

Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach (*Prunus persica*)

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Abstract. Field gas exchange measurements on intact peach (*Prunus persica* (L.) Batsch) leaves indicate that leaf nitrogen content (N_L) and leaf weight per unit leaf area (W_a) are highly correlated with CO_2 assimilation rate (A) and mesophyll conductance (g_m). Therefore, N_L and W_a were used to study seasonal relationships between leaf carboxylation capacity and natural light exposure in tree canopies. From mid-season onwards, N_L and W_a were linearly correlated with light exposure expressed as the amount of time during a clear day that a leaf was exposed to a photosynthetic photon flux density (Q) of $\geq 100 \mu\text{mol m}^{-2} \text{s}^{-1}$. The data support the hypothesis that whole-tree photosynthesis is optimized by partitioning of photosynthetic capacity among leaves in deciduous tree canopies with respect to natural light exposure.

Key-words: photosynthetic capacity; nitrogen partitioning; light acclimation; peach.

Introduction

It has been well established that the photosynthetic characteristics of individual leaves of a broad range of plant species are strongly influenced by the light environment in which they are grown (Bjorkman & Holmgren, 1963; Chabot & Chabot, 1977; Charles-Edwards, Charles-Edwards & Sant, 1974; Louwse & Zweerde, 1977). Generally, leaves growing in high light environments (sun leaves) attain light saturation at higher light flux densities, have higher light-saturated rates of photosynthesis, and have higher light compensation points than leaves growing in low light environments (shade leaves). These differences in photosynthetic characteristics have been related to differences in protein and chlorophyll content as well as leaf anatomy and physiology (Boardman, 1977; Chabot & Chabot, 1977; Nobel, Zaragoza & Smith, 1975; Patterson, Duke & Hoagland, 1978; Prioul, Brangeon & Reyss, 1980). However, most of the available information on leaf photosynthetic acclimation to light environment is from experiments conducted under controlled environmental conditions on annual or herbaceous perennial plant

species over relatively short time periods for the purpose of studying photosynthetic acclimation processes in individual leaves. Much less information is available on seasonal photosynthetic acclimation within tree canopies involving allocation of leaf constituents such as leaf N content (N_L) or leaf weight per unit leaf area (W_a) under natural canopy light conditions.

Using previously published relationships between N_L and leaf photosynthetic capacity as a basis for a series of econometric models, Mooney & Gulmon (1979) predicted that carbon gain for a whole plant canopy would be maximized when leaf N is distributed such that the leaves in the micro-environments receiving the greatest amount of light would have the highest N_L . Field (1983) attempted to test this hypothesis by looking at leaf age, N_L , and light-microsite relationships within the canopy of a drought-deciduous, California, chapparral shrub (*Lepechinia calycina* Benth. Epl.). Although he succeeded in demonstrating some of the advantages in N-redistribution to maximize carbon gain, his data did not show consistent relationships between N_L and light microenvironments.

Previous research with peach (*Prunus persica*) and other temperate-deciduous trees has indicated that leaf photosynthetic capacity is often highly correlated with N_L , W_a , or leaf thickness (DeJong, 1982; Barden, 1974; Kappel & Flore, 1983; Marini & Marini, 1983; McMillen & McClendon, 1983). In this paper we will first confirm that these relationships exist for peach (*Prunus persica* (L.) Batsch cv. Springcrest) under the local field conditions for these experiments. We will then proceed to test the general concept of optimization of leaf N by analysing the seasonal relationships between N_L and natural light exposure in peach tree canopies.

Materials and methods

Plant material

The plants used in these studies were 10-year-old peach trees (*Prunus persica* (L.) Batsch cvs. Springcrest and O'Henry) located at the Kearney Agricultural Center of the University of California, Parlier, California (near Fresno). These trees were trained to

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a standard open vase configuration and received routine horticultural care suitable for commercial fruit production including: pruning, fertilization, irrigation, pest control, etc. The Springcrest peach tree used for light measurements was not pruned in the winter prior to the measurements in order to obtain a leaf canopy density comparable to trees growing under non-horticultural conditions.

Leaf CO₂ assimilation measurements

Leaf gas-exchange measurements were conducted in the field with a mobile, field, gas-exchange laboratory. Measurements were made on intact, mature leaves located in various areas of the tree canopy. During measurement, leaves were exposed to full sunlight by manipulating the tree canopy to eliminate natural canopy shading. Individual leaves were enclosed in a cylindrical, temperature-controlled, stirred cuvette similar to that described by DeJong (1982). Leaf temperatures were maintained at $27.5 \pm 1.0^\circ\text{C}$ by circulating water to a heat-exchange plate in the cuvette from a temperature-controlled water bath (RC-3 Lauda, Brinkmann Instruments Inc., Westbury, NY). Leaf temperature was measured to the nearest 0.1°C using three type E (chromel-constantan) thermocouples (0.002 cm diameter wire) appressed to the abaxial leaf surface and monitored with a digital thermocouple thermometer (Model 2190A, John Fluke Mfg. Co. Inc., Everett, WA). Gas exchange measurements were made with an open-system, gas-analysis apparatus similar to that described by Augustine *et al.* (1976). CO₂ concentrations were measured with a differential IR gas analyser (225 MKIII, ADC Ltd, Hoddesdon Herts, U.K.). Water vapour concentrations were measured with a relative humidity sensor (Model 5121, Weathertronics Inc., West Sacramento, CA) maintained at a constant, known temperature. Flow rates were controlled and measured with an electronic mass flow controller (FC-260, Tylan Inc., Carson, CA). The water vapour pressure gradient between the leaf and the air in the cuvette was maintained at less than 2.0 kPa.

Leaf assimilation (A), leaf conductance to water vapour (g_L), and intercellular CO₂ concentrations were calculated from measurements of CO₂ flux, water vapour flux, and leaf temperature measurements according to von Caemmerer & Farquhar (1981). Mesophyll conductance was calculated as a residual (Jarvis, 1971) with the assumptions that the CO₂ compensation point was $50 \mu\text{mol mol}^{-1}$ and the CO₂ response curve was linear between intercellular CO₂ concentrations of 50 and $200 \mu\text{mol mol}^{-1}$. Previous research with peach indicates that these assumptions are reasonable (DeJong, 1982, 1983). Immediately after each individual leaf measurement, the leaf was excised from the tree, leaf area was determined with an electronic leaf-area meter (LI-3000, LI-COR Inc.,

Lincoln, NE), and the leaf was dried at 75°C for a minimum of 48 h. N_L of the same leaf was determined by modified Kjeldahl analysis as developed by Carlson (1978).

Canopy light measurements

Canopy light measurements were made using 14 photosynthesis light sensors similar to those described by Biggs *et al.* (1971) for measuring photosynthetically active radiation at wavelengths between 400 and 700 nm. Each sensor was individually calibrated with a quantum sensor (LI-1905, LI-COR Inc., Lincoln, NE). The 14 sensors were monitored with two portable, battery-operated, dataloggers (CR21 Micrologger, Campbell Scientific Inc., Logan, UT). The loggers were programmed to scan each sensor every 10 s and log the data as a frequency distribution to determine the amount of time each sensor was exposed to sunlight within specific quantum flux density ranges. The specific ranges of quantum flux densities (Q) were 00–100, 100–250, 250–400, 400–550, 550–700, and $\geq 700 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Canopy light distributions were measured in two peach trees in two different ways. In one tree (the unpruned Springcrest tree) light sensors were placed directly above specific pairs of leaves in various locations from the top to the bottom of the tree canopy. Light data were then collected over two clear, sunny days. After collection of the light data, the pairs of leaves below each light sensor were harvested and the sensors were moved to other locations directly above pairs of leaves in the same tree. The light and leaf sampling were repeated over the next clear, 2-day period. After collecting the second set of samples in the Springcrest tree, the light sensors were moved to a pruned O'Henry peach tree and placed at specific locations along the primary branches of the tree. This tree was chosen because it had been trained to have four major branches, one in each direction of the compass. At the first sensor setting in this tree, sensors were placed at right angles and approx. 20 cm out from both sides of the primary north and south branches at 1, 2, and 3 m from the ground. An additional sensor was placed at the tip of each primary branch so that the tree contained 14 sensors at specified locations. These sensors were monitored over two clear, sunny days and then moved to similar locations on the major east and west branches. After each measuring period, the nearest fully expanded leaves adjacent to the light sensors were harvested.

All leaves harvested in these light studies were immediately taken to the laboratory for measurement of leaf area and dried at 75°C for a minimum of 48 h. N_L of each individual leaf was subsequently determined as stated previously.

These sampling procedures produced two daily light exposure histograms for each of 28 leaves per

tree for each sampling period. Data were collected over approximate monthly sampling periods from late April to early October.

Results

Gas exchange measurements

In this study, A , g_m and g_l measured in the field were curvilinearly related to N_L per unit leaf area (Fig. 1). However, g_m was the measurement that was most highly correlated with N_L . The more curvilinear nature of the relationship between A and N_L was apparently related to factors affecting a curvilinear relationship between g_l and N_L per unit leaf area. The relationship between A , g_m , g_l , and W_a (Fig. 2) was very similar to those for N_L per unit leaf area (Fig. 1), except that the correlation coefficients were lower.

The apparent similarities in these relationships can be accounted for by the highly positive correlation between N_L per unit leaf area and W_a (Fig. 3).

When A and N_L were both expressed on a leaf dry-weight basis the two parameters were linearly related (Fig. 4). Even though significant ($P = 0.01$), the correlation coefficients for this relationship were

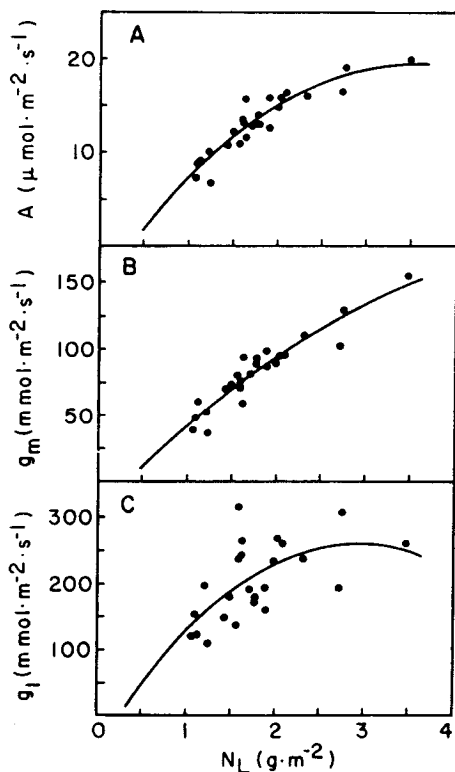


Figure 1. The relationship between leaf N content per unit leaf area (N_L) and CO_2 assimilation rate (A), mesophyll conductance (g_m), and leaf conductance to water vapour (g_l) in peach leaves. Regression statistics are: $Y = -4.427 + 13.57X - 1.929 X^2$ ($r = 0.934$), $Y = -23.51 + 71.17X - 6.332 X^2$ ($r = 0.941$), and $Y = -50.26 + 211.3X - 35.89 X^2$ ($r = 0.632$) for (A), (B) and (C), respectively.

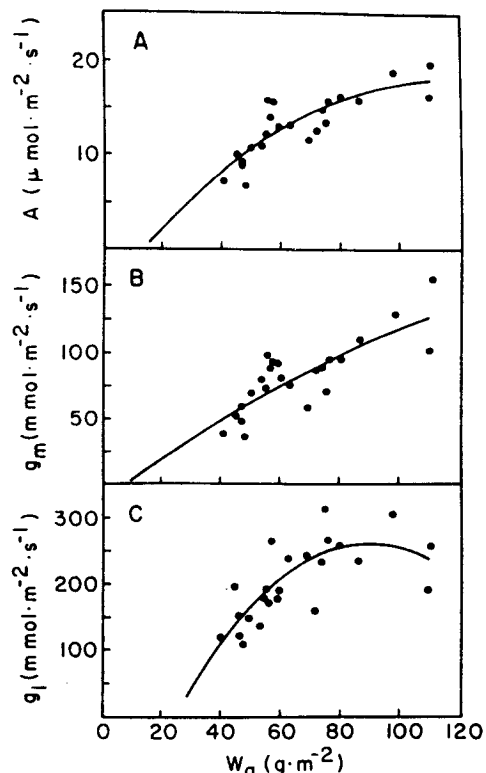


Figure 2. The relationship between leaf weight per unit leaf area (W_a) and CO_2 assimilation rate (A), mesophyll conductance (g_m), and leaf conductance to water vapour (g_l) in peach leaves. Regression statistics are: $Y = -4.941 + 0.395X - 0.0017 X^2$ ($r = 0.858$), $Y = -13.20 + 1.755X - 0.0043 X^2$ ($r = 0.815$), and $Y = -236.3 + 11.02X - 0.061 X^2$ ($r = 0.772$) for (A), (B) and (C), respectively.

much lower than for the relationships between A and g_m with N_L on a leaf-area basis.

Canopy light exposure and N_L measurements

Detailed analysis of canopy light exposure and N_L data from the late June and early July measurements on the O'Henry peach tree indicated that there was a

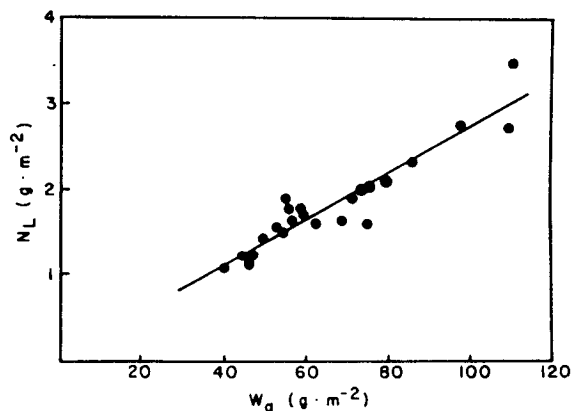


Figure 3. The relationship between leaf N content per unit leaf area (N_L) and leaf weight per unit leaf area (W_a) for leaves used for photosynthetic measurements. $Y = 0.002 + 0.027 X$ ($r = 0.939$).

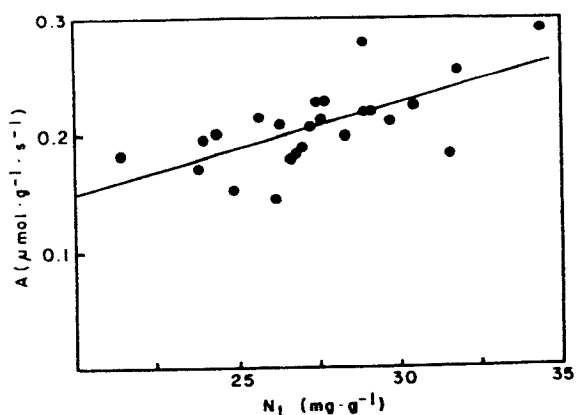


Figure 4. The relationship between leaf CO₂ assimilation rate per unit leaf dry weight (*A*) and leaf N content per unit dry weight (*N_L*). $Y = -0.005 + 0.008X$ ($r = 0.648$).

strong correlation between the daily amount of light a leaf experienced and *N_L*. Furthermore, of the light categories used in these experiments, *N_L* was most highly correlated with the time of exposure to $Q \geq 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 1).

The seasonal pattern of the relationship between *N_L* per unit leaf area and the number of hours of daily leaf exposure to $Q \geq 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ are shown in Fig. 5 for the unpruned Springcrest peach tree and in Fig. 6 for the pruned O'Henry peach tree. Early in the season the correlation between *N_L* and light exposure, and the slope of the relationship, is less than on subsequent dates (Figs 5 & 6). Correlations between *N_L* and light exposure were greatest in late June and July for both trees; however, the slope of the relationships tended to increase as the season progressed. Seasonal patterns of the relationship between *W_s* and light exposure were similar to those for *N_L* on an area basis but the correlation coefficients for the *W_s* relationships were always less than for the corresponding *N_L* relationship (data not shown).

Discussion

Previous laboratory measurements of peach leaf photosynthesis have indicated a linear relationship between leaf photosynthetic capacity and *N_L* per unit

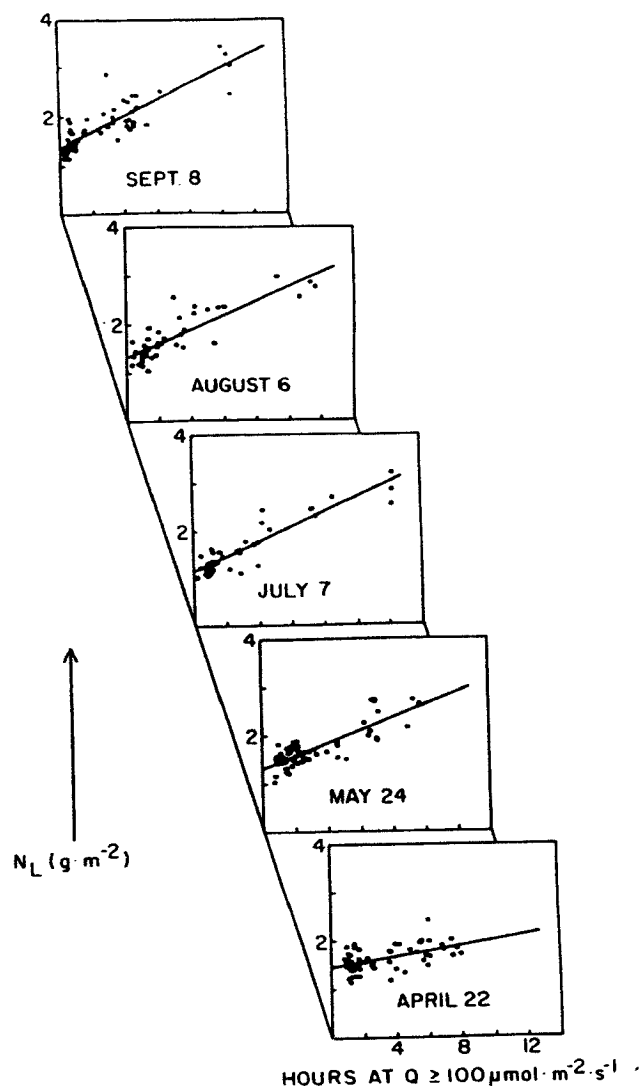


Figure 5. The relationship between leaf N content per unit leaf area (*N_L*) and light exposure expressed as daily hours of $Q \geq 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the unpruned Springcrest peach tree at five sampling periods. The regression statistics are: $Y = 1.46 + 0.05X$ ($r = 0.493$), $Y = 1.319 + 0.13X$ ($r = 0.819$), $Y = 1.17 + 0.15X$ ($r = 0.915$), $Y = 1.31 + 0.14X$ ($r = 0.849$) and $Y = 1.35 + 0.16X$ ($r = 0.856$) for April through September, respectively.

Table 1. Summary of the linear correlation coefficients between cumulative hours of daily exposure to a given range of light flux densities (*Q*) and *N_L* measured on the O'Henry peach tree during late June and early July.

<i>Q</i> ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Correlation coefficient (<i>r</i>)
≥ 700	0.831
≥ 550	0.837
≥ 400	0.848
≥ 250	0.865
≥ 100	0.895

leaf area (DeJong, 1982). In that research, *N_L* was found to be highly correlated with *g_m*. The present research confirms a high relationship between *g_m* and *N_L* under field conditions. In the field, however, the relationship between *A* and *N_L* is also strongly influenced by *g_i* which is influenced by environmental factors independent of *N_L*. Since *g_m* is an estimation of the carboxylation capacity of a leaf independent of environmental influences on *g_i*, the high correlation between *N_L* and *g_m* indicates a relationship between *N_L* and leaf carboxylation capacity. Evans (1983) has also shown a curvilinear relationship between *A* and *N_L* on a leaf area basis in wheat. However, in the

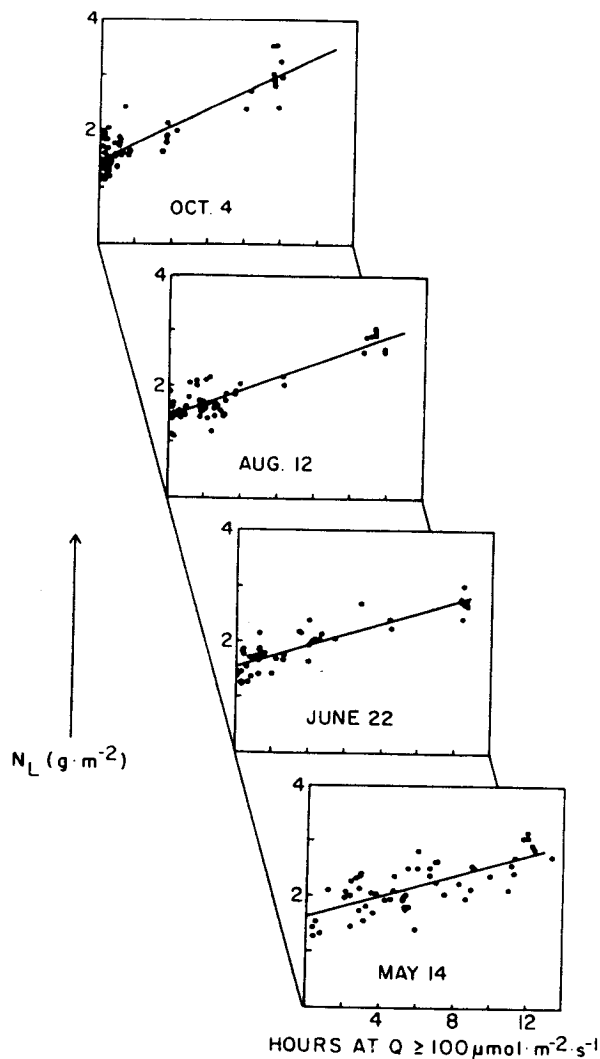


Figure 6. The relationship between leaf N content per unit leaf area (N_L) and leaf light exposure expressed as daily hours at $Q \geq 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the O'Henry peach tree at four sampling periods. The regression statistics are: $Y = 1.62 + 0.09X$ ($r = 0.733$), $Y = 1.54 + 0.10X$ ($r = 0.896$), $Y = 1.44 + 0.12X$ ($r = 0.887$), and $Y = 1.42 + 0.16X$ ($r = 0.894$) for May through October, respectively.

same paper he showed a highly linear correlation between ribulose biphosphate carboxylase activity and N-content on a leaf-area basis. This indicates that those plants apparently had the photosynthetic enzyme capacity to maintain a linear relationship between A and N_L but other factors limited A at the time of measurement. Farquhar, von Caemmerer & Berry (1980) have presented theoretical evidence for a strong dependence of A on N_L and the partitioning of N_L between carboxylase nitrogen and chlorophyll nitrogen.

There have been numerous recent papers reporting a linear relationship between A and N_L on a leaf dry weight basis (Mooney, Ferrar & Slayter, 1978; Mooney & Gulmon, 1979; Gulmon & Chu, 1981). In

work with the Californian shrub *Lepechinia calycina*, Field & Mooney (1983) have reported higher correlations between A and N_L when both were calculated on a leaf dry-weight basis rather than on a leaf-area basis. This may be because they were dealing with effects of leaf age and variations in W_a that were independent of photosynthetic capacity.

Most previous studies of photosynthetic acclimation to light have involved measurement of differences that develop between plants after they have been exposed to discrete light treatments either by placing the plants in artificial lighting conditions or in a shade regime using natural light. Although such studies have yielded information about the process of photosynthetic acclimation to light, the light regimes used in those studies vastly oversimplify the complexity of natural light environments in tree canopies.

Very few leaves in a tree canopy are exposed to constant light flux densities over a defined, uninterrupted time period. Light measurements in this study indicate that most leaves are exposed to relatively high light flux densities for varying lengths of time. Within a tree canopy, shade leaves are not leaves that develop under a continuous low level of light but are leaves that experience longer periods of shade than other more exposed leaves. The tree canopy is made up of a gradient of leaves ranging from those exposed to long periods of high light and various mixtures of intermediate and low light, to some minimal period of high light and longer periods of intermediate and low light. Furthermore, natural shade light involves more than just reduction in flux densities but also involves changes in spectral composition with a tendency toward lower red:far-red ratios (Federer & Tanner, 1966). In order to get a clearer understanding of the complexity of light patterns in natural shading conditions, we chose to characterize the canopy light environment by measuring the amount of time during clear days that leaves were exposed to particular light flux densities. DeJong (1983) showed that photosynthesis in field-grown peach leaves from well-exposed portions of the canopy approaches light saturation at Q between 500 and $700 \mu\text{mol m}^{-2} \text{s}^{-1}$. Therefore, as indicated above, all light above $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ was considered in one category and light below that level was separated into five additional categories. The light data indicated that the amount of time that each leaf was exposed to levels of light above light compensation ($Q \geq 100 \mu\text{mol m}^{-2} \text{s}^{-1}$) was most highly correlated with N_L . These data do not indicate that all light above Q of $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ was equally effective in the acclimation response but rather that, for the light measurement methods used in this study, this measurement yielded the highest overall correlations with N_L . In fact the data in Table 1 indicate that the exposure times at or above the other light levels were also highly correlated with N_L .

The seasonal changes in the relationships between N_L and light exposure correspond to the seasonal pattern of canopy development in deciduous trees. In California, initial leaf growth in these cultivars occurs in the early part of March. During that initial canopy development period, there is relatively little shade within the tree canopy. By mid-April, there is a significant amount of within-canopy shading and N_L begins to reflect a relationship between N_L and light exposure. Apparently, as the canopy develops, differences in light exposure become more distinct and predictable and N_L is adjusted accordingly. The increasing slope between N_L and light exposure as the season progresses is consistent with the concept that leaf N is being reallocated from shaded leaves to more exposed leaves of the tree canopy (Field, 1983).

The data presented in this paper support the hypothesis of Mooney & Gulmon (1979) suggesting redistribution of leaf N in response to light environment as a natural means for maximizing whole-plant carbon gain. These data clearly show that N_L (and therefore leaf photosynthetic capacity) is not uniformly distributed over a tree canopy and that this distribution is related to natural light microenvironment.

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