Trees (1989) 3: 89–95

Structure and Function
Trees

# Partitioning of leaf nitrogen with respect to within canopy light exposure and nitrogen availability in peach (*Prunus persica*)

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**Summary.** Relationships between leaf nitrogen content and within canopy light exposure were studied in mature nectarine peach trees (*Prunus persica* cv. Fantasia) that had received 0, 112, 196, 280 or 364 kg of fertilizer nitrogen per hectare per year for the previous 3 years. The relationships between light saturated leaf $CO_2$ assimilation rates and leaf nitrogen concentration were also determined on trees in the highest and lowest nitrogen fertilization treatments. The slope of the linear relationship between leaf N content per unit leaf area and light exposure was similar for all nitrogen treatments but the y-intercept of the relationship increased with increasing N status. The slope of the relationship between leaf N content per unit leaf area and light saturated $CO_2$ assimilation rates was greater for the high N trees than the low N trees, but maximum measured leaf $CO_2$ assimilation rates were similar for both the high and low N treatments. A diagrammatic model of the partitioning of leaf photosynthetic capacity with respect to leaf light exposure for high and low nitrogen trees suggests that the major influence of increased N availability is an increase in the photosynthetic capacity of partially shaded leaves but not of the maximum capacity of highly exposed leaves.

**Key words:** Nitrogen partitioning – Photosynthesis – Light acclimation

## Introduction

Plant productivity is dependent on plant photosynthetic efficiency and the efficiency with which photosynthates are partitioned. Plant photosynthetic efficiency is not only dependent on the photosynthetic characteristics of individual leaves but also on the partitioning of photosynthetic capacity between leaves within a plant canopy (Mooney and Gulmon 1979; Field 1983; DeJong 1982). Furthermore, leaf photosynthetic capacity has been shown to be highly correlated with leaf nitrogen content in several plant species (Hirose and Werger 1987a, b; DeJong 1983; Field and Mooney 1986; Van Keulen et al. 1989). DeJong and Doyle (1985) and Hirose and Werger (1987a) demonstrated that leaf photosynthetic capacity and leaf nitrogen content are apparently partitioned among leaves within a plant canopy with respect to natural field light exposure.

These relationships between leaf nitrogen content, leaf photosynthetic capacity and leaf light exposure provide a new opportunity to study the interactions between plant nitrogen status, nitrogen partitioning and photosynthesis, under field conditions. Although it is well established that nitrogen availability can have large affects on leaf nitrogen content and leaf photosynthesis (Natr 1975), less is known about the effect of nitrogen availability on nitrogen partitioning. The large effects of nitrogen availability on plant growth and size has made nitrogen partitioning difficult to study within plant canopies. Previous research has demonstrated that leaf nitrogen is distributed within peach tree canopies along gradients of canopy light exposure. This relationship can be used as an independent standard to determine how nitrogen availability affects N partitioning within the tree canopies. In other words, does nitrogen availability alter the slope or the intercept of the relationship between leaf nitrogen content per

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unit leaf area and leaf light exposure? Is there a greater tendency to partition leaf nitrogen along gradients of canopy light exposure when nitrogen is limiting than when nitrogen is plentiful?

The purpose of this research was to: (1) determine the effect of plant nitrogen status on the partitioning of leaf nitrogen content per unit leaf area with respect to natural canopy leaf light exposure in field grown peach trees and, (2) determine the relationship between leaf nitrogen content and leaf photosynthetic capacity in canopies of differing nitrogen status.

## Materials and methods

*Plant material.* The plants used in these studies were 11-year-old nectarine trees (*Prunus persica* cv. Fantasia) located at the Kearney Agricultural Center of the University of California, Parlier, California (near Fresno). These trees were trained to a standard "open vase" configuration and received routine horticultural care suitable for commercial fruit production including pruning, fruit thinning, harvesting, irrigation, pest control, etc. In 1983 the orchard was subdivided into three research blocks for nitrogen fertilization experiments. The blocks contained five subplots, each receiving 0, 112, 196, 280, or 364 kg $ha^{-1} \cdot year^{-1}$ of fertilizer nitrogen. Trees in 0 nitrogen plots were totally dependent on nitrogen available in the soil and irrigation water and began showing symptoms of N deficiency after the 1st year of treatment. The latter four treatments all received 112 kg $ha^{-1}$ fertilizer nitrogen applied as $NH_4NO_3$ or $(NH_4)_2SO_4$ in late summer after fruit harvest. In the 280 and 364 kg $ha^{-1} \cdot year^{-1}$ treatments, another 168 kg $ha^{-1}$ of nitrogen was applied as $NH_4NO_3$ or $(NH_4)_2SO_4$ in early spring. The 196 and 364 kg $ha^{-1} \cdot year^{-1}$ treatments received an additional fertilization of 84 kg $ha^{-1}$ of nitrogen as $Ca(NO_3)_2$ in late May.

*Canopy light measurements.* In these experiments with peach the canopy develops rapidly in the spring but extension shoot growth virtually stops by 1 July (DeJong et al. 1987). The light exposure and $CO_2$ exchange measurements in this experiment were carried out after this period of maximum shoot extension growth. Canopy light measurements were made using 14 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-190S, LI-COR Inc., Lincoln, Neb., USA). The 14 sensors were monitored with two portable, battery-operated dataloggers (CR21 Micrologger, Campbell Scientific Inc., Logan, Utah, USA). 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 photo flux densities (Q) were 0–100, 100–250, 250–400, 400–550, 550–700, and greater than 700 $\mu mol\ m^{-2} s^{-1}$.

Canopy light distributions were measured in trees of each of the five N treatments by placing light sensors directly above specific pairs of leaves in various locations from the top to the bottom of the tree canopy. Light data in a specific tree were collected over 2 clear, sunny days. After collection of the light data, 2 leaves below each sensor were harvested and the sensors were moved to other locations directly above pairs of leaves in a tree from a different nitrogen treatment.

All leaves harvested in the light studies were immediately taken to a laboratory for measurement of leaf area with an electronic leaf area meter (LI-3000, LI-COR Inc., Lincoln, Neb., USA). The leaf samples were dried at 75° C for a minimum of 48 h. Nitrogen content per unit leaf area ($N_A$) of each individual leaf was subsequently determined by modified Kjeldahl analysis as developed by Carlson (1978).

These sampling procedures produced two daily light exposure histograms for each of 28 leaves per tree for each nitrogen treatment in a given sampling series. Canopy light data were collected from late June through August in 1985 and 1986. Previous research indicated that there was very little seasonal affect on the relationship between leaf N content and leaf light exposure from mid-June through August (DeJong and Doyle 1985).

*Leaf $CO_2$ 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° C ± 1.0° 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, USA). 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, Wash., USA). Gas-exchange measurements were made with an open-system, gas-analysis apparatus similar to that described by Augustine et al. (1976). $CO_2$ concentrations were measured with a differential IR gas analyzer (225 MKIII, ADC Ltd, Hoddesdon, Herts, UK). Water vapor concentrations were measured with a relative humidity sensor (Model 5121, Weathertronics Inc., West Sacramento, Calif., USA) maintained at a constant, known temperature. Flow rates were controlled and measured with an electronic mass flow controller (FC-260, Tylan Inc., Carson, Calif., USA). The water vapor 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 vapor ($g_l$), and intercellular $CO_2$ concentrations were calculated from measurements of $CO_2$ flux, water vapor flux, and leaf temperature measurements according to von Caemmerer and Farquhar (1981). Mesophyll conductance was calculated as a residual (Jarvis 1971) with the assumptions that the $CO_2$ compensation concentration was 50 $\mu mol\ mol^{-1}$ and the $CO_2$ response curve was linear between intercellular $CO_2$ concentrations of 50 and 200 $\mu mol\ mol^{-1}$. 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 and the leaf was dried at 75° C for a minimum of 48 h. $N_A$ of the same leaf was determined as stated previously.

## Results

### Canopy light exposure and $N_A$ measurements

Analysis of the canopy light exposures and $N_A$ (nitrogen per unit leaf area) data indicated that there was a statistically significant correlation between the daily amount of light a leaf experienced and $N_A$ in trees from all five N treatments. As with previous experiments $N_A$ was highly correlated with the daily time of exposure to $Q > 100\ \mu\text{mol m}^{-2}\text{s}^{-1}$ (DeJong and Doyle 1985). The relationships between $N_A$ and the number of hours of daily light exposure to $Q > 100\ \mu\text{mol m}^{-2}\text{s}^{-1}$ are shown in Fig. 1. As tree nitrogen status increased, an increasing proportion of sampled leaves were exposed to fluxes of $Q > 100\ \mu\text{mol m}^{-2}\text{s}^{-1}$ for less than 30 min per day. Since this increasing proportion of low-light leaves had the tendency to skew the relationship toward those leaves, all leaves that received less than 30 min per day of $Q > 100\ \mu\text{mol m}^{-2}\text{s}^{-1}$ were eliminated from the statistical analysis. An analysis of covariance indicated that the slopes of the relationships between $N_A$ and $Q > 100\ \mu\text{mol m}^{-2}\text{s}^{-1}$ were not significantly different between the nitrogen treatments but the elevation of the line (i.e., the y-intercept) increased significantly with increasing nitrogen availability ($\alpha < 0.001$).

Leaf nitrogen content per unit dry weight ($N_W$) was poorly correlated with light exposure in all nitrogen treatments (Fig. 2), however an analysis of covariance indicated that these correlations were statistically significant ($\alpha < 0.001$). Mean leaf $N_W$ ($\text{g} \cdot \text{g}^{-1} \cdot 100$) increased with increasing levels of nitrogen availability (2.24, 2.40, 2.73, 2.83 and 2.93, for the 0, 112, 196, 280 and 364 kg $\text{ha}^{-1}$ $\text{year}^{-1}$ treatments, respectively). $N_A$ and leaf weight per unit area ($W_A$) were highly correlated at all nitrogen treatments (Fig. 3). An analysis of covariance indicated that there were statistically significant increases in the slope of the relationship between $N_A$ and $W_A$ with increasing nitrogen availability ($\alpha < 0.001$).

### *Gas-exchange measurements*

In this study leaf assimilation (A) was linearly related to $N_A$ in leaves with $N_A < 3.0\ \text{g m}^{-2}$ (Fig. 4). Leaf mesophyll conductance calculated as a residual was also related to $N_A$ in a pattern similar to A vs $N_A$ (data not shown). In leaves with $N_A > 3.0\ \text{mg m}^{-2}$, A and $g_m$ were quite variable and generally not correlated with increasing $N_A$. Maximum measured rates of A were similar for both the 0 N and the 364 kg $\text{ha}^{-1}$ $\text{year}^{-1}$ N treatment. However, assimilation rates of the leaves with the lowest $N_A$ were lower for the high nitrogen trees than the low nitrogen trees. Therefore, the slope of the A to $N_A$ relationship was greater for the high nitrogen trees than for the low nitrogen trees (Fig. 4).

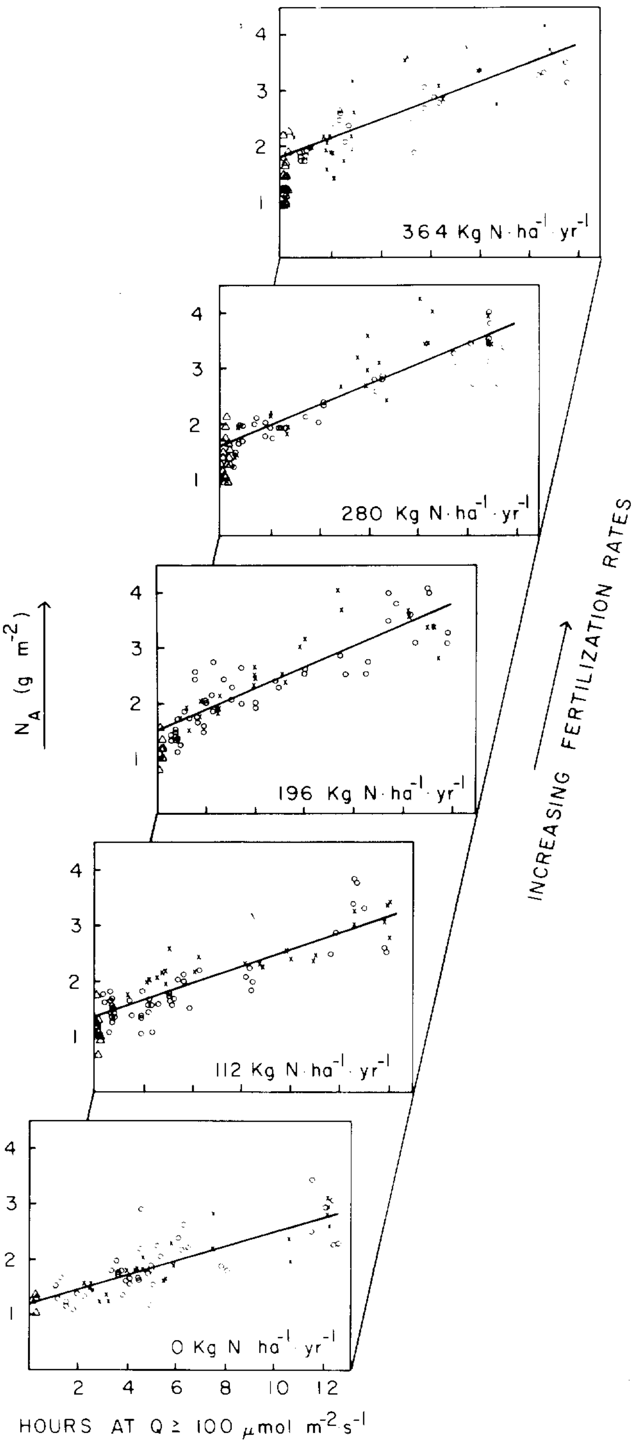

**Fig. 1.** The relationship between nitrogen per unit leaf area ($N_A$) and leaf light exposure (measured as the number of hours in a day that the leaf was exposed to $Q \geq 100\ \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) for trees in each of five N fertilization treatments. *Open circles* are data from 1985, *x* for 1986 data. *Triangles* are for leaves exposed to $\leq 30$ mins at $Q \geq 100\ \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The regression statistics are: $Y = 1.20 \pm 0.17x$ ($r = 0.81$), $Y = 1.36 + 0.15x$ ($r = 0.87$), $Y = 1.52 + 0.19x$ ($r = 0.88$), $Y = 1.60 + 0.18x$ ($r = 0.89$) and $Y = 1.81 + 0.17$ ($r = 0.82$) for nitrogen treatments 0, 112, 196, 280 and 364, respectively

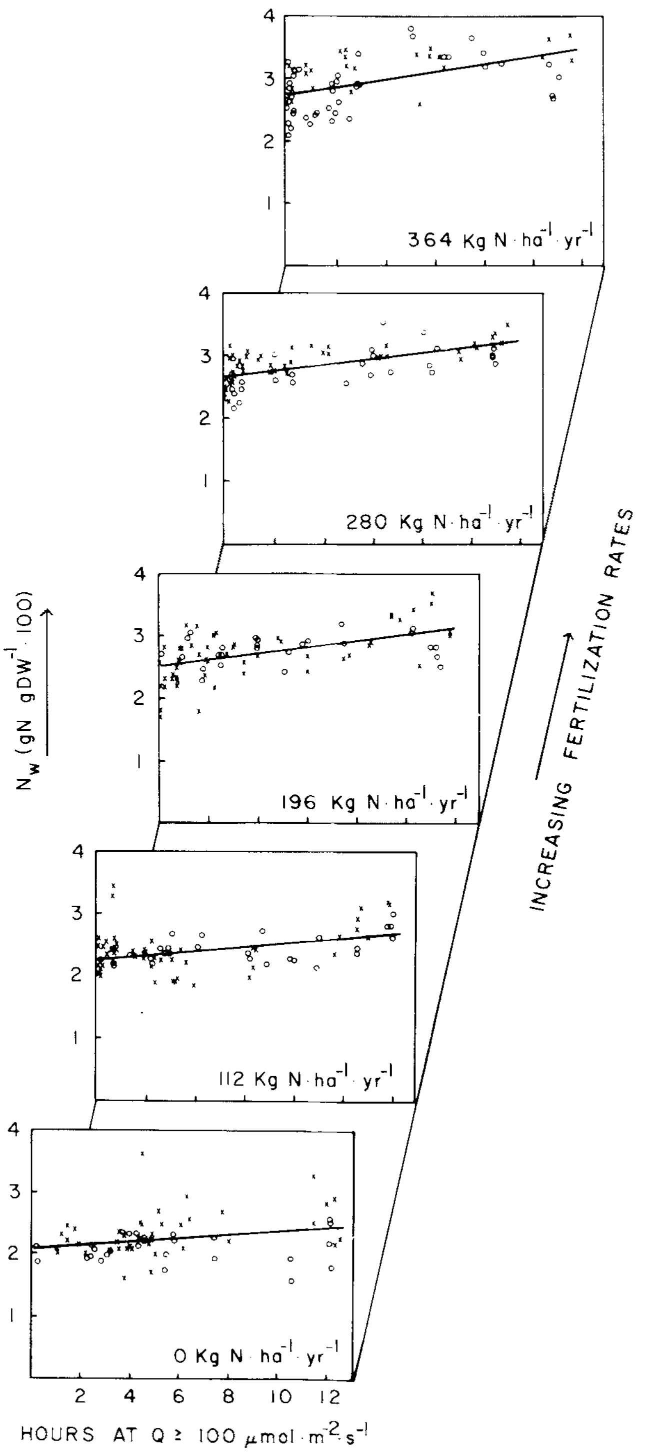

**Fig. 2.** The relationship between nitrogen per unit leaf dry weight ($N_W$) and leaf light exposure (measured as the number of hours in a day that the leaf was exposed to $Q \geq 100$ μmol · m$^{-2}$ · s$^{-1}$) for trees in each of five N fertilization treatments. *Open circles* are for 1985 data, *x* for 1986 data. The regression statistics are: $Y = 2.09 + 0.03x$ ($r = 0.29$), $Y = 2.27 + 0.03x$ ($r = 0.41$), $Y = 2.52 + 0.05x$ ($r = 0.53$), $Y = 2.65 + 0.05x$ ($r = 0.65$), and $Y = 2.75 + 0.06x$ ($r = 0.52$) for nitrogen treatments 0, 112, 196, 280 and 364, respectively

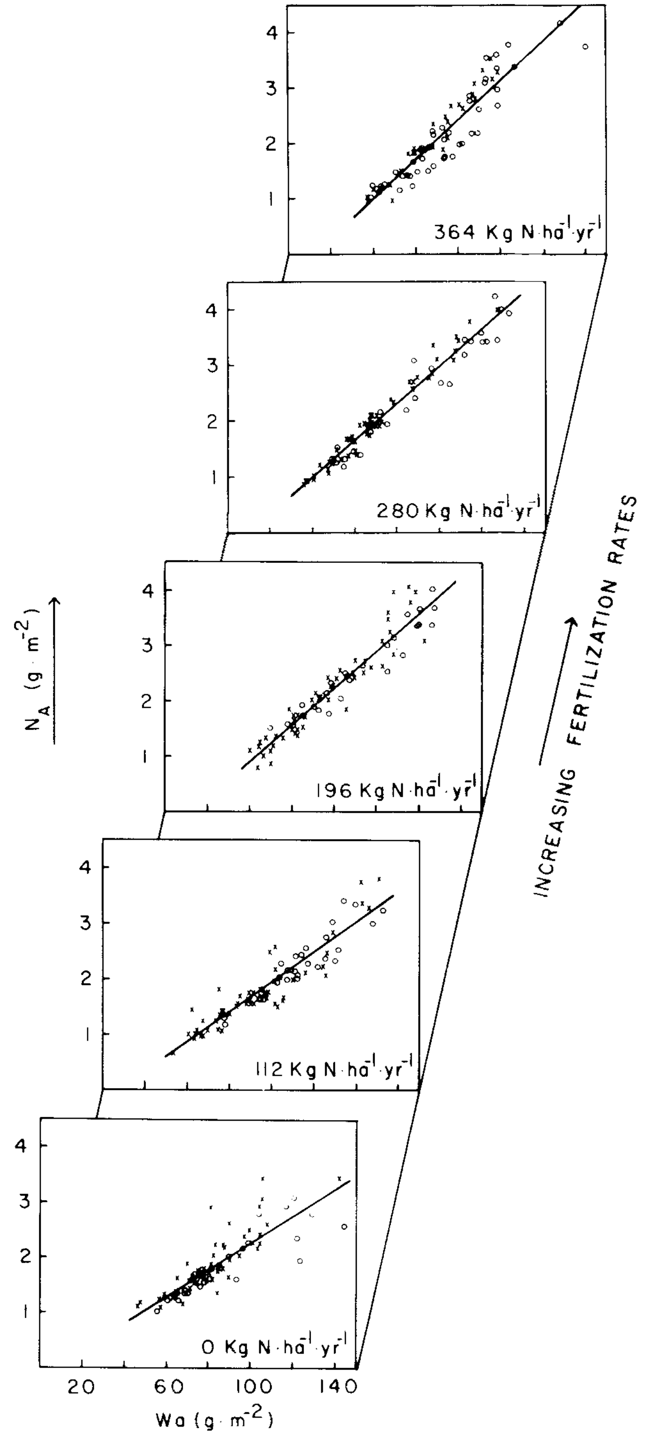

**Fig. 3.** The relationship between nitrogen per unit leaf area ($N_A$) and dry weight per unit area ($W_A$) for trees in each of five N fertilization treatments. *Open circles* are for 1985 data, *x* for 1986 data. The regression statistics are: $Y = -0.16 + 0.024x$ ($r = 0.84$), $Y = -0.21 + 0.27x$ ($r = 0.93$), $Y = -0.44 + 0.033x$ ($r = 0.95$), $Y = -0.34 + 0.033x$ ($r = 0.98$) and $Y = -0.40 + 0.035x$ ($r = 0.93$) for nitrogen treatments 0, 112, 196, 280 and 364, respectively

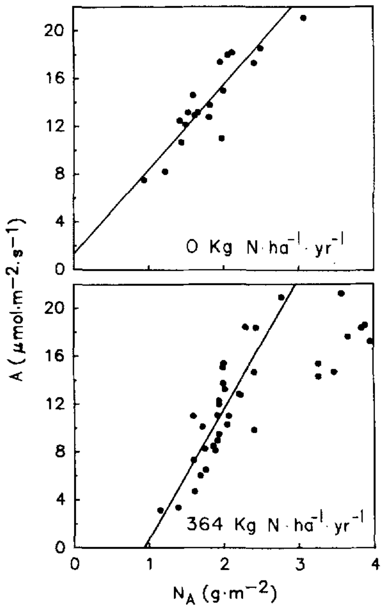

**Fig. 4.** The relationship between net leaf $CO_2$ assimilation rate ($A$), and N content per unit leaf area ($N_A$) in trees that received 0 and 364 kg·N·ha$^{-1}$·year$^{-1}$. Regression statistics on data with $N_A < 3.0$ gm$^{-2}$ are: $Y = 1.35 + 7.08x$ ($r = 0.87$) and $Y = -10.1 + 10.8x$ ($r = 0.84$)

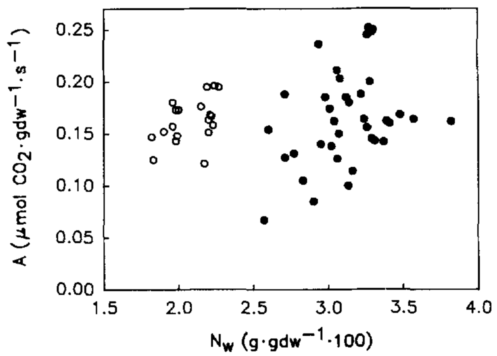

**Fig. 5.** The relationship between net leaf $CO_2$ assimilation rate per unit leaf dry weight ($A$) and N content per unit leaf dry ($N_W$) for unfertilized trees (*open circles*) and trees receiving 364 kg N·ha$^{-1}$·year$^{-1}$ (*closed circles*)

There were no statistically significant correlations between A expressed on a dry weight basis (μmol $CO_2$ g$^{-1}$ s$^{-1}$) and $N_W$ (g g$^{-1}$ × 100) either when leaves of a given nitrogen treatment were analyzed separately or together (Fig. 5).

## Discussion

In a previous paper DeJong and Doyle (1985) showed that there was a linear relationship between leaf nitrogen content per unit leaf area and leaf light exposure in peach tree canopies. The present research shows that although application of fertilizer nitrogen had substantial effects on tree nitrogen status, it had little effect on partitioning nitrogen along gradients of leaf light exposure except for shifting more leaves into low exposure ranges due to increased leaf development. When the highly shaded leaves are eliminated from the analysis it appears that additional fertilizer nitrogen increased the basal level of nitrogen per unit leaf area at a given light level but did not significantly affect the slope of the relationship between $N_A$ and $Q > 100$ μmol m$^{-2}$s$^{-1}$ (Fig. 1). Thus it appears that the plant's basic strategy for partitioning leaf nitrogen per unit leaf area with respect to leaf light exposure is not altered by plant nitrogen status.

The general relationships between $N_A$ and A reported in this paper for the trees receiving 0 and 364 kg ha$^{-1}$ year$^{-1}$ of fertilizer nitrogen are in basic agreement with those previously reported by DeJong and Doyle (1985) for peach trees grown at an intermediate nitrogen status. Minimum rates of A were achieved at approximately 1 g m$^{-2}$ of leaf nitrogen and maximum rates were achieved at about 3 g m$^{-2}$ for leaves of both nitrogen treatments. The causes for the variability in A and gm at $N_A$ greater than 3 g m$^{-2}$ in the high nitrogen treatment are not apparent. Regardless of this variability it does appear that maximum rates of A are achieved at around 3 g m$^{-2}$, and that the relationship between A and $N_A$ is reasonably linear between 1 and 3 g m$^{-2}$.

The maximum rates of assimilation achieved by leaves from both treatments were similar (21 μmol m$^{-2}$s$^{-1}$) but the minimum rates of A were lower for the high nitrogen treatment than the low nitrogen treatment (3.3 and 7.5 μmol m$^{-2}$ s$^{-1}$, respectively). The latter is probably related to the fact that the canopies of the low nitrogen trees were less dense and minimum leaf light exposures were usually above 1 h at $Q \geq 100$ μmol m$^{-2}$s$^{-1}$ (Fig. 1) whereas the high nitrogen trees had very dense canopies and many leaves were much more shaded. Data in Fig. 1 indicate that leaves of the highest nitrogen treatment that were exposed to $Q \geq 100$ μmol m$^{-2}$s$^{-1}$ for 1 h had $N_A = 1.8$ g m$^{-2}$. Thus, according to Fig. 4, A for leaves of a comparable time of light exposure would be 9 μmol m$^{-2}$s$^{-1}$.

If trees of both the highest and the lowest N fertilization treatment have the same maximum rate of leaf A, what is the photosynthetic response of the tree canopy to increased N availability? To address this we can use the relationships from Figs. 1 and 4 to estimate how A may be related to canopy light exposure in trees with differing N

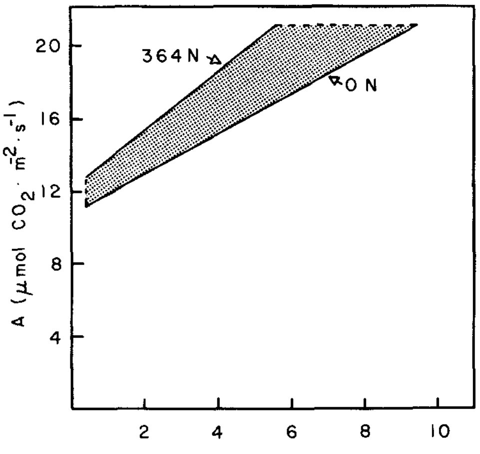

**Fig. 6.** The relationship between *A* measured at light saturation and daily leaf light exposure (hours at $Q \geq 700\ \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) above light saturation for low and high N trees. The *shaded area* represents the leaf photosynthetic advantage in the high N canopies relative to the low N canopies

status. Figure 6 is a diagrammatic model of the canopy photosynthetic response to nitrogen fertilization in peach trees. Since actual leaf photosynthesis in the canopy should be more closely related to hours of light exposure > light saturation, data in Fig. 1 were transformed into $N_A$ vs $Q > 700\ \mu\text{mol m}^{-2}\text{s}^{-1}$ [$(Q > 700\ \mu\text{mol m}^{-2}\text{s}^{-1}) = Q > 100\ \mu\text{mol m}^{-2}\text{s}^{-1} \times 0.82 - 0.39$); $R = 0.99$)]. No attempt was made to account for A in leaves exposed to less than 30 min at $Q > 700\ \mu\text{mol m}^{-2}\text{s}^{-1}$ and it was assumed that all leaves with $N = 3.0\ \text{g m}^{-2}$ are potentially capable of maximum A.

This model indicates that although the maximum rate of A is similar for trees of the highest and lowest nitrogen treatment, the maximum rate of A is achieved in leaves with less time of exposure to $Q > 700\ \mu\text{mol m}^{-2}\text{s}^{-1}$ in high nitrogen trees than in low nitrogen trees. Thus the hatched area is a diagrammatic indication of the potential photosynthetic advantage of the high nitrogen treatment compared to the low treatment. Unfortunately the potential advantage cannot be quantified further without data regarding the amount of leaf area in various light exposure categories. Nevertheless, it is apparent that on a whole canopy basis the high nitrogen trees may have a significantly higher potential for daily carbon fixation than the low nitrogen trees in spite of the fact that maximum As are similar.

In recent years there have been a number of attempts to develop general relationships between leaf nitrogen content and A (Field and Mooney 1986; Van Keulen et al. 1988) both between and within given plant species. The present research indicates that the development of such general relationships should be approached carefully. In peach there is a good relationship between A and nitrogen when comparing leaves from trees with similar nitrogen status. However, that relationship changes with plant nitrogen status and is not apparent if A and leaf nitrogen are expressed on a dry weight basis (Fig. 5). The fact that both the high and low nitrogen trees in these experiments had similar maximum A does not mean that there was no photosynthetic response to fertilizer nitrogen. The effect of fertilizer nitrogen on nitrogen partitioning, rather than $A_{max}$, may have been apparent because the plants were grown and measured under field conditions with natural patterns of solar radiation and canopy development. Many studies involving photosynthetic responses to nitrogen fertilization are done on small plants under greenhouse or growth chamber condtions where light is distributed relatively evenly throughout the plant canopy. Under such conditions gradients of light exposure are usually minimized and leaf nitrogen is probably distributed more evenly among the leaves. Thus, if there is a shortage of nitrogen all leaves may experience a reduction in leaf nitrogen content and $A_{max}$ decreases. Furthermore, annual plants develop very rapidly and there may not be as much time to partition or adjust leaf nitrogen or $A_{max}$ to correspond with light gradients in the plant canopy.

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Received February 7, 1989