Specific Leaf Weight and Nitrogen Allocation Responses to Light Exposure within Walnut Trees

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Abstract. Exposure to photosynthetically active radiation and the consequent effect on leaf mass per unit leaf area (SLW) and nitrogen (percent dry weight and µg·mm⁻²) allocation within tree canopies was investigated in walnut (Juglans regia 'Serr' and 'Hartley') trees. Percent contribution of discrete light flux densities below light saturation (100-700 µmol·s⁻¹·m⁻²) to the total light exposure of individual spurs, exposed up to 9 hour-day⁻¹ to saturating light (>700 µmol·s⁻¹·m⁻²), was minimal (<1 hour), indicating that individual spurs were either exposed or shaded most of the day. SLW and N content per unit leaf area of individual spurs were highly correlated (second-order polynomial curve fit) with light exposure within the tree canopy, indicating uneven allocation of available N for optimal utilization. Nitrogen expressed as percent dry weight was not correlated with light exposure and SLW. Leaf N content per leaf area was highly correlated (linear fit) with SLW.

Productivity of plants depends on net photosynthesis, which, in turn, may be limited by light, among other factors. Numerous laboratory studies have evaluated the photosynthetic response curves to light. Light saturation of walnut is approached at photosynthetic photon fluxes of 600 to 800 µmol·s⁻¹·m⁻² (Tombesi et al., 1983) and that of cherry, peach, and plum at 400 to 700 µmol·s⁻¹·m⁻² (DeJong, 1983) and pecan requires 675 µmol·s⁻¹·m⁻² (Crews et al., 1980) for light saturation of photosynthesis.

In the orchard, net photosynthesis may be limited by various factors besides light, i.e., temperature, CO₂ concentration, and water deficit (reduced stomatal conductance). Nevertheless, as a result of excessive vegetative growth, light may limit individual leaf photosynthesis in commercial orchards. In practice, light measurements are not taken routinely and researchers generally assume that light exposure is variable within the tree canopy, where photosynthesis proceeds, analogous to laboratory studies, at nonsaturating light intensities. Many walnut orchards in California are extremely shaded as a result of complete canopy closure. We aimed to evaluate light fluxes within these dense canopies and the consequent effects on specific leaf weight and N allocation among leaves within the trees. Specific leaf weight and leaf N expressed on an area basis have been related to light exposure in other fruit trees (Avery, 1977; Barden, 1974, 1977, 1978; Crips, 1972; DeJong, 1982; DeJong and Doyle, 1985; Delong et al., 1989; Jackson and Palmer, 1977; Kappel and Flore, 1983; Marini and Marini, 1983; MacMillen and McClendon, 1983; Weinbaum et al., 1989).

Quantitative evaluation of this relationship should be helpful in formulating management practices (i.e., pruning and N nutrition) for walnuts.

The orchard. Five individual-tree replicates of 'Serr' and 'Hartley' Persian walnut trees, grafted on black walnut (Juglans hind-sii) rootstock, were selected for measurements in a commercial orchard near Winters, Calif. Trees were 16 years old and planted 8.5 x 8.5 m, with cultivar rows oriented east–west. Tree height was 8 to 10 m, with the canopies closed near the top. The trees were only lightly pruned for 3 years before the study and not pruned at all in the year of the study.

Light measurements. Transmittance of photosynthetic photon flux (PPF, 400–700 nm) and sunfleck measurements under tree canopies were taken on 15 July 1989 with an 80-cm 80 sensor Light Ceptometer (model SF-80; Decagon Devices, Pullman, Wash.). The ceptometer can be used to measure PPF and to take sunfleck readings simultaneously. Percent photosynthetically active radiation (PAR) transmittance was calculated as the ratio of below to above canopy irradiance. Above-canopy irradiance was measured in an open field. Below-canopy irradiance varied and, therefore, readings were averaged from measurements taken in three positions along tree rows: a) walking on both sides of trunks, along tree rows (one reading each step, 20 readings per tree, averaged); and in a circle; b) around tree trunks; and c) between tree trunks. With positions b and c, one reading was taken every 45° (eight readings per circle, averaged for each position). Only relative values of the sunfleck readings could be measured using a manual threshold setting because of the extreme shade under the canopy. The manual light threshold for shade was set in a shed under homogeneous light exposure of 17 µmol·s⁻¹·m⁻² PAR.

Measurements of PAR above individual spurs were carried out under clear skies in 1989 following canopy closure (6-25 June

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were sampled immediately after irradiance was disregarded because of high variance of battery-operated data loggers (CR21 microsider considered to be minor. Irradiance above 700 consisted of the fraction of time that the sensors were programmed to scan each sensor respectively). Irradiance was measured around and 26 June to 8 July in 'Serr' and 'Hartley', and within the canopies of three to four trees, at a total of 55 positions for each cultivar, according to Delong and Doyle (1985). Two battery-operated data loggers (CR21 micrologger; Campbell Scientific, Logan, Utah), each with seven quantum sensors, were used. Sensors were individually calibrated with a quantum sensor (LI-1905; LI-COR, Lincoln, Neb.) and positioned horizontally, immediately above individual spurs. The data loggers were programmed to scan each sensor once every 10 sec and to log the data as an average over 4-h intervals. The logged data consisted of the fraction of time that the sensors were exposed to light of <100, 100–250, 250–400, 400–550, 550–700, and >700 µmol·s·m·m, respectively.

Leaflet sampling and analysis. Leaflets were sampled immediately after irradiance measurements were completed on each spur. Leaf areas were measured with a Delta T area meter (Decagon, Seattle, Wash.), then washed, dried at 55C, and ground to pass a reflect the prevailing light conditions under closed-canopy walnut orchards and the magnitude of differences between two distinct cultivars. These differences in canopy light characteristics may occur because 'Serr' is a more vigorous cultivar, with a different tree and leaf morphology, resulting in a denser and slightly more shaded canopy than 'Hartley'.

Nitrogen content and SLW of individual spur leaves were correlated with the total daily light exposures measured immediately above the spur. Measurements were taken soon after the canopy was fully developed, and the specific leaf weight of the spur leaves was established (S.A.W., unpublished data). SLW and micrograms N/mm were significantly correlated with total daily light exposure (Figs. 1 and 2); second-order polynomial correlations (r) characterized SLW and N for both cultivars. Linear correlations (rather than polynomial) with similar r values could be fit to the data relating SLW and N to PPF, but the data deviated from the curve fit at the low end of the curve. Leaf N, as percent dry weight (% DW), was not correlated with light exposure. SLW and N (area basis) were linearly correlated (Figs. 1 and 2). The high correlations (r = 0.9) indicate a very strong relationship, when taking into account a 10% analytical error in N determination.

Light was measured above the spur, while SLW and N were measured on several leaflets below, shading each other to some extent. The correlations between light measurements and SLW and N (area basis) probably would have been even higher if they had been made for individual leaflets and for extended periods. The SLW value may reflect an integrated value of the incident light better than light sensors positioned above spurs could measure.

Light exposure time measurements were logged at 4-h intervals and at five specific light flux ranges that contribute to daily photosynthesis. The results were calculated and expressed as percent energy contribution (daily photon flux, Fig. 3), based on daily exposure hours (Fig. 4) to specific light flux ranges. Both expressions are presented, since either a short exposure (contribution) time at high light or long exposure time at low light fluxes can (theoretically) contribute significantly to daily photosynthesis.

In extreme shade, = 60% of the intercepted PAR energy came, from light fluxes of 100 to 700 µmol·s·m·s distributed evenly within this range (Fig. 3). The percent contribution of specific light flux ranges below saturation decreased exponentially as the total daily light interception increased. However, when incident PPF was expressed as exposure time to various light flux ranges, it became apparent that the combined contribution of 100 to 700 µmol·s·m·s was = 1 h·day at most (Fig. 4). The rest of the time the spur was in darkness (at night) or <100 µmol·s·m·s. Furthermore, the 100 to 700 µmol·s·m·s contribution was minimal for shaded spurs. The percent contribution to daily light exposure of light fluxes between light compensation and light saturation were, therefore, greater in shaded than in exposed leaves, but the absolute exposure time to these intermediate light fluxes was minimal. Ap-
can support fruit growth by importing carbohydrate. The photosynthetic characteristics of either on their own or by using carbohydrate was minimal. Such a light regime in the canopy only extreme high- and low-light zones were soon after canopy closure, to PPF of >100 µmol·s⁻¹·m⁻². Within the canopy of a shaded walnut either highly exposed (exterior of canopy) or the exposure of the outer canopy, but also orchard basis, where planting densities limit not be valid in fruit trees not only on an Baker, 1988). Our data from walnut indicate that the premise of the above argument may still be true, at least for mature leaves in these very shaded tree canopies.

### Literature Cited


### Table 1. Relative sunfleck (SF) measurement and transmittance of photosynthetically active radiation (PAR) under the canopies of ‘Serri’ and ‘Hartley’ walnut trees on 15 July 1989 in Winters, Calif.

<table>
<thead>
<tr>
<th>Time (HR)</th>
<th>Relative SF</th>
<th>PAR (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0930</td>
<td>Hartley/Serr</td>
<td>1.63</td>
</tr>
<tr>
<td>1145</td>
<td>Hartley/Serr</td>
<td>1.66</td>
</tr>
<tr>
<td>1315</td>
<td>Hartley/Serr</td>
<td>1.33</td>
</tr>
</tbody>
</table>

Means and st of three types of measurements (around trunks and between canopies along tree rows, and walking on two sides of trees along tree rows).