

Influence of canopy light environment and nitrogen availability on leaf photosynthetic characteristics and photosynthetic nitrogen-use efficiency of field-grown nectarine trees

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Summary Relationships between CO₂ assimilation at light saturation (A_{\max}), nitrogen (N) content and weight per unit area (W_A) were studied in leaves grown with contrasting irradiances (outer canopy versus inner canopy) and N supply rates in field-grown nectarine trees *Prunus persica* L. Batsch. cv. Fantasia. Both A_{\max} and N content per unit leaf area (N_A) were linearly correlated to W_A , but leaves in the high-N treatment had higher N_A and A_{\max} for the same value of W_A than leaves in the low-N treatment. The curvilinear relationship between photosynthesis and total leaf N was independent of treatments, both when expressed per unit leaf area ($A_{\max A}$ and N_A) and per unit leaf weight ($A_{\max W}$ and N_W), but the relationship was stronger when data were expressed on a leaf area basis. Both $A_{\max A}$ and N_A were higher for outer canopy leaves than for inner canopy leaves and $A_{\max W}$ and N_W were higher for leaves in the high-N treatment than for leaves in the low-N treatment.

The relationship between A_{\max} and N resulted in a similar photosynthetic nitrogen-use efficiency at light saturation (A_{\max} NUE) for both N and light treatments. Photosynthetic nitrogen-use efficiency was similar among treatments throughout the whole light response curve of photosynthesis. Leaves developed in shade conditions did not show higher N-use efficiency at low irradiance.

At any intercellular CO₂ partial pressure (C_i), photosynthetic CO₂ response curves were higher for outer canopy leaves and, within each light treatment, were higher for the high-N treatments than for the low-N treatments. Consequently, most of the differences among treatments disappeared when photosynthesis was expressed per unit N. However, slightly higher assimilation rates per unit N were found for outer canopy leaves compared with inner canopy leaves, in both N treatments.

Because higher daily irradiance within the canopies of the low-N trees more than compensated for the lower photosynthetic performances of these leaves compared to the leaves of high-N trees, daily carbon gain (and N-use efficiency on a daily assimilation basis) per leaf was higher for the low-N

treatment than for the high-N treatment in both outer and inner canopy leaves.

Keywords: carbon assimilation, irradiance, nitrogen partitioning, peach, photosynthesis, *Prunus persica*.

Introduction

Leaf photosynthetic capacity at saturating light (A_{\max}) is closely correlated with leaf N content in several species (DeJong 1983, Field and Mooney 1986, Hirose and Werger 1987, Keulen et al. 1989). Field and Mooney (1986) found that light-saturated photosynthetic nitrogen-use efficiency (A_{\max} NUE) is correlated with leaf N content among different species.

It has been suggested that when light is the source of variation in leaf N content, the photosynthesis:N relationship shows great scatter because of partitioning of N among the different N fractions (Evans 1989b). Acclimation to low light has been reported for several species in conjunction with a reduction in the fraction of N invested in electron transport and carboxylation proteins (Björkman 1968, Medina 1971, Terashima and Evans 1988, Evans 1989a). Although this diminishes N-use efficiency at high irradiance (A_{\max} NUE), N-use efficiency at low irradiance may be enhanced (Evans 1989b).

Field (1983) suggested that N would be allocated optimally in a plant canopy when the marginal increase in assimilation (A) with an increase in N was constant throughout the canopy. This hypothesis is supported by several studies on N allocation in a variety of tree and crop species indicating that more N is allocated to the sites at higher irradiance at the top of the canopy (Field 1983, DeJong and Doyle 1985, Hirose and Werger 1987, Evans 1989a, Hirose et al. 1989, Leuning et al. 1991a, 1991b, Ellsworth and Reich 1993, Hollinger 1996).

Evans (1989b) suggested that, in a field canopy, the A_{\max} -N relationship may be steeper as a result of the combined effect of N partitioning within the canopy and the light effect on N partitioning. It was concluded that the assessment

of light and N effects on the A_{\max} :N relationship under natural field conditions is desirable but difficult to achieve.

We have studied the relationship between leaf photosynthesis and N content and photosynthetic nitrogen-use efficiency under contrasting irradiances and N supply rates in field-grown nectarine trees *Prunus persica* L. Batsch. cv. Fantasia. We tested three hypotheses: (1) the photosynthesis:N relationship is similar when light or N availability are sources of variation in leaf N content; (2) acclimation to low light reduces the photosynthetic NUE at saturated irradiance or increases it at low irradiance, or both; and (3) the daily photosynthetic NUE characteristics of leaves on low-N trees are higher than those of leaves on high-N trees. We also determined the relationships between leaf weight per unit area (W_A) and leaf photosynthesis and N content.

Materials and methods

Plant material

Four-year-old nectarine trees were used. The orchard is located at the Pomology Department experimental field of the University of California, Davis, CA. Trees were trained to a perpendicular V configuration (DeJong et al. 1994) and received routine horticultural care suitable for commercial fruit production including pruning, fruit thinning, harvesting, irrigation, and pest control. In 1994, the orchard was divided in four nitrogen treatments with four randomly distributed replications. For the present experiment, two trees of the zero nitrogen and two trees of the 300 kg of N ha⁻¹ treatments were chosen. The zero-N (low-N) trees were reduced in size and had pale foliage compared to other (high-N) trees but were normal in other respects. There were no other apparent symptoms of N deficiency.

Gas exchange measurements and leaf parameters

Gas exchange measurements were made with a portable computerized open-system IRGA (LI-6400, Li-Cor, Inc., Lincoln, NE). A cool light source (6400-02 LED) was mounted on the leaf chamber as the source of variable light. All measurements were taken with cuvette temperature set at 27 °C and relative humidity at 50%.

Photosynthetic light response curves and CO₂ response curves were measured on "sun" (outer canopy) leaves and "shade" (inner canopy) leaves (two of each from two trees in each of the N treatments). All measurements were made on mid-shoot leaves on shoots of similar vigor. The most shaded leaves in the bottom-center of the canopy were chosen for the inner canopy leaves. Measurements were taken between 0900 and 1200 h on four consecutive clear days (day of the year 206–209) about a week before fruit harvest. Each day, one light response curve and one CO₂ response curve was generated on one leaf in each of the four treatments (i.e., high-N + sun, high-N + shade, low-N + sun and low-N + shade). To compensate for possible diurnal effects, the order of the four treatments was changed every day.

For light response curves, the cuvette CO₂ partial pressure was fixed at 35 Pa and irradiance was gradually decreased from

2000 to zero $\mu\text{mol m}^{-2} \text{s}^{-1}$ (minimum waiting time between steps was 2 min and measurements were taken when stability was achieved). For CO₂ response curves, light was kept at 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and the cuvette CO₂ partial pressure was gradually decreased. Light curves were fitted according to Thornley (1976). Maximum electron transport (J_{\max}) and maximum carboxylation ($V_{c,\max}$) rates were calculated as described by Farquhar et al. (1980).

To be sure that sample leaves for light and CO₂ curves were representative, additional measurements of photosynthesis were made for each treatment at saturating light and a CO₂ partial pressure of 35 Pa on the same days as the curve measurements. When measuring gas exchange on shade treatments, leaves were induced with saturating light at a CO₂ partial pressure of 35 Pa. Measurements were not taken until photosynthesis was constant. Mid-shoot leaves of similar age were chosen for all measurements to avoid leaf age and senescence effects. After gas exchange measurements, leaves were harvested and their areas measured with an area meter (Li-Cor Model LI-3000). Leaves were then weighed after drying at 70 °C for 72 h. Leaf N was determined by modified Kjeldahl analysis (Carlson 1978).

Light measurements

The daily course of irradiance was monitored at each treatment site with photodiodes previously calibrated with a quantum sensor (Li-Cor Model LI-190). Data were recorded every 30 s by a battery-operated data logger (CR21 Micrologger, Campbell Scientific Inc., Logan, UT). The sensors were placed on the leaf adaxial surface parallel to the leaf lamina and were kept in place by the electrical wires. The natural orientation of the leaves was not affected by the attachment of the sensors. Light was measured on four outer canopy leaves (two on the east and two on the west side of the tree) and four inner canopy leaves of both trees in each N treatment. The leaves were different from those used for gas exchange measurements, but leaf choice was representative of the sites where photosynthesis was measured. Irradiance data were collected from 0600 to 2000 h during one clear day soon after completion of the gas exchange measurements.

Irradiance recorded by each sensor, together with the photosynthetic characteristics (light curves) of the leaves of the treatment corresponding to that sensor were used to calculate the daily assimilation of a hypothetical leaf placed at each sensor site. The mean of the estimates of single-leaf daily carbon gains was then calculated for each treatment (i.e., high-N + sun; high-N + shade; low-N + sun; low-N + shade).

Results

Light-saturated photosynthesis per unit area (A_{\max}) and leaf weight per unit area (W_A) were linearly correlated within each N treatment (Figure 1). Sun (outer canopy) leaves had twofold higher W_A than shade leaves, regardless of N treatment. Low-N sun leaves tended to have higher W_A than high-N sun leaves, but similar trends were not apparent in shade leaves. Leaf N

content per unit area (N_A) was also linearly correlated to W_A within each N treatment (Figure 2).

In both N treatments, A_{\max} and N_A were curvilinearly correlated ($r^2 = 0.85$, $P < 0.001$) (Figure 3). Plotting data separately for each N treatment did not improve the regression coefficient ($r^2 = 0.82$ for high-N and $r^2 = 0.86$ for low-N). Virtually all sun leaves had higher A_{\max} and N_A than shade leaves. Within each light treatment, leaves in the high-N treatments had higher A_{\max} and N_A than leaves in the low-N treatments.

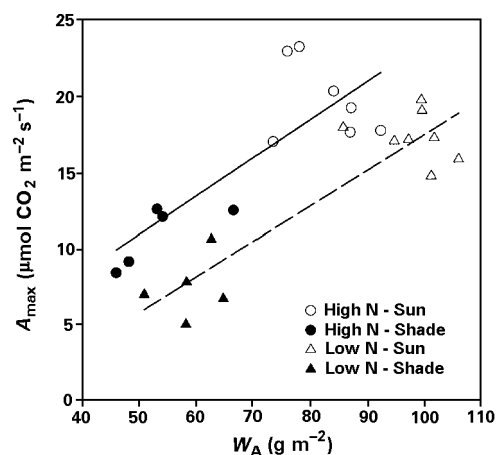


Figure 1. Relationship between light-saturated photosynthesis per unit area (A_{\max}) and leaf weight per unit area (W_A) in nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves). The regression statistics are: $A_{\max} = -1.46 + 0.24W_A$ ($r^2 = 0.90$; $P < 0.01$) for the high-N treatment and $A_{\max} = -5.8 + 0.23W_A$ ($r^2 = 0.97$; $P < 0.01$) for the low-N treatment.

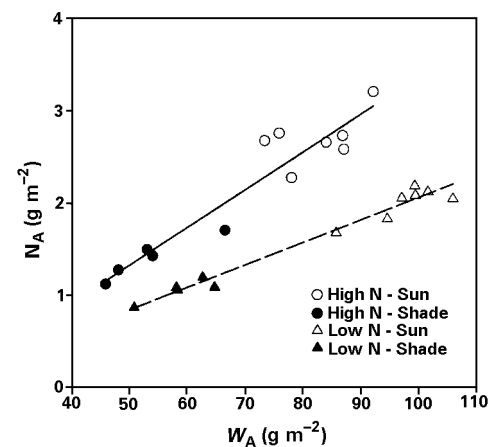


Figure 2. Relationship between N content per unit area (N_A) and leaf weight per unit area (W_A) in nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves). The regression statistics are: $N_A = -0.70 + 0.04W_A$ ($r^2 = 0.90$; $P < 0.01$) for the high-N treatment and $N_A = -0.37 + 0.024W_A$ ($r^2 = 0.97$; $P < 0.01$) for the low-N treatment.

On a unit dry weight basis, light-saturated photosynthesis ($A_{\max W}$) and nitrogen (N_W) were curvilinearly correlated ($r^2 = 0.64$, $P < 0.001$) although with a lower regression coefficient than when both were expressed on an area basis (Figure 4). Plotting data separately for each N treatment reduced the regression coefficients (0.17 and 0.44 for high-N and low-N, respectively). Leaves of the high-N treatment had higher N_W than leaves of the low-N treatments. Within each N treatment, sun leaves had higher N_W than shade leaves.

Light-saturated photosynthetic nitrogen-use efficiency ($A_{\max}/N_A = A_{\max}NUE$) was similar among treatments and no definite trend was apparent when it was plotted against N_A (Figure 5). The $A_{\max}NUE$ was not increased at high irradiance

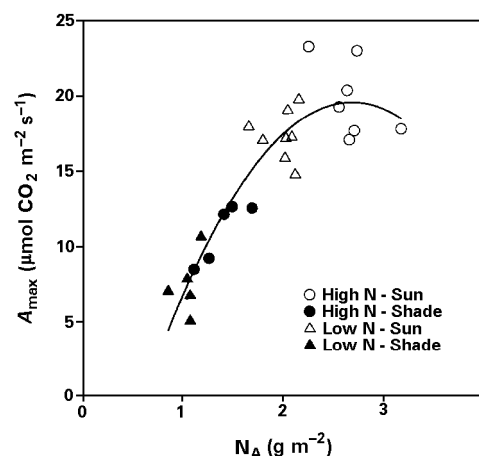


Figure 3. Relationship between light-saturated photosynthesis per unit area (A_{\max}) and N content per unit area (N_A) in nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves). The regression statistics are: $A_{\max} = -13.04 + 24.14N_A - 4.48N_A^2$ ($r^2 = 0.85$; $P < 0.001$).

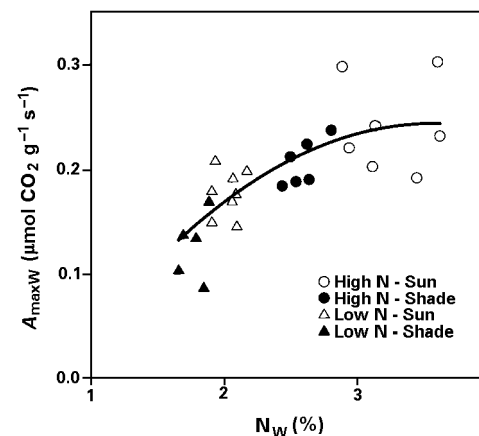


Figure 4. Relationship between light-saturated photosynthesis per unit weight ($A_{\max W}$) and N content per unit weight (N_W) in nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves). The regression statistics are: $A_{\max W} = -0.204 + 0.259N_W - 0.037N_W^2$ ($r^2 = 0.63$; $P < 0.01$).

indicating that both sun and shade leaves partitioned N into similar fractions (i.e., in the electron transport and carboxylation proteins).

The photosynthetic responses to light of leaves in the four treatments reflected the differences in photosynthetic capacity shown in Figure 3, throughout the whole range of irradiances (Figure 6). At any irradiance, CO₂ assimilation (*A*) was always higher for sun leaves than for shade leaves. Within each light treatment, high-N leaves had higher *A* than low-N leaves except at very low light (initial slopes of the *A*-PFDF curves in Figure 6 were 0.036, 0.031, 0.061 and 0.061 for the low-N + shade, high-N + shade, low-N + sun and high-N + sun, respectively).

Photosynthetic nitrogen-use efficiency (ANUE) was similar among all treatments at any irradiance (Figure 7). When *A* was expressed per unit N, the four curves seemed to overlap over the whole light range and the differences among treatments largely disappeared (initial slopes of the ANUE-PFDF curves in Figure 7 were 0.036, 0.023, 0.032 and 0.023 for low-N + shade, high-N + shade, low-N + sun and high-N + sun, respectively).

The photosynthetic response to intercellular CO₂ concentration (*C_i*) also reflected differences in photosynthetic capacity among the treatments (Figure 8). When *A* was expressed per unit N, the differences were greatly reduced (Figure 9). In particular, the difference between N treatments virtually disappeared both for sun and shade leaves, but shade leaves had lower ANUE than sun leaves.

Maximum electron transport (*J_{max}*) and maximum carboxylation (*V_{c,max}*) rates also differed among treatments (Table 1). Both *J_{max}* and *V_{c,max}* were much higher in sun leaves than in shade leaves, and within light treatments they were higher for high-N leaves than for low-N leaves. When *J_{max}* and *V_{c,max}* were expressed per unit N, the differences between treatments were greatly reduced; however, shade leaves had lower values than sun leaves.

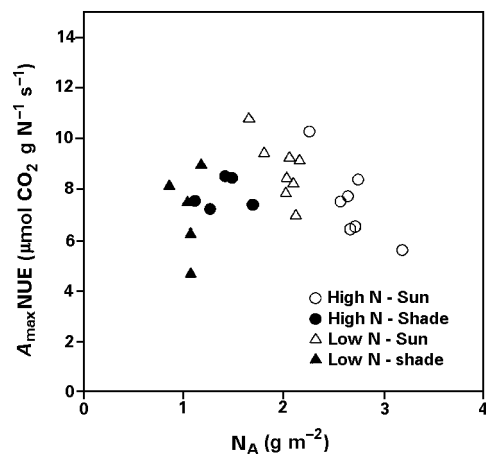


Figure 5. Relationship between light-saturated photosynthetic N-use efficiency (*A_{max}NUE*) and N content per unit area (*N_A*) in nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves).

Mean daily carbon gain of sun (outer canopy) leaves was higher in the low-N treatment than in the high-N treatment because of higher available irradiance (Table 2). The daily carbon gain of a single leaf in the most shaded positions of the canopy was very low, because of the low irradiance. Carbon gain of shade leaves was about 10% of that of sun leaves in the

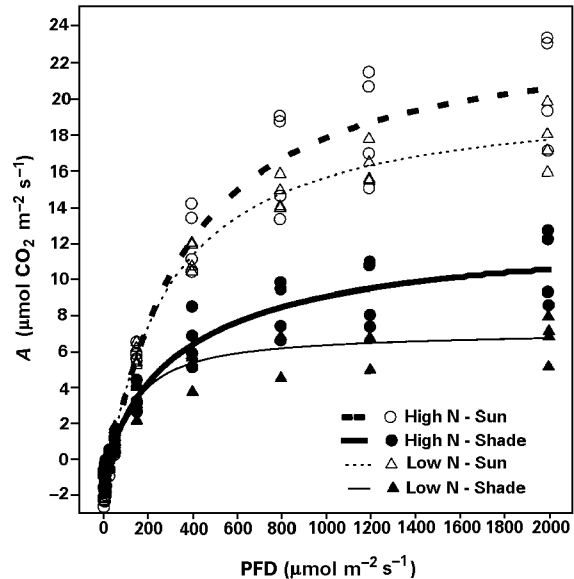


Figure 6. The CO₂ assimilation (*A*) response curve to light (PFDF) in nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves).

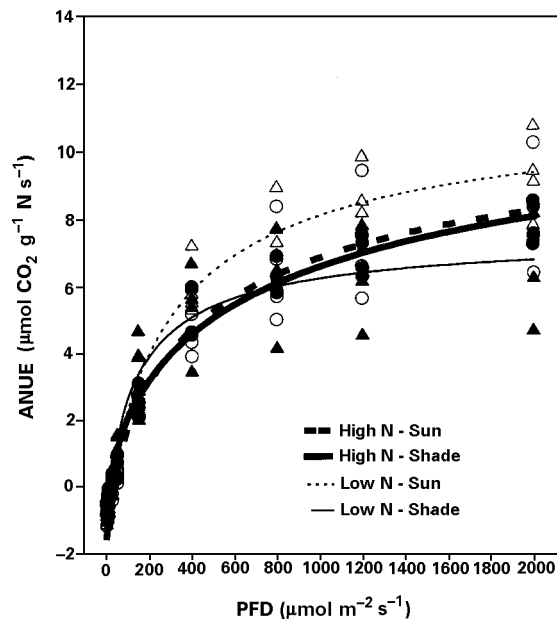


Figure 7. Photosynthetic nitrogen-use efficiency (ANUE) response curve to light (PFDF) in nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves).

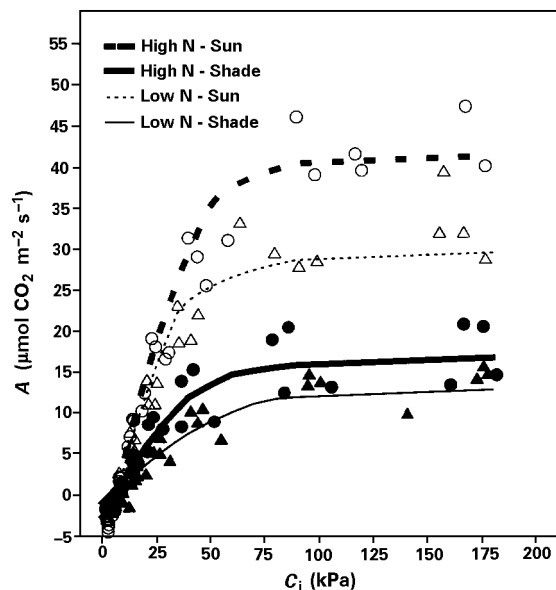


Figure 8. The CO_2 assimilation (A) response curve to intercellular CO_2 concentration (C_i) of nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves).

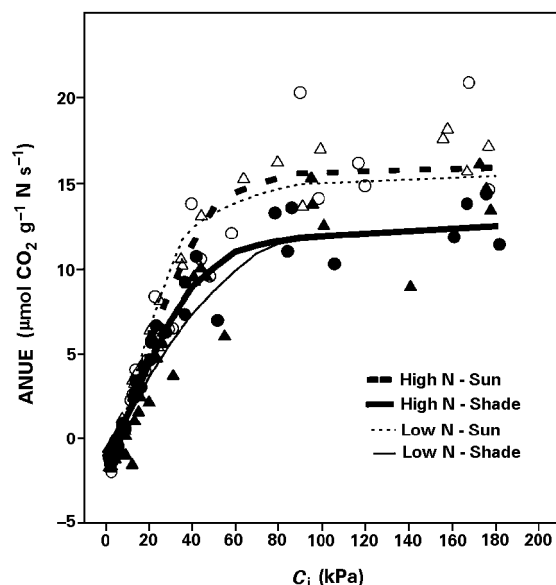


Figure 9. Photosynthetic N-use efficiency (ANUE) response curve to intercellular CO_2 concentration (C_i) of nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves).

low-N treatment and virtually zero (negative, but with standard error including zero) in the high-N treatment. Leaf N-use efficiency on a daily assimilation basis (daily carbon gain/ N_A = Daily NUE) was proportional to daily available irradiance and therefore higher for sun leaves than for shade leaves and higher for low-N trees than for high-N trees. Examples of

Table 1. Maximum electron transport (J_{\max}) and maximum carboxylation ($V_{c,\max}$) rates and their values per unit leaf nitrogen (J_{\max}/N and $V_{c,\max}/N$) in nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves).

	High N		Low N	
	Sun	Shade	Sun	Shade
J_{\max} ($\mu\text{Eq m}^{-2} \text{s}^{-1}$)	300	95	195	80
$V_{c,\max}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	100	40	85	25
J_{\max}/N ($\mu\text{Eq g}^{-1} \text{N s}^{-1}$)	115	71	101	78
$V_{c,\max}/N$ ($\mu\text{mol g}^{-1} \text{N s}^{-1}$)	38	30	44	24

calculated daily patterns of assimilation at each site and N treatment are shown in Figure 10.

Discussion

Relationship between leaf weight per unit area and A_{\max} and N_A content

Light-saturated photosynthesis (A_{\max}) and N_A were curvilinearly correlated. Both A_{\max} and N_A were linearly correlated with W_A across light treatments, but different correlations were found for the two N treatments. These results are consistent with previous literature. Increases in available irradiance seem to induce proportional increases in both A_{\max} and W_A (Chazdon and Field 1987, DeJong et al. 1989, Harrington et al. 1989), whereas the effect of N availability is variable (Sage and Pearcy 1987a, Walters and Reich 1989). Both A_{\max} and W_A are negatively related across different species (Field and Mooney 1986, Reich et al. 1991b). In most cases, variability in the A_{\max} - W_A relationship is associated with similar variability in the N_A - W_A relationship so that A_{\max} and N_A are closely related. This is also true when the time of the season is the source of variation in N_A (Reich et al. 1991a).

Photosynthesis and N relationship

Assimilation of CO_2 and leaf N were correlated independently of whether light or N availability was the source of variation in leaf N content. The correlation was similar whether expressed on a unit area or a unit weight basis. Correlation on a unit weight basis has been found among different species (Field and Mooney 1986), and within one species, throughout the season (Reich et al. 1991a) and may be a globally important feature of plant functioning (Reich et al. 1997). However, within a species at a given moment of the season, $A_{\max}W$ and N_W are not always correlated (Chazdon and Field 1987, DeJong et al. 1989, Harrington et al. 1989, Hollinger 1996). This could be because variation in N_W in response to light is small compared to variation in N_A , which sums the variation in N_W and W_A . Within each N treatment, we found little variation in N_W in response to light, but there was a large variation in N_W (from 2 to 3% N) between N treatments. Within this wide range of N_W , $A_{\max}W$ correlated well with N_W . These results suggest that photosynthesis and N correlate on both a unit area and a

Table 2. Mean \pm SE daily photosynthetic active radiation (PAR), daily CO₂ assimilation and daily nitrogen-use efficiency in nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves).

	Daily intercepted PAR (mol m ⁻² day ⁻¹)	Daily assimilation (mmol CO ₂ m ⁻² day ⁻¹)	Daily NUE (mmol CO ₂ g ⁻¹ N day ⁻¹)
<i>High H</i>			
Sun	23.53 \pm 0.19	327.5 \pm 16.0	128 \pm 6
Shade	2.37 \pm 1.63	-5.3 \pm 10.4	-4 \pm 8
<i>Low N</i>			
Sun	29.32 \pm 0.84	429.4 \pm 15.3	223 \pm 8
Shade	3.56 \pm 0.31	38.5 \pm 2.6	38 \pm 2

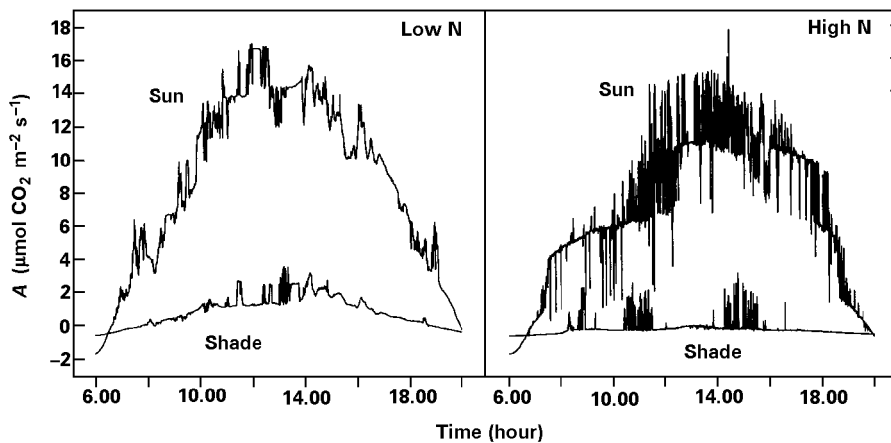


Figure 10. Daily assimilation in nectarine tree leaves at contrasting irradiances and N availabilities (High N = 300 kg N ha⁻¹; Low N = 0 kg N ha⁻¹; Sun = outer canopy leaves; Shade = inner canopy leaves).

unit weight basis but, in the absence of variability in soil N fertility, the small variation of N_w (compared to the variation in N_A) makes this correlation hard to detect.

We used a curvilinear function to express the relationship between A_{max} and N. Good correlations were also found with linear models, but compared with the curvilinear model, the correlations were weaker and had a positive intercept, both on a per unit area basis and a unit weight basis (not shown). The negative intercept of the curvilinear fit is more biologically acceptable because it allows for some N to be in the leaf before any photosynthesis occurs. Curvilinear relationships between photosynthesis and leaf N content have been found in some species (Nevins and Loomis 1970, Takano and Tsunoda 1971, Wong 1979, Lugg and Sinclair 1981, Gulmon and Chu 1981, Evans 1983, Evans and Terashima 1988) but not in others (Sage and Percy 1987b, Küppers et al. 1988). Possible reasons for the curvature have been extensively discussed by Evans (1989b).

Acclimation to low light and photosynthetic N-use efficiency

Photosynthetic nitrogen-use efficiency was similar in both N treatments at all irradiances. Although the correlation between photosynthesis and N_A does not prove causation, there is evidence that total leaf N usually reflects the concentration of nitrogenous compounds responsible for maximum assimilation rates (Field and Mooney 1986, Evans 1989b). It has been argued that, when light is the source of variation in N content,

the A_{max} -N relationship may not be generally valid because of a different partitioning of N into the various N fractions (Evans 1989b). When sun versus shade leaves were compared at the same N content, a 2-fold increase in A_{max} (and therefore in A_{max} NUE) was found in *Spinacia* (Terashima and Evans 1988), *Pisum* (Evans 1987) and *Piper auritum* H.B. & K. (Walters and Field 1987). In a tree canopy, this should reduce the A_{max} NUE of shade leaves and increase the slope of the A_{max} - N_A relationship. However, the response to the light environment in the partitioning of N into leaves is species-specific (Evans 1989b). In nectarine trees, we found a similar photosynthetic nitrogen-use efficiency among light and N treatments, both at saturating light (A_{max} NUE) and at other flux densities (ANUE), suggesting that, within a leaf, N partitioning does not play a major role in field-grown nectarine trees when either light or N availability are the source of variation in leaf N content.

Further information on within-leaf N partitioning was obtained by studying photosynthetic CO₂ response curves which allowed calculation of J_{max} and $V_{c,max}$ (Farquhar et al. 1980). The assimilation rate at high CO₂ intercellular partial pressure (C_i) reflects the rate of electron transport (von Caemmerer and Farquhar 1981, Evans 1987, Evans and Terashima 1988). Assimilation at low C_i (initial slope of the curve) is proportional to maximum RuBP carboxylase activity (von Caemmerer and Farquhar 1981, Evans 1983, Ferrar and Osmond 1986, von Caemmerer and Edmondson 1986). In the present study, J_{max} and $V_{c,max}$ were similar between nitrogen treatments when

expressed per unit N, but slightly lower for shade leaves than for sun leaves. If these activities are proportional to the N invested in related nitrogenous compounds, this would indicate a slightly higher partitioning of leaf N into electron transport and carboxylation proteins in shade leaves than in sun leaves. Higher N partitioning into RuBP carboxylase at high irradiances than at low irradiances has been found for spinach (Terashima and Evans 1988), *Atriplex patula* L. (Medina 1971) and *Solidago virgaurea* L. (Björkman 1968), but not in *Phaseolus* and *Alocasia* (Seemann et al. 1987). Higher electron transport rates per unit N at high irradiance have been found in several but not all species (for a review see Evans 1989b). In our study, the differences in J_{\max} and $V_{c,\max}$ per unit N were relatively small (compared to the 2.5-fold increase in electron transport capacity found in *Spinacia*, for a given N content, from shade to sun leaves; Terashima and Evans 1988) and did not result in a clear difference in assimilation per unit N at ambient CO₂.

Importance of leaf photosynthetic characteristics and NUE relative to the daily carbon gain

Compared with high-N trees, the higher available irradiance on the low-N trees more than compensated for the lower photosynthetic performances of individual leaves, resulting in a higher single leaf daily carbon gain (Table 2). The higher irradiance was a result of the smaller size and less dense canopy of the low-N trees (data not shown). The lower single-leaf daily carbon gain of the high-N trees does not extend to the canopy level, it only represents the mean carbon gain of sun and shade leaves placed at the light sensor site. Possible effects of midday depression in photosynthetic rates were not considered. The larger and denser canopies of the high-N trees intercepted more light (unpublished data) and had higher leaf assimilation rates at the same irradiance (higher light-photosynthetic response curves for both sun and shade leaves) than leaves of low-N trees. Therefore, our data suggest that the higher daily carbon gain of the high-N tree canopies compared with the low-N tree canopies is achieved by a lower contribution of individual leaves, because of lower light availability, and probably results in much lower NUE on a daily carbon basis (i.e., lower daily carbon gain and higher N content of leaves). The investment in total leaf area and leaf mass in a tree canopy, which affects light distribution and varies with soil N availability, is another means of N partitioning (in addition to single leaf N content and N partitioning among leaf N fractions) and represents an important factor when studying N partitioning and NUE on a daily carbon assimilation basis (Anten et al. 1995).

Conclusions

In nectarine tree canopies, N content was higher in outer, sun-exposed leaves than in inner shade leaves and the increase in leaf N content was correlated with photosynthetic capacity. The increase in N and photosynthesis was proportional so that photosynthetic nitrogen-use efficiency was similar, at any irradiance, for leaves under all light and N availability treatments.

Our data also suggest that the light environment had a slight effect on N partitioning into the different leaf N fractions. However, this partitioning seemed to be relatively small and did not noticeably affect the overall light-saturated photosynthetic nitrogen-use efficiency. On a daily assimilation basis, nitrogen-use efficiency seemed to be affected more by available irradiance than by leaf photosynthetic characteristics.

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