Estimating seasonal nitrogen dynamics in peach trees in response to nitrogen availability

JOSEP RUFAT[1] and THEODORE M. DeJONG[2,3]

[1] *Institut de Recerca i Tecnologia Agroalimentàries (IRTA), Àrea de Tecnologia Frutícola, Centre UdL-IRTA, Alcalde Rovira Roure 177, 25198 Lleida, Spain*

[2] *Department of Pomology, University of California, Davis, CA 95616, USA*

[3] *Author to whom correspondence should be addressed*

Summary The PEACH computer simulation model of reproductive and vegetative growth of peach trees (Grossman and DeJong 1994) was adapted to estimate seasonal nitrogen (N) dynamics in organs of mature peach (*Prunus persica* (L.) Batsch cv. O'Henry) trees grown with high and low soil N availability. Seasonal N accumulation patterns of fruits, leaves, stems, branches, trunk and roots of mature, cropping peach trees were modeled by combining model predictions of organ dry mass accumulation from the PEACH model with measured seasonal organ N concentrations of trees that had been fertilized with either zero or 200 kg N ha^{-1} in April. The results provided a comparison of the N use of perennial and annual organs during the growing season for trees growing under both low and high N availability.

Nitrogen fertilization increased tree N content by increasing organ dry masses and N concentrations during the fruit growing season. Dry mass of current-year vegetative growth was most affected by N fertilization. Whole-tree N content of fertilized trees was almost twice that of non-fertilized trees.

Although N use was higher in fertilized trees, calculated seasonal N accumulation patterns were similar for trees in both treatments. Annual organs exhibited greater responses to N fertilization than perennial organs. Estimated mean daily N use per tree remained nearly constant from 40 days after anthesis to harvest. The calculations indicated that fertilized trees accumulated about 1 g N tree^{-1} day^{-1}, twice that accumulated by non-fertilized trees. Daily N use by the fertilized orchard was calculated to be approximately 1 kg N ha^{-1}, whereas it was approximately 0.5 kg N ha^{-1} for the non-fertilized trees. During the first 25–30 days of the growing season, all N use by growing tissues was apparently supplied by storage organs. Nitrogen release from storage organs for current growth continued until about 75 days after anthesis in both N treatments.

Keywords: crop modeling, fertilizer requirements, fruit tree growth, Prunus persica.

Introduction

Nitrogen (N) is generally the most important macronutrient in crop fertilization, and N supply often restricts final yield of peaches. During the growing season, a significant amount of N is removed from orchard soils (Batjer et al. 1952, Rogers et al. 1955, Weinbaum et al. 1992). Although a high percentage of leaf N is remobilized to perennial organs before leaf abscission (Taylor and Van den Ende 1969, Stassen et al. 1981*b*, Castagnoli et al. 1990), stored N is insufficient to maintain commercial crop yields. Fertilization with N is required to maintain tissue N status (Taylor and Van den Ende 1969, Weinbaum et al. 1984*a*), crop yields (Taylor and Van den Ende 1970, Saenz et al. 1997) and vegetative growth (Taylor and Van den Ende 1969, Stassen et al. 1981*a*).

Leaf and stem N content is influenced by several factors including environmental conditions, management practices and physiological factors. Decreases in leaf N concentration throughout the fruit growth period have been reported in peach trees (Taylor and May 1967, Taylor and Van den Ende 1969) and can be attributed to dilution of N in growing leaves and stems in the spring and the remobilization of N from leaves to organs, including fruit, that have greater N demand in summer. In peach, N concentrations in fruit are similar to concentrations in foliage (Cummings 1973).

Weinbaum et al. (1984*b*) reported that the presence of fruits may influence N uptake, and it seems that N demand, mainly in the shoot, may regulate N uptake by roots. Fertilizer timing experiments in peach have indicated that nutrient uptake is greatest during the period of fruit growth (Stassen et al. 1981*a*, Muñoz et al. 1993). The nutritional status of plants may also influence N uptake. Feigenbaum et al. (1987) confirmed that the recovery of fertilizer N by N-starved orange trees grown in the field was greater than in trees previously supplied with abundant fertilizer N.

Knowledge of the effects of N availability on dry matter partitioning to vegetative and harvestable portions of fruit trees is fundamental to understanding relationships between fertilization and seasonal growth and as a basis for improved crop management. Seasonal patterns of fruit (Grossman and DeJong 1995*a*, Saenz 1996), leaf and stem dry mass (Grossman and DeJong 1995*b*) and seasonal patterns of N concentration in fruit, leaf and stem have been reported for peach trees

(Taylor and May 1967, Taylor and Van den Ende 1969, Stassen et al. 1981*a*, 1981*b*, 1982), but attempts to quantitatively integrate N content and dry matter partitioning in peach trees have been limited to young trees that could be sequentially harvested for tissue analysis (Habib et al. 1989, 1993).

The development of computer simulation models of annual carbon supply and demand in peach trees (e.g., Grossman and DeJong 1994) provides an opportunity to examine relationships between tissue N contents and dry matter partitioning in mature trees. The PEACH model is a state-variable model in which nitrogen-stimulated differences in fruit, leaf, current-year stem, branch, trunk, and root dry mass accumulation can be modeled by integrating differences in organ growth potentials and the supply of photosynthates.

The objectives of this study were to determine the effects of N availability on the seasonal patterns of N concentration and dry mass accumulation in different parts of peach trees and to use the PEACH crop simulation model to estimate the effect of N availability on seasonal N budgets.

Materials and methods

Field studies

Seven-year-old "O'Henry" peach (*Prunus persica* L. Batsch) trees on Lovell rootstock, trained to a perpendicular-V pruning system (DeJong et al. 1994) and growing at the U. C. Davis Wolfskill Experimental Farm (Winters, CA; 38°31′ N, 121°58′ W), were used for this study. The trees had been planted on a Yolo clay loam soil at a spacing of 5.18×1.83 m (1055 tree ha^{-1}). "O'Henry" is a late season cultivar with fruit harvested in early August.

For 3 years before the study began in spring 1996, trees received either 200 kg N ha^{-1} (urea) in early spring (high N treatment; HN), or no N fertilization (low N treatment; LN). In the HN treatment, N fertilizer was applied manually and immediately incorporated with irrigation provided by microsprinklers placed every 4 m along the row. During the 1996 season, an additional application of 50 kg N ha^{-1} was applied to HN-treated trees on May 21 to ensure high N availability.

The experimental plot consisted of two blocks and two N treatments. Each experimental unit consisted of a row of seven trees, of which the central five were sampled. Treatments were separated by border rows receiving the same treatments to avoid the influence of adjacent N treatments. Trees were managed according to commercial practices for pest and weed control, hand thinning and pruning. Trees were irrigated weekly with microsprinklers.

In 1996, bloom was monitored on four tagged shoots on each tree in the two blocks of each N treatment by counting the number of open flowers daily. Full bloom was considered to be the date on which 50% or more of the flowers of each shoot were open. An average full bloom date was established for each N treatment.

Fruits were harvested in accordance with commercial picking standards. Plots were harvested twice. Fruit number and fresh mass per tree were recorded at harvest and a subsample

of the harvested fruit was oven-dried and weighed to calculate a fresh/dry mass conversion factor. A notional date of harvest was calculated based on a weighted mean (using fruit mass) of the two harvest dates.

Fruit and current-year stem and leaf samples from trees in both N treatments were collected at 14-day intervals from anthesis until harvest. All samples were dried to constant weight at 65 °C. Ten average-size fruits per tree were collected from each treatment block from fruit set until mid-June. At the end of the season, only five fruits per tree were collected. Four current-year stems and leaves per tree were collected at each sample date. Samples of current-year stems were at least 10 cm long, and selected leaves and stems were not adjacent to fruits. Fruit growth was regressed against time using cubic splines (Hunt 1979, Grossman and DeJong 1995*a*) fitted to the logarithmically transformed mass data (Grossman and DeJong 1995*a*). Leaf sampling was repeated until June 1997, and data from both seasons were used to construct curves for the seasonal pattern of stem and leaf N content. Fruit and stem sampling was repeated until June during 1997 to validate the results of the previous year.

On July 18 and August 8, 1996 (Day of year (DOY) 200 and 220), the total growth of current-year organs (fruits, stems and leaves) of four trees of both treatments was measured. All fruits were harvested and shoots more than 5 cm long were separated into watersprouts (rapidly growing shoots ≥ 6 mm basal diameter) and stems with their respective leaves. Fresh mass, dry mass and N content of each organ were determined.

Total N concentration was determined by Kjeldhal digestion, following the procedure of Carlson (1978), based on the transfer of ammonia by diffusion through hollow silicone fibers into a flowing stream of water, followed by detection by electrical conductivity. Leaf area was determined on the sampled leaves with an electronic leaf area meter (LI-3000, Li-Cor Inc., Lincoln, NE).

Model calculations

The PEACH computer simulation model of annual carbon supply and demand in peach trees (Grossman and DeJong 1994) is a state-variable model in which fruit, leaf, current-year stem, branch, trunk and root mass are state variables, and minimum and maximum air and soil temperatures, degree-days, solar radiation and canopy light interception are the driving variables. Photosynthetic carbon assimilation and stored carbohydrates supply carbon required for maintenance respiration and growth.

Because the PEACH model assumes adequate N supply, high N (HN) simulations were run using default model data for photosynthesis and light interception. For the low N (LN) treatment, leaf photosynthetic rate was reduced to 86% and 63% for full sun and shade leaves, respectively, and light interception was reduced by 83% (Rosati et al. 1999).

"O'Henry" fruit dry mass values from 1996 were fit with a cubic spline function with knots at 450 and 900 degree-days to obtain growth calibration curves for the HN and LN treatments, respectively. The 1994 fruit dry mass values (Saenz 1996) were used to validate the modeled curves. The general

patterns for stem and leaf relative growth rates (RGR) were assumed to be similar to the model previously developed for the "Cal Red" cultivar (Grossman and DeJong 1994), which ripens at approximately the same time as "O'Henry." New coefficients were estimated based on data from trunk, scaffold and branch measurements (data not shown) and data from total growth of current-year organs on trees in the HN and LN treatments. Data from trees excavated during the dormant period in 1994 (Table 1) were used to develop branch, wood, and root initial dry mass input data for the model, and the data at the end of the season (Niederholzer 1997) were used to validate modeled values.

Mean bloom and crop load data from the 1994 study (Saenz 1996) were also used as model input data. Nitrogen-fertilized "O'Henry" trees bloomed on March 7, 1994, and fruit was harvested on August 13. There was an accumulated total of 2164 degree-days (minimum and maximum thresholds of 7 and 35 °C, respectively). For non-fertilized trees, bloom occurred on March 9, 1994, and harvest was on August 2. Total degree-days accumulated were 1953.

Seasonal N concentration algorithms for trees in the HN and LN treatments were developed from data for fruits, leaves and stems obtained in 1996. Algorithms were validated with leaf and fruit N concentration data from Saenz (1996). Initial N concentrations for branch, wood, and root input data were obtained from analysis of trees excavated during the dormant period in 1994 (Niederholzer 1997). Seasonal patterns of N concentrations reported by Stassen et al. (1983) were adjusted based on N concentrations measured in the HN and LN treatments and used to estimate daily branch, wood and root N concentrations. An inverse logistic function ($y = (1 + Be^{-kx})/M$) versus degree-days was fitted for all organ N concentration

data by the nonlinear regression (PROC NLIN) procedure in the SAS statistical software package (SAS Institute, Cary, NC). Parameter values for M, B and k are listed in Table 2.

Total N content of each organ was estimated as the product of total organ dry mass (calculated from the PEACH model for each day) and the simultaneous estimate of N concentration of each organ. Nitrogen accumulation rate (NAR) was determined with the equations described by Ryugo (1988) for dry mass:

$$NAR = (N_2 - N_1)(t_2 - t_1)^{-1},$$

where N_2 and N_1 are total N organ content at time t_2 and t_1, respectively.

Weather data for 1994 and degree-days used in the PEACH Model were obtained from the California Irrigation Management Information System (CIMIS) weather station located at the Wolfskill Experimental Orchard in Winters, CA. In 1996, data from CIMIS weather stations in both Davis and Winters, CA, were used. For degree-day calculations, the single sine with horizontal cutoff was used, with minimum and maximum threshold temperatures of 7 and 35 °C, respectively (Zalom et al. 1983, DeJong and Goudriaan 1989). All data were expressed as accumulated degree-days from time of full bloom.

Results and discussion

Fruit growth

Seasonal patterns of fruit dry mass (Figure 1) were similar in the HN and LN treatments. However, during Stage III, fruits from non-fertilized trees grew more rapidly than fruits from

Table 1. Mean dry mass, N content, N concentration and % total N for each organ from excavated trees in 1994 (Niederholzer 1997) and modeled dry mass output values for LN and HN treatments.

Organ	February 1994				August 1994				Model output August 1994
	Total DW (g tree^{-1})	Total N (g tree^{-1})	% N	% Total N	Total DW (g tree^{-1})	Total N (g tree^{-1})	% N	% Total N	Total DW (g tree^{-1})
High nitrogen treatment									
Fruit					5792.0	44.0	0.76	22.7	5137
Stem					1408.0	15.1	1.08	7.8	2082
Leaf					2888.0	86.4	2.99	44.5	3034
Branch	672.0	3.6	0.54	5.3	1031.0	3.6	0.35	1.9	1005
Trunk	7728.0	20.9	0.27	30.5	11290.0	19.2	0.17	9.9	9234
Root	5615.0	44.0	0.78	64.2	4595.0	23.7	0.52	12.2	5931
Fruit thin					83.0	1.9	2.24	1.0	
TOTAL	14015.0	68.5		100.0	27087.0	193.9		100.0	26423
Low nitrogen treatment									
Fruit					5140.0	21.5	0.42	21.7	5139
Stem					653.0	4.1	0.63	4.1	754
Leaf					1307.0	31.2	2.39	31.5	1384
Branch	502.0	2.8	0.56	5.3	770.0	2.6	0.34	2.6	550
Trunk	7868.0	20.5	0.26	39.1	11390.0	18.1	0.16	18.3	8288
Root	5190.0	29.1	0.56	55.5	5140.0	18.4	0.36	18.6	6408
Fruit thin					227.0	3.2	1.40	3.2	
TOTAL	13560.0	52.4		100.0	24627.0	99.1		100.0	22523

Table 2. Parameter values for N concentration curves for each organ. An inverse logistic function ($y = (1 + Be^{-kx})/M$) was fitted versus day of year for all organ N concentrations using the nonlinear regression procedure (PROC NLIN) of the SAS statistical software package.

Organ	High N treatment			Low N treatment		
	M	B	k	M	B	k
Fruit	1.02	205.61	0.04657	1.75	182.59	0.03831
Stem	1.12	204.03	0.04590	1.54	1261.45	0.05832
Leaf	35.72	150.00	0.00211	32.45	150.00	0.00383
Trunk	5.88	30271.68	0.14935	6.25	43407.80	0.15272
Root	2.55	1.84	0.00790	3.85	1.93	0.00698
Branch	2.86	32109.41	0.14995	2.94	51592.67	0.15252

fertilized trees and continued to be larger than fruits from HN-treated trees until the first harvest. The calculated weighted mean harvest date was 2 days earlier in the LN treatment than in the HN treatment, and anthesis for HN-treated trees was 1 day earlier than anthesis for LN-treated trees. Therefore, the mean fruit growth season was 3 days longer in the HN treatment than in the LN treatment in 1996.

The larger fruit (Figure 1) on non-fertilized trees compared with fertilized trees during Stage III, before harvest, suggests that differences in fruit size were caused not by differences in nutrient availability but by differences in crop load, which was highest in HN-treated trees. Because the trees were hand-thinned, it is difficult to determine if the differences in crop load were a result of initial fruit set or were caused by differences in the way workers who did the thinning responded to the appearance of LN-treated trees. If resource availability (photosynthate supply) had been reduced by the LN treatment, lower crop growth rates would have been expected compared with HN-treated trees. As reported by Lilleland (1932) and Saenz et al. (1997), N deficiency appears to affect sink demand by decreasing the length of the fruit growth period.
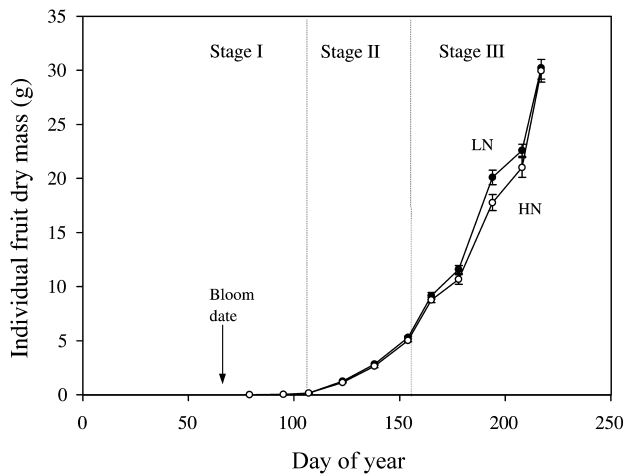
Nitrogen content in fruits, leaves and stems

Fruits and stems had similar patterns of seasonal N concentration, with % N rapidly decreasing during the first 2 months, followed by a slower decrease until harvest. Leaf N concentrations decreased more gradually over the season (Figure 2). The largest significant differences in N concentration between the treatments were on DOY 152–157 and were consistent for the three organ types (Figure 2). This period coincided with the beginning of fruit Stage III (Figure 1). Decreasing N concentrations throughout the season in various organs have been attributed to the dilution of N in growing organs in the spring. During fruit growth, translocation of N from leaves to fruits seems to occur during the last fruit development stages. In the

Figure 1. Seasonal patterns of mean individual fruit dry mass accumulation for non-fertilized trees (LN; ●) and trees fertilized with 200 kg N ha⁻¹ (HN; ○) applied in spring to "O'Henry" peach trees. Each value represents the mean of fruit samples from 10 trees. Bars represent ± 1 standard error of the mean.
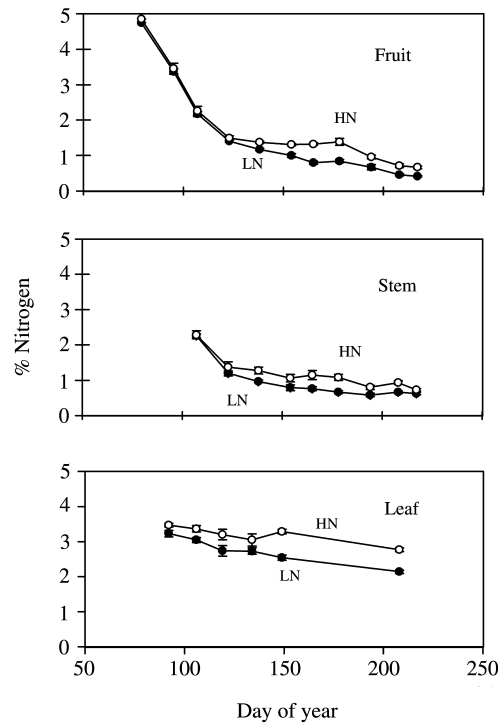

Figure 2. Seasonal patterns of N concentration in fruit, stems and leaves of "O'Henry" peach trees receiving either low (LN; ●) or high (HN; ○) rates of N application. Each value represents the mean of fruit samples from 10 trees. Bars represent ± 1 standard error of the mean.

fall, remobilization of N from leaves to storage tissues also occurs (Taylor and May 1967, Taylor and Van den Ende 1969, Stassen et al. 1981*a*).

Model responses of dry mass growth to N treatments

Modeled fruit dry mass values increased with degree-days after bloom following a double-sigmoidal growth curve. Model outputs of total tree fruit dry mass were similar for fertilized and non-fertilized trees (Figure 3) and similar to measured values (Table 1).

The seasonal pattern of modeled leaf and stem growth is similar to that reported by Berman (1996) for the same peach cultivar and Grossman and DeJong (1995*c*) for early and late maturing peach cultivars, with a linear increase in stem growth and a logistic increase in leaf growth over the season. Niederholzer (1997) obtained similar dry mass values at harvest for both organs in response to similar treatments (Table 1). The model dry mass values for branches showed a linear total dry mass growth pattern similar to the pattern in other perennial parts of the tree, and the value at harvest was almost the same as the value reported in a previous study (Niederholzer 1997) (Table 1). Total modeled wood growth (trunk and scaffolds) was similar to the linear increase reported by Berman (1996)

and Grossman and DeJong (1995*c*). Compared with data from Niederholzer (1997), the model underestimated dry mass partitioning to wood at the time of fruit harvest by 18 and 23% for HN- and LN-treated trees, respectively. On the other hand, modeled root dry mass at harvest was higher than that from excavated trees. Because simulated total tree dry mass and dry mass from excavated trees were similar, the model apparently needs to be adjusted for wood and root growth. For roots, the difficulty in measuring root turnover and mass of fine roots left in the soil could explain some of the differences between the modeled root output and excavation data.

Modeled total tree dry mass at harvest in the HN and LN treatments was similar to tree dry mass of fertilized and non-fertilized excavated trees in 1994 (Niederholzer 1997) (Table 1). Differences between HN and LN total dry mass (Table 1) could result from increased light interception and leaf photosynthesis (A_{max}) in response to N fertilization. DeJong (1982) reported a positive relationship between leaf N concentration and photosynthetic rate in peach trees. Thus, the modeled nutrient availability for whole-tree growth was probably increased by N fertilization, as suggested by DeJong et al. (1989). The potential vegetative organ growth for the LN treatment was lower than that in the HN treatment, apparently as a result of lower dry mass partitioning to vegetative growth in response to competition between vegetative and reproductive growth (Grossman and DeJong 1995*c*).

Calculated N increments in response to N treatments

Combining the dry mass output data from the PEACH model for fruits, leaves, stems, branches, wood and roots with the N concentrations from the fitted functions (Table 2) allowed an estimation of the seasonal N accumulation in each part of the tree (Figure 4). Although trees in both N treatments had similar N accumulation patterns for the respective organs and there were few differences in the proportion of total N in each organ, N contents of HN organs were higher than N contents of LN organs during the whole fruit growth period. Because of high leaf N concentrations, leaves accounted for the highest accumulated N content among all tree organs during the season (Figure 4). Only fruits in the LN treatment were calculated to have a higher N content than leaves at harvest, because of the relatively higher yield per total biomass in LN-treated trees compared with HN-treated trees.

Because of their storage function, the perennial organs had some stored N at the beginning of the season. The calculations indicated that, by the time of bloom, stored N had already been depleted. During the growing season until harvest, calculated N contents decreased gradually in the trunk and root. Although a decrease in N content after bloom was estimated for branches, it was very small, and immediately before harvest there was a slight increase in N content. The calculations indicate large differences in N accumulation between current-year growth and perennial organs in fertilized trees. As reported by Munoz et al. (1993), during the growing season, most of the N in peach trees was estimated to go into the fruits, leaves and shoots. Feigenbaum et al. (1987) reported similar results in mature citrus trees.
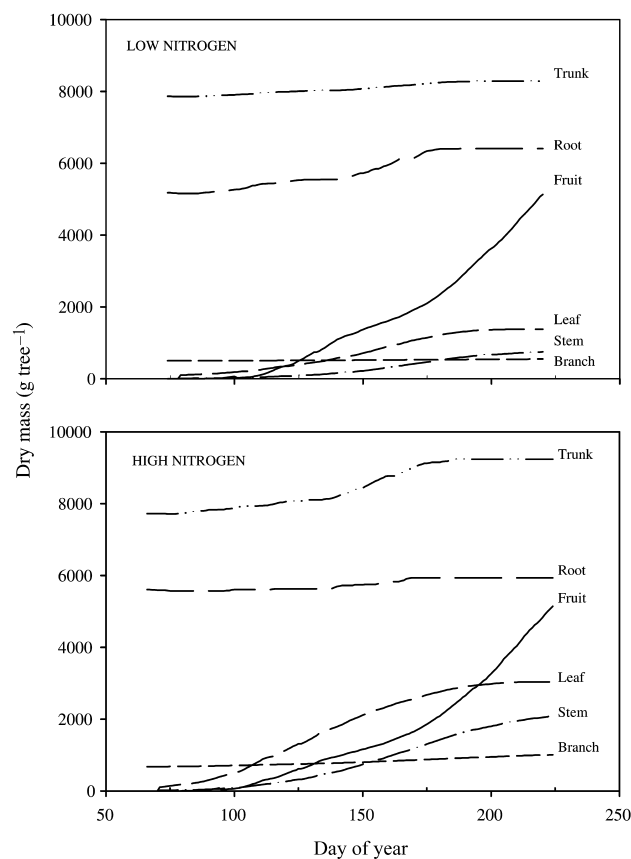

Figure 3. Estimated seasonal patterns of total dry mass distribution for the different parts of trees in the low and high N treatments. The PEACH model output data are a result of using the values from excavated dormant trees (Niederholzer 1997) as input data.
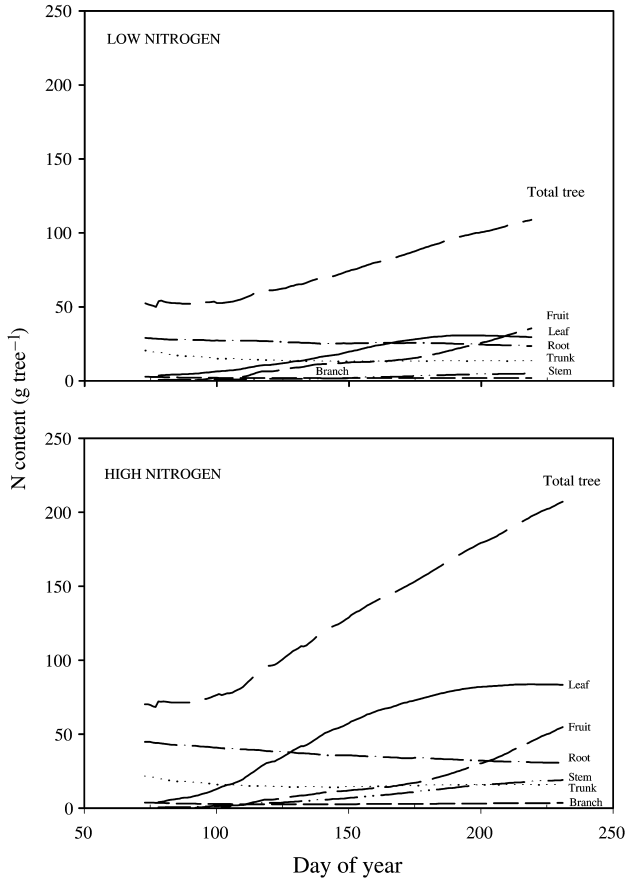
Figure 4. Estimated seasonal patterns of total N distribution in the different parts of low and high N treatment trees. Each curve value is the product of total organ dry mass modeled for each day and the simultaneous estimate of N concentration for the respective organ.
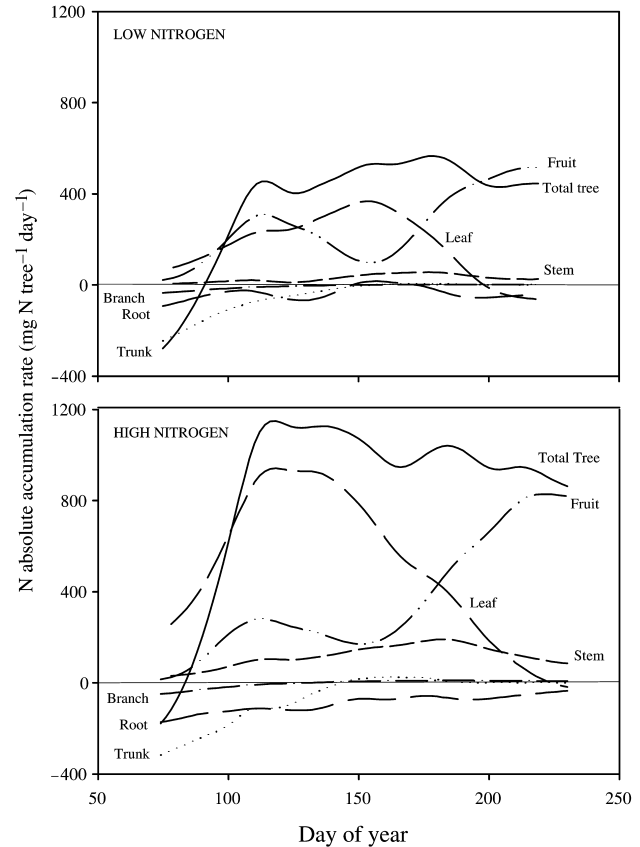

Figure 5. Estimated seasonal patterns of N absolute accumulation rate in the different parts of low and high N treated trees. Each curve value is the result of using the equation NAR = $(N_2 - N_1)(t_2 - t_1)^{-1}$, where N_2 and N_1 are the total N organ content at times t_2 and t_1.

The calculated N increments indicate that the leaves and fruit demanded more N than perennial tissues. Leaves had the highest calculated absolute net assimilation rate (NAR) in the HN treatment (Figure 5) during the first 100 days of vegetative growth and their N accumulation rate started decreasing as full canopy was achieved. Although calculated absolute NAR values were lower for LN-treated trees than for HN-treated trees during the season, a similar N accumulation pattern was obtained (Figure 5), but at a lower rate because of strong N competition from fruits. At an early stage, developing peach and apricot fruits apparently compete successfully with newly expanding foliage for available nutrients (Kriedemann 1968). From anthesis to DOY 150, the high estimated rate of N accumulation was apparently the result of immature leaves acting as sinks. As the season progressed, the calculations indicated that mature leaves were capable of translocating nitrogenous compounds to other organs. After DOY 170 (close to full canopy), the resulting parabolic decrease in NAR indicated that the leaf N requirement to build N components was proportional to the demand of the rest of the organs and may reflect the capacity of leaves to act as protein reservoirs (Chapin et al. 1990). This decreasing trend in NAR resulted in negative NAR estimates for vegetative organs in both treatments close

to harvest time. The strong fruit N demand at that time, in addition to stem N demand, contrasted with the calculated net N outflow from the leaves.

The calculated N requirement of fruit increased sharply early in the season, particularly for LN-treated trees (Figure 5). The increase corresponded to the exponential increase in dry weight in the early stage of fruit growth, and was followed by a period of decreasing fruit NAR (Figure 5) corresponding with the second stage of fruit development (pit hardening) when cell division is thought to decrease (Lilleland 1932). The rapid resumption of growth (cell enlargement) in the last stage of fruit growth paralleled an increase in NAR. The calculated NAR increased almost linearly (Figure 5) during the second half of the season, with similar values in both N treatments.

Branches were calculated to have little N gain or loss over the entire season. The estimated NAR for roots was negative during almost all of the fruit development period. The estimated trunk NAR recovered from negative values by DOY 140 for HN-treated trees and by DOY 150 for LN-treated trees. Subsequently, values were close to zero. Minimum values for trunk and root coincided with the starting values.

These calculations indicate a net release of N from storage

organs to current-year organs. The N apparently supplied by these organs decreased with time, as uptake from the soil increased. This corresponds to previous reports that most N release takes place during the first 2 months after anthesis (Deng et al. 1989). Nutrient uptake is a function of demand (Richards and Rowe 1977, Weinbaum et al. 1994) and is thought to be independent of remobilization from storage (Weinbaum et al. 1984a). After harvest, a positive net N storage occurs as a result of a large decrease in the N demand from growth (Stassen et al. 1983).

Estimated total tree NAR was most affected by the high leaf and fruit NAR values over the season. The integrated value for the whole tree takes into account the increases and decreases in N content in each organ, and provides an estimate of seasonal tree N use. Absolute nitrogen accumulation rates increased rapidly during the vegetative spring flush (until DOY 110), which occurred in both HN- and LN-treated trees. After the spring flush, NAR in the HN-treated trees plateaued at about 1 g N tree^{-1} day^{-1} until harvest (Figure 5). For this orchard, this is equivalent to approximately 1 kg N ha^{-1} day^{-1}. For LN-treated trees, the values were approximately 50% less (Figure 5) and the estimated N use was about 0.5 kg N ha^{-1} day^{-1}.

Calculations of negative total NAR indicate an outflow of tree N early in the season (Figure 5), which is unlikely. Any N released from perennial parts during this period was probably redistributed to developing buds, but the calculations did not account for this because growth was calculated only after bud break.

References

Batjer, L.P., B.L. Rogers and A.H. Thompson. 1952. Fertilizer applications as related to nitrogen, phosphorus, potassium, calcium and magnesium utilization by apple trees. Proc. Am. Soc. Hortic. Sci. 60:1–6.

Berman, M.E. 1996. Effects of competition among sinks and environmental factors on growth and carbon partitioning in peach (Prunus persica). Ph.D. Diss. Univ. California, Davis, 132 p.

Carlson, R.M. 1978. Automated separation and conductimetric determination of ammonia and dissolved carbon dioxide. Anal. Chem. 50:1528–1531.

Castagnoli, S.P., T.M. DeJong, S.A. Weinbaum and R.S. Johnson. 1990. Autumn foliage applications of ZnSO₄ reduced leaf nitrogen remobilization in peach and nectarine. J. Am. Soc. Hortic. Sci. 115: 79–83.

Chapin, F.S., III, E.-D. Schulze and H.A. Mooney. 1990. The ecology and economics of storage in plants. Annu. Rev. Ecol. Syst. 21:427–447.

Cummings, G.A. 1973. The distribution of elements in 'Elberta' peach tree tissues and the influence of potassium and magnesium fertilization. J. Am. Soc. Hortic. Sci. 98:474–477.

DeJong, T.M. 1982. Leaf nitrogen content and CO₂ assimilation capacity in peach. J. Am. Soc. Hortic. Sci. 107:955–959.

DeJong, T.M. and J. Goudriaan. 1989. Modeling peach fruit growth and carbohydrates requirements: reevaluation of the double sigmoid growth pattern. J. Am. Soc. Hortic. Sci. 114:800–804.

DeJong, T.M., K.R. Day and R.S. Johnson. 1989. Partitioning of leaf nitrogen with respect to within canopy light exposure and nitrogen availability in peach (Prunus persica). Trees 3:89–95.

DeJong, T.M., K.R. Day, J.F. Doyle and R.S. Johnson. 1994. The Kearney Agricultural Center Perpendicular "V" (KAC-V) orchard system for peaches and nectarines. HortTechnology 4:362–367.

Deng, X., S.A. Weinbaum and T.M. DeJong. 1989. Use of labeled nitrogen to monitor transition in nitrogen dependence from storage to current-year uptake in mature walnut trees. Trees 3:11–16.

Feigenbaum, S., H. Bielorai, X. Erner and S. Dasberg. 1987. The fate of ¹⁵N labelled nitrogen applied to mature citrus trees. Plant Soil 97:178–187.

Grossman, Y.L. and T.M. DeJong. 1994. PEACH: a simulation model of reproductive and vegetative growth in peach trees. Tree Physiol. 14:329–345.

Grossman, Y.L. and T.M. DeJong. 1995a. Maximum fruit growth potential and seasonal patterns of resource dynamics during peach growth. Ann. Bot. 75:553–560.

Grossman, Y.L. and T.M. DeJong. 1995b. Maximum fruit growth potential following resource limitation during peach growth. Ann. Bot. 75:561–567.

Grossman, Y.L. and T.M. DeJong. 1995c. Maximum vegetative growth potential and seasonal patterns of resource dynamics during peach growth. Ann. Bot. 76:473–482.

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.

Habib, R., P. Millard and M.F. Proe. 1993. Modelling the seasonal nitrogen partitioning in young sycamore (Acer pseudoplatanus) trees in relation to nitrogen supply. Ann. Bot. 71:453–459.

Hunt, R. 1979. Plant growth analysis: the rationale behind the use of the fitted mathematical function. Ann. Bot. 43:245–249.

Kriedemann, P.E. 1968. ¹⁴C translocation patterns in peach and apricot shoots. Aust. J. Agric. Res. 19:775–780.

Lilleland, O. 1932. Growth study of the peach fruit. Proc. Am. Soc. Hortic. Sci. 29:8–12.

Muñoz, N., J. Guerri, F. Legaz and E. Primo-Millo. 1993. Seasonal uptake of ¹⁵N-nitrate and distribution of absorbed nitrogen in peach trees. Plant Soil 150:263–269.

Niederholzer, F.J.A. 1997. The influence of peach tree nitrogen status, cropload, and localized soil nitrogen enrichment on whole tree nutrient and dry matter accumulation, local root growth and nitrate uptake rates. Ph.D. Thesis. Univ. California, Davis, 138 p.

Richards, D. and R.N. Rowe. 1977. Root–shoot interactions in peach: the function of the root. Ann. Bot. 41:1211–1216.

Rogers, B.L., L.P. Batjer and H.D. Billingsley. 1955. Fertilizer applications as related to nitrogen, phosphorus, potassium, calcium and magnesium utilization by peach trees. Proc. Am. Soc. Hortic. Sci. 66:7–12.

Rosati, A., G. Esparza, T.M. DeJong and R.W. Pearcy. 1999. Influence of canopy light environment and nitrogen availability on leaf photosynthetic charactersitics and photosynthetic nitrogen-use efficiency of field-grown nectarine trees. Tree Physiol. 19: 173–180.

Ryugo, K. 1988. Fruit culture: its science and art. John Wiley, New York, 344 p.

Saenz, J.L. 1996. Nitrogen nutrition as a modifier of fruit sink activity and resource availability for fruit growth in peach (Prunus persica (L.) Batsch). M.S. Thesis. Univ. California, Davis, 89 p.

Saenz, J.L., T.M. DeJong and S.A. Weinbaum. 1997. Nitrogen stimulated increases in peach yield are associated with extended fruit development period and increased fruit sink capacity. J. Am. Soc. Hortic. Sci. 122:772–777.

Stassen, P.J.C., J.H. Terblanche and D.K. Strydom. 1981a. The effect of time and rate of nitrogen application on development and composition of peach trees. Agroplantae 13:55–61.

Stassen, P.J.C., H.W. Stindt, D.K. Strydom and J.H. Terblanche. 1981b. Seasonal changes in nitrogen fractions of young Kakamas peach trees. Agroplantae 13:63–72.

Stassen, P.J.C., O. Bergh, C.W.J. Bester and M.M. Du Preez. 1982. Reserves in full-bearing peach trees. Carbohydrate reserves and their implications to orchard practices. Deciduous Fruit Grower 32:424–430.

Stassen, P.J.C., M.M. Du Preez and J.D. Stadler. 1983. Reserves in full-bearing peach trees. Macro-element reserves and their role in peach trees. Deciduous Fruit Grower 33:200–206.

Taylor, B.K. and L.H. May. 1967. The nitrogen nutrition of the peach tree. II. Storage and mobilization of nitrogen in young trees. Aust. J. Biol. Sci. 20:289–411.

Taylor, B.K. and B. Van den Ende. 1969. The nitrogen nutrition of the peach tree. IV. Storage and mobilization of nitrogen in mature trees. Aust. J. Agric. Res. 20:869–881.

Taylor, B.K. and B. Van den Ende. 1970. The nitrogen nutrition of the peach tree. V. Influence of rate of application of calcium ammonium nitrate fertilizer on yield, tree growth and nitrogen content of fruit. Aust. J. Exp. Agric. Anim. Husb. 10:214–217.

Weinbaum, S.A., I. Klein, F.E. Broadbent, W.C. Micke and T.T. Muraoka. 1984a. Use of isotopic nitrogen to demonstrate dependence of mature almonds trees on annual uptake of soil nitrogen. J. Plant Nutr. 7:974–990.

Weinbaum, S.A., I. Klein, F.E. Broadbent, W.C. Micke and T.T. Muraoka. 1984b. Effects of time of nitrogen application and soil texture on the availability of isotopically labeled fertilizer nitrogen to reproductive and vegetative tissue of mature almond trees. J. Am. Soc. Hortic. Sci. 109:339–343.

Weinbaum, S.A., R.S. Johnson and T.M. DeJong. 1992. Causes and consequences of overfertilization in orchards. HortTechnology 2: 112–121.

Weinbaum, S.A., F.J.A. Niederholzer, S. Ponchner, R.C. Rosecrance, R.M. Carlson, A.C. Whittlessey and T.T. Muraoka. 1994. Nutrient uptake by cropping and defruited field-grown "French" prune trees. J. Am. Soc. Hortic. Sci. 119:925–930.

Zalom, F.G., P.B. Goodell, L.T. Wilson, W.W. Barnett and W.J. Bentley. 1983. Degree-days: the calculation and use of heat units in pest management. Division of Agriculture and Natural Resources, Univ. California, Leaflet 21373, Berkeley, 9 p.