumes is summarized in Table 2. The pertinent transpiration data were published by Ran et al. (1992) and will not be repeated here. The transpiration per gram dry matter (reciprocal of the data in Table 2) increased after harvest and pruning, especially in the 40- and 80-L treatments. This stemmed from a reduced dry matter production rate (DMPR) in the postharvest growth stage as compared with that of the preharvest growth stage (Fig. 2), while maintaining the same transpiration rate. Older leaves and higher temperatures in the postharvest period could explain these observations. The difference in P (Eq. [5]) between small and large treatment volumes diminished considerably after harvest. Because the seasonal variation exceeded the root volume variation in P , nearly no difference in all-season average P values among volumes was observed (Table 2).

The fractions of DM in the studied tree organs, according to which partitioning of daily DM additions among tree parts was calculated, were similar for the various root volumes (Table 3). An exception was the DM fraction of the trunk, which decreased with increasing container volume.

The ratio of thin root to total root weight (TRR, Table 3) was used to calculate weight of absorbing roots from estimated total root weight. At harvest (Day 163), the TRR

Table 2. Total dry matter production to cumulative transpiration ratio (P , Eq. [5]) as a function of container volume and tree growth stage.[†]

Time period [‡]	Container volume, L				
	5	10	20	40	80
Day of year	g L ⁻¹				
114-163	4.34	2.64	3.10	6.00	4.21
164-253	1.89	2.49	2.41	1.78	1.61
114-253	2.53	2.53	2.61	3.11	2.30

[†] Cumulative evaporation from Class A pan was 433 mm for the period from Day 114 to Day 163 and 944 mm for Day 164 to Day 253. Tree stand was 1 tree 2.5 m⁻².

[‡] Day 114 = blooming; Day 163 = fruit harvest; Day 253 = end of season.

Fig. 2. Dry matter accumulation by 3-yr-old fruiting peach trees as a function of time and container volume. Circled and noncircled symbols represent experimental and computed (Eq. [5]) results, respectively.

Table 3. Partitioning of dry matter (DM) among tree organs, and the thin to total root weight ratio (TRR) as a function of container volume and growth stage.†

Time period	Container volume	Tree organ§					TRR
		L	B	T	R	F	
	L	% of total DM in tree					
Day 144	5	—	0.46	0.32	0.21	—	0.53
	10	—	0.42	0.30	0.28	—	0.46
	20	—	0.44	0.28	0.27	—	0.44
	40	—	0.50	0.24	0.26	—	0.43
	80	—	0.49	0.24	0.27	—	0.37
Day 163	5	0.16	0.30	0.25	0.13	0.15	0.42
	10	0.19	0.30	0.22	0.19	0.10	0.37
	20	0.19	0.33	0.17	0.14	0.17	0.36
	40	0.18	0.33	0.19	0.20	0.10	0.34
	80	0.16	0.34	0.16	0.19	0.14	0.28
Day 253	5	0.23	0.41	0.18	0.18	—	0.64
	10	0.25	0.37	0.17	0.21	—	0.62
	20	0.25	0.42	0.18	0.15	—	0.52
	40	0.21	0.39	0.18	0.22	—	0.54
	80	0.22	0.41	0.17	0.20	—	0.40

† Thin roots: <1 mm in diameter.

‡ Day 114 = blooming; Day 163 = fruit harvest; Day 253 = end of season.

§ L = leaves; B = branches; T = trunk + root collar; R = roots; F = fruits.

in all treatments was appreciably smaller than on Day 114 or Day 253, due to the fruit sink competition for carbohydrates. Similar results have been published for tomato (Hurd et al., 1979).

The total DM vs. time functions calculated from Eq. [5] and data in Tables 2 and 3 are presented for the five container volumes in Fig. 2.

Nitrate Uptake

The effect of container volume on cumulative $\text{NO}_3\text{-N}$ uptake by 3-yr-old trees from blooming to harvest (Fig. 3a) or from blooming to end of season (Fig. 3b) was nearly linear. Simulation of N uptake vs. container volume was more successful when done according to the constant Q_N/DM concept than by the Michaelis-Menten approach. The shortcoming of the Michaelis-Menten simulation (Fig. 3) could have stemmed from three sources: (i) estimation of fine root weight as a function of time (Fig. 4) may have been in error; (ii) the fine roots (<1 mm) may not be an

Fig. 3. Experimental and simulated total N uptake as a function of container volume (a) from blooming (Day 114) to fruit harvest (Day 163) and (b) from blooming to end of season (Day 253). M&M and Q_N/DM : simulated according to the Michaelis-Menten and the constant Q_N/DM approaches, respectively.

Fig. 4. Fine root (<1 mm in diameter) weight of 3-yr-old peach trees as a function of time along the growing season and container volume. Experimental points are circled; the remaining points were calculated as described in the text.

accurate representation of the fraction of roots participating in NO_3 uptake, particularly for the 40- and 80-L trees; and (iii) the Michaelis-Menten parameters were determined from 20-L trees, which may not be representative of larger volume roots. The lower fine root weight in 80-L

Fig. 5. Nitrogen partitioning among organs of 3-yr-old fruiting peach tree as a function of container volume at (a) Day 163, harvest, and (b) Day 253, end of season. Experimental and simulated results are presented by empty and filled symbols, respectively. Simulation made according to the constant Q_N/DM approach ($= 0.02$).

than in 40-L trees on Day 253 (Fig. 4) suggests that the first explanation may be most important. It is unlikely that the method of estimating DM production during the season from daily transpiration caused the poor simulation by the Michaelis-Menten approach, as this method was used for the constant Q_N/DM approach as well.

The constant Q_N/DM approach is consistent with the functional equilibrium concept used in annual crop simulations (Wilson, 1988). This concept maintains that the photosynthesis rate is proportional to the nutrient uptake rate, and that plants achieve this balance by adjusting the relative size of their shoot and root masses (Johnson and Thornley, 1987). Our results indicate that the constant Q_N/DM approach can be applied on a daily basis, as was recently shown by Gastal and Saugier (1989) for tall fescue.

Nitrogen Partitioning

At harvest and at the end of the season, the effect of container volume on N partitioning among tree organs was slight (Fig. 5). A similar effect was obtained on DM distribution (Ran et al., 1992). Considering the SE of the presented data (Fig. 5), the agreement between empirical and model partitioning results is good. Note that the computations were done according to the constant Q_N/DM approach only. The poorest agreement was obtained for N

Fig. 6. Nitrogen concentration in dry matter of various 3-yr-old peach tree organs (%) as a function of time along the growing season. Container volume = 20 L; Circled and noncircled symbols represent experimental and simulated results, respectively. Simulation made according to the constant Q_N/DM approach ($= 0.02$).

fraction in roots of 80-L trees; at harvest (Day 163) the model overestimated it appreciably (28 vs. 19% of total N), while at the end (Day 253) it was underestimated (17 vs. 27%).

The fraction of N in leaves, trunk, and roots was similar on Day 163 and Day 253 for all container volumes. The fraction of N in branches on Day 253 increased relative to the fraction on Day 163.

Nitrogen Concentration in Tree Organs

Nitrogen concentration in the dry matter of tree organs decreased in the following order: leaves, roots, fruits, branches, and trunk (Fig. 6). At blooming, fruit harvest, and end of the season, N concentration in specific organs differed due to root volume effects by <10%. Results for 5-, 10-, 40- and 80-L trees are not presented, as they were similar to the 20-L volume treatment. The variations in experimental results along the season were meaningful only for leaves and branches, where a maximum and a minimum of N concentration at harvest, respectively, were observed.

The model predicted small temporal variations in N concentration in all treatments. The predicted fluctuations (up to $\pm 20\%$) diminished as root volume increased. In all volumes, prediction of N concentration in leaves at harvest was least satisfactory (30% deviation in 5-L and 16% deviation in 80-L trees), followed by N concentration in fruits. In perennial organs, which have defined DM and N values at blooming, N concentration was more successfully simulated than for annual organs, where the initial values had to be approximated. The underestimation of N concentration in leaves may have been related to initial conditions of the model, or to an unsatisfactory partitioning coefficient of N to this organ.

CONCLUSIONS

Data indicate that peach trees have a N-concentration-stat mechanism, which sustained a nearly constant N concentration in tree organs along the growing season in all studied root volumes. Trees with restricted root systems

absorbed less N per unit time from the N solution than did trees with larger root systems. To maintain the characteristic N concentration, trees with small root volumes produced less dry matter than trees with unrestricted root volumes, creating the observed differential growth and fruit yield. The signal to reduce the tree growth rate to maintain the constant N concentration could be mediated by cytokinin concentration in the canopy, which is expected to be a function of root volume as well.

The modified model of Habib and coworkers predicted the root volume effect on temporal N uptake and partitioning in fruiting peach trees. This may serve as a positive verification of the improved model and its governing assumptions. The reasonable agreement between simulated and experimental results encourage further testing of the model under field conditions to assess its suitability for the prediction of temporal N uptake and N concentration in tree organs for cultural management purposes.

REFERENCES

- Bar-Yosef, B., S. Schwartz, T. Markovich, B. Lucas, and R. Assaf. 1988. Effect of root volume and nitrate solution concentration on growth, fruit yield, and temporal N and water uptake by apple trees. *Plant Soil* 107:49-56.
- Black, J.D.F., and D.W. West. 1974. Water uptake by an apple tree with various proportions of the root system supplied with water. p. 432-433. *In Proc. Int. Drip Irrig. Congr., 2nd, San Diego, CA.*
- Dasberg, S., H. Bieloryi, and Y. Erner. 1981. Partial wetting of the root zone and nitrogen effects on growth and quality of Shamouti oranges. *Acta Hort.* 119:103-108.
- Frith, G.L.T., and D.G. Nicholas. 1974. Effect of nitrogen fertilizer application to part of the root system. p. 434-436. *In Proc. Int. Drip Irrig. Congr., 2nd, San Diego, CA.*
- Gastal, F., and B. Saugier. 1989. Relationships between nitrogen uptake and carbon assimilation in whole plants of tall Fescue. *Plant Cell Environ.* 12:407-416.
- Gerard, C.J., P. Sexton, and G. Shaw. 1982. Physical factors influencing soil strength and root growth. *Agron. J.* 74:875-879.
- Habib, R., and P. Monestiez. 1987. Croissance vegetative et repartition de l'azote chez le jeune pecher: approche par modelisation. p. 161-175. *In Colloque INRA-CTIFL sur les recherches Fruitières, 7eme, Bordeaux, France.*
- Habib, R., A.M. de'Cockborne, P. Monestiez, and F. Lafolie. 1989. An experimental test of a nitrogen uptake and partitioning model for young trees. *Tree Physiol.* 5:403-421.
- Hurd, R.G., A.P. Gay, and A.C. Mountifield. 1979. The effect of partial flower removal on the relation between root, shoot, and fruit growth in the indeterminate tomato. *Ann. Appl. Biol.* 93:77-89.
- Johnson, I.R., and J.H.M. Thornley. 1987. A model of shoot:root partitioning with optimal growth. *Ann. Bot. (London)* 60:133-142.
- Levin, I., R. Assaf, and B. Bravado. 1979. Soil moisture and root distribution in apple orchards irrigated by tricklers. *Plant Soil* 52:31-40.
- Ran, Y., B. Bar-Yosef, and A. Erez. 1992. Root volume influence on dry matter production and partitioning as related to nitrogen and water uptake rates by peach trees. *J. Plant Nutr.* 15:713-726.
- Skene, K.G.M. 1975. Cytokinin production by roots as a factor in the control of Plant growth. p. 356-396. *In J.G. Torrey and D.T. Clarkson (ed.) The development and function of roots.* Academic Press, London.
- Wilson, J.B. 1988. A review of evidence on the control of shoot:root ratio in relation to models. *Ann. Bot. (London)* 61:433-439.