Nitrogen Stimulated Increases in Peach Yields Are Associated with Extended Fruit Development Period and Increased Fruit Sink Capacity

J.L. Saenz, T.M. DeJong, and S.A. Weinbaum
Department of Pomology, University of California, One Shields Avenue, Davis CA 95616

ADDITIONAL INDEX WORDS. fruit growth, source, sink strength, relative growth rate, thinning

ABSTRACT. This study was designed to characterize the mechanisms of N-stimulated peach *Prunus persica* (L.) Batsch productivity. The effects of N fertilization on potential assimilate availability (source capacity) and on the growth capacity of individual fruit (sink capacity) were assessed. On heavily thinned trees, fertilization did not stimulate fruit growth rates relative to those on nonfertilized trees, suggesting that fruit growth rates were not assimilate-limited throughout the period of fruit development. However, N fertilization resulted in a longer fruit development period and increased the growth potential of individual fruit by 20% (fresh mass) and 15% (dry mass) vs. controls. In unthinned trees, N fertilization increased total fruit yield by 49% (fresh mass) and 40% (dry mass) compared to the unthinned, nonfertilized controls. N fertilization increased total fruit yield per tree in unthinned peach trees by extending the fruit development period and thus increasing the amount of assimilate accumulated for fruit growth. The fruit development period was prolonged both by assimilate deprivation associated with increasingly higher crop loads and by N fertilization. Thus, the prolongation of the peach fruit development period by N-fertilization appears inconsistent with the role of N in increasing assimilate availability for fruit growth. We conclude that N fertilization stimulates peach yields by increasing the period for fruits to use assimilates (sink capacity). The effect of N on assimilate availability was not directly evaluated. The timing of fertilizer N availability did not influence fruit growth potential.

The principal yield components in fruit trees are fruit number per tree and fruit mass at maturity. Both of these variables may be influenced by nitrogen (N) fertilization (Blake, 1925; Cain and Mehlenbacher, 1956; Forde and Proebsting, 1945; Taylor and van den Ende, 1970). Nitrogen also influences time of bud break (Stassen, 1981), fruit development period (Lott, 1931; Reeve and Neufield, 1959; Stembridge et al., 1962), flower density (DeJong and Day, 1991), and fruit set (DeJong and Day, 1991; Stassen et al., 1981). An important aspect of the complex influence of N on tree development and productivity is its role in assimilate availability for vegetative and reproductive growth. Nitrogen influences tree photosynthetic capacity including photosynthetic rate (DeJong, 1982; DeJong et al., 1989) and leaf area (Ashley, 1931; Taylor and van den Ende, 1969; Stassen et al., 1981).

Although peach fruits are capable of photosynthesis (Pavel and DeJong, 1993b), they are classified as "sinks" because their growth is sustained principally by leaf photosynthesis (Coombe, 1976). That fruit growth frequently occurs at the expense of vegetative growth is indicative of the dominance of fruit as carbon sinks (Bollard, 1970; Grossman and DeJong, 1995a, 1995b).

Interfruit competition for assimilates can limit fruit growth and final fruit size in heavily cropping trees (Ryugo, 1988; DeJong and Grossman, 1996). Heavy thinning of immature fruit, to minimize interfruit competition for assimilates allows the remaining fruit to approach their full genetic growth potential (Grossman and DeJong, 1995b).

Although it is well known that N fertilization can increase commercial yields in peach (Ritter, 1956) it is not clear whether these increases in yield are due to indirect effects, i.e., increases in

assimilate availability for fruit growth or to direct effects, i.e., increases in the growth potential (sink capacity) of individual fruit, or both. Recent research using heavily thinned and over-cropped peach trees provides an experimental approach to analyzing these questions (DeJong and Grossman, 1995).

Under low interfruit competition, differences in final fruit size have been correlated with fruit cell number (Bain and Robertson, 1951; Bradley, 1959; Smith, 1950). Therefore, cell division may be a major component of fruit sink capacity. Flower initiation occurs in the summer preceding anthesis (Tufts and Morrow, 1925), and cell division in fruit is mostly completed during the first 4 to 5 weeks after anthesis (Reeve and Neufield, 1959; Massia et al, 1992; Zanchin et al, 1994). Therefore, we hypothesized that fall application of fertilizer N to N-deficient trees may support the growth of larger fruit than on trees in which N is limiting during the period of cell division.

The primary objectives of this study were to a) assess whether N-deprivation limits individual fruit growth potential under low levels of interfruit competition that minimize possible effects of assimilate limitation and b) determine whether N-promoted fruit growth depends primarily on increases in the availability of assimilates (source capacity) or increased fruit growth potential (sink capacity). A secondary objective was to determine whether the timing of N supplementation to N-deficient trees affects fruit growth potential.

Materials and Methods

Nine-year-old 'O'Henry' peach (*Prunus persica* L. Batsch) trees on 'Lovell' rootstock, spaced 5.18 × 1.83 m (1055 trees/ha at the Univ. of California, Davis, Wolfskill Experimental Farm, Winters, Calif.) received no N fertilization during the 1993 growing season. In order to distinguish between source- and sink-limited peach fruit growth, the study was conducted using trees under different levels of soil N fertilization and various levels of relative assimilate availability for individual fruit growth. The effect of N availability on fruit growth potential, was tested on

772

Table 1. The effect of N fertilization on mean N concentration of fully exposed leaves throughout the experimental period.[z]

| | Leaf N concn (% dry mass) | | | | |
| | Sampling date | | | | |
Nitrogen treatment	27 Sept. 1993	22 Oct. 1993	21 Apr. 1994	19 May 1994	22 July 1994
No N	1.98 a[y]	1.77 c	2.83 b	2.59 b	2.42 b
Spring N	2.02 a	1.82 c	4.13 a	3.64 a	3.00 a
Split N	2.01 a	2.00 b	4.15 a	3.54 a	3.15 a
Fall N	1.92 a	2.12 a	4.11 a	3.53 a	3.20 a

[z]Nitrogen-fertilization treatments were applied 28 Sept. 1993 (fall application) and 9 Apr. 1994 (spring application). Spring and fall N consisted of N at 200 kg·ha^{-1} in the spring and fall, respectively, and Split N consisted of N at 100 kg·ha^{-1} in the fall plus N at 100 kg·ha^{-1} in the spring.
[y]Different letters within columns indicate that means differ significantly using the Tukey mean separation test ($P \leq 0.05$).

heavily thinned trees to minimize the likelihood that fruit growth may be source-limited (Grossman and DeJong, 1995 a, 1995b). The effect of N fertilization on assimilate availability for total fruit growth was tested using unthinned trees, to determine the availability of assimilates for maximum fruit yield.

The field experiment was designed as a split-plot with four N fertilizer treatments replicated four times as main plots in a randomized complete block design. Three fruit thinning treatments were assigned to subplots within each main plot. Each of the sixteen fertilizer treatment main plots consisted of 45 trees (5 rows × 9 trees per row) with the 3 thinning treatments applied to the center 21 trees (one 7-tree-row per thinning subplot).

Four N-fertilization treatments were used to establish a range of N availability and several temporal patterns of N availability. Treatments consisted of 1) fall N treatment receiving N at 200 kg·ha^{-1} on 28 Sept. 1993; 2) split N treatment receiving N at 100 kg·ha^{-1} on 28 Sept. 1993 and 9 Apr. 1994; 3) spring N treatment receiving N at 200 kg·ha^{-1} on 9 Apr. 1994, 5 weeks after full bloom (AFB); 4) and a control treatment, which received no N fertilizer during the 1993 and 1994 seasons. Nitrogen fertilizer was applied manually as NH_4NO_3 within the wetted zone of the microsprinklers. The fertilization was followed by an irrigation immediately after application.

Thirty mid-shoot leaves per N treatment plot (ten leaves per thinning subplot) were sampled periodically between 27 Sept. 1993 and 22 July 1994 to assess the impact of fertilization on tree N status. Thus, at each sampling, 480 leaves were collected (16 N plots × 3 thinning subplots per N plot × 10 leaves per thinning subplot). Leaves were dried for 48 h at 65 °C in a forced-air oven and ground to pass a screen (140 mesh/cm^2), and total N was determined conductimetrically according to Carlson (1978, 1986).

Bloom was monitored on seven tagged shoots per each N treatment plot, and the number of open flowers on tagged shoots was counted daily during the blooming period. Full bloom was defined as the date when ≥50% of the flowers of each tagged shoot were open. A mean full bloom date was established for each N treatment. Subsequent fruit growth was described based on these bloom dates as days after full bloom (AFB). Full bloom dates were compared using SAS's (SAS Institute, Cary, N.C.) General Linear Model procedure. This procedure was also used to compare treatment effects on the length of fruit growth periods and on the harvest date.

Relative assimilate availability per fruit was adjusted by regulating the number of developing fruit per tree. Three different thinning treatments (i.e., severity of immature fruit removal) were established in each of the four N treatments. The three thinning

Table 2. The relationship between thinning severity and N fertilization on fruit number per tree at harvest, final fruit dry mass, and fresh mass per fruit and tree.

Thinning severity[z]	Nitrogen treatment[y]	Crop load (no. fruit/tree)	Mass/fruit (g/fruit)		Fruit mass/tree (kg/tree)	
			Dry	Fresh	Dry	Fresh
Heavy	No N	98.6 a[x]	33.7 a	196.9 a	3.3 b	19.4 b
	Spring N	101.1 a	39.3 b	240.7 b	4.0 a	24.3 a
	Split N	99.5 a	38.1 b	231.2 b	3.8 ab	22.9 a
	Fall N	105.4 a	39.0 b	235.4 b	4.1 a	24.8 a
Commercial	No N	223.0 a	23.2 a	142.5 a	5.2 b	31.7 b
	Spring N	199.4 a	29.5 b	201.3 b	5.9 ab	40.1 a
	Split N	217.8 a	29.7 b	192.8 b	6.4 a	41.8 a
	Fall N	213.7 a	30.0 b	191.4 b	6.4 a	40.9 a
Unthinned	No N	460.2 a	15.6 a	99.1 a	7.1 b	45.5 b
	Spring N	466.4 a	21.5 b	147.0 b	10.0 a	68.3 a
	Split N	541.4 a	18.3 b	129.1 b	9.8 a	69.0 a
	Fall N	498.9 a	20.1 b	133.6 b	10.0 a	66.1 a

[z]Thinning was performed 4–7 Apr. 1994. Heavy thinning consisted of leaving ≈120 fruit/tree, commercial thinning ≈210 fruit/tree, and nonthinned ≈450–550 fruit/tree.
[y]Nitrogen fertilization was applied on 28 Sept. 1993 (fall application) and 9 Apr. 1994 (spring application). Spring and fall N consisted of N at 200 kg·ha^{-1} in the spring and fall, respectively, and split N consisted of N at 100 kg·ha^{-1} in the fall plus N at 100 kg·ha^{-1} in the spring.
[x]Different letters indicate significant differences within thinning treatments ($P \leq 0.05$).

Table 3. The effect N fertilization rate and timing on full bloom date.

Nitrogen treatment[z]	Full bloom (calendar day)
No N–Spring N	67.7 a[y]
Split N	65.8 b
Fall N	65.0 b

[z]N-fertilization was applied on 28 Sept. 1993 (fall application) and 9 Apr. 1994 (spring application). Spring N and fall N consisted of N at 200 kg·ha^{-1} in the spring and fall, respectively, and Split N consisted of N at 100 kg·ha^{-1} in the fall plus N at 100 kg·ha^{-1} in the spring.

[y]Different letters indicate significant difference ($P \leq 0.05$) using Tukey test.

treatments were heavy thinning (leaving ≈120 fruit/tree), commercial thinning (leaving ≈210 fruit/tree), and no thinning (resulting in a crop load ≈450 to 550 fruit/tree). Thinning was carried out according to commercial practice (i.e., 4–7 Apr. 1994).

Tree care followed commercial practices of pest and weed control, and summer pruning. Trees were irrigated weekly with microsprinklers which supplied 80% of potential evapotranspiration measured with a standard reference pan in an adjacent orchard.

Fruit were harvested according to commercial picking standards using flesh pressure and background color as the main indices for fruit selection. Most subplots were harvested twice. Data on fruit number and fresh mass were recorded for individual trees at harvest, and a 10-fruit subsample was dried to constant mass at 65 °C to get the fresh/dry mass conversion factor. Harvest data were analyzed by ANOVA for general variance and mean separation was performed using the Tukey test ($P \leq 0.05$).

Harvest dates were calculated using a weighted average based on the relative number of mature fruit at each of two harvest dates. The fruit development period was calculated by subtracting the date of full bloom for each nitrogen block from the date of harvest of each individual tree.

Ten-fruit samples from each seven-tree heavily thinned subplot (one to two fruit per tree per sampling) were collected 18 times at

4- to 14-d intervals to describe fruit development between 3 weeks after bloom and harvest. As a result of this sampling procedure, crop loads on heavily thinned trees were reduced from ≈120 fruit/tree at thinning to ≈100 fruit/tree at harvest. In addition to standard plots of accumulation of mass over time, fruit growth vs. time curves were fitted as cubic splines (Grossman and DeJong, 1995a; Hunt, 1982) using the least-squares regression on logarithmically transformed mass data (Grossman and DeJong, 1995a). Instantaneous estimates of fruit relative growth rate (RGR), the rate of increase in mass per unit of mass per unit of time, were calculated using the first derivatives of the cubic spline equations (Grossman and DeJong, 1995a).

Results

Leaf N deficiency symptoms were observed on trees throughout the experimental plot before initiation of the experiment, and marginal deficiency ($\leq 2.1\%$ N), according to Beutel et al., 1983, was confirmed by leaf analysis in September 1993 (Table 1) before the fall application. Trees receiving a fall fertilization (fall N and split-N treatments) maintained higher leaf N concentrations in October relative to leaf N concentrations of trees that had not yet received a N application (control and spring N treatments, Table 1).

Fertilizer application increased mass per fruit and total fruit yield per tree at final harvest within each thinning treatment (Table 2). The timing of N applications did not significantly influence mass per fruit and total fruit mass per tree (Table 2).

Nitrogen and thinning treatments influenced the phenology of fruit development. Fall N advanced the bloom date by 2 d (Table 3) but delayed the average date of harvest by 7 to 12 d (Table 4). Fertilization and heavy crop loads (unthinned treatment) prolonged the fruit development period, i.e., delayed fruit maturation (Table 4). The fruit development periods were similar and shortest in nonfertilized trees, regardless of fruit load (Table 4). Fertilization exerted a much greater effect (maximum difference 14 d) on the length of the fruit development period than crop load (maxi-

Table 4. The effect of N fertilization on average harvest date, and length of the fruit development period. Comparisons have been done within each thinning treatment.

Thinning severity[z]	Nitrogen treatment[y]	Harvest date[x] (calendar day)	Length of fruit development period[x] (d)
Heavy	No N	213.3 a	145.6 a
	Spring N	221.4 b	153.7 b
	Split N	220.5 b	154.7 b
	Fall N	220.2 b	155.2 b
Commercial	No N	214.2 a	146.5 a
	Spring N	224.5 b	156.8 b
	Split N	225.0 b	159.3 b
	Fall N	223.4 b	159.0 b
Unthinned	No N	215.9 a	148.2 a
	Spring N	227.3 b	159.6 b
	Split N	227.5 b	161.9 b
	Fall N	227.6 b	162.6 b

[z]Thinning was performed 4–7 Apr. 1994. Heavy thinning consisted of leaving ≈120 fruit/tree, commercial thinning ≈210 fruit/tree, and nonthinned ≈450 to 550 fruit/tree.

[y]Nitrogen fertilization was applied on 28 Sept. 1993 (fall application) and 9 Apr. 1994 (spring application). Spring and fall N consisted of N at 200 kg·ha^{-1} in the spring and fall, respectively, and split N consisted of N at 100 kg·ha^{-1} in the fall plus N at 100 kg·ha^{-1} in the spring.

[x]Three-way ANOVA results indicated significant differences ($P \leq 05$) in harvest data and length of fruit development period with respect to thinning level within each N treatment and between N treatments across all thinning levels. There were also significant interactions between N treatment and thinning level. Different letters indicate significant differences ($P \leq 05$) between N treatments within each thinning level using the Tukey mean separation test.
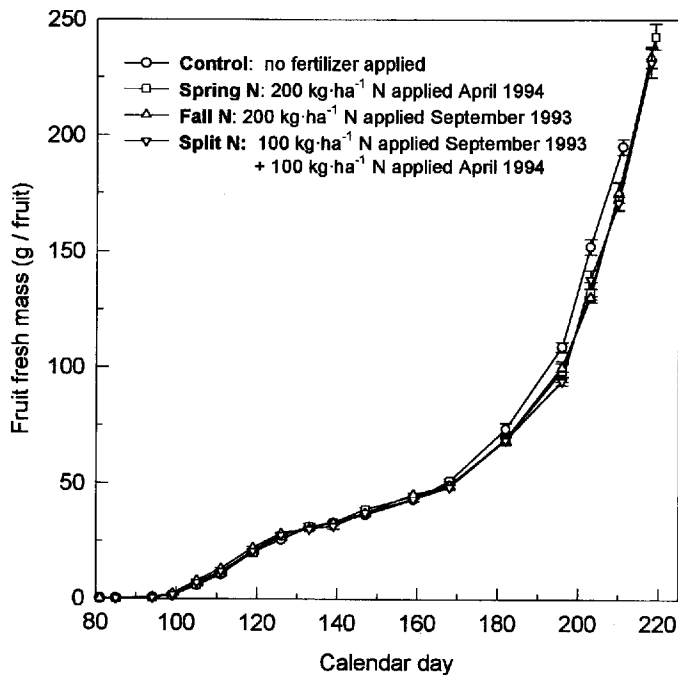
774

Fig. 1. Seasonal patterns of mean fruit fresh mass (g) of 'O'Henry' peaches as influenced by nitrogen treatments. Fruit were collected from heavily thinned trees. Bars represent ±1 standard error.

mum difference between thinning treatments was 6 d; Table 4).

Within unthinned trees, the assimilates available for fruit growth on fertilized trees were 49% (fresh mass) and 40% (dry mass) greater than on nonfertilized trees at final harvest (Table 2). Nitrogen fertilization increased the growth potential of individual fruit, as estimated from the mass per fruit at harvest. The mean mass of fruits at harvest on heavily thinned fertilized trees was 20% (fresh mass) and 15% (dry mass) greater than on heavily thinned nonfertilized trees (Table 2). Nevertheless, the fruit on nonfertilized heavily thinned trees were heavier on any specific date during the last 30 d of growth (until harvest; Figs. 1 and 2) and also had a higher RGR than fruit on fertilized trees during the corresponding periods of growth (Figs. 3 and 4).

Relative growth rate (RGR) was calculated using spline equation regression from 110 calendar days to harvest because the previous period (80 to 110 calendar days) showed a pattern not compatible with the spline equation. The three fertilization treatments were combined because their patterns of fruit growth were similar from 110 calendar days to harvest (Figs. 1 and 2) and their fresh and dry masses and RGRs did not differ statistically during this period (data not shown). Initial high fruit RGRs decreased sharply until reaching a minimum around 150 calendar days for fresh mass (Fig. 3) and 170 to 175 calendar days for dry mass (Fig. 4) and increased gradually thereafter until harvest. From 110 calendar days to harvest, fresh mass RGR of fruit on fertilized trees tended to be lower than the RGR of fruit of nonfertilized trees on any specific date, but significant differences were detected only from 110 to 125 calendar days and 165 to 195 calendar days (Fig. 3). From calendar day 190 until harvest, the fresh mass RGR of fruit of nonfertilized trees decelerated (Fig. 3). During this same period, fruit dry mass RGR of nonfertilized trees was almost parallel to that of fertilized trees (Fig. 4), showing a different behavior than described for fresh mass (Fig. 3). Calculated fruit dry mass RGR of nonfertilized trees was higher than fertilized trees on

specific days between 110 to 135 and 185 to 205 calendar days (Fig. 4). During the period between the minimum RGR values and harvest, the highest fruit RGRs for fresh and dry mass of all treatments were reached at the last sampling date just before harvest (Figs. 3 and 4).

Discussion

Nitrogen fertilization clearly increased the growth potential of fruit as indicated by increases in individual fruit mass and total fruit yields (Table 2). Nitrogen-stimulated increases in fruit growth potential could be mediated either by prolonging the fruit developmental period or increasing the fruit RGRs. The design of this experiment attempted to distinguish between these two possibilities by allowing all fruit from heavily thinned trees to reach or approach a sink-limited condition and, thus, attain their maximum RGRs (Grossman and DeJong, 1995 a, 1995b; Pavel and DeJong, 1993a). If sink-limited conditions were not achieved, fruit RGR on nonfertilized trees during Stage III of fruit growth should have been lower than on fertilized trees because nonfertilized trees should have had less assimilates for fruit growth, and Stage III is the most source-limited period (Grossman and DeJong, 1995b). But the expected sink-limited condition was evident from higher fresh and dry masses (Figs. 1 and 2) and higher dry mass RGR (Fig. 4) of fruit of nonfertilized trees compared to fruit of fertilized trees on all sampling dates until nonfertilized trees were harvested. Therefore, differences in assimilate availability for fruit growth during most of the fruit development period were unlikely to have caused the observed differences in fruit growth. Other studies have reported accumulations of total nonstructural sugars in N-deficient plants relative to N-sufficient plants—perhaps reflecting N-limited organ initiation and development (DeJong et al., 1984). Alternatively, one might argue that the fruit of the N-fertilized trees could be assimilate limited rather than sink limited due to stimulation of excessive vegetative growth by N fertilization and
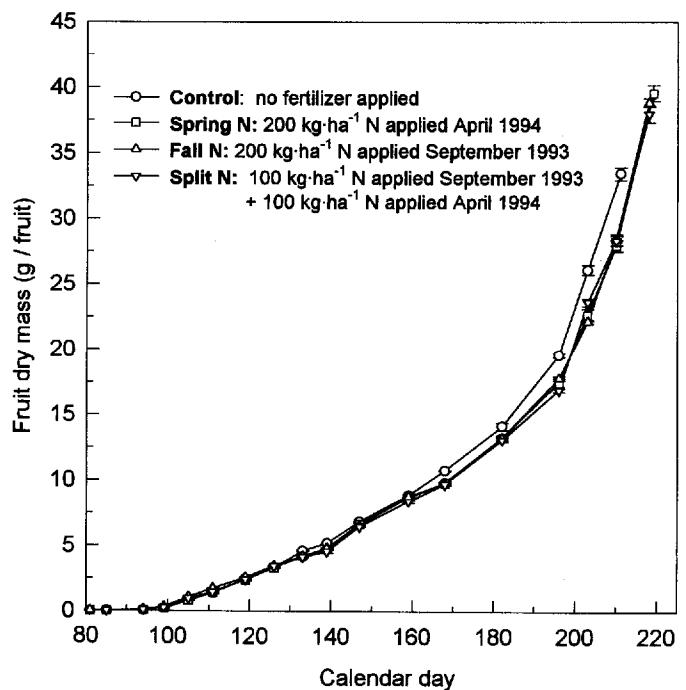

Fig. 2. Seasonal patterns of mean fruit dry mass (g) of 'O'Henry' peaches as influenced by N treatments. Bars represent ±1 standard error (where not visible, bars fit within the symbol).
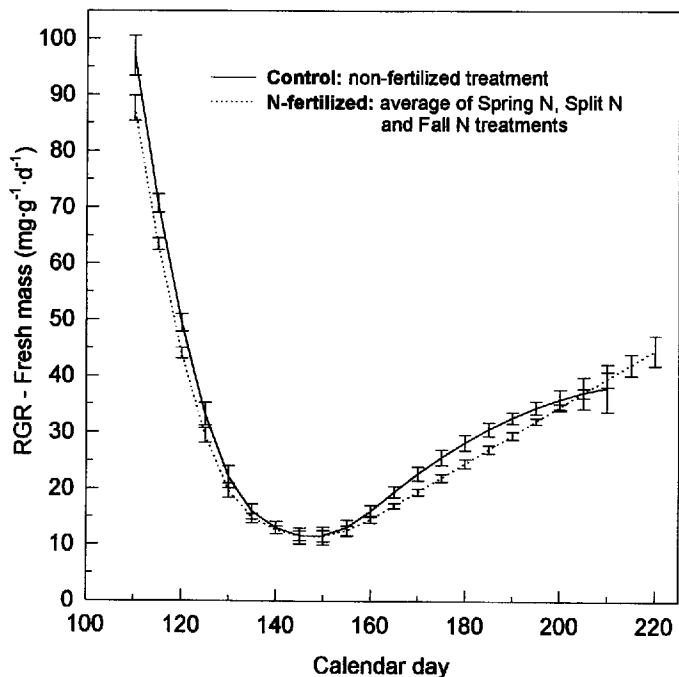
Fig. 3. Seasonal patterns of relative growth rate (RGR) for fruit (fresh mass) of N-fertilized and nonfertilized 'O'Henry' peach trees. Lines represent first derivative of exponential spline equations. Bars indicate ±1 standard deviation of the expected value of RGR at 5 calendar day intervals.

in this study (unpublished data), and other studies have indicated increases in canopy photosynthesis in response to N fertilization (DeJong et al., 1989).

Within each fertilizer treatment, the fruit development period increased with increasing fruit load: the higher the fruit load per tree the longer the fruit growth period (Table 4). This suggests that the extended period of fruit development and maturation associated with severe interfruit competition was a consequence of a reduced assimilate availability per fruit.

Nitrogen fertilization delayed fruit maturation (Table 4). Among fertilized trees, a positive relationship was observed between crop load per tree (reduction in assimilate availability per fruit) and duration of the fruit growth period. In other words, greater interfruit competition resulted in a prolonged fruit growth period. If the N effect on the fruit growth period was mediated primarily by N-enhanced assimilate availability, then we might anticipate earlier maturation of fruit on fertilized trees, but the opposite response was observed. Therefore, it is apparent that N stimulation of the fruit development period was independent of a N effect on assimilate availability.

Our data do not support the hypothesis that fall N fertilization would increase fruit growth potential relative to fruit on trees not receiving N fertilization until termination of fruit cell division during the postbloom period. The lack of differences in fruit mass or total fruit yield at harvest between fall (Fall N and Split N) and spring N-fertilized trees (Table 2) suggests that the level of N availability between floral differentiation in summer (Tufts and Morrow, 1925) and the early postbloom period did not limit early mesocarp development. It is not known whether the stimulation of fruit growth was direct, i.e., an N effect on fruit cell division, cell enlargement, or cell maturation, or was indirect, such as through increased levels of various hormones (Buban et al., 1978).

N deprivation resulted in lower total fruit dry mass per tree by 18%, 16%, and 29% on the heavily thinned, commercially thinned,
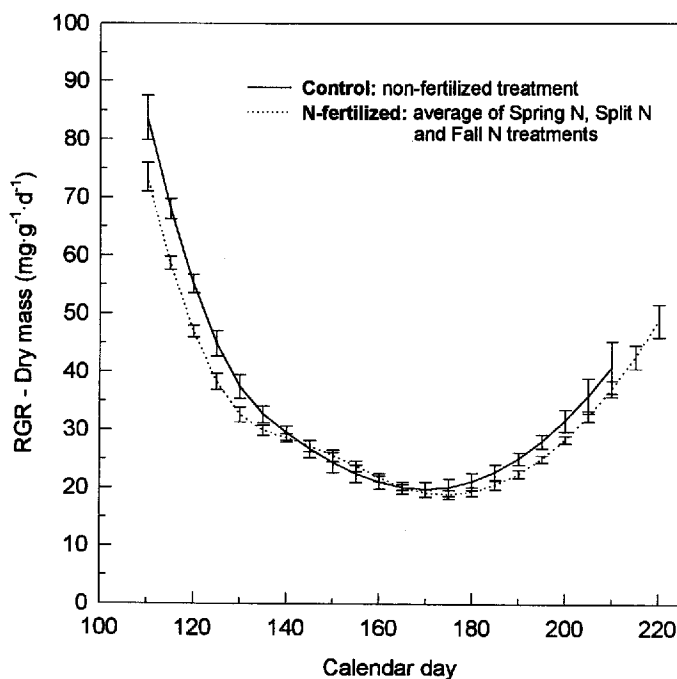
the competition of vegetative growth with fruit growth. This seems unlikely since the collective final crop on fertilized unthinned trees was substantially greater than on nonfertilized trees. Although the dry mass fruit RGRs on heavily thinned nonfertilized trees were greater than those on heavily thinned N-fertilized trees on specific dates (Fig. 4), the slopes of the dry mass RGR curves are parallel through the later period of fruit growth. Therefore, if RGRs were normalized for developmental time, it is unlikely that there would be any difference and most (if not all) of the differences in final fruit size can be accounted for by differences in the length of fruit development period. Since peaches accumulate >70% of their final dry mass during the last few weeks of growth (Grossman and DeJong, 1995a), the longer fruit maturation is delayed, the longer the period of rapid fresh and dry mass accumulation. This is apparently the major reason why fruit on N-fertilized trees exhibited a higher final fruit size potential than fruit from nonfertilized trees.

Although the longer fruit growth development period increased the total fruit dry mass of comparably cropped heavily thinned N-fertilized trees by 15% to 24% compared to nonfertilized trees; the total fruit dry mass of nonthinned N-fertilized trees was 38% to 40% greater than nonthinned nonfertilized trees (Table 2). The difference in percentage yield increase associated with N fertilization between the heavily thinned and nonthinned treatments was apparently due to increased assimilate available for fruit growth and the longer fruit development period of the unthinned trees. As indicated above, fruit growth on heavily thinned trees was apparently not assimilated limited, whereas the small mean fruit sizes on the nonthinned trees clearly indicate that assimilates limited fruit growth on these trees (Grossman and DeJong, 1995b). If more assimilates were not available for fruit growth on N-fertilized trees, the percent stimulation of fruit dry mass per tree on thinned and nonthinned trees should have been similar. Furthermore, vegetative growth was greater in the trees receiving N fertilization

Fig 4. Seasonal patterns of relative growth rate (RGR) for fruit (dry mass) of fertilized and nonfertilized 'O'Henry' peach trees. Lines represent first derivative of exponential spline equations. Bars indicate ±1 standard deviation of the expected value of RGR at 5 calendar day intervals.

and nonthinned treatments, respectively, compared to the N-fertilized trees (Table 2). Currently, the range of leaf N concentrations considered indicative of adequate N availability is 2.4% to 3.3% N (Beutel et al., 1983). Our documentation of a lower yield on trees with a mean July leaf N concentration of 2.42% compared to 3.00% to 3.12% on fertilized trees (Table 1) indicates that the currently accepted standards may need reevaluation.

Literature Cited

Ashley, T.E. 1931. Some vegetative responses of the peach to applications of nitrate of soda. Proc. Amer. Soc. Hort. Sci. 28:28–33.

Bain, J.M. and R.M. Robertson. 1951. The physiology of growth of apple fruits I. Austral. J. Sci. Res. 4:75–91.

Beutel, J., K. Uriu, and O. Lilleland. 1983. Leaf analysis for California deciduous fruits. Soil and plant tissue testing in California, Univ. of Calif. Bul. 1879.

Blake, M.A. 1925. The growth of the fruit of the Elberta peach from blossom bud to fruit maturity. Proc. Amer. Soc. Hort. Sci. 22:29–39.

Bollard, E.G. 1970. The physiology and nutrition of developing fruits, p. 387–420. A.C. Hulme (ed.). In: The biochemistry of fruits and their products. vol. I. Academic Press, London.

Bradley, M.V. 1959. Mean cell size in the mesocarp of mature peaches of different sizes. Proc. Amer. Soc. Hort. Sci. 73:120–124.

Buban, T., A. Varga, J. Tromp, E. Knegt, and J. Bruinsma. 1978. Effects of ammonium and nitrate nutrition on the levels of zeatin and amino nitrogen in xylem sap of apple rootstocks. Z. Pflanzenphysiol. 89:289–295.

Cain, J.C. and R.J. Mehlenbacher. 1956. Effects of nitrogen and pruning on trunk growth in peach. Proc. Amer. Soc. Hort. Sci. 67:139–143.

Carlson, R.M. 1978. Automated separation and conductimetric determination of ammonia and dissolved carbon dioxide. Anal. Chem. 50:1528–31.

Carlson, R.M. 1986. Continuous flow reduction of nitrate to ammonia with granular zinc. Anal. Chem 58:1590–1591.

Coombe, B.G. 1976. The development of fleshy fruits. Annu. Rev. Plant Physiol. 27:207–228.

DeJong, T.M. 1982. Leaf nitrogen content and CO_2 assimilation capacity in peach. J. Amer. Soc. Hort. Sci. 107:955–959.

DeJong, T.M. and K.R. Day. 1991. Relationships between shoot productivity and leaf characteristics in peach canopies. HortScience 26:1271–1273.

DeJong, T.M. and Y.L. Grossman. 1995. Quantifying sink and source limitations on dry matter partitioning to fruit growth in peach trees. Physiol. Plant. 95:437–443.

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.

Forde, H.I. and E.L. Proebsting. 1945. Utilization of ammonia supplied to peaches and prunes at different seasons. Hilgardia 16:411–425.

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.

Hunt, R. 1982. Plant growth curves. Edward Arnold, London.

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

Lott, R.V. 1931. Some fruiting responses of the peach to applications of nitrate of soda. Proc. Amer. Soc. Hort. Sci. 28:23–27.

Massia, A., A. Zanchin, N. Rascio, and A. Ramina. 1992. Some biochemical and ultrastructural aspects of peach fruit development. J. Amer. Soc. Hort. Sci. 117:808–815.

Pavel, E.W. and T.M. DeJong. 1993a. Source- and sink-limited growth periods of development peach fruit indicated by relative growth rate analysis. J. Amer. Soc. Hort. Sci. 118:820–824.

Pavel, E.W. and T.M. DeJong. 1993b. Estimating the photosynthetic contribution of developing peach (Prunus persica) fruits to their growth and maintenance carbohydrate requirements. Physiol. Plant. 88:331–338.

Reeve, R.M. and C.H.H. Neufeld. 1959. Observations on the histology and texture of Elberta peaches from trees of high and low levels of nitrogen nutrition. Food Res. 24:552–563.

Ritter, C.M. 1956. Effect of varying rates of nitrogen fertilization on young Elberta peach trees. Proc. Amer. Soc. Hort. Sci. 68:48–55.

Ryugo, K. 1988. Fruit culture. Its science and art. Wiley, New York.

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). MS thesis, Univ. of California, Davis.

Smith, W.H. 1950. Cell-multiplication and cell-enlargement in the development of the flesh of the apple fruit. Ann. Bot. 14:23–38.

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

Stembridge, G.E., C.E. Gambrell, H.J. Sefick, and L.O. Van Blaricom. 1962. The effect of high rates of nitrogen and potassium on the yield, quality, and foliar mineral composition of Dixigem peaches in the South Carolina sandhills. Proc. Amer. Soc. Hort. Sci. 81:153–161.

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. Austral. J. Agr. 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. Austral. J. Expt. Agr. Animal Husbandry 10:214–217.

Tufts, W.P. and E.B. Morrow. 1925. Fruit bud differentiation in deciduous fruits. Hilgardia 1:3–14.

Winkler, A.J. 1930. The relation of number of leaves to size and quality of table grapes. Proc. Amer. Soc. Hort. Sci. 27:158–160.

Zanchin, A., C. Bonghi, G. Casadoro, A. Ramina, and N. Rascio. 1994. Cell enlargement and cell separation during peach fruit development. Intl. J. Plant Sci. 155:49–56.

J. Amer. Soc. Hort. Sci. 122(6):772–777. 1997.

777