Distribution of leaf mass per unit area and leaf nitrogen concentration determine partitioning of leaf nitrogen within tree canopies

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Summary   Distribution of leaf nitrogen with respect to leaf mass per unit area (M_a), nitrogen per unit mass (N_m) and nitrogen per unit area (N_a) within peach (*Prunus persica* L.) tree canopies was studied in two field experiments. In one experiment, leaf light exposure and M_a were measured on leaves from different canopy positions of peach trees subjected to five nitrogen (N) fertilization treatments. Leaf light exposure and M_a were linearly related and the relationship was independent of N fertilization. In a subsequent experiment, N fertilizer was applied to previously unfertilized trees in midsummer, after shoot growth had terminated. Application of N fertilizer did not affect mean canopy M_a. Fertilization increased N_m of all leaves throughout the canopy compared with non-fertilized trees. No significant relationship between N_m and M_a was found in either fertilized or control trees. There was a linear relationship between N_a and M_a and the slope of the relationship was increased by N fertilizer application. We conclude that distribution of N_a in peach tree canopies is primarily a function of M_a partitioning with light and N_m, which is related to soil N availability.

Keywords: modeling, nitrogen allocation, nitrogen fertilization, photosynthesis, Prunus persica.

Introduction

Nitrogen (N) partitioning within plant canopies is considered optimal when leaf N is distributed along the canopy light gradient to maximize carbon assimilation per unit N (Field 1983, Hirose and Werger 1987). This hypothesis is supported by several studies showing that leaf N concentration per unit area or per unit mass is proportional to the irradiance available at the leaf sites (Gulmon and Chu 1981, Field 1983, DeJong and Doyle 1985, Hirose and Werger 1987, Walters and Field 1987, Evans 1989*b*, Lemaire et al. 1991, Leuning et al. 1991, Ellsworth and Reich 1993, Kull and Niinemets 1993, Hikosaka et al. 1994, Reich and Walters 1994, Niinemets 1995, 1997, Hollinger 1996).

However, in many species, a strong correlation exists between leaf N concentration and light exposure within the canopy only when N is expressed per unit leaf area (N_a). When N

is expressed per unit mass (N_m), some species exhibit increasing (Kull and Niinemets 1993), constant (DeJong et al. 1989, Weinbaum et al. 1989, Klein et al. 1991, Ackerly 1992, Ellsworth and Reich 1993, Harley and Baldocchi 1995, Hollinger 1996, Niinemets 1997), or decreasing (Ellsworth and Reich 1992, Kull and Niinemets 1993, Reich and Walters 1994, Niinemets 1995, 1997) N_m with increasing light.

The different relationships between N_a and N_m with light can be explained by considering that N_a is the product of leaf mass per unit area (M_a) and N_m ($N_a = M_a N_m$). Parameter M_a is positively related to leaf irradiance (Jackson 1967, Lewandowska and Jarvis 1977, Chabot et al. 1979, Gulmon and Chu 1981, Marini and Barden 1982, Jurik 1986, Weinbaum et al. 1989, Sanchez and Righetti 1990, Klein et al. 1991, Campbell et al. 1992, Kull and Niinemets 1993, Wayne and Bazzaz 1993, Reich and Walters 1994, Niinemets 1997). Increased M_a is the result of increased leaf thickness, palisade depth and mesophyll cell density (Chabot et al. 1979, Jurik 1986, Wooge and Barden 1987, Witkowski and Lamont 1991, Thompson et al. 1992). The correlation between M_a and light is usually strong and results in a positive relationship between N_a and irradiance even when N_m is constant or decreases with increasing light.

The close correlation between M_a (and N_a) and light exposure has led to the conclusion that M_a is a species-specific estimate of long-term leaf light conditions (Niinemets 1997). Furthermore, it has been suggested that M_a distribution in canopies provides a means of distributing N_a within plant canopies (Ellsworth and Reich 1993). The distribution of M_a in tree canopies explains 95% of the distribution of N_a in *Acer saccharum* Marsh., and modeled integrated canopy photosynthesis is higher when based on observed M_a distribution compared with other potential M_a distribution patterns (Ellsworth and Reich 1993). Similar results have been predicted by the model of Gutschick and Wiegel (1998).

Although M_a may explain most of the N_a partitioning within a given canopy, the relationship between M_a and N_a is dependent on tree nitrogen nutrition status, and the slope of the N_a–M_a relationship increases with increasing N fertilization (DeJong et al. 1989, Walters and Reich 1989, Rosati et al. 1999). Nitro-

gen fertilization generally increases N_m (Gulmon and Chu 1981, Beutel et al. 1983, DeJong et al. 1989, Thompson et al. 1992, Saenz et al. 1997) and consequently N_a for any given M_a. Therefore, M_a may be sufficient for scaling relationships (i.e., estimating N_a and photosynthesis) across different soil nutrient regimes; however, the mechanisms underlying the interaction between N fertilization and the partitioning of N with light gradients are not yet well understood.

Furthermore, the relationship between M_a and irradiance has not been extensively studied across different soil N availabilities and there is no clear evidence that the M_a–light relationship is independent of N fertilization. Many authors (Oxman et al. 1977, Longstreth and Nobel 1980, Gulmon and Chu 1981, Jurik et al. 1982) have found that, with increasing N fertilization, M_a is reduced for a given irradiance above the plants. However, because light was not measured at the single leaf level, the reduction in M_a may have been caused by increased shading at the leaf level as a result of increased canopy size of the N-fertilized plants.

We have investigated whether M_a is partitioned along canopy light gradients independently of plant N nutrition and whether N fertilization affects N_m independently of light availability at the leaf site. To test these hypotheses, the relationship between (M_a) and leaf irradiance was studied across different N fertilization regimes. The effects of N fertilization on the partitioning of N within the tree canopy were studied by observing changes in the N_m–M_a and the N_a–M_a relationships following N fertilization of N-deficient peach trees.

Materials and methods

The first part of this study is a further elaboration of data from DeJong et al. (1989). Plants were 11-year-old nectarine trees (*Prunus persica* cv. Fantasia) fertilized with 0, 112, 196, 280 or 364 kg ha^{-1} year^{-1} of nitrogen fertilizer. The latter four treatments received 112 kg ha^{-1} during late summer of the previous year. Trees in the 196, 280 and 364 kg ha^{-1} year^{-1} treatments received the additional fertilizer during shoot growth in early spring.

Canopy light (PAR) at single leaf sites was measured after maximum shoot elongation during two clear days on trees in each of the five nitrogen treatments. Light data were expressed as the number of hours at photon flux densities (PFD) greater than 100 μmol m^{-2} s^{-1}. After collection of the light data, the leaves were harvested and immediately taken to a laboratory for leaf area measurement and then dried for dry mass measurement and nitrogen analysis. Leaf mass per unit area (M_a) and nitrogen concentration per unit mass (N_m) and per unit area (N_a) were subsequently calculated. Details on experimental design, plant material, laboratory analysis and light measurements are provided in DeJong et al. (1989).

In a subsequent experiment, we used 14-year-old peach trees (*Prunus persica* cv. Flamecrest), growing at the Kearney Agricultural Center, University of California, Parlier, California. Trees were trained to a standard open-vase configuration and, with the exception of N fertilization, received routine horticultural care suitable for commercial fruit production includ-

ing pruning, fruit thinning and harvesting, irrigation, and pest control. During the 5 years before the experiment, the trees received no N fertilizer and exhibited moderate N deficiency. Ten homogeneous, randomly chosen trees were selected and 10 shoots ranging from the lower inside to upper outside of the canopy of each tree were tagged. On July 12 (Day of year (DOY) 193), five of the 10 trees were fertilized with ammonium sulfate fertilizer corresponding to 366 kg N ha^{-1} and irrigated within a few hours after fertilizer application. Fully expanded mid-shoot leaves (one from each tagged shoot) were collected at intervals for the remainder of the season on DOY 193, 200, 206, 220, 234, 255 and 283 (July 12 and 25, August 8 and 22, September 12 and October 10, respectively). Sample leaves were harvested between 0800 and 1000 h, immediately taken to a laboratory for measurement of leaf area and then dried for 72 h at 70 °C. Nitrogen content was determined as described by DeJong et al. (1989). Values of M_a and N_a were subsequently calculated.

Data were analyzed by comparing the slopes and intercepts of linear regression models (Kleinbaum and Kupper 1978).

Results

Analysis of M_a data from the initial experiment (DeJong et al. 1989) indicated that the M_a–light exposure relationship was unaffected by N fertilization (Figure 1, data shown for lowest and highest fertilization treatments only). Plotting M_a against leaf light exposure (expressed as daily time of exposure to PFD > 100 μmol m^{-2} s^{-1}) resulted in a linear relationship that did not vary significantly with N fertilization. There were no significant trends in regression slope or intercept with increasing fertilization, and the lowest and highest fertilization treatments had the most similar regression parameters. The linear regressions were fit using all available data, including those for leaves with less than 0.5 h of exposure to PFD > 100 μmol m^{-2} s^{-1}, which were excluded in the original analysis by DeJong et al. (1989).

In the subsequent experiment, there was no significant relationship between N_m and M_a in either fertilized or control trees
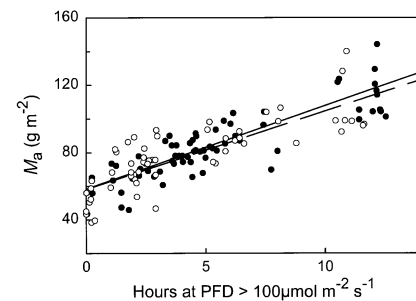

Figure 1. Relationship between leaf mass per unit area (M_a) and leaf light exposure (expressed as daily time of exposure to PFD > 100 μmol m^{-2} s^{-1}) for peach trees fertilized with 0 (closed circles; solid line ($y = 4.95x + 58.3$; $r^2 = 0.77$, $P < 0.001$)) and 364 (open circles; dashed line ($y = 4.96x + 57.3$; $r^2 = 0.667$, $P < 0.001$)) kg ha^{-1} year^{-1} of N fertilizer.

at any sampling date (Figure 2, data shown only for three dates). Leaf N concentration was relatively constant throughout the wide range of M_a found within the canopies. However, N_m was higher in fertilized trees than in control trees within 2 weeks after fertilizer application and the differences in N_m between the two treatments continued to increase for the rest of the season (Figures 2 and 3B).

When leaf N concentration was expressed on an area basis, N_a was linearly correlated with M_a ($P < 0.001$ and r^2 between 0.70 and 0.91 for all regressions) in both fertilized and control trees (Figure 2). However, starting from DOY 220 and for all subsequent dates, fertilized trees had significantly ($P < 0.05$) higher slopes of the N_a–M_a relationship than control trees, whereas there was no significant difference in the intercepts. None of the intercepts of these regressions for both fertilized and control trees was significantly different from zero. The comparatively higher slopes of the N_a–M_a relationship in fertilized trees were mainly a result of a strong decrease in the slope of the relationship in the unfertilized trees during the season (Figure 3C).

The seasonal pattern of mean canopy M_a per treatment and per date (50 leaves) was not affected by nitrogen fertilization (Figure 3A). Both fertilized and control trees had similar seasonal patterns with almost constant values of M_a during the season.

The fertilization treatment dramatically affected seasonal values of both N_m and N_a expressed as the mean canopy value per treatment and per date (Figures 3B and 3D). At the last sampling date, both N_m and N_a were about 30% higher in fertilized trees than in control trees.
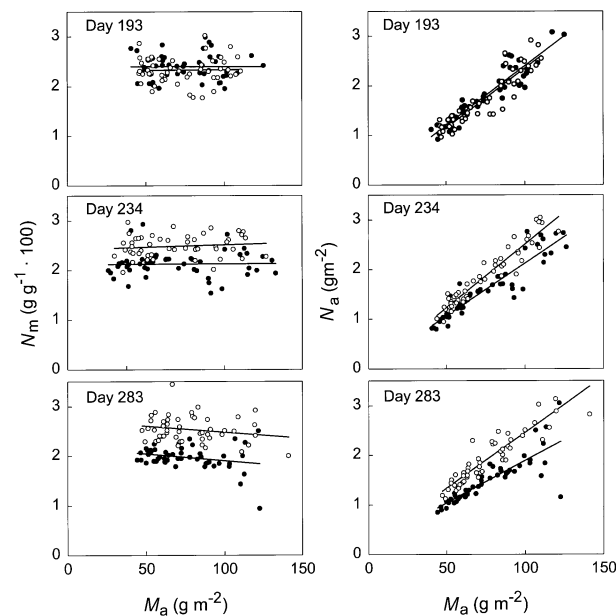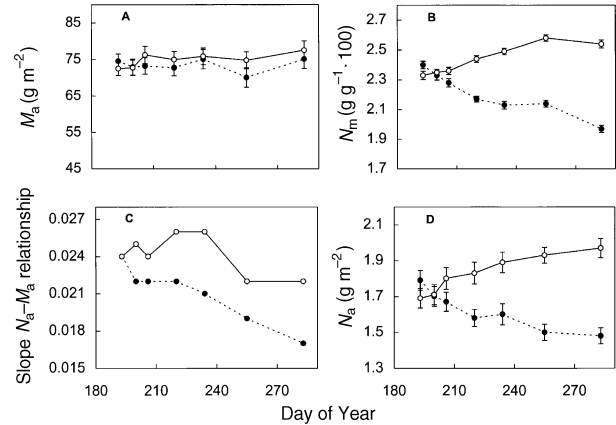

Figure 3. Seasonal patterns in mean canopy values of leaf mass per unit area (M_a; A), leaf nitrogen per unit mass (N_m; B), the slope of the N_a–M_a relationship (C), and leaf nitrogen per unit area (N_a; D). Open circles and solid lines represent fertilized trees; and closed circles and dashed lines represent control trees. Error bars represent the SE of the means.

Discussion

Partitioning of leaf mass was related to canopy light gradients independently of N fertilization (Figure 1). Correlation between M_a and light availability at the leaf site has been extensively documented (Jackson 1967, Lewandowska and Jarvis 1977, Chabot et al. 1979, Gulmon and Chu 1981, Marini and Barden 1982, Jurik 1986, Weinbaum et al. 1989, Sanchez and Righetti 1990, Klein et al. 1991, Campbell et al. 1992, Kull and Niinemets 1993, Wayne and Bazzaz 1993, Reich and Walters 1994, Niinemets 1997). However, the M_a–light relationship has usually been investigated within one canopy or plant community without variation in soil N availability. If soil N availability is varied during shoot growth, the main effect of N fertilization is an increase in canopy size and intercepted light with distribution of total canopy N into larger leaf mass (Gulmon and Chu 1981, DeJong et al. 1989, Walters and Reich 1989, Thompson et al. 1992). Greater canopy size results in increased canopy self-shading and the optimum LAI developed for a given pool of N depends on the species, but generally increases with increasing soil N availability (Dingkuhn et al. 1990, Anten et al. 1995, Hirose et al. 1997). Increased canopy size following N fertilization is also associated with a reduction in M_a for a given irradiance above the plants (Oxman et al. 1977, Longstreth and Nobel 1980, Gulmon and Chu 1981, Jurik et al. 1982). Our data suggest that a given irradiance at the leaf level corresponds to a given M_a, independently of soil N availability and its effect on canopy size and light distribution. Therefore, the reduction in M_a often associated with N fertilization may result from increased shading, because soil N availability does not affect the response of M_a to light. Thus, M_a may be considered a species-specific estimate of long-term light conditions as suggested by Niinemets (1997), even across different N nutrition regimes.

Figure 2. Relationship between leaf N per unit mass (N_m) and leaf N per unit area (N_a) and leaf mass per unit area (M_a) on Days of year 193, 234, 283. Fertilizer treatment was applied on Day 193. Open circles represent fertilized trees; and closed circles represent control trees.

Nitrogen fertilization did not affect the mean canopy value of M_a (Figure 3A). Both fertilized and unfertilized trees had similar seasonal patterns of M_a. Because N fertilizer was applied after maximum shoot elongation in the second experiment, light availability on the tagged shoots was similar between fertilized and control trees. Lower M_a values on fertilized trees would probably have been found if N fertilization had been applied early enough to stimulate extensive canopy growth and thereby significantly increase canopy self-shading.

Although soil N availability did not affect the M_a–light relationship, N fertilization resulted in a continuous increase in N_m relative to the control trees (Figure 3B). However, the increase in N_m was relatively homogeneous within the canopy at all dates and no significant relationship was found between N_m and M_a in either fertilized or control trees, even during the early dates after N fertilization of the N-deficient trees (Figure 2). That is, leaves with the highest M_a had N concentrations similar to leaves with the lowest M_a. These results are consistent with studies on other tree species (Weinbaum et al. 1989, Klein et al. 1991, Ellsworth and Reich 1993, Harley and Baldocchi 1995, Hollinger 1996, Niinemets 1997). Although N_m was constant across the wide range of canopy M_a values within each nitrogen treatment, fertilized trees had higher leaf N concentration than control trees (cf. Gulmon and Chu 1981, Beutel et al. 1983, DeJong et al. 1989, Thompson et al. 1992, Saenz et al. 1997). Therefore, N fertilization did not result in preferential allocation of N, but rather caused a general increase in N_m at all sites independently of leaf irradiance. A previous study on peach trees (DeJong et al. 1989) showed a slight positive relationship between light exposure and N_m (r^2 from 0.08 to 0.42 for all regressions) and N_m only increased about 10–20% over the range of irradiances within each N fertilization treatment. Niinemets (1997) listed peach trees among those with constant N_m with varying irradiance. Although N_m in peach tree canopies may vary by about 10–20% (DeJong et al. 1989) or not at all (this study) in response to light within each N fertilization treatment, M_a varies about 3-fold (DeJong et al. 1989, Rosati et al. 1999), indicating that N_a ($N_a = N_m M_a$) is mostly affected by M_a.

Nitrogen fertilization increased the slope of the N_a–M_a relationship (Figures 2 and 3C) and mean canopy N_a (Figure 3D). Previous data (DeJong et al. 1989, Walters and Reich 1989, Rosati et al. 1999) also indicate that the slope of the N_a–M_a relationship increases with increasing N fertilization. The difference in the slope between fertilized and control trees increased during the season, probably as a result of increasing N uptake with time after fertilizer application. We conclude, therefore, that the slope of the N_a–M_a relationship increases proportionally with total N availability, whereas the intercept remains at zero. This relationship is independent of the source of variation in N availability, whether the source is time after application or amount applied.

Because N fertilization did not induce partitioning of N_m toward outer leaves (high M_a), the increase in the slope of the N_a–M_a relationship must have resulted from a uniform increase in N_m in response to fertilization. This effect can be explained by considering that N_a is the product of N_m and M_a. If leaf N concentration is constant within one N fertilization treatment, (i.e., one canopy), N_m becomes the slope of a linear relationship between N_a and M_a with a zero intercept. Consequently, if N fertilization increases N_m uniformly in the canopy, then the slope of the N_a–M_a relationship is also increased, whereas the intercept remains near zero. Thus, the apparent higher partitioning of leaf N on an area basis (N_a) toward the outer-canopy leaves with increasing soil N availability results from the homogeneous distribution of leaf N concentration (N_m) in leaves of different mass (M_a).

Previous research on the leaf nitrogen–light relationship has focused on N partitioning in terms of N_a, thereby confounding the variation in both N_m and M_a and preventing estimation of leaf construction costs on whole-plant energy capture (Givnish 1988). In our study, the distribution of M_a along the light gradient and the uniform increase in N_m within the canopy with increasing N availability appeared to be independent phenomena. Therefore, it seems that, in peach trees or in species with constant N_m throughout the light gradient, N_a can be modeled as the product of M_a, which depends on leaf light exposure independent of N fertilization, and N_m, which varies with total N availability independent of irradiance. Given the close relationship between N_a and photosynthesis, this proposed modeling of canopy N_a distribution could be extended to modeling of photosynthetic properties (Gulmon and Chu 1981, Field and Mooney 1986, Hirose and Werger 1987, DeJong et al. 1989, Walters and Reich 1989, Keulen et al. 1989). For a given N_a, variations in within-leaf N partitioning among the different photosynthetic N fractions in response to light could be included (Björkman 1968, Medina 1971, Terashima and Evans 1988, Evans 1989a). However, in peach trees as well as in *Acer saccharum*, within-leaf N partitioning appears to have a limited effect on leaf photosynthetic properties compared with within-canopy N_a (Niinemets and Tenhunen 1997, Rosati et al. 1999). Seasonal and age effects on M_a and N_m could also be included in such models (Reich et al. 1991); however, the gradient in leaf N concentration may only be strongly affected by leaf age under N-deficient nutrition (cf. Hikosaka et al. 1994).

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