Influence of branch autonomy on fruit, scaffold, trunk and root growth during Stage III of peach fruit development

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Summary We studied the influence of branch autonomy on the growth of reproductive and vegetative organs by establishing different patterns of fruit distribution within and between large branch units (scaffolds) in mature peach trees (*Prunus persica* (L.) Batsch cv. 'Elegant Lady'). Different patterns of fruit distribution were established by defruiting either whole scaffolds (uneven fruit distribution between scaffolds; US) or several selected hangers (small fruiting branches) per tree (uneven fruit distribution between hangers; UH). The effects of these patterns were compared with the effects of an even fruit distribution treatment (EVEN) in which fruits were thinned to achieve maximum uniformity of fruit distribution within the canopy. The desired fruit loads were obtained by differentially thinning the remaining bearing parts. On a tree basis, the response of mean fruit mass to fruit load was strongly affected by fruit distribution. The steepest mean fruit mass to fruit load relationship was found in US trees, whereas the relationship in UH trees was intermediate between the US and EVEN trees. On a scaffold basis, differences in fruit size between EVEN and US trees with similar fruit loads, though statistically significant, were relatively small, indicating that scaffolds were almost totally autonomous with respect to dry matter partitioning to fruit during the final stage of peach fruit growth. Hangers also appeared to exhibit significant autonomy with respect to the distribution of dry matter during the final phase of fruit growth. Branch autonomy was evident in scaffold growth: defruited scaffolds in the US treatment grew more than fruited scaffolds, and fruit distribution treatments had little impact on scaffold cross-sectional area on a tree basis. On the other hand, as observed for fruit growth, branch autonomy did not appear to be complete because the fruited scaffolds grew more in US trees than in EVEN trees under heavy cropping conditions. However, the effect of fruit distribution occurred only over short distances, and was negligible on organs located farther away from the source of heterogeneity (fruits), such as the trunk and roots.

Keywords: fruit distribution, fruit load, tree water status.

Introduction

Carbon movement through the plant appears to be constrained to certain directions at specific times, and it is widely acknowledged that large branches on mature trees are relatively autonomous with respect to their carbon budget during the growing season, i.e., after initial shoot elongation has ceased (Sprugel et al. 1991). Branch autonomy becomes more prominent after the initial spring flush, probably because the spring flush is supported in part from root and trunk carbon reserves (Dickson 1991, Lacointe et al. 1995). However, from late spring until the end of the season, branches import little carbon and either use current photosynthates or export them to other organs of the plant (trunk and roots) (Sprugel et al. 1991). In peach trees (*Prunus persica* (L.) Batsch cv. 'Spring Lady'), most shoot elongation occurs during the first 15 weeks after anthesis, whereas branch diameter growth continues until autumn (Grossman and DeJong 1995).

Carbohydrate partitioning among plant organs is thought to be driven by differences in organ sink strength (i.e., growth potential) (DeJong 1999). A hierarchy of sink strengths has been established: fruits > young leaves and stem tips > mature leaves > cambia > roots > storage tissue (Kramer and Kozlowski 1979). Because the capacity to generate carbon is unevenly distributed in the tree (some branches are shaded whereas others are well lit) and fruit competition represents a functional limitation to final fruit size (Wardlaw 1990), we predicted that heterogeneity in fruit distribution in a tree affects its capacity to supply dry matter to fruits.

In addition, the impact of organ competition on growth may be modulated by the degree of autonomy occurring in any particular location. For instance, growth of fruits that are localized in a specific portion of a tree may be more influenced by fruit-to-fruit competition if that portion is relatively autonomous compared with a nonautonomous region in which carbon resources are obtained from the tree as a whole. Because both shoot and root growth are usually enhanced when fruit load decreases (Williamson and Coston 1989, Kappel 1991,

Grossman and DeJong 1995), it is commonly assumed that reductions in fruit load increase the total amount of carbohydrates available for growth of other organs (Wardlaw 1990, Grossman and DeJong 1994). Therefore, if fruit growth is supported autonomously within branches, a tree with a heterogenous fruit distribution has more surplus carbon available for root and stem growth than a tree with uniform fruit distribution. When fruit carbon demand is low, net carbon gain per tree may decrease because of low net assimilation rate per unit of leaf area (DeJong 1986*b*, Gucci et al. 1991, Palmer 1992); however, this decrease can be partially compensated for by the development of more leaves in defruited trees (Wünsche and Palmer 1997). Within the conceptual framework of branch autonomy, we therefore hypothesized that heterogeneity in fruit distribution will (1) reduce dry matter allocated to fruits, and (2) enhance the growth of organs other than fruits (e.g., scaffolds, trunks and roots) even when overall crop loads per tree are similar. We predicted that these effects would increase with increasing fruit load. Our study objective was to evaluate the growth responses of fruit and vegetative organs, including the main trunk, scaffolds and roots, to different patterns of fruit distribution in mature peach trees with varying fruit loads.

To study these growth responses under the most favorable conditions, tree fruit load was manipulated during the part of the season when fruit sink strength was expected to be greatest, that is during the phase of maximum fruit growth (Stage III; Grossman and DeJong 1995) in peach. A transport–competition model for fruit growth was used (DeJong and Grossman 1995) to quantify the degree of branch autonomy for fruit growth. To obtain different patterns of fruit distribution, either whole scaffolds or several selected fruiting shoots per tree were defruited at the onset of Stage III of fruit development. The desired fruit loads were obtained by differentially thinning the remaining bearing parts.

Materials and methods

Orchard conditions

Seventy-eight trees from 11 rows of 10-year-old 'Elegant Lady' peach (*Prunus persica*) trees, on 'Lovell' rootstock, were selected for uniformity in a block at the UC Davis Wolfskill Experimental Orchard, Winters, CA. The orchard was planted in a high density formation (5.5 × 2 m spacing) and trained to a Kearney perpendicular-V with two main scaffolds per tree (DeJong et al. 1995). Trees received standard commercial dormant pruning and 100 kg ha^{-1} N fertilization in the spring before the experiment. The trees were irrigated twice weekly by microjet sprinklers, receiving 100% replacement of reference evapotranspiration (ET$_0$, data obtained from the California Irrigation Management System for Winters). There was no rainfall during the experimental period.

Thinning treatments

Thinning treatments were applied just before the start of Stage III, the final exponential phase, of fruit growth on May 15. Three main bearing pattern treatments were established according to differences in fruit distribution in the tree: (1) fruits distributed evenly (EVEN); (2) fruits distributed unevenly by totally defruiting one of the two available main branches (scaffolds) per tree (uneven distribution between scaffolds; US); and (3) fruits distributed unevenly by totally defruiting selected fruiting shoots (hangers) from both scaffolds (uneven distribution among hangers; UH). A hanger is defined as a 1-year-old shoot selected during dormant pruning for fruiting in the next growing season. Three fruit thinning sub-treatments were imposed to obtain a range of fruit loads within each main fruit bearing treatment. In general, the scaffolds or hangers in each bearing treatment were unthinned, lightly thinned or normally thinned (Table 1). In UH trees, the desired range of fruit counts per tree was achieved by manipulating the proportion of defruited hangers; for the low and normal crop loads, one out of two hangers was defruited, whereas for the heavy crop load, only one out of three hangers was defruited. Additionally, the fruited hangers were slightly thinned in the low crop load treatment (Table 1). Although these sub-treatments were applied as discrete treatments on the individual scaffolds, they provided a continuous range of crop loads per tree or scaffold, ranging from heavily cropped to lightly cropped (Table 2). In addition to the three bearing treatments, a fourth treatment was defined by selecting six trees that were thinned to a low crop load of < 50 fruits tree^{-1} (Table 1), which were used to estimate the potential fruit growth response for the particular orchard and study period. The number of trees in the US treatment was twice that in the EVEN and UH treatments, because scaffolds were used as the reference unit for comparisons. Eighteen trees were assigned to the EVEN and UH treatments and 36 trees were assigned to the US treatment. These trees were chosen for homogeneity in fruit load and assigned to the different bearing treatments following a completely randomized spatial distribution.

Fruit harvest

Fruits were harvested on July 2, about one week before commercial maturity, in order to avoid significant fruit drop. All fruits were removed from each scaffold and counted. Crop fresh mass for each scaffold was determined and a 30-fruit subsample per tree was collected. The sample was weighed before and after drying at 65 °C in a forced air draft oven. Relative dry mass was calculated as the ratio of sample fresh mass to dry mass. Mean fresh mass and mean dry mass per fruit were calculated by dividing total crop fresh mass and total crop dry mass, respectively, by total fruit number.

Water status measurements

Because cropping can influence tree water status and thereby affect fruit dry matter accumulation (Berman and DeJong 1996), water status was measured at key points during the experiment. Stem water potential (Ψ_{stem}) (McCutchan and

Table 1. Cropping patterns and applied thinning strategies pertaining to the bearing treatments.

Bearing treatment–thinning sub-treatment	Definition	Treatment abbreviation
Potential fruit growth	Heavily thinned to a minimum crop load (50 fruits tree^{-1})	PFG
Even distribution of fruits		EVEN
Maximum crop	Both scaffolds unthinned	EVEN-M
Heavy crop	Both scaffolds lightly thinned	EVEN-H
Normal crop	Both scaffolds normally thinned	EVEN-N
Uneven distribution of fruits—scaffold defruited		US
Scaffold defruited + heavy crop	One scaffold defruited, other scaffold unthinned	US-H
Scaffold defruited + normal crop	One scaffold defruited, other scaffold lightly thinned	US-N
Scaffold defruited + low crop	One scaffold defruited, other scaffold normally thinned	US-L
Uneven distribution of fruits—hanger defruited		UH
Hanger[1] defruited + heavy crop	Both scaffolds with selected hangers (1 out of 3) defruited. Other hangers unthinned.	UH-H
Hanger defruited + normal crop	Both scaffolds with selected hangers (1 out of 2) defruited. Other hangers unthinned.	UH-N
Hanger defruited + low crop	Both scaffolds with selected hangers (1 out of 2) defruited. Other hangers lightly thinned.	UH-L

[1] A hanger is a 1-year-old shoot selected during dormant pruning for fruiting in the next growing season.

Shackel 1992) was measured with a pressure chamber (Soil Moisture Equipment, Santa Barbara, CA). Measurements were made at solar noon on shaded leaves located close to the base of each scaffold. Leaves were bagged for at least 1 h before measurement. The leaf bags were plastic sheaths covered with aluminum foil. Midday leaf conductance (g_l) was measured under light-saturated conditions with a portable steady state porometer (Model LI-1600, Li-Cor, Lincoln, NE). We measured Ψ_{stem} and g_l on one and two leaves per scaffold, respectively, in all trees of the treatment–sub-treatment combinations that represented the most extreme fruit load and bearing patterns conditions, i.e.: (1) maximum crop load (EVEN-M); (2) scaffold-defruited + heavy crop load (US-H); and (3) potential fruit growth (PFG) treatments. Measurements were taken on 3 days during Stage III of fruit growth:

just after fruit thinning (May 19), mid-Stage III (June 6) and one week before fruit harvest (June 24).

Analysis of treatment effects and quantification of limitations in fruit growth

To analyze the effects of the bearing patterns on final fruit mass, fresh mass and dry mass were plotted against fruit count per tree. Regression analysis was used to account for a possible interaction of the bearing treatments with crop load. In addition, to test the possibility of a favorable influence of a completely defruited scaffold on the fruit mass of the neighboring loaded scaffold, the same data were expressed on a scaffold basis. This procedure was valid only for comparisons of EVEN and US treatments because both treatments had evenly distributed fruits at the scaffold level.

Table 2. Crop load, sample size and ranges achieved with the different thinning treatments.

Treatment and sub-treatment	Sample size (no. trees)	Mean no. fruits per tree	Min–max no. fruits per tree
Potential fruit growth (PFG)	6	51	44–59
Maximum crop (EVEN-M)	6	640	448–899
Heavy crop (EVEN-H)	6	550	369–702
Normal crop (EVEN-N)	6	260	211–321
Scaffold defruited + heavy crop (US-H)	12	360	224–463
Scaffold defruited + normal crop (US-N)	12	223	106–280
Scaffold defruited + low crop (US-L)	12	152	90–392
Hanger defruited + heavy crop (UH-H)	6	482	283–763
Hanger defruited + normal crop (UH-N)	6	429	314–530
Hanger defruited + low crop (UH-L)	6	200	164–224

Quantification of the limitation of fruit growth by the different bearing patterns was carried out according to the procedure described by DeJong and Grossman (1995), which enables estimation of the degree of sink and source limitation on fruit growth. In our study, the focus was on calculation of the transport–competition component of the supply limitation (TRANS–COMP$_{lim}$), because we were interested in testing if fruit distribution affected this component. The calculation requires a continuous function of dry mass fruit growth rate that is dependent on fruit load. The different intensities of fruit thinning provided the required range of fruit loads. A brief summary of the calculations is outlined.

Potential relative growth rate (RGR$_{pot}$) was calculated as:

$$RGR_{pot} = \frac{\log_e W_{2(PFG)} - \log_e W_{1(PFG)}}{T_2 - T_1} \qquad (1)$$

where $W_{2(PFG)}$ and $W_{1(PFG)}$ are the mean individual fruit dry masses at harvest dates T_2 and T_1, corresponding to the trees of the PFG treatment with a minimum number of fruits (50 per tree). We estimated $W_{1(PFG)}$ from dry mass and fruit counts from five defruited scaffolds (US treatment) at the time of fruit thinning. Total potential fruit sink demand rate (SINK$_{pot}$; g day^{-1}) for trees with different numbers of fruits per tree or scaffold was modeled as:

$$SINK_{pot} = \frac{(W_1^* e^{(RGR_{pot} (T_2 - T_1))} - W_1^*)n}{T_2 - T_1} \qquad (2)$$

where n is fruit number and W_1^* is mean fruit dry mass at the onset of Stage III, which was calculated based on the initial mean fruit size developed from data obtained on defruited scaffolds and applied to EVEN trees. The potential source supply rate (SOURCE$_{pot}$) was estimated from fruit growth under source-limited conditions, such as on EVEN trees in the maximum crop treatment (EVEN-M):

$$SOURCE_{pot} = \frac{(W_{2(EVEN-M)} - W_{1(EVEN-M)})n}{T_2 - T_1} \qquad (3)$$

The rate of actual total fruit dry mass growth rate (FGR$_{actual}$) during a growth period was calculated as:

$$FGR_{actual} = \frac{(W_2 - W_1)n}{T_2 - T_1} \qquad (4)$$

where n is number of fruits per sample unit.

The data obtained per tree were fitted to linear ($y = a + bx$) and logarithmic ($y = \sqrt{a + b\ln x}$) functions for SINK$_{pot}$ and FGR$_{actual}$, respectively. The data obtained per scaffold were fitted to quadratic and simple logarithmic expressions for SINK$_{pot}$ and FGR$_{actual}$, respectively. The transport–competition limitation parameter, TRANS–COMP$_{lim}$, was calculated from the estimates of the previously fitted functions. If SINK$_{pot}$ > SOURCE$_{pot}$, fruit growth may have been limited by both supply limitation and transport–competition limitation. In this case, TRANS–COMP$_{lim}$ was calculated as:

$$TRANS-COMP_{lim} = \frac{SOURCE_{pot} - FGR_{actual}}{SOURCE_{pot}} \qquad (5)$$

However, when SINK$_{pot}$ < SOURCE$_{pot}$, source supply did not limit fruit growth and the entire source limitation was due to transport–competition limitation:

$$TRANS-COMP_{lim} = \frac{SINK_{pot} - FGR_{actual}}{SINK_{pot}} \qquad (7)$$

Vegetative growth measurements

The cross-sectional area of the trunk (TCSA) and the two scaffolds per tree (SCSA) were calculated from circumference tape measurements. To minimize error in circumference measurements, two pins were placed in opposite sides of the branch to mark the place of the initial reading. These measurements were repeated four times during Stage III of fruit growth. Growth rates of TCSA and SCSA during Stage III were calculated as:

$$GR = \frac{CSA_f - CSA_i}{T_f - T_i} \qquad (7)$$

where CSA_f and CSA_i are the final and initial values of cross-sectional area, respectively, and $T_f - T_i$, the elapsed time in days between measurements. The evolution in growth rate during Stage III was calculated for the treatment and sub-treatment combinations that represented the extreme fruit load and bearing pattern conditions, i.e.: (1) maximum crop load (EVEN-M); (2) scaffold defruited + high crop load (US-H); and (3) potential fruit growth (PFG) treatments.

Root growth measurements

Root growth was evaluated by an ingrowth bag method (Majdi 1996, Finer and Laine 2000). The day after fruit thinning, holes were dug in the alleyways on either side of each tree. The cut ends of roots with a mean diameter of 8 mm and located about 20 cm below the soil surface were inserted into a mesh bag filled with root-free growing medium. Each bag contained 1.8 l of 100% calcined clay (Turface^{TM}, Profile Products, IL) with a bulk density of 0.67 g cm^{-3}. One root was inserted in each bag. The root bags were custom-made with root cloth that cannot be penetrated by roots. The nutrient content of the growth medium was enriched by submerging each bag in Hoagland's solution No. 1 before placing the bags in the soil. A total of three trees (12 bags) were sampled for each of the EVEN, US and PFG treatments. In the case of the UH treatment, root growth of three trees (12 bags) of only the highest cropping load sub-treatment was evaluated (UH-H).

Statistical analysis

The significance of treatment effects on water relations was evaluated by repeated measures analysis of variance (ANOVA). The effect of treatments on the sensitivity of fruit fresh and dry mass to fruit load was tested by analysis of covariance (ANCOVA) using the test of heterogeneity of slopes. Daily patterns for TCSA and SCSA growth during Stage III of fruit growth were analyzed for all sub-treatments, but only the extreme fruit thinning treatments are reported. For clarity, regressions between accumulated growth values and fruit load data were averaged by sub-treatments. The effect of the fruit distribution treatments was analyzed by ANCOVA that tested for heterogeneity in the slope of treatment responses to fruit load. Particular differences in the slopes between the EVEN and either the US or UH treatment were subsequently tested by orthogonal contrasts. To analyze the effect of the US treatment on growth rate of either defruited or fruited scaffolds, data for each sub-treatment were subjected to one-way ANOVA. Both ANOVA and ANCOVA tests were performed by considering trees and scaffolds as sample units.

Results

Thinning treatments resulted in a continuous range of fruit loads from 100 to 850 fruits tree^{-1}, with overlap in fruit count among the thinning sub-treatments. However, because we defruited half of each US tree, the highest counts in this treatment did not exceed 463 fruits (Table 2), whereas UH trees had as many as 763 fruits per tree (Table 2).

Higher fruit loads were significantly correlated with more negative values of Ψ_{stem} and higher values of g_1 (Table 3). Fruit relative dry mass was unaffected by fruit load and remained constant among the thinning sub-treatments (Table 3).

Mean fruit dry mass at harvest was strongly correlated with fruit load (Figure 1). The different bearing patterns affected the response of fruit mass to fruit load (Figure 1). In general, a higher degree of fruit clumpiness was correlated with steeper
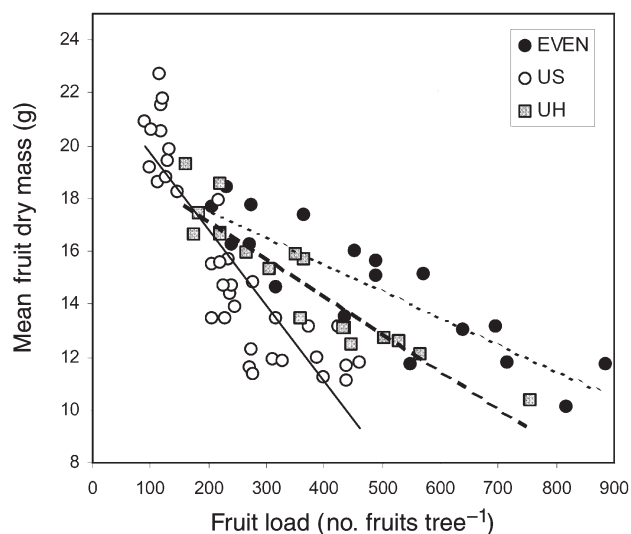

Figure 1. Relationships between mean fruit dry mass and fruit load per tree at the end of Stage III of peach fruit development. Simple linear functions were fitted to dry mass relationships. Each value represents a tree mean. Definitions: EVEN = even fruit distribution; US = uneven fruit distribution–scaffold defruited; and UH = uneven fruit distribution–hanger defruited.

slopes of the relationship between mean fruit fresh or dry mass and fruit load (Figure 1; Table 4). That is, the relationships for US trees had the steepest slopes, whereas the relationships for EVEN trees had the shallowest slopes (Figure 1). The slopes

Table 4. Probabilities for test of heterogeneity of slopes in ANCOVA for mean final fruit fresh mass and dry mass as a function of number of fruits per tree or scaffold. Each tree represents a statistical unit. See Table 1 for definition of abbreviations.

ANCOVA	Fruit fresh mass	Fruit dry mass
Comparison with tree as sample unit		
Treatment (TRT)	0.0028[*1]	0.0108[*]
Covariable (no. fruits)	0.0001	0.0001
Heterogeneity of slopes (TRT × no. fruits)	0.0001	0.0001
Contrast of treatment slopes		
EVEN versus US	0.0001	0.0001
EVEN versus UH	0.1129	0.1522
Comparison with scaffold as sample unit		
Treatment (TRT)	0.0081	0.0082
Covariable (no. fruits)	0.0001	0.0001
Heterogeneity of slopes (TRT × no. fruits)	0.2900	0.1925
Least squares means for TRT effect (g fruit^{-1})		
EVEN	100.3 b[2]	15.4 b
US	107.1 a	16.2 a
UH	91.4 c	13.8 c

[1] When the heterogeneity of the slopes is significant, the assumptions for a covariance analysis are invalid and therefore the probabilities followed by an asterisk are not relevant.
[2] Different letters indicate significance differences at $P < 0.05$ (Student *t*-test).

Table 3. Effects of fruit load on midday stem water potential (Ψ_{stem}), midday stomatal conductance (g_1) and fruit relative dry mass (RDM) for trees in the treatments with the extreme fruit distributions.

Treatments and sub-treatments	Ψ_{stem} (MPa)	g_1 (mmol m^{-2} s^{-1})	Fruit RDM (%)
Maximum crop (EVEN-M)	−0.66 a[1]	324 a	14.9
Scaffold defruited + heavy crop (US-H)	−0.60 b	290 b	14.9
Potential fruit growth (PFG)	−0.55 c	257 c	15.3
Probability[2]	0.0005	0.0004	0.6883

[1] Within a column, different letters indicate significant differences at $P < 0.05$ (Duncan's test).
[2] Significance of the thinning treatments, time and time × treatment effect in the repeated measurements ANOVA.
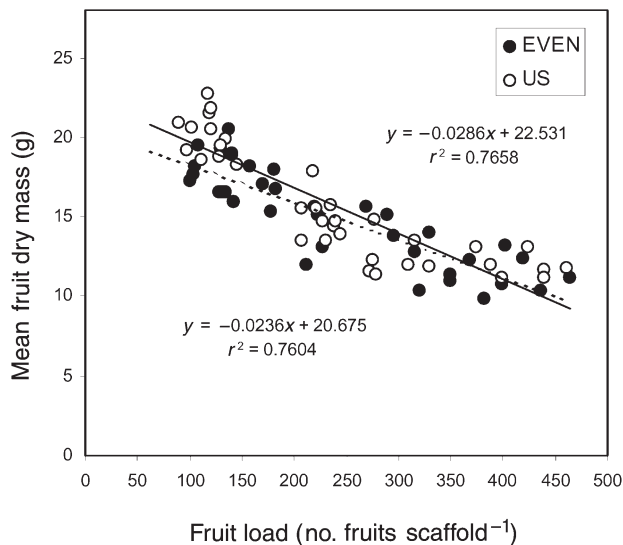
Figure 2. Relationships between mean fruit dry mass and fruit load per scaffold at the end of Stage III of peach fruit development. Data were fitted by simple linear functions. Each value represents a tree mean. Definitions: EVEN = even fruit distribution; and US = uneven fruit distribution–scaffold defruited.
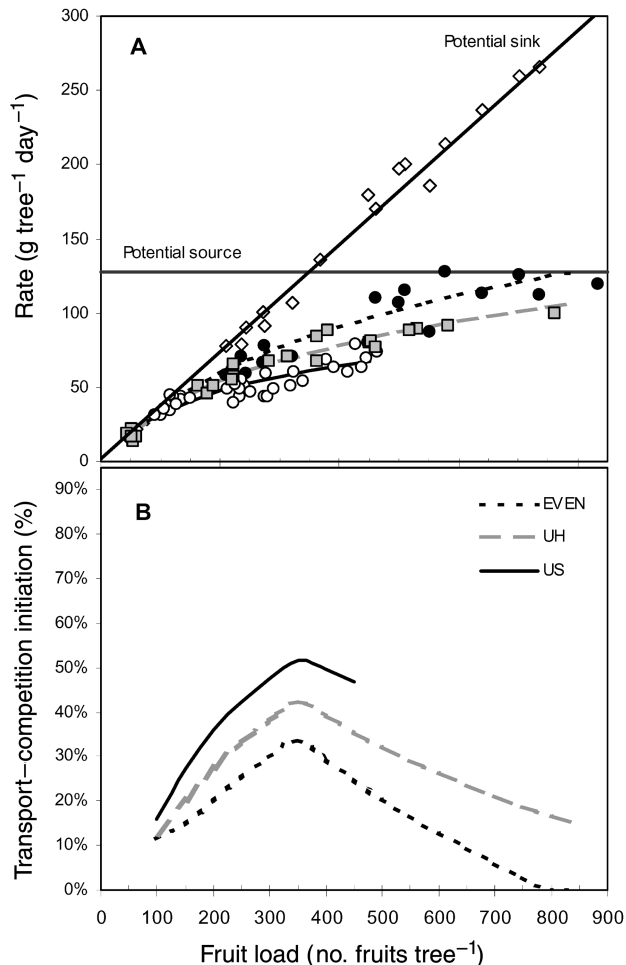

Figure 3. Relationships between fruit load and rates of potential sink demand, potential source supply, actual total fruit dry mass growth (A) and transport–competition limitation on a tree basis for Stage III of peach development (B). In panel A, the solid horizontal line represents potential source supply and the solid line fitted to the open diamonds represents potential sink demand. Potential sink data was calculated according to Equation 2. Closed circles, open circles and shaded squares represent the actual growth rates of even fruit distribution (EVEN), uneven fruit distribution–scaffold defruited (US) and uneven fruit distribution–hanger defruited (UH) treatments, respectively.

differed significantly between treatments (Table 4). When fruit dry mass was expressed per scaffold, differences between the slopes were not significant, but there was a marginal treatment effect on dry mass, indicating a slight advantage for fruit on US trees (Table 4 and Figure 2).

Differences between bearing treatments in actual fruit growth rates (FGR$_{actual}$) were not evident at low fruit loads but increased progressively with increasing fruit load per tree (Figure 3A). The EVEN trees tended to accumulate the highest total fruit dry mass, whereas US trees had the lowest fruit dry mass growth rate (Figure 3A). On the other hand, the TRANS–COMP limitation rates manifested a peak at about 350 fruits tree^{-1} and progressively decreased at both lower and higher fruit loads (Figure 3B). Maximum limitation rates for fruit growth were about 52% in US trees, whereas limitations were slightly lower in UH trees (42%) and lowest in EVEN trees (33%) (Figure 3B). When the same calculations were performed on a scaffold basis, FGR$_{actual}$ for EVEN and US trees had similar trends and the calculated TRANS–COMP limitations were only an average of 4% higher in EVEN trees than in US trees (Figure 4A). Maximum limitations were observed at 150 fruits per scaffold, and the limitations at this crop load were similar to those of EVEN trees when calculated on a tree basis (Figures 3B and 4B).

The daily increases in TCSA and SCSA differed between trees with different fruit loads (Figures 5A and 5B). When fruit load was greatest (EVEN-M sub-treatment), there was almost no SCSA growth or even a slight TCSA shrinkage. The reason for this TCSA shrinkage is unknown; however, it was unrelated to water stress because Ψ_{stem} values were high in trees in all treatments (< −0.7 MPa, Table 3). At the lowest cropping load (PFG), there were steady and noticeable in-

creases in SCSA and TCSA with time (Figures 5A and 5B). Scaffolds of US-H trees grew at rates that were intermediate between those of PFG and EVEN-M trees, but the standard errors for the US-H sub-treatment were substantially larger than for any other sub-treatment (Figure 5A).

The relationship between fruit load at the scaffold level and the mean growth rate of both scaffolds per tree (fruited and defruited scaffolds) was linear (Figure 6A). In general, higher fruit loads resulted in lower SCSA growth; however, this response was not evident in US trees in which growth rates seemed to be independent of the mean fruit load of both scaffolds (Figure 6A). The scaffold growth response of UH trees appeared to follow the same general trend as in trees with evenly distributed fruit (Figure 6A). The fruit load effect in US
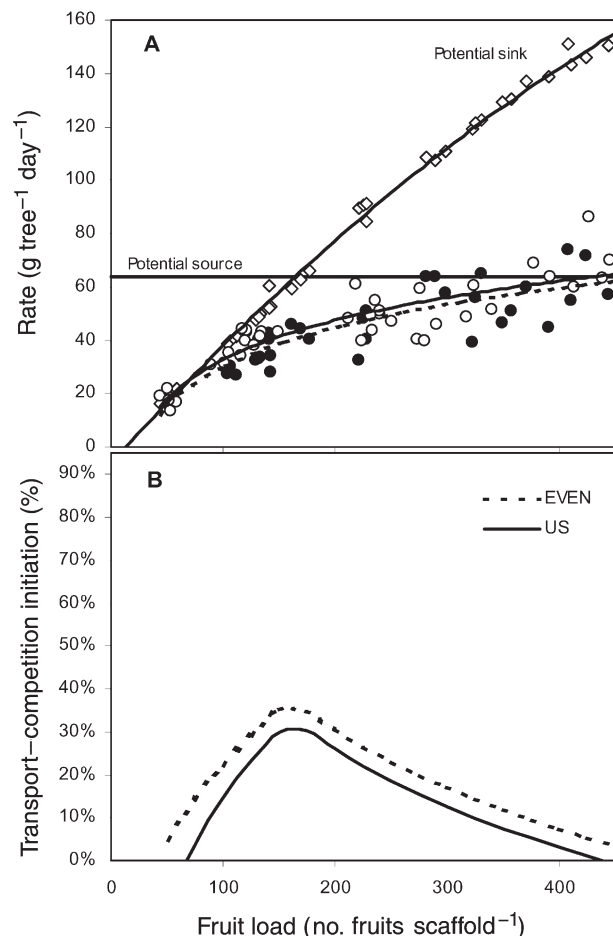
Figure 4. Relationships between fruit load and rates of potential sink demand, potential source supply, actual total fruit dry mass growth (A) and transport–competition limitation on a scaffold basis (B) for Stage III of peach fruit development. In panel A, the solid horizontal line represents potential source supply and the solid line fitted to open diamonds represents potential sink demand. Potential sink data were modeled using the ACTUAL fruit size data from the EVEN treatment and multiplied by the corresponding fruit load. Symbols: ● = actual growth rate of even fruit distribution treatment (EVEN); and ○ = actual growth rate of uneven fruit distribution–scaffold defruited (US) treatment. In panel B, the dotted and solid lines represent EVEN and US treatments, respectively.
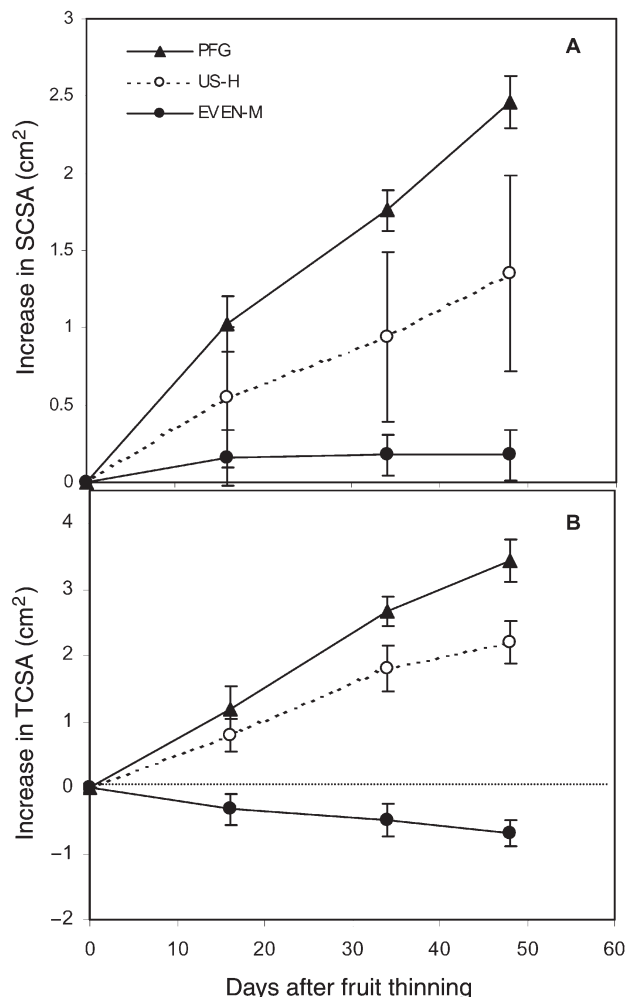

Figure 5. Seasonal patterns of the increase in mean scaffold cross-sectional area (SCSA) (A) and trunk cross-sectional area (TCSA) (B) for the extreme fruit distribution treatments. Each symbol represents the mean of six trees in the even fruit distribution–maximum crop (EVEN-M) and potential fruit growth (PFG) treatments and 12 trees in the uneven fruit distribution–scaffold defruited–heavy crop (US-H) treatment. Bars indicate ± standard error.

trees was more evident when the response of scaffold growth to scaffold fruit load was analyzed only for the loaded scaffolds, rather than based on the mean of both scaffolds (Figure 6B). Nevertheless, the fruit load effect in the US trees appeared to be weaker than in trees in the other treaments (Figure 6B). Analysis of covariance (ANCOVA) revealed that the slope of the SCSA growth to fruit load relationship in the loaded scaffold of US trees was significantly different from that in EVEN trees; therefore, data from US trees were considered separately from the general regression (Figure 6B). A significant difference was found for the two highest fruit load sub-treatments (US-N and US-H) when we compared growth

of the fruited scaffolds with the non-fruited scaffold of US trees (Table 5). In these sub-treatments, non-fruited scaffolds surpassed the growth of the fruited scaffolds and in the case of US-H trees, the values more than doubled (Table 5).

The response of trunk growth (TCSA) to fruit load was strong and linear (Figure 7). Fruit number per tree explained up to 90% of the variation in trunk growth (Figure 7). Although trunk growth (TCSA) of US trees had a tendency toward positive residuals in the general regression (Figure 7), based on the ANCOVA, differences in the slopes of the regressions for US and EVEN trees were not statistically significant (Table 6). The fruit load effect on trunk growth (TCSA) in UH trees did not differ from that in other treated trees (Figure 7).

Root growth was strongly related to fruit load with a tendency toward saturation at high fruit loads (> 350 fruits tree^{-1})
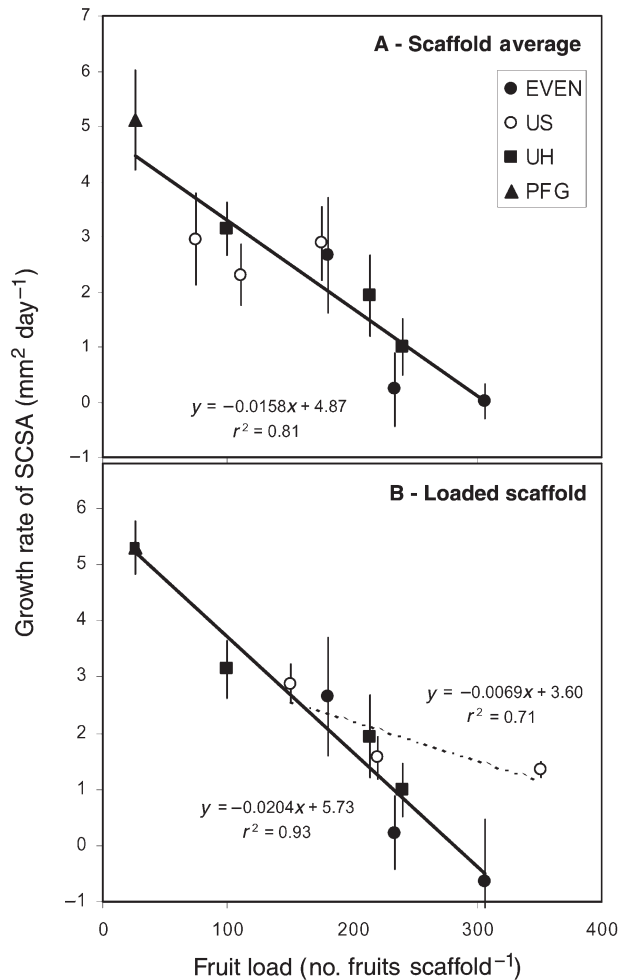
Figure 6. Relationships between scaffold growth in cross-sectional area (SCSA) and scaffold fruit load for various fruit distribution treatments, for both scaffolds averaged per tree (A) and only for the loaded scaffolds in the case of the uneven distribution–scaffold defruited treatment (US) (B). Data from the US treatment were excluded from the general linear fitting. Each observation represents the mean of six trees for the potential fruit growth (PFG) treatment and for each sub-treatment in the even fruit distribution (EVEN) treatment, whereas 12 trees were averaged per sub-treatment for the US treatment. Bars indicate ± standard error. Definition: UH = uneven fruit distribution–hanger defruited.

(Figure 8). No clear patterns emerged between fruit distribution treatments designed to allow differentiation from the general relationship that was observed between root growth and crop load (Figure 8).

Discussion

The cropping treatments in this study produced clear differences in the responses of fruit dry mass growth to fruit load. The impact of fruit distribution on total dry mass allocated to fruit was most evident at the highest fruit loads, with US trees and, to a lesser extent, UH trees having a reduced capacity to accumulate fruit dry matter. However, when data for US and

Table 5. Effects of fruit load and absence of fruit on adjacent scaffolds (uneven fruit distribution treatment, US) on growth rate of cross-sectional area measured at the base of the scaffold. The fruit load on the bearing scaffold was low, normal and high for US-L, US-N and US-H, respectively.

Scaffold type	Thinning sub-treatments		
	US-L	US-N	US-H
Fruited (mm^2 day^{-1})	2.88	1.56 b[1]	1.34 b
Non-fruited (mm^2 day^{-1})	3.02	3.05 a	4.40 a
Probability[2]	0.8278	0.0058	0.0001

[1] Within a row, similar letters indicate no statistical significance between sub-treatments according to the Duncan's test at $\alpha < 0.05$.
[2] Probability of effect of presence or absence of fruit in one-way ANOVA.

EVEN trees were normalized by expressing the values per scaffold, most differences between them disappeared, indicating that branches operated mostly as independent units. In US trees and within EVEN and UH trees, the defruited scaffold had little influence on fruit growth of the fruited scaffold. This evidence of autonomy in large branches is in general agreement with other experiments in which vegetative sinks or sources were manipulated instead of fruit sinks (Stephenson 1980, Honkanen and Haoukioja 1994). Furthermore, the reduction in accumulation of fruit mass in UH trees compared with EVEN trees indicates that branch autonomy was functional at the level of smaller branch units (i.e., the hanger level). This supports the conclusion of Audergon et al. (1993) that peach branches older than 3 years can be considered inde-
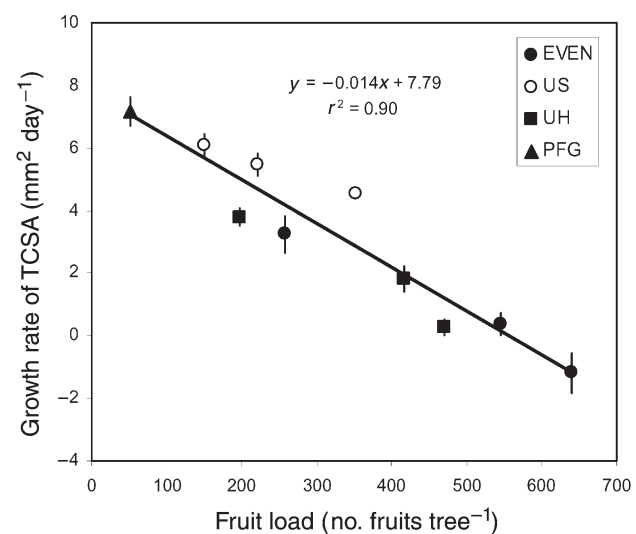

Figure 7. Relationships between trunk cross-sectional area (TCSA) and fruit load in the fruit distribution treatments. Each observation represents the mean of six trees for the potential fruit growth (PFG) treatment and for each sub-treatment in the even fruit distribution (EVEN) treatment, whereas 12 trees were averaged per sub-treatment for the uneven fruit distribution–scaffold defruited (US) treatment. Bars indicate ± standard error. Definition: UH = uneven fruit distribution–hanger defruited.

Table 6. Probabilities for the test of heterogeneity of slopes in ANCOVA for cross-sectional area growth response of the loaded scaffold (SCSA) and trunk (TCSA) to fruit load on a scaffold and tree basis, respectively.

Parameter	Source/Treatments	Probability
SCSA	Treatment (TRT)	0.0590[1]
	Covariable (Fruit load; FL)	0.0001
	Heterogeneity slopes (TRT × FL)	0.0076
	Contrast of slopes	
	EVEN versus US	0.0019
	EVEN versus UH	0.2581
TCSA	Treatment (TRT)	0.3289
	Covariable (Fruit load; FL)	0.0001
	Heterogeneity slopes (TRT × FL)	0.1331
	Contrast of slopes	
	EVEN versus US	0.0727
	EVEN versus UH	0.2024

[1] When heterogeneity of slopes is significant, the assumptions for a covariance analysis are not valid and therefore the probability is not relevant.

pendent units. However, these findings contrast with a similar study on apple where it was observed that branch autonomy was negligible with respect to translocation of carbon between fruited and defruited halves of apple trees (Palmer et al. 1991). We have no explanation for the discrepancy between our data with peach and the study of Palmer et al. (1991) with apple. We note, however, that the study with apple involved central leader apple trees on size-controlling rootstock (M9), and crop load adjustments were made on two sides of the same main leader, whereas our study on peach involved two-leader (scaffolds) trees on vigorous rootstock (Lovell). Thus, the discrepancy between studies may relate to species (peach versus apple), rootstock vigor (vigorous versus size-controlling) or training system.

Reductions in fruit dry mass that occurred when fruits were distributed in clumps on hangers were partly a result of a fruit competition effect and partly a transport limitation effect (DeJong and Grossman 1995). The latter effect probably occurred because clumped fruit distribution leaves large areas of branches without fruit, thereby increasing the distance from fruits to the sources of carbohydrates. The TRANS–COMP calculations, which quantified the limitations due to transport and competition, indicated that US trees had the highest TRANS–COMP values and EVEN trees had minimum values. Nevertheless, our TRANS–COMP limitation values per tree in the optimum fruit distribution (EVEN) treatment (33% at maximum) were larger than the values reported for Stage III in another mid-season maturing cultivar (DeJong and Grossman 1995). In the study of DeJong and Grossman (1995), fruits were thinned early in the fruit growth period and fruit growth was subsequently followed through the various fruit growth stages. In their study, TRANS–COMP began at a maximum of 25% and decreased to almost 0% in the later stages of fruit growth, and the different TRANS–COMP values were attributed to differences in fruit developmental stage. In our study, fruit thinning was delayed until the onset of Stage III, and the calculated TRANS–COMP response was limited only to Stage III of fruit growth. The lower TRANS–COMP limitations calculated by DeJong and Grossman (1995) may be a function of response to time, because thinning and the progressive decrease in TRANS–COMP rates could be the result of progressive vascular reorientation through development in the fruit stems after fruit thinning (Sachs et al. 1993). Thus, the relatively higher TRANS–COMP limitations calculated in our experiment may be a result of the short term of the experiment after thinning.

The calculation of TRANS–COMP limitation on a scaffold basis indicated that the limitation rates were similar in US and EVEN trees, with an advantage of only about 4% in fruit growth in the US treatment. This advantage reflects less than complete branch autonomy or an effect mediated by tree water status (Table 3). Although the impact of bearing patterns on total dry mass allocated to fruits increased with fruit load, the values of TRANS–COMP limitation were generally reduced at crop loads higher than 350 fruits per tree. This effect was predicted because when the maximum potential source supply rate is attained at high fruit loads, the proportion of supply limitation becomes more prominent than the transport–competition effect.

Reproductive growth apparently competes with vegetative growth during Stage III of fruit development because fruits are stronger sinks than growing shoots (Grossman and DeJong 1995). Accordingly, under the conditions of the fruit load prevailing in the most heavily thinned treatment (PFG), vegeta-
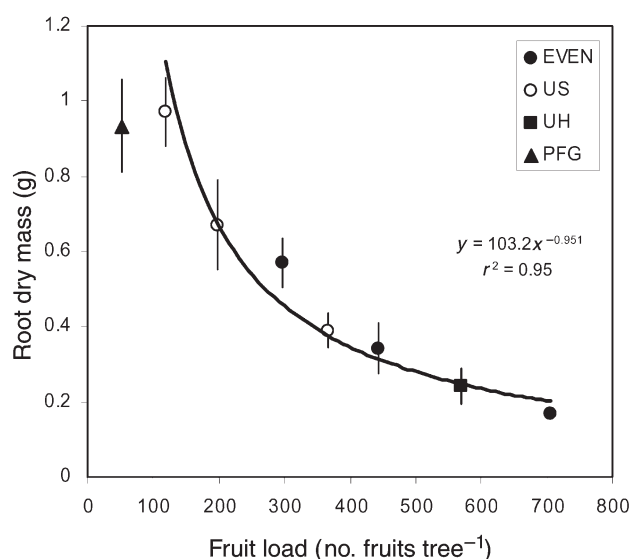

Figure 8. Relationships between root dry mass growth and fruit load in the fruit distribution treatments. Each observation represents the mean of three trees for the potential fruit growth (PFG) treatment and for each sub-treatment in the even fruit distribution (EVEN), uneven fruit distribution–scaffold defruited (US) and uneven fruit distribution–hanger defruited (UH) treatments. Bars indicate ± standard error.

$y = 103.2x^{-0.951}$
$r^2 = 0.95$

tive growth continued at constant high rates throughout Stage III of fruit growth. In general, fruit load had a dramatic impact on growth of SCSA and TCSA and the fruit distribution treatments also appeared to cause major differences on individual scaffolds; defruited scaffolds grew at higher rates than the fruited scaffolds in the US treatment. The high growth rates of the defruited scaffold can be explained by the lack of fruit growth competition in the defruited branch and thus by the existence of a surplus of carbon confined to this scaffold. The growth rate difference between fruited and defruited scaffolds indicates significant branch autonomy.

On the other hand, not all growth differences are necessarily related to carbon immobility. Differences in carbon acquisition per tree or scaffold are expected, because net assimilation rates in peach leaves are associated with fruit demand for carbon (DeJong 1986*b*, Ben Mimoun et al. 1996). However, these differences are often compensated for by the development of new canopy on the defruited scaffolds (Wünsche and Palmer 1997). Furthermore, if there were a significant effect of defruiting on the net assimilation rate of one scaffold while the adjacent scaffold was cropped, this would indicate that scaffolds are autonomous with respect to carbon demand as well as carbon supply.

In retrospect, the finding that scaffold growth of UH and EVEN trees was similar is not surprising, because growth was measured at the scaffold level. Likewise, differences in SCSA growth between adjacent scaffolds may have been cancelled out on a whole-tree basis because tree-averaged SCSA data resulted in a nonsignificant effect of fruit distribution treatments.

Although branch autonomy for scaffold growth appeared to be significant, it was not absolute. Loaded scaffolds grew more under heavy cropping conditions in US trees than in EVEN trees, indicating that some carbon probably moved from the defruited scaffold to the fruited scaffold. This possible carbon movement did not seem to involve trunk growth, because TCSA in the US trees was not significantly different from that in the EVEN or UH trees for similarly cropped conditions.

Growth of the root system was unaffected by fruit distribution treatments. Because root growth was sensitive to fruit load but did not benefit from an apparent lack of total branch autonomy, this may indicate that, during Stage III of fruit development, roots were unable to compete equally with scaffolds for carbon resources. It appears that the incomplete branch autonomy was only apparent among the aboveground organs and at a local level, thus defining a broader unit of autonomy that may isolate the aboveground part of the tree from the root system. This behavior supports the functional equilibrium concept between aboveground and belowground parts of the tree which holds that current-year growth in fine roots is thought to be proportional to the production of new leaves (Kozlowski et al. 1991). Calculations performed with a carbon balance model, in which root growth is supported by carbohydrates residual to aboveground growth, indicates that, with modest fruit loads, little carbon is available for root growth

during Stage III (PEACH model, Grossman and DeJong 1994). This may explain the high sensitivity of root growth to fruit load at medium crop loads (100–300 fruits tree^{-1}), whereas at higher crop loads, root growth occurred at a minimal but constant rate. The strong response of root growth to fruit load is in accordance with the concept that roots are weaker carbon sinks relative to other vegetative organs (Heim et al. 1979, Kramer and Kozlowski 1979).

In summary, scaffold branches appeared to function primarily as autonomous units in supplying carbon for Stage III fruit growth, when peach fruits are believed to be strong sinks. Fruiting hangers also exhibited significant autonomy relative to the distribution of dry matter within the tree. We predicted that extreme heterogeneity in fruit distribution would produce a growth enhancement in organs other than fruits, including the root system. However, this enhancement was observed only in organs at short distances from the fruit positions (i.e., defruited scaffolds grew more than fruited scaffolds), but not in organs located farther away from the source of heterogeneity such as the trunk and roots.

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