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Seasonal patterns of vegetative growth and competition with reproductive sinks in peach (*Prunus persica*)

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SUMMARY

Growth of leaves, wood, and stems were studied over an entire growing season on four year old peach (*Prunus persica* (L.) Batsch.) trees having no crop, commercial crop loads, or heavy crop loads. Leaf, wood, and stem growth were reduced on cropping trees relative to defruited trees. The presence of fruit reduced leaf biomass growth during Stage I and II of fruit growth but not thereafter. Wood biomass growth was reduced by the presence of fruit during all stages of fruit growth. Stem biomass growth was most strongly affected by fruit during Stage III of fruit growth. Carbon partitioning to stems appeared to be influenced by both fruit sink demands and overall developmental capacity for secondary radial growth. Total above-ground biomass production was similar in all three treatments, despite significantly greater leaf area in defruited trees. The total carbohydrate cost of the above ground biomass (the sum of biomass costs, calculated growth and maintenance respiration costs) was estimated to be similar for all three treatments. Cropping reduced root starch content and flowering density but did not influence percent fruit set during the subsequent growing season relative to non-cropped trees.

Carbon partitioning patterns are the complex result of growth by plant organs and competition among different organs for carbohydrates (DeJong, 1999). Peach (*Prunus persica* (L.) Batsch.) trees are assemblages of carbohydrate sinks including fruit, stems, growing leaves, frame wood and roots. The processes of partitioning among these different organs is of interest because the balance of vegetative and reproductive growth has important consequences for tree morphology and productivity. Carbon investment into leaves and the stems supporting them increases a tree's total photosynthetic capacity. Investment into stems and trunk determines tree size, which also affects the capacity for carbon gain. Investment into reserves affects the subsequent season's growth and cropping potential. Fruit are dependent upon these vegetative and reserve components for assimilates, yet they compete with vegetative sinks for carbohydrates, and suppress their growth.

Vegetative growth suppression by fruit growth is well documented in apple (Forshey and Ellving, 1989; Maggs, 1965), and peach (Grossman and DeJong, 1993b; Miller and Walsh, 1988; Proebsting, 1958) however, the timing of this vegetative growth suppression is not well documented.

In addition to competing with vegetative organs, growing fruit may compete with developing flower initials (Monsees and Goldschmidt, 1982) and reduce the amount of fruit set in the following season. Also, fruit may compete with storage sinks, reducing the amount of storage carbohydrate at the end of the season. This could significantly affect crop growth in the following season, as growth of flower buds and early fruit growth are dependent upon reserves of carbohydrates (Loescher et al., 1990). Because vegetative organs supply carbohydrates, and fruit growth suppresses vegetative growth, one would expect reduced total productivity in cropping trees (Reekie and Bazzaz, 1987). However, it has often been observed that cropping trees have greater dry matter production than defruited trees, despite reduced leaf area (Wright, 1989; Forshey and Ellving, 1989), suggesting that vegetative sink potential limits biomass accumulation in non-fruiting trees.

The growth rate of an organ is determined by its growth potential and its competitive ability to obtain resources relative to other sinks (DeJong, 1999). Biomass growth potential is the capacity for dry weight gain by an organ, given a non-limiting supply of resources (Ho et al., 1989; Wareing and Patrick, 1975). The actual growth realized by an organ is equal to, or below its growth potential, depending upon the level of resource competition from other organs. Growth potentials are not temporally fixed but can fluctuate throughout an organ's developmental course (Grossman and DeJong, 1995a, b). Thus, the relative competitive ability of an organ is dynamic, as fluctuations occur in both its own capacity for growth, as well as, in the growth capacity of competing sinks (Wardlaw, 1990).

Three phases of peach fruit sink activity have been identified (Grossman and DeJong, 1995a; Pavel and DeJong, 1993). During stages I and III in fruit development (Connors, 1919), growth is often source-limited in normally cropping trees. At these times, fruit growth is limited as a result of competition from other fruit and vegetative sinks. Between these two source-limited periods (Stage II), fruit growth is usually sink-limited.

Fruit growth carbohydrate demands shift as fruit develop through the three growth stages and are harvested. This fluctuating crop demand for carbohydrates should affect the growth of the vegetative
sinks which compete with the crop. In peach, Miller and Walsh (1983) observed changes in vegetative growth rates corresponding to fruit growth phases. However, their study did not include a defruted treatment and did not quantify total vegetative potential or the degree to which the growth of different vegetative components was reduced below their potential. Grossman and De Jong (1995a) observed periods of source limitation to stem growth during phases of intense fruit sink activity. However, source and sink limitations to leaf and wood growth were not measured.

This project was undertaken to expand upon previous studies in peach by quantifying total yearly, above-ground vegetative growth potential and determining at what periods during the season the presumed competition for carbohydrates reduced growth of vegetative organs below their genetic potential. The seasonal growth of stems, leaves and wood were studied with differing levels of competition from fruit. Vegetative growth responses were measured in the absence of fruit, with “normal” competition from fruit (commercial crop loads) and with heavy fruit competition (high crop loads). The objectives of the study were to: (1) quantify the vegetative growth potential for young peach trees, (2) quantify the degree to which crop depresses actual vegetative biomass growth below potential levels, (3) describe the seasonal dynamics of canopy growth, total sink potential and biomass productivity, and (4) to investigate the effect of different fruit loads on the following season’s crop.

MATERIALS AND METHODS

Four year old ‘O’Henry’ peach trees (Prunus persica, (L.) Batsch) on ‘Lovell’ rootstock were used at the UC Davis Wolfskill Experimental Orchard (Winters, CA). ‘O’Henry’ is a late season cultivar with fruit harvested in early August. Trees were trained to a perpendicularr-V, (De Jong et al., 1994) planted at 5.5 x 2 m spacing. Trees received irrigation and pest control equivalent to standard commercial practice.

Prior to bloom, 115 trees were selected for uniformity of trunk diameter and randomly assigned one of three thinning treatments. Fruit thinning treatments were imposed on 28 March, two weeks after full bloom. The thinning treatments were as follows: Defruted (DF), with all fruit removed, Commercially Thinned (CT), with fruit thinned to commercial crop loads (~150 fruit per tree), and Unthinned (UT) with no fruit removed (250–350 fruit per tree).

At six times throughout the growing season, five trees from each thinning treatment were sampled. Sampling dates were assigned to correspond with different developmental stages of fruit growth. The timing of fruit development in ‘Cal Red’, a cultivar similar to ‘O’Henry’, was described by Grossman and De Jong (1995a) and this information, plus visual observation of growing fruit, was used to estimate the timing of development in ‘O’Henry’. Sampling dates were 1 April (onset of initial rapid fruit and shoot growth, Stage I), 15 May (onset of the sink-limited fruit growth period, Stage II), 30 June (onset of rapid fruit growth, Stage III), 5 August (fruit harvest), 21 September and 6 November (leaf fall).

On each harvest date, all fruit on each sample tree were harvested, counted and total crop fresh weight recorded. A fruit subsample of ten fruits per harvested tree was collected and dried to determine fresh-dry weight ratio and to calculate total crop dry weight.

Shoot biomass was estimated by harvesting every fourth stem along the primary scaffold branches on each tree. Leaves were stripped from harvested stems, dried and weighed. Individual stem lengths and dry weights were measured.

Girth marks were painted on the trunks and at three heights along each scaffold on six trees from each thinning treatment. Diameters were measured at these locations using digital calipers (Mitutoyo Corp, Japan) every two weeks. Diameter measurements were made one day after irrigation, at the same time of day (0800 hours) on each sampling date, to reduce variation from diurnal shrinkage and swelling. Using diameter measurements and the measured distances between sampling points, the volume growth of the entire trunk and frame was calculated for each tree throughout the season. Wood samples were collected from the mid-scaffold region from four trees in October to determine wood density, using fresh volume and dry weight. Using the mean wood density value, tree volume growth was used to estimate wood dry weight growth.

Absolute growth rates were calculated on an accumulated degree-day basis. Temperature data were obtained from the California Irrigation Management Information System (CIMIS) weather station in Winters. Degree-days were calculated on the UC IPM IMPACT computer system, using the single-sine method (Zalom et al., 1983) with thresholds at 7°C and 35°C. Means and standard errors were calculated using SAS (SAS Institute, Cary NC, USA). Absolute growth rates (AGR’s) were calculated by randomly pairing samples from consecutive dates. Means were compared using Tukey’s Mean Separation test at a significance level of 0.05.

Daily standing biomass of leaves, stems, fruit and wood for each treatment were modelled using mean biomass values and calculated growth rate values. Hourly respiration rates for each organ type were calculated using published specific respiration rates, respiratory quotients (Q) (Grossman and De Jong, 1994a) and hourly temperature data from CIMIS. Estimated respiration by each organ type was calculated by multiplying specific respiration rate by estimated dry weight, and the hourly values were summed for the entire season.

Growth respiration and biomass costs of each organ were calculated using the mean end-of-season stem and wood biomass values, plus leaf biomass values from the date of maximum leaf biomass (August in cropping trees, September in defruted trees), plus the mean crop dry weight values for each treatment. Growth respiration was calculated by multiplying each biomass value by growth respiration coefficients from Grossman and De Jong (1994b). Carbohydrate costs were calculated using carbon equivalent weight values from Grossman and De Jong (1994b).

Samples were collected in January of the subsequent year from the six trees from each crop load treatment sampled the previous November to determine starch content of various tree components in each treatment.
Trunk wood was sampled by drilling 2 cm into the trunk with a hand-drill and collecting the shavings. Trunk bark/phloem was removed with a 2 cm diameter cork borer. One year stems were sampled and the wood and bark/phloem were separated. Roots with diameters ranging from 5 to 20 mm were sampled by excavating within 1.0 m of the trunk of the trees. Root wood and bark/phloem were separated. All samples were dried at 90°C and enzymatically assayed for starch, as described in Weinbaum et al. (1994).

Five trees from each of the thinning treatments, which were not sampled during the previous year, were selected for analysis of bloom, fruit set and yield. The trees were dormant-season pruned and eight shoots on each tree were tagged before bloom. Flower density was determined at full bloom (12 March). Three weeks later, the number of growing fruit on the tagged shoots was recorded. Trees were then thinned to a commercial crop load. The mature fruit were harvested in August and crop fresh weight was recorded and crop dry weight was estimated using the fresh-dry ratio of a ten-fruit subsample from each tree.

RESULTS

The fruit thinning treatments had major effects on the amount of dry matter partitioned to fruit ranging from nothing in the DF treatment to a mean of 2.73 and 4.41 kg per tree in the CT and UT treatments, respectively. As expected, leaf biomass growth was greater in the DF treatment than in the two cropped treatments (Figure 1A). Leaf biomass accumulation ceased by the end of the fruit growth period in the cropping treatments but continued into September in the DF treatments (Figure 1A). Mean leaf biomass absolute growth rates during Stage I and II of fruit growth tended to be higher in the DF treatment compared with the fruited treatments but were not significantly different during the Stage III period (Figure 1B). No treatment differences in leaf area per unit dry weight were observed (data not shown), so leaf biomass values were proportional to leaf area values. The DF treatment trees had significantly greater leaf area than the CT or UT treatment trees for much of the season.

Wood biomass increased linearly in all three treatments throughout most of the season (Figure 2A). From 30 June onward, wood biomass in the DF treatment was significantly greater than in the cropping treatments. During the fruit growth period (Stages I, II and III), wood biomass absolute growth rates of DF trees were significantly higher than that of UT trees, and were higher than that of CT trees during Stage II, Stage III and the first post-harvest interval (Figure 2B). Wood biomass growth rates of the fruiting treatments appeared
to recover in the first interval after harvest compared with stage III of fruit growth. All treatments were similar by the last growth interval in the fall.

Stem biomass accumulation was significantly greater in DF trees at the end of Stage I and Stage III of fruit growth but by the end of the season the commercial cropped trees were not different from the DF trees. (Figure 3A). Mean stem biomass AGR was higher in DF than cropping trees during Stages I and III, but AGRs were essentially equal during Stage II and the first post-harvest period (Figure 3B).

Total stem length per tree was greatest in the DF treatment, and was significantly greater than the cropping treatments at the end of the season (Figure 4A). Stem specific weight (average dry weight per unit length of stem) was significantly higher in the DF trees than in the cropping treatments at the end of Stage I and Stage III. However, by the time of leaf fall, stem specific weight was roughly equal (within 7%) for all treatments (Figure 4B).

Calculated total above-ground biomass production at the end of the growing season was virtually the same for all treatments; 9.52, 10.02 and 9.85 kg per tree for the DF, CT and UT treatments, respectively. The fraction of above-ground biomass partitioned to vegetative growth was 100% for the DF trees, 56% for CT trees and 44% for UT trees (Figure 5).

The estimated carbohydrate cost of the above-ground biomass was calculated for each treatment using mean biomass values, growth rates and weather station temperature data. Estimated total carbohydrate costs were very similar (within 5%) for all three treatments (Figure 6). However, maintenance respiration was estimated to be somewhat higher for the treatment with the greatest leaf biomass (DF) and lowest in the treatment with the greatest fruit load (UT).

Fig. 3 A: Seasonal pattern of stem biomass accumulation. Symbols represent the treatment mean ± SE (n = 5). Asterisks indicate defruted (DF) treatment means that are significantly different from both commercially thinned (CT) and unthinned (UT) treatment means (Tukey's Studentized Range Test, P<0.05). B: Mean stem biomass absolute growth rates for each sampling interval. Error bars represent SEs. Within each time interval, means labelled with different letters are significantly different from one another (Tukey's Studentized Range Test, P<0.05).

Fig. 4 A: Seasonal pattern of total tree stem length. Symbols represent the treatment mean ± one SE (n = 5). Asterisks indicate defruted (DF) treatment means that are significantly different from both commercially thinned (CT) and unthinned (UT) treatment means (Tukey's Studentized Range Test, P<0.05). B: Seasonal pattern of specific stem weight. Symbols represent the treatment mean ± one SE. Asterisks indicate DF treatment means that are significantly different from both CT and UT treatment means (Tukey's Studentized Range Test, P<0.05).

Fig. 5 Annual above-ground biomass distribution in peach trees that were defruted (DF), commercially thinned (CT) and unthinned (UT). Leaf and fruit biomass data on fruiter trees were collected on 5 August before fruit and leaf drop. Leaf data on DF trees was from 21 September, and stem and wood values were from 5 November.
Wood and bark/phloem from the trunk, roots and stem wood were analysed for starch content (Figure 7). Very little starch was detected in the one-year bark or trunk bark (data not shown). High starch concentrations were measured in the roots, with root bark being over 15% starch by dry weight. Starch concentrations did not vary among treatments, except in the root bark, where concentrations were significantly greater in the DF treatment than in the UT treatment. Root bark starch values for the CT treatment were intermediate.

The bloom densities (flowers per meter of stem) in DF and CT trees in March of the year subsequent to flowering treatments were significantly greater than in UT trees (Table 1). Percent initial fruit set did not differ statistically among treatments (Table 1), but final fruit density (fruit per metre of stem) was significantly higher in the DF and CT treatments than in the UT treatment (Table 1). Trees were thinned to nearly identical crop loads, and crop dry weight at harvest was not significantly different among treatment trees in the year after the cropping treatment was applied (Table 1).

**DISCUSSION**

As anticipated from previous studies (Miller and Walsh, 1985; Proebsting, 1998), crop load had a substantial influence on leaf, stem and wood growth in this study (Figure 1–4). The effect of crop load on vegetative growth began to appear during the first stage of fruit growth and stem growth was statistically different between defruited and cropped trees at the first sampling interval (Figure 4). These results differ from the data of Miller and Walsh (1988) because the latter did not impose a defruited control and also did not apply their thinning treatments until after Stage I of fruit growth. However, these data are in general agreement with stem and leaf growth data reported by Grossman and DeJong (1995b) for different cultivars and with predictions from the PEACH growth simulation model developed by Grossman and DeJong (1994b).

The relatively constant rate of growth of the wood component during most of the season (Figure 2) is intriguing, given the relatively variable growth rate of the other components. These trends in estimated wood biomass accumulation also agree with peach trunk diameter data reported by Grossman and DeJong (1995b) but differ from wood dry weight data reported by Miller and Walsh (1988) for peach trees growing in Maryland. Other more general studies on trunk diameter growth in trees (Barnett, 1995; Young and Kramer, 1982) indicate that a relatively constant rate of wood growth is typical in many trees. The fact that the trajectory for wood biomass growth appears to have been determined quite early in the season in the present study (Figure 2) warrants further investigation.

Perhaps one of the most interesting aspects regarding vegetative growth in this study is that stem biomass per unit length of new stems was statistically identical at the end of the season in spite of apparent differences earlier during development (Figure 4). During periods of rapid fruit growth (high reproductive sink demand), specific stem length in cropped trees fell significantly below that of defruited trees. However, during periods of reduced fruit demand, stem biomass per unit length increased in stems of cropping trees to match the stems on defruited trees. These results suggest that radial secondary thickening in current season stems is determinate.
Apparently, the average diameter and density of the one-year stems reached their "potential" value regardless of cropping treatment. Allometric relationships of this nature are known to be genetically determined in forest tree species and are used by tree breeders for selection of desired biomass allocation traits. For example, in Douglas fir, traits such as wood density and the ratio of stem wood to total biomass are highly heritable (St. Clair, 1994). Kervella et al. (1994) have similarly demonstrated genotypic differences among peach cultivars in the relationship between stem diameter and length. These relationships may be important for studying and understanding the dynamics of dry matter partitioning in peach trees. As also shown by Grossman and DeJong (1995b), stem extension growth does not temporally correspond to stem dry weight growth and the present study indicates that extension growth apparently creates a relatively fixed potential sink for stem diameter growth but that potential may be fulfilled anytime during the season when there is adequate resource availability to meet the demand. This is in agreement with the guiding principles proposed by DeJong (1999) for logically modelling the biomass partitioning process in peach trees.

Above-ground vegetative biomass production in CT and UT trees was reduced 44 and 56%, respectively, compared with DF trees (Figure 5). While UT trees had twice as many fruit as CT trees, stem length, leaf biomass and wood biomass were not halved relative to CT trees. Thus, the increased fruit loads in the UT trees compared with the CT trees resulted in increased inter-fruit competition and smaller fruits, as well as modest reductions in vegetative growth. This response is what is generally predicted by the PEACH model (Grossman and DeJong, 1994b) and is in agreement with the concept that biomass partitioning in plants is primarily regulated by competition between semi-autonomous organs and their location and relative sink effectiveness (DeJong, 1999).

Leaf area was about 30% greater in DF trees than in cropping trees, and DF trees also had significantly more stem length (Figure 4A) and thus larger canopies than cropping trees. Despite having a larger canopy, total above-ground biomass production in DF trees was not significantly different from that of cropping trees. Similar results have been reported for apple by Maggs (1963) and Heim et al., (1979) but other researchers have reported increased biomass production by cropping trees despite lower total leaf area (Forshey and Elfving, 1989). In contrast, Kappel (1991) reported that above-ground biomass production by defruited sour-cherry trees exceeded that of cropping trees. These three types of response can be rationalized by understanding the processes of carbon acquisition and partitioning that are involved. If defruited trees have the potential for increased stem and leaf growth as apparently was the case in the present experiment, then the increased leaf growth should result in increased canopy size and consequently greater canopy light interception if the canopies are not crowded or shaded by adjacent trees. This should lead to increased or at least the same total biomass accumulation during the season. On the other hand, if the vegetative/shoot growth of defruited trees is limited by the effects of a size-controlling rootstock, root restriction in a potted plant, nutrient deficiencies or some similar limitation, one would anticipate that crop load would enhance overall tree biomass production because fruit sinks represent increased biomass growth potential that would not be limited by the same factors as vegetative organs. The presence of fruits has also been reported to increase leaf photosynthetic rate in fruit trees (Gucci et al., 1995) but this response is also variable (Forshey and Elfving, 1989). In situations where vegetative sinks are limited by rootstocks or other means, one would expect fruit to have a strong influence on photosynthesis (Foyer and Galter, 1996) but in peaches on vigorous rootstocks this response has been reported to be relatively minor (DeJong, 1986). When maintenance respiration, growth respiration and the carbohydrate costs of the various organs were estimated, the total estimated carbohydrate costs of the above ground organs was roughly equal for all treatments (Figure 6).

This suggests that any fruit stimulated enhancement of leaf photosynthesis in the fruited trees relative to the defruited trees was compensated by the greater leaf area of the defruited trees.

However, to fully estimate whole-tree carbon gain, root growth and respiration would have to be accounted for. If roots constitute a major sink, and DF trees produced substantially more root biomass than cropping trees, then significant differences in whole-tree carbon gain could have existed between treatments. In a peach carbon budget model developed by Grossman and DeJong (1994b), it was estimated that root growth and respiration of a cropping peach tree utilized one third of the seasonal photosynthetic production. Miller and Walsh (1988) observed high root growth rates during periods of low sink demand by fruit, and Maggs (1963) reported root biomass growth to be over three times greater in defruited than cropping apple trees. Thus, different levels of partitioning to below-ground sinks could constitute a major productivity difference between treatments not visible in the above ground data presented here.

Since heavy crop loads are well known to cause decreases in carbohydrate storage in perennial organs (Monselise and Goldschmidt, 1982), the lack of significant differences in the starch concentration of trunk wood and stem wood among the treatments (Figure 7) indicates that there was probably enough time between fruit maturity and leaf fall to recover from any difference that may have occurred earlier in the season due to differences in crop load. Actually these starch results correspond with the fact that stem biomass per unit stem length had recovered by the last vegetative growth measurement in November (Figure 4B).

Even though the starch concentrations were similar in the wood and stems, the larger size of these components in the defruited treatment trees relative to the cropping trees (Figures 2 and 3) indicates that the defruited trees did have more total reserves for the following season. Furthermore, root bark starch concentrations were more than 20% higher in defruited trees than unfruited trees (Figure 7).
The fact that fruit density on stems of trees in the unthinned treatment was less than the two other treatments during the subsequent cropping year was apparently primarily the result of reduced bloom density (Table I). The reduced bloom density may have been the result of differences in the rate of recovery of stem biomass growth after fruit harvest as indicated in Figure 4. Since peach is known to differentiate flower buds during August and September (Garcia, 1980; Tufts and Morrow, 1925), significant delays in stem maturation may have influenced fruit bud initiation and differentiation process in the unthinned treatment trees. Nevertheless, differences in total fruit set between the previous season’s fruiting treatments were minor enough to be ameliorated by normal fruit thinning practices.

Thus, there was no effect of previous season treatments on fruit yield in the subsequent season (Table 1). These results correspond to the fact that alternate bearing is rarely considered a significant factor in commercial peach production (Monselise and Goldschmidt, 1982).

Although there is ample documentation in the literature that cropping influences vegetative growth and dry-matter partitioning in fruit trees, this research provides some seasonal context for when differences occur between cropping and non-cropping trees. Furthermore, this study documents the resilience of the peach tree as a cropping system indicating that recovery begins to occur immediately after harvest in young trees and cropping effects on yield potential in the subsequent year can be negligible.

REFERENCES


