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# Net Photosynthesis, Specific Leaf Weight, and Flowering of Peach as Influenced by Shade

**Richard P. Marini[1] and Donald L. Sowers[2]**
*Department of Horticulture, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061*

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***Abstract.*** **'Redhaven' peach *[Prunus persica* (L.) Batsch] trees were shaded to five light levels [100%, 45%, 23%, 17%, and 9% photosynthetic photon flux (PPF)] for four different periods. Net photosynthesis (Pn), measured under the various shade levels, increased nonlinearly with increasing percent PPF. After 18 days of shading, specific leaf weight (SLW) was positively and linearly related to percent PPF. After shade removal, Pn and SLW returned to control levels in 26 and 4 days, respectively. Flower density was positively related to percent PPF when trees were shaded from 16 June to 4 July or 4-31 July, but not from 31 July to 30 Sept. of the previous year.**

Orchard profitability depends on efficient absorption and use of light. Productivity of young orchards has been improved by increasing tree density (Erez, 1982; Layne and Tan, 1984), but as plantings mature, shading may become a problem. Shading reduced flower bud initiation (Cain, 1971), fruit size and quality (Jackson et al., 1971; Seeley et al., 1980), and plant fresh weight (Barden, 1974) of apple. Photosynthetic characteristics of apple (Barden, 1974) and peach (Kappel and Flore, 1983) leaves were influenced by exposure to diverse light environments. Compared to sun-grown leaves, shade-grown leaves generally had lower net photosynthetic (Pn) rates at saturating light levels and lower dark respiration rates and specific leaf weight (SLW). These characteristics not only depended on the light regime under which leaves developed, but also were influenced

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[1]Associate Professor.
[2]Research Technician.

Table 1. Net photosynthesis (Pn) (μmol·s$^{-1}$·m$^{-2}$) of young and old 'Redhaven' peach leaves, exposed to various photosynthetic photon fluxes (PPF), on trees shaded during three periods during the season.

| Shade period and % PPF | Date of measurement: 15 June | | 18 June | | 3 July | | 8 July | | 30 July | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Age of leaves: Young | Old | Young | Old | Young | Old | Young | Old | Young | Old |
| 16 June-4 July | Not shaded | | Shaded | | | | Not shaded | | | |
| 100 | 12.3 | 14.0 | 12.2 | 12.5 | 20.5 | 20.5 | 20.5 | 21.5 | 18.0 | 13.5 |
| 45 | 11.5 | 12.0 | 9.7 | 10.4 | 22.1 | 18.9 | 22.0 | 20.5 | 20.8 | 17.0 |
| 23 | 10.7 | 14.1 | 5.9 | 9.1 | 13.5 | 7.7 | 20.5 | 11.2 | 18.1 | 19.4 |
| 17 | 9.8 | 10.7 | 7.5 | 8.9 | 14.1 | 8.4 | 16.6 | 22.2 | 19.8 | 15.4 |
| 9 | 12.6 | 12.9 | 4.0 | 4.4 | 8.9 | 6.8 | 17.2 | 18.4 | 18.1 | 21.7 |
| Significance | NS | NS | L | L | L, Q | L, Q | L | L | NS | NS |
| $R^2$ | --- | --- | 0.70 | 0.81 | 0.61 | 0.73 | 0.31 | 0.36 | --- | --- |
| 4-31 July | Not shaded | | | | | | Shaded | | | |
| 100 | --- | --- | --- | --- | 16.3 | 21.1 | 24.5 | 20.8 | 15.4 | 14.5 |
| 45 | --- | --- | --- | --- | 18.4 | 21.0 | 15.9 | 11.9 | 11.2 | 13.6 |
| 23 | --- | --- | --- | --- | 25.4 | 21.2 | 7.0 | 8.6 | 7.7 | 9.6 |
| 17 | --- | --- | --- | --- | 19.1 | 20.0 | 4.9 | 6.3 | 11.2 | 11.6 |
| 9 | --- | --- | --- | --- | 19.8 | 21.9 | 3.5 | 5.8 | 7.7 | 9.1 |
| Significance | --- | --- | --- | --- | NS | NS | L, Q | L | L | L |
| $R^2$ | --- | --- | --- | --- | --- | --- | 0.89 | 0.78 | 0.45 | 0.38 |
| 16 June-31 July | Not shaded | | | | Shaded | | | | | |
| 100 | --- | --- | --- | --- | 19.8 | 18.1 | 23.8 | 17.6 | 19.4 | 17.7 |
| 45 | --- | --- | --- | --- | 19.6 | 13.3 | 16.1 | 14.5 | 19.4 | 16.6 |
| 23 | --- | --- | --- | --- | 12.4 | 10.5 | 10.3 | 5.8 | 15.6 | 10.5 |
| 17 | --- | --- | --- | --- | 14.5 | 12.1 | 11.9 | 9.8 | 9.3 | 8.2 |
| 9 | --- | --- | --- | --- | 6.3 | 5.6 | 4.7 | 2.8 | 6.8 | 3.7 |
| Significance | --- | --- | --- | --- | Q | L | L, Q | L | L,Q | L,Q |
| $R^2$ | --- | --- | --- | --- | 0.43 | 0.58 | 0.91 | 0.74 | 0.65 | 0.69 |

'Average available PPF was 1128, 1560, 1478, 1102, and 1350 μmol·s$^{-1}$·m$^{-2}$ for 15 and 18 June and 3, 8, and 30 July, respectively.
$^{NS,L,Q}$Nonsignificant and significant ($P < 0.05$) linear and quadratic terms, respectively (n = 3). Coefficients of determination ($R^2$) are for the combined regression model for Pn vs. PPF.

by subsequent light conditions (Barden, 1974). Improved light penetration into fruit tree canopies following various types of summer pruning may improve the photosynthetic- characteristics of previously shaded leaves (Day et al., 1989; Marini and Barden, 1982; Marini, 1985; Taylor and Ferree, 1984).

The purpose of this study was to determine the effects of several light regimes on Pn and SLW of leaves and on flower bud initiation of peach trees.

Three-year-old 'Redhaven' trees spaced 7.3 × 5.2 m were used for whole-tree shade treatments in 1986. Dome-shaped structures supported by PVC pipe were covered with 51%, 73%, 80%, or 92% neutral-density black polypropylene shade fabric (E.C. Geiger, Harleysville, Pa.) that provided 45%, 23%, 17%, and 9% PPF. Nonshaded trees served as controls. Temperature under the shade fabric ranged 1 to 3C above ambient. Trees were shaded during one of four periods: 16 June-4 July, 4-31 July, 31 July-30 Sept., and 16 June-30 Sept. Full bloom occurred on 3 Apr. and fruit were harvested 23 July-8 Aug. There were three single-tree replicates in a completely randomized design, with a factorial arrangement of five shade levels and four shade periods. PPF was recorded at 10-sec intervals at a weather station 5.5 km from the orchard, and data were integrated for each 24-hr period. Total available PPF (mol·m$^{-2}$) was 2756 from bloom until 16 June, 1060 for 16 June-4 July, 1255 for 4-31 July, and 1864 for 31 July-30 Sept. Average PPF was 38.3, 55.8, 48.3, and 31.6 mol·m$^{-2}$·day$^{-1}$ for the same four periods.

Net photosynthesis was measured on sunny days (when PPF was 1100 to 1560 μmol·s$^{-1}$·m$^{-2}$ from 1030 to 1330 HR) with an Analytical Development Corp. (P.K. Morgan Instruments, Andover, Mass.) $CO_2$ analyzer (model LCA-2) equipped with a Parkinson broad leaf chamber. The air flow rate was 6.7 ml·s$^{-1}$, and the ambient $CO_2$ concentration ranged from 330 to 380 mg·liter$^{-1}$. Net photosynthesis of two leaves on the south side of each tree was measured on 15 and 18 June and 3, 8, and 30 July. On 15 June, one leaf (old leaf) had been unfolded for ≈ 4 weeks and was fully expanded, whereas the other leaf (young leaf) was about one-half expanded. When trees were shaded, Pn was measured under the shade fabric. Test leaves were not shaded, except by the shade fabric. After removal from the leaf chamber, leaves were excised, and leaf areas were measured with a LI-COR (LI-3000, Lincoln, Neb.) portable leaf area meter. Leaves were then dried at 60C for 96 hr, and SLW was calculated for each leaf.

On 21 Apr. 1987, during full bloom, the lengths of 10 1-year-old shoots from around each tree were recorded. Flowers per shoot were recorded and flower density (FD) was calculated as flowers/m of shoot length (Lombard et al., 1988).

Analysis of variance indicated there were shade level × shade period x measurement date interactions ($P \leq 0.05$). Leaf age usually interacted with shade period and measurement date. Therefore, where appropriate, regression analyses were performed for each leaf age per measurement date per shade period to determine the influence of PPF on Pn and percent PPF on SLW and FD.

When measured under the shade fabric, Pn generally increased with increasing PPF (Table 1). Net photosynthesis, measured under the shade fabric, was linearly and quadratically related to PPF after 2 days (18 June) and 18 days (3 July) of shade, respectively, for trees shaded 16 June-4 July. Partial cloud cover during Pn measurements on 8 July caused a range of PPF from 600 to 1480 μmol·s$^{-1}$·m$^{-2}$. Therefore, 4 days after shade removal (8 July), Pn of leaves measured in full sun was linearly related to PPF. Leaves totally recovered 27 days (30 July) after shade removal. When measured under the shade fabric, Pn of young and old leaves was quadratically and linearly related to PPF, respectively, after 4 days (8 July) of shade for trees shaded 4-31 July. Net photosynthesis of both leaf ages was linearly related to PPF after 26 days (30 July) of shade. When old leaves were shaded from 16 June to 31 July, Pn measured under the shade fabric was linearly related to PPF after 18 (3 July) and 23 (8 July) days of shade, and the relationship became quadratic after 43 (30 July) days of shade. Net photosynthesis of young leaves shaded 16 June-31 July was nonlinearly related to PPF on all three dates.

Greenhouse-grown apple leaves develop-

Table 2. Specific leaf weight (SLW) ($mg \cdot cm^{-2}$) of young and old 'Redhaven' peach leaves as influenced by percent photosynthetic photon flux (PPF) on trees shaded during three periods during the season.

| Shade period and % PPF | Date of measurement: 15 June | | 18 June | | 3 July | | 8 July | | 30 July | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Age of leaves: Young | Old | Young | Old | Young | Old | Young | Old | Young | Old |
| 16 June-4 July | Not shaded | | Shaded | | | | Not shaded | | | |
| 100 | 6.0 | 6.5 | 6.3 | 6.5 | 6.7 | 6.8 | 6.7 | 7.4 | 7.7 | 7.6 |
| 45 | 6.4 | 5.6 | 5.8 | 5.9 | 4.9 | 6.1 | 5.4 | 6.5 | 6.8 | 7.6 |
| 23 | 6.0 | 6.1 | 6.0 | 6.0 | 4.3 | 5.9 | 4.9 | 5.9 | 6.3 | 7.3 |
| 17 | 5.8 | 6.8 | 5.9 | 6.1 | **4.1** | 5.6 | 4.7 | 6.9 | 6.5 | 7.7 |
| 9 | 6.0 | 5.5 | 5.1 | 5.5 | **3.5** | 5.5 | 5.3 | 6.7 | 7.2 | 6.6 |
| Significance | NS | NS | Q | NS | L | L | L, Q | NS | NS | NS |
| $R^2$ | --- | --- | 0.38 | --- | 0.87 | 0.75 | 0.82 | --- | --- | --- |
| 4-31 July | Not shaded | | | | | | Shaded | | | |
| 100 | --- | --- | --- | --- | 6.6 | 6.9 | 6.7 | 6.4 | 7.7 | 7.0 |
| 45 | --- | --- | --- | --- | 6.2 | 6.8 | 5.9 | 6.7 | 6.8 | 6.3 |
| 23 | --- | --- | --- | --- | 6.8 | 6.3 | 5.5 | 6.4 | 6.0 | 6.3 |
| 17 | --- | --- | --- | --- | 6.0 | 7.0 | 5.3 | 6.0 | 5.7 | 6.1 |
| 9 | --- | --- | --- | --- | 6.2 | 7.2 | 5.1 | 6.1 | 5.3 | 5.6 |
| Significance | --- | --- | --- | --- | NS | NS | L | NS | Q | Q |
| $R^2$ | --- | --- | --- | --- | --- | --- | 0.64 | --- | 0.87 | 0.42 |
| 16 June-31 July | Not shaded | | | | Shaded | | | | | |
| 100 | --- | --- | --- | --- | 6.3 | 7.3 | 6.2 | 6.6 | 7.5 | 7.1 |
| 45 | --- | --- | --- | --- | 5.3 | 6.2 | 4.7 | 6.2 | 5.6 | 6.8 |
| 23 | --- | --- | --- | --- | 4.5 | 5.7 | 4.5 | 5.4 | 5.1 | 6.7 |
| 17 | --- | --- | --- | --- | 3.6 | 5.6 | 4.2 | 5.4 | 4.6 | 6.5 |
| 9 | --- | --- | --- | --- | 3.8 | 5.4 | 3.2 | 5.8 | 4.0 | 5.4 |
| Significance | --- | --- | --- | --- | Q | L | Q | L | L | Q |
| $R^2$ | --- | --- | --- | --- | 0.69 | 0.77 | 0.84 | 0.43 | 0.90 | 0.59 |

[NS,L,Q]Nonsignificant or significant ($P < 0.05$) linear and quadratic terms, respectively (n = 3). Coefficients of determination ($R^2$) are for the combined regression model for SLW vs. % PPF.

Table 3. Flower density (FD) of 'Redhaven' peach shoots in 1987 as influenced by percent photosynthetic photon flux (PPF) during four periods during the 1986 season.

| PPF (%) | Shade period: 16 June-4 July | 4-31 July | 31 July-30 Sept. | 16 June-30 Sept. |
|---|---|---|---|---|
| | *FD (flowers/m of shoot length)* | | | |
| 100 | 50 | 43 | 41 | 43 |
| 45 | 47 | 51 | 37 | 30 |
| 23 | 37 | 41 | 42 | 20 |
| 17 | 34 | **44** | 44 | 25 |
| 9 | 28 | **31** | **40** | 4 |
| Significance | L | Q | NS | Q |
| $R^2$ | 0.68 | 0.48 | --- | 0.56 |

[NS,L,Q]Nonsignificant and significant ($P < 0.05$) linear and quadratic terms, respectively (n = 30). Coefficients of determination ($R^2$) are for the regression model of FD vs. percent PPF.

ing for 3 weeks in 20% PPF had reduced Pn when measured in saturating light, and Pn increased slightly following 3 weeks in full sun, but declined further following an additional 3-week shade treatment (Barden, 1974). After being grown under a range of PPF for nearly 3 months, SLW and Pn of peach leaves were positively related to percent PPF (Kappel and Flore, 1983). Shade leaves became light-saturated between 400 and 600 $\mu mol \cdot s^{-1} \cdot m^{-2}$, whereas sun leaves became saturated between 600 and 800 $\mu mol \cdot s^{-1} \cdot m^{-2}$. Under saturating light, Pn of leaves grown in 9% PPF was 55% that of nonshaded controls (Kappel and Flore, 1983). In our study, when measured in full sun, Pn of peach leaves grown in 9% PPF for 18 days (16 June-4 July) and then exposed to full sun for 4 days was 83% that of nonshaded controls.

Specific leaf weight tended to decline with increased intensity and duration of shade, but young leaves were most affected by shade (Table 2). When young leaves were shaded 16 June-4 July, SLW was significantly related to percent PPF after 2 days (18 June) of shade and further declined after 18 days (3 July) of shade. When young leaves were shaded 16 June-31 July, SLW declined initially, but did not decline further after 45 days (30 July) of shade. Compared to young leaves, SLW of old leaves declined more slowly upon shading and increased more rapidly upon shade removal. After being grown in 20% PPF for 3 weeks, SLW of greenhouse-grown apple leaves was similar to the preshade level, but was only 75% that of nonshaded control leaves (Barden, 1974). Specific leaf weight of leaves that were shaded for 3 weeks, followed by 3 weeks of full sun, increased at the same rate as nonshaded control leaves (Barden, 1974). Peach leaves may respond more rapidly than apple to changing PPF. In our study, SLW of young leaves grown in 23% PPF for 18 days (3 July) was 64% of that of nonshaded controls, but, 26 days after shade removal (30 July), SLW increased to 82% of the controls (Table 2).

Reduced SLW of leaves sampled from shaded locations of apple trees has been attributed to fewer palisade cell layers and smaller cell size (Wooge and Barden, 1987). In our study, leaf dry weight, but not leaf area, usually correlated with percent PPF (data not shown). Since SLW changed quite rapidly in response to changing PPF, these changes may be due to accumulated soluble carbohydrates, rather than changes in leaf morphology.

Measured in saturating light, Pn has been correlated with SLW when leaves were shaded for 3 to 9 weeks (Barden, 1977) or when leaves were sampled from various locations in the tree canopy (Marini and Barden, 1981; Marini and Marini, 1983). In our study, Pn was not correlated with SLW ($P > 0.05$), except for leaves shaded 16 June-31 July and measured on 30 July. More than 3 weeks of shade are apparently required to change leaf morphology enough to influence Pn. This study also differed from previous studies in that Pn of field-grown leaves was measured under shade, whereas previous studies used greenhouse-grown trees and Pn was measured under saturating light conditions (Barden, 1974, 1977). Field-grown leaves may respond differently to low light conditions than greenhouse-grown leaves. Compared to greenhouse-grown apple leaves (Barden, 1974), Pn of peach leaves in this study recovered more rapidly from a previous shade treatment. In addition, SLW of peach leaves in this study declined to a greater extent when shaded and increased to a greater extent upon shade removal.

When trees were shaded 16 June-30 Sept.,

shoot length increased linearly with increasing percent PPF, but shade during the other periods did not influence shoot length (data not shown). When trees were shaded 16 June-4 July, FD increased linearly with increasing percent PPF (Table 3). There was a nonlinear positive relationship between FD and percent PPF for trees shaded 4-31 July or 16 June-30 Sept. Heavy shading to 9% PPF 16 June-4 July and 4-31 July reduced FD to 56% and 72% of the nonshaded controls, respectively. When trees were shaded 16 June-30 Sept., FD was nonlinearly related to percent PPF and shading to 9% PPF reduced FD to 9% of the control.

Results from this study indicate that shading for several days has a negative influence on SLW and Pn of peach leaves. However, SLW and Pn will return to normal levels rather quickly upon exposure to full sun. Therefore, summer pruning to improve light penetration into peach canopies may improve the photosynthetic efficiency of interior-canopy leaves. Early season shading (16 June-4 July), before 'Redhaven' harvest in late July, was most detrimental to flower bud initiation, and subsequent exposure to full sun did not counteract the 18-day shade period. Therefore, in the mid-Atlantic region, within-canopy shading must be avoided during June and July.

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