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Photosynthetic Photon Flux Influences Macroelement Weight and Leaf Dry Weight per Unit of Leaf Area in Prune Tree Canopies

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Abstract. **The relationship between canopy position and foliage concentrations of several phloem-mobile and -immobile essential nutrients was determined over a 20-fold range of average incident photosynthetic photon flux (PPF) (50 to 1000 $\mu mol \cdot s^{-1} \cdot m^{-2}$) in 7-year-old prune (*Prunus domestica* L., syn. 'Prune d'Agen') tree canopies. Mineral weight per unit of leaf area (LA) increased with increasing PPF within the canopy according to the relationship N > Ca > Mg > K > P. Dry weight per leaf area (DW/LA) increased 3-fold over the range of light exposures sampled. Leaf nutrient concentration expressed as percent dry matter (DM) did not vary with PPF. Both DW/LA and leaf N/LA appear to integrate the light microenvironment at the canopy coordinates of leaves sampled and may be correlated with photosynthetic capacity. Thus, these parameters may have diagnostic value in orchard management and crop production.**

With the exception of several studies in apple and citrus (Haynes and Goh, 1980; Jackson and Palmer, 1977; Koo and Sites, 1956), plant nutritionists and horticulturists have virtually ignored the relationship between foliage position within fruit tree canopies and the concentrations of mineral nutrients within those leaves. Leaf N expressed on a leaf unit area (LA) basis has exhibited a strong positive correlation with photosynthetic photon flux (PPF) within canopies of peach (DeJong, 1982; DeJong, 1983; DeJong and Doyle, 1985). Our purpose was to determine if similar variation might occur with respect to allocation of other essential plant nutrients. We measured the PPF at five positions differing in light exposure within canopies of French prune trees and correlated these measurements with the net allocation of several phloem-mobile and -immobile nutrients within leaves from those positions.

Materials and Methods

Plant materials. Seven-year-old French prune trees were growing on Myrobalan seedling rootstocks located in a commercial orchard near Orland, Calif. Trees were planted 2.74 m apart within the row, with 4.87 m between rows. The trees had been minimally pruned until year 7 and had borne commercial crops since year 4.

Measurement of photosynthetic photon flux (PPF). Irradiance was measured using five light sensors as described by DeJong and Doyle (1985). Each sensor was individually calibrated with a quantum sensor (LI-1905, LI-COR). The five sensors were monitored with a portable, battery-operated microdata logger (CR21 Micrologger, Campbell Scientific, Logan, Utah). The datalogger was programmed to scan each channel every 5 sec and log the data as an average over 6-hr periods defined as 2400–0600, 0600–1200, 1200–1800, and 1800–2400 HR. Only the readings from 0600–1200 and 1200–1800 HR accumulated relevant PPF values. As PPF accumulated between 0600–1200 and 1200–1800 HR were nearly identical (Table 1), we have plotted the PPF data collected at various sensor positions between 0600–1200 HR against the leaf nutrient levels measured at those sensor positions (Figs. 1 and 2). Quantum sensors were attached to a vertical pole at 130, 191, 252, 312, and 434 cm above the ground. The last was in full sun and is indicative of the PPF experienced by the most exposed leaves. The pole with attached sensors was positioned on the south side of each tree 1 m from the trunk. PPF was measured continuously in each tree over 3 to 4 clear days before moving to the next tree replicate. Precautions were taken so that sensors located at higher levels within the canopy did not affect light readings of sensors located below. Ten single-tree replicates were selected at random from two rows of the orchard. PPF was measured between early July and early August.

Table 1. Relationship between sensor positions in tree canopies and average PPF during two time intervals. Sensor positions refer to distance above ground within the canopy.

Sensor position above ground (cm)	Average PPF ($\mu mol \cdot s^{-1} \cdot m^{-2}$) Interval (HR)	
	0600–1200	1200–1800
130	56	45
191	201	167
252	375	312
312	473	506
434	921	1110

Leaf sampling and analysis. Twenty leaves per sensor position per tree were sampled within 2 hr at the time of fruit harvest in August. Leaf samples were collected within 20 cm of each sensor. This permitted correlation between leaf nutrient levels and PPF experienced by the leaves sampled. Leaf areas were measured using a Delta T leaf area meter (Decagon). Leaves were washed in a weak detergent solution, rinsed in tap water several times, given a final rinse in distilled water, dried in a forced-air oven at 55C, and ground in a Wiley mill to pass a 20-mesh screen. Nitrogen was determined by a Kjeldahl procedure (Weinbaum and Neumann, 1977); K, Ca, and Mg by flame photometry; and P by the amino naphthol sulfonic acid method as described by Uriu and Crane (1977). Data were subjected to linear regression analyses.

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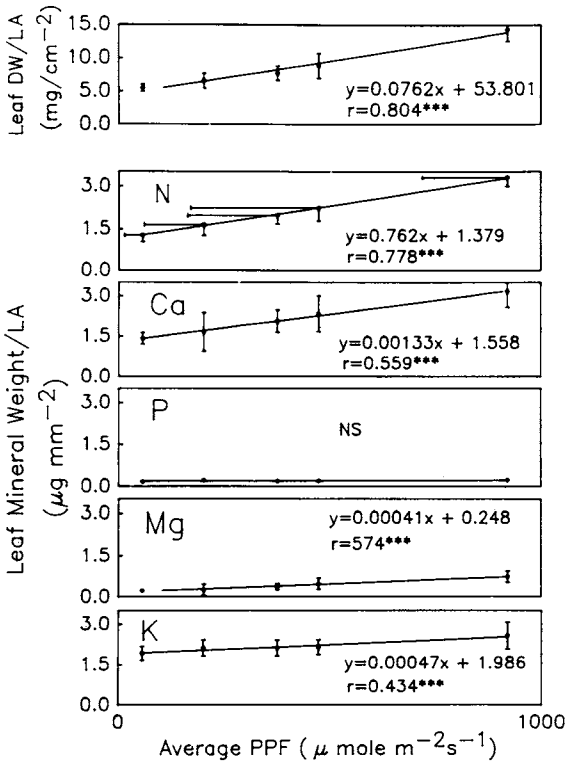

Fig. 1. Plots of leaf mineral weights per unit of leaf area (LA) and leaf dry weight/LA (DW/LA) vs. average PPF between 0600 and 1200 HR in prune tree canopies. Each data point in the figure is located at the mean (± SD) of five composite leaf analyses (10 leaves per analysis) at each sensor position and the average PPF at those sensor positions for the 10 replicate trees. See N plot for SDs of PPF. Regression statistics for each figure, however, were based on analysis of all 50 data points (i.e., five sensor positions per tree times 10 replicate trees). ^{NS}Not significant; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

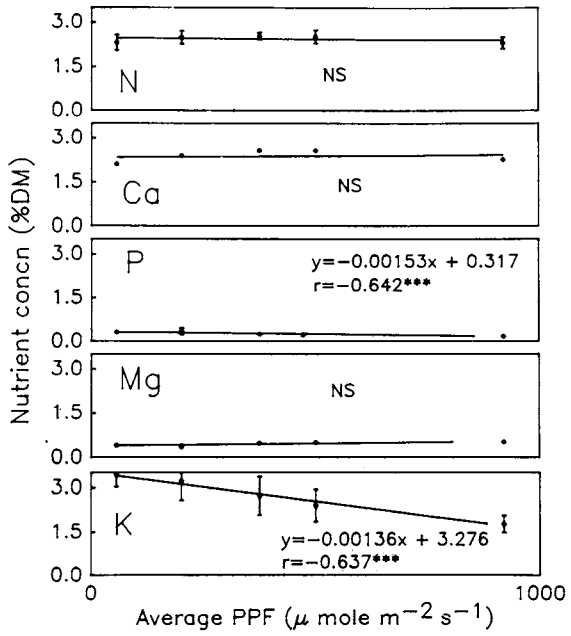

Fig. 2. Plots of leaf nutrient concentrations based on percent dry matter (%DM) vs. average PPF between 0600 and 1200 HR in prune tree canopies. Each data point in the figure is located at the mean (± SD) of five composite leaf analyses (10 leaves per analysis) at each sensor position for the 10 replicate trees. Regression statistics for each figure, however, were based on analysis of all 50 data points (i.e., five sensor positions per tree times 10 replicate trees). ^{NS}not significant; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

Results

PPF increased 20-fold over the range of sensor positions and associated canopy exposures (Table 1). Dry weight per unit of leaf area (DW/LA) increased regularly with increasing PPF and nearly 3-fold over the range of PPF measured from the most shaded (50 μmol·s^{-1}·m^{-2}) to the most exposed portions of the canopy (1000 μmol·s^{-1}·m^{-2}; Fig. 1).

The relationship between leaf mineral content and PPF varied among nutrients and was influenced greatly by the basis of expression. Leaf N/LA, Ca/LA, and Mg/LA exhibited strong positive correlations with increasing PPF (Fig. 1). This trend was less evident in the case of K, and absent in the case of P. The variability in average PPF and leaf N/LA is indicated by lines representing 1 SD at the various sensor positions (Fig. 1, N plot). Variability was smallest at the most shaded (130 cm) and most exposed positions (434 cm; Table 1). Greater variability occurred among the 10 tree replicates at intermediate sensor positions; i.e., at 191, 252, and 312 cm above ground (Table 1; Fig. 1, N plot). The correlations between average PPF and N/LA would presumably be better than our data indicate if we knew the precise PPF at the positions occupied by the leaves sampled. In fact, our leaves were sampled up to 20 cm from the sensor positions and actual PPF at these positions could vary appreciably from the sensor readings.

Leaf concentrations of N, Ca, and Mg did not vary with increasing PPF when expressed as percent dry matter (DM) (Fig. 2). The exception to this generalization was percent K, which decreased markedly, and percent P, which decreased slightly with increasing PPF (Fig. 2).

Changes in the net nutrient allocation with increasing PPF may also be expressed on a molar basis. These data are thus normalized to reflect the influence of PPF on nutrient element accumulation expressed as number of ions (Table 2). Molar concentrations of leaf nutrients increased with increasing PPF according to the same order as occurred when expressed as mineral weight per LA; i.e., N > Ca > Mg > K > P (Table 2). Rates of nutrient accumulation (relative to N, taken as 100), are also presented. N/LA increased at a 3-fold greater rate with increasing PPF than Ca/LA, 7-fold greater than Mg/LA, and 9-fold greater than K/LA (Table 2).

Discussion

The greater accumulation of phloem-immobile nutrients such as Ca (McClung and Lott, 1956) in exposed vs. shaded leaves (Fig. 1) is presumed to result from mass flow of the xylem solution. Water flux through transpiring organs is probably the principal mechanism determining the initial distribution of xylem solutes among transpiring leaves (Fiscus et al., 1983; Neumann and Nooden, 1984; Syvertsen and Graham, 1985). Shade increases stomatal resistance (Jordan et al., 1975), reduces transpiration (Rom and Ferree, 1986), and presumably also reduces the flux of nutrients to less-exposed leaves within the tree canopy. As Mg is a constituent of the chlorophyll molecule, it follows that leaf Mg content may be correlated with leaf chlorophyll concentrations in different regions of the canopy.

Phosphorus and K were less influenced by PPF than were N,

Table 2. Responsiveness of leaf dry weight per unit of leaf area (DW/LA; mg DW/cm^2) and leaf mineral weight per LA (in μg·mm^{-2} and μmol·mm^{-2}) to changes in average PPF (μmol·s^{-1}·m^{-2}).

Parameter	Linear correlation of leaf mineral weight/LA and leaf DW/LA on Δ PPF	Slope A[z] (×10^{-4})	Change relative to N	Slope B[y] (×10^{-5})	Change relative to N
A) Leaf mineral weight/LA					
N	*	24.0	(100)	17.1	(100)
P	NS	---	---	---	---
K	*	7.2	30	1.84	11
Ca	*	20.0	83	4.99	29
Mg	*	5.7	24	2.35	14
B) Leaf DW/LA	*	1040	4333	---	---

[z]A = slope of Δ leaf mineral weight/LA (μg·mm^{-2}) divided by Δ PPF.
[y]B = slope of Δ leaf mineral weight/LA (μmol·mm^{-2}) divided by a Δ PPF. The relative change in nutrient concentration with change in PPF is thus expressed on a molar basis.
[NS,*]Not significant or significant at $P = 0.05$, respectively.

Ca, and Mg (Fig. 1), presumably because they are less intensively incorporated into leaf macro-molecules or otherwise immobilized in leaves than the latter.

In contrast to expression of leaf nutrient content on the basis of LA (Fig. 1), concentrations of N and Ca expressed as a percentage of DM (Fig. 2) did not vary with PPF. We reported previously (Erez and Weinbaum, 1985) that N concentrations expressed as percent DM were the same in exposed and shaded portions of walnut tree canopies, but leaf N/LA and leaf DW/LA were 100% greater in the exposed as compared with the shaded portion of those canopies. Leaf nutrient concentrations, expressed as percent DM, may be influenced by changes in both leaf mass and leaf nutrient content. Apparent seasonal decreases in leaf nutrient concentration (expressed as percent DM) may be due to seasonal increases in leaf mass (Marini and Marini, 1983; Oland, 1963) rather than actual decreases in leaf nutrient content (Rogers et al., 1953). Mineral weight/LA, therefore, more accurately reflects differences in leaf nutrient content than does leaf nutrient concentration expressed as percent DM. If leaves are sampled from different geographical regions, orchards, trees, different regions within a tree canopy (i.e., developing under different PPF), sampling dates, crop loads, etc., leaf nutrient concentrations expressed as percent DM may not be indicative of actual nutrient partitioning. Although leaf samples may have the same percentage N (percent DM basis), leaf nutrient content may differ markedly if DW/LA of the samples are dissimilar. Our data (Fig. 1) and extensive documentation in other tree species (Barritt et al., 1987; Barden, 1977; Barden, 1978; Doud and Ferree, 1980; Erez and Weinbaum, 1985; McClung and Lott, 1956; Porpligia and Barden, 1980; and Syvertsen, 1987) indicate that leaf DW/LA varies with PPF within canopies.

Both leaf DW/LA and leaf N/LA increased with increasing PPF in prune tree canopies (Fig. 1). Allocation of leaf N along light flux gradients within prune tree canopies is consistent with data obtained in other species (DeJong and Doyle, 1985; Fiscus et al., 1983). Nitrogen is incorporated increasingly into cellular proteins under high PPF and the enzyme 1,5-bisphosphate carboxylase (RUBISCO), which may constitute up to 80% of soluble leaf protein (Huffaker, 1982), preferentially accumulates in the most exposed leaves (DeJong and Doyle, 1985). We hypothesize that whole-tree photosynthesis may be optimized by the greater relative partitioning of leaf N among the most exposed leaves of the canopy because leaf N/LA has been found to exhibit a highly significant positive correlation with photosynthetic capacity (DeJong and Doyle, 1985). Thus, leaf analysis to determine leaf N/LA may be indicative of both the light microenvironment and leaf photosynthetic capacity at the canopy coordinates sampled. Flowering (Jackson and Sweet, 1972) and fruit set (Stephenson, 1981) have been related positively to light exposure, and fruit development reportedly depends in large measure on photoassimilates supplied by adjacent leaves (Stephenson, 1981). Leaf N/LA may indicate the level of photosynthate available to developing fruit, particularly in heavily cropped trees.

Leaf nutrient concentration expressed on a dry weight basis is useful in detecting nutrient deficiencies and determining the need for fertilization. The present study has shown, however, that leaf N/LA, but not leaf N concentration (percent DM), appears to be a sensitive indicator of the light microenvironment. Also, leaf N/LA is more highly correlated with leaf photosynthetic capacity (at least in *Prunus* spp.) than is leaf N percent DM (T.M. DeJong, personal communication). Leaf N/LA and leaf DW/LA (which also varied significantly with PPF, Fig. 1) may have applications as diagnostic tools in tree fruit culture with respect to canopy management (tree spacing, pruning, etc.) and production characteristics known to be sensitive to low light (e.g., flowering, fruit set, and fruit quality).

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