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# Patterns of Leaf Mass, Area and Nitrogen in Young Northern Hardwood Forests

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ABSTRACT.—Patterns of leaf mass per unit area (LMA) and area-based foliar N concentration (N area) through the canopy were examined for seven tree species growing in reference and fertilized plots of two early successional northern hardwood stands in New Hampshire. Increases in LMA with height in the canopy were significantly related to increasing average daily photosynthetically active radiation (PAR). As expected, the slopes of regressions between LMA and PAR (*i.e.*, plasticity) were higher for shade tolerant than intolerant species in both stands. Fertilization increased leaf area index in both stands. For the shade intolerant species (*Prunus pensylvanica, Betula papyrifera*), average canopy LMA increased in response to fertilization but no response was observed in the more tolerant species (*Acer* spp., *Fagus grandifolia, Betula allegheniensis*). The slopes of regressions between N area and PAR were highly significant, with higher plasticity of N area for shade tolerant than intolerant species. Average canopy N area increased in response to fertilization, and the response was particularly large for the intolerant species. The increase in N-area for these species was associated with the significant response of shaded foliage, as sun exposed foliage showed no response to fertilization.

## INTRODUCTION

Most tree species live in spatially and temporally varying light environments, and plasticity in foliage properties is essential to the photosynthetic performance of individual trees. The range of irradiances normally encountered by foliage of different species varies with tree life histories; for example, relatively uniform irradiances are encountered both by species that grow rapidly in height after large-scale disturbance (and maintain most foliage in a high light environment) and by species that always reside in the forest understory. Shade tolerant species generally exhibit a more plastic response to light availability than intolerant species (Goulet and Bellefleur, 1986).

The ratio of leaf mass to area (LMA) is sensitive to the light environment of individual leaves. Thin leaves (low LMA) maximize energy capture per unit respiratory cost at low light (Chabot *et al.,* 1979) while thick leaves maximize light use at high irradiances (Jurik, 1986). Ellsworth and Reich (1993) concluded that variation in LMA within the canopy of mature sugar maple (*Acer saccharum* Marsh.) was the most important plastic response conferring high efficiency to whole-tree photosynthesis in this late-successional, shade tolerant species. Similarly, Goulet and Bellefleur (1986) observed that the high shade tolerance of late- successional species resulted largely from the highly plastic response of LMA, whereas early-successional intolerant species produce only leaves adapted for high light.

Other plastic traits contribute to the efficiency of whole-canopy photosynthesis, including leaf orientation (*e.g.,* leaf angles; Ford and Newbould, 1971), leaf biochemistry (especially the amounts of light harvesting pigments and carboxylation enzymes; Evans, 1989) and

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nutrient allocation throughout the canopy. Ellsworth and Reich (1993) observed that variation in photosynthetic capacity within the sugar maple canopy resulted from differences in nitrogen content per unit leaf area (N area) associated with the light availability gradient through the canopy, a result that supports the general notion that allocation of N throughout the plant canopy optimizes daily whole-canopy photosynthesis (Hirose and Werger, 1987).

Following large-scale disturbances in eastern deciduous forests, canopy closure is very rapid and competition for light is intense with the ultimate success of various species depending upon height growth and shade tolerance (Marks, 1975). In northern hardwood stands a dominance hierarchy is established in the competition for light based upon the life history traits of the species available to colonize (Bormann and Likens, 1979) and, thus, different species achieve canopy dominance at different stages of succession. The fastest growing and most shade intolerant species (Harlow *et al.*, 1979), such as pin cherry (*Prunus pensylvanica* L.) and paper birch (*Betula papyrifera* Marsh.), dominate early in succession. Species with intermediate shade tolerance such as yellow birch (*Betula alleghenieniensis* Michx.) and red maple (*Acer rubrum* L.) may follow, eventually giving way to the slower growing but extremely tolerant sugar maple and beech (*Fagus grandifolia* Ehrh). Thus, during growth to maturity in northern hardwood forests, canopies of these three classes of tree species typically would use different ranges of irradiances and might be expected to exhibit differences in the plasticity of foliar traits across light environments (Goulet and Bellefleur, 1986).

The objectives of the present study were: (1) to quantify within-crown variations in LMA and N-area in relation to the shade tolerance of the principal tree species during the early stages of stand development in northern hardwood forests and (2) to examine the response of these relationships to changes in soil nutrient availability resulting from long-term fertilization treatments. We expected the relaxation of nutrient (especially N) constraints to canopy photosynthesis to be accompanied by shifts in patterns of N allocation to foliage and possibly changes in the plastic response of LMA. For example, increased nitrogen availability often results in decreased LMA (Oxman *et al.*, 1977; Longstreth and Nobel, 1980; Jurik, 1986), although the contrary also has been observed (Yoshida and Coronel, 1976). Fahey *et al.* (1998) observed that the light regime in young northern hardwood stands was altered by fertilization because of increases in stand leaf area and changes in foliage height distribution. By quantifying the responses of LMA and foliar N to fertilization in these stands, we also hoped to improve general understanding of the interactions of light and nutrient availability in regulating interspecific competition. We expected that changes in the plastic responses of LMA and N-area under increased nutrient availability would not reflect simply the response to changing light distribution; rather, we hypothesized that, because nutrient availability directly constrains the structural plasticity of foliage, the magnitude of variation in LMA and N area with light availability would be greater in fertilized stands.

## METHODS

*Study sites and treatment.*—The research was conducted in two early successional northern hardwood stands in the White Mountain National Forest, central New Hampshire. The stands were chosen on the basis of similarity in site characteristics (elevation, slope, soils and pre harvest forest composition) and high abundance of pin cherry to be part of a larger study of forest response to fertilization (Fahey *et al.*, 1998). Each stand originated following clearcut harvest; the younger stand was cut in 1978 and the older stand in 1972. This research focussed on six species from a range of shade tolerance classes: very intolerant (pin cherry, paper birch), mid tolerant (yellow birch, red maple) and very tolerant (sugar maple, beech) (Harlow *et al.,* 1979). We also studied the very tolerant, obligate understory species, striped maple (*Acer pensylvanicum* L.).

In each stand two 17 × 17 m plots were established within relatively uniform forest. One plot was chosen to be a reference and the other was fertilized. A balanced fertilizer including micronutrients was added to the soil surface in six applications at 4 wk intervals during the growing season (May–October) from 1989 through 1996. The annual macronutrient additions were (in $g/m^2$): N = 16.7, P = 5.8, K = 25.4, Ca = 31.0 and Mg = 3.7. This dose was chosen to roughly triple nitrogen availability in early successional northern hardwoods (Mou *et al.,* 1993) and, hence, to greatly relax nutrient limitation. Additional detail on the sites and treatment can be found in Fahey *et al.* (1998).

*Leaf area index and light measurements.*—Total leaf area index (LAI) was measured by collecting litterfall using a network of 11 litter traps (0.18 $m^2$ each) in each plot, counting the number of leaves of each species and measuring the average area per leaf on a random subsample of 12–18 leaves of each species for each collection. As detailed below, an independent estimate of LAI was available using readings from a plant canopy analyzer.

The light environment was characterized in each of the four study plots by first quantifying the vertical distribution of leaf area and then using the Beer-Lambert equation with an empirical light extinction coefficient to estimate available light through the canopy. Beginning near the top of the canopy and ending at ground level, a vertical sequence of 10–13 LAI readings with a plant canopy analyzer (model LAI-2000, LiCor Inc., Lincoln, Nebraska) was taken at eight points along the perimeter of the plot. The average LAI at each height was computed using open sky readings from a paired sensor placed in a nearby clearing. All LAI measurements were made at dawn or dusk to approximate isotropic skylight distribution. Because both leafy and woody components were included in these profiles, a correction for the woody components was made by measuring "leaf-off" LAI of woody components only in the fall of 1995. For details on this methodology, *see* Fahey *et al.* (1998).

The amount of short-wave radiation reaching a particular level in the canopy ($Q_i$) was calculated from the Beer-Lambert equation (Larcher, 1995):

$$Q_i = Q_o \times \exp(-k \times LAI_i)$$

where $Q_o$ is incoming PAR at the top of the canopy; k is the extinction coefficient; and $LAI_i$ is the cumulative leaf area index at canopy at level i. $Q_o$ was calculated from solar radiation data collected at the nearby Hubbard Brook Experimental Forest; the average short-wave radiation flux for June and July of 1995 and 1996 was 19.11 $MJ/m^2 \cdot d$. The ratio of energy in the PAR waveband to total radiation is approximately 0.5 (Campbell, 1981). Since this ratio is fairly constant across a wide-range of atmospheric conditions (Campbell, 1981), average growing season $Q_o$ was estimated at our study sites as 9.56 $MJ/m^2 \cdot d$.

The extinction coefficient (k) varies significantly with LAI, according to observations from eastern deciduous forests (Brown and Parker, 1994). We estimated k for each plot (Table 1) from the litterfall LAI measurements and the highly significant regression of k on LAI from the data of Brown and Parker (1994). A comparison of LAI estimates based upon litterfall and plant canopy analyzer readings indicated that the latter method gave consistently lower values by an average 13%. We used the litterfall LAI value to estimate k and the plant canopy analyzer to distribute LAI among canopy layers.

*Foliage measurements.*—In midsummer 1995 representative trees of each species were harvested from areas adjacent to the reference plots. In the older stand sample size was three trees (for beech, red maple, sugar maple and striped maple) or four trees (for pin cherry,

TABLE 1.—Forest characteristics of reference (R) and fertilized (F) plots in the two study sites in central New Hampshire

| Age | Treatment | Canopy height (m) | Leaf area index | k[1] | % Nitrogen[2] in foliage |
|---|---|---|---|---|---|
| 19 y | R | 9.2 | 3.76 | 0.84 | 1.79–2.46 |
| | F | 12.0 | 5.69 | 0.62 | 2.35–3.10 |
| 25 y | R | 11.9 | 5.87 | 0.60 | 1.81–2.39 |
| | F | 14.0 | 6.63 | 0.51 | 2.36–3.20 |

[1] k: light extinction coefficient

[2] Range of values across species; in the younger fertilized plot, excluding red maple (1.32%)

paper birch and yellow birch). In the younger stand sample sizes were larger because the trees were smaller; 14 for pin cherry, six for each of the birches, five for red maple and three for beech, sugar maple and striped maple. Each tree was divided into 1 m height increments and all the foliage for each increment was removed. Random subsamples of 20–30 leaves from each increment were stored in plant presses for laboratory analysis of LMA and N. Total leaf mass for each increment was measured after drying to constant mass at 60 C. These values were used to calculate weighted average LMA and N-area for each species.

In the fertilized plots a different procedure was employed (midsummer 1996) so that destructive harvest of trees in these plots could be minimized. While using a height pole to classify 1 m height increments on sample trees, several twigs were pruned from each height increment using a pruning pole. In the older stand it was necessary to harvest (as above) two large pin cherry and paper birch trees because pruning was impractical above 12 m height. Three trees of each species were sampled in each stand, except for pin cherry, yellow birch and paper birch ($n = 4$). Only two sugar maple trees were available for sampling in the older fertilized plot and none in the younger one. All leaf samples were stored in plant presses until analyzed.

For each leaf sample blade area was measured using a leaf area meter (model 3100, LiCor Inc., Lincoln, Nebraska). The leaves were oven dried to constant mass at 60 C and each leaf was weighed to ±0.1 mg. Samples were pooled within height increments for each species and plot and ground to pass a fine screen (hole size = $0.04\ mm^2$). Nitrogen concentration was measured colorimetrically on these samples following a micro-kjeldahl digestion by the sodium salicylate method.

*Analysis.*—LMA was calculated as the ratio of mass to area for each individual leaf and the mean LMA was calculated at each height increment for each sample tree. As an index of plasticity in foliage morphology, the slope of the regression between LMA and estimated light availability for each height increment was calculated using the General Linear Model of SYSTAT (Wilkinson *et al.*, 1992). Significant differences between the slopes of these regressions were determined by nonoverlap in the 90% confidence intervals calculated using Student's *t* distribution (Neter and Wasserman, 1974); the relaxed confidence interval was used because we anticipated high error in the estimates of light available to each leaf and height increment. Nitrogen content of foliage on a unit leaf area basis (N area) was calculated from mean values of LMA and foliar mass-based concentrations of N for each height increment in each plot. The same procedure as for LMA was used to calculate and compare regressions of N area vs. light.

Differences in LMA and N area between species were analyzed by one-way analysis of variance. Student's *t* statistic was used to compare stand LAI (litter trap method) and foliar

TABLE 2.—Intercepts and slopes of linear regressions between estimated light availability (MJ m$^{-2}$ d$^{-1}$) and leaf mass per unit area (g m$^{-2}$) in the two study sites in central New Hampshire. Within columns, slopes with the same letter are not significantly different ($P > 0.10$). Significant differences in the slopes between reference and fertilized plots for a species are indicated by asterisks (*)

| | Reference | | | Fertilized | |
|---|---|---|---|---|---|
| Species | Intercept | Slope | | Intercept | Slope |
| A. 19-year-old forest | | | | | |
| Pin cherry | 30.8 | $4.40^{a}$ | | ns | ns[1] |
| Paper birch | 36.9 | $6.81^{ab}$ | | 60.2 | 4.20 |
| Yellow birch | 24.7 | $6.24^{ab}$ | | ns | ns |
| Red maple | 32.8 | $9.53^{c}$ | | ns | ns |
| Sugar maple | 27.6 | $10.9^{bc}$ | | na[2] | na |
| American beech | 16.5 | $10.6^{c}$ | | ns | ns |
| Striped maple | 15.7 | $9.31^{bc}$ | | 25.8 | 5.76 |
| B. 25-year-old forest | | | | | |
| Pin cherry | 40.8 | $3.65^{a}$ | | ns | ns |
| Paper birch | 54.7 | $3.72^{a}$ | | 77.6 | $2.84^{a}$ |
| Yellow birch | 38.7 | $5.09^{ab}$ | * | 53.1 | $7.97^{b}$ |
| Red maple | 43.4 | $7.16^{b}$ | | 53.8 | $11.6^{b}$ |
| Sugar maple | 37.3 | $5.84^{b}$ | * | 21.2 | $26.8^{c}$ |
| American beech | 34.7 | $5.86^{b}$ | * | 31.7 | $11.0^{b}$ |
| Striped maple | 22.7 | $11.2^{c}$ | | 30.6 | $12.9^{b}$ |

[1] ns—not significant ($P > 0.05$)

[2] na—not available

N concentration for each species between reference and fertilized plots in each stand. We also computed the linear regressions between foliar N concentration (mass-based) vs. canopy height increments for each species. Finally, we compared the response to fertilization of LMA and N area of sun and shade foliage of each species using Student's *t* statistic. Sun foliage was defined as the upper two height increments and shade foliage as that receiving less than 20% of maximum light availability; pin cherry sometimes had no foliage below this threshold and shade foliage was defined as the two lowest height increments (<25% maximum light).

## RESULTS

*Leaf mass per unit area.*— LMA increased significantly with height in the canopy for all species in the reference plots, and this relationship appeared to be curvilinear and differed greatly among species (data not shown). A linear relationship between LMA and estimated PAR was observed for all species. Generally, the $r^2$ values for these regressions exceeded those for LMA vs. log (height), and the following analysis concentrates on the relationships with light. Slopes of the regression of LMA vs. PAR were significant ($P < 0.05$) for all species in both reference plots (Table 2) and $r^2$ values ranged from 0.66 to 0.99. The rankings of species based on the slope of the LMA-PAR regression were similar in both of the reference plots; significantly higher values were generally observed for beech and the maple species than for pin cherry and the two birch species (Table 2). LAI was significantly higher ($P < 0.05$) in fertilized than reference plots in both stands (Table 1). The effect of fertilization on LMA was not consistent among species; this fertilization effect was complicated by the fact that fertilization also affected the penetration of light through the canopy. Although

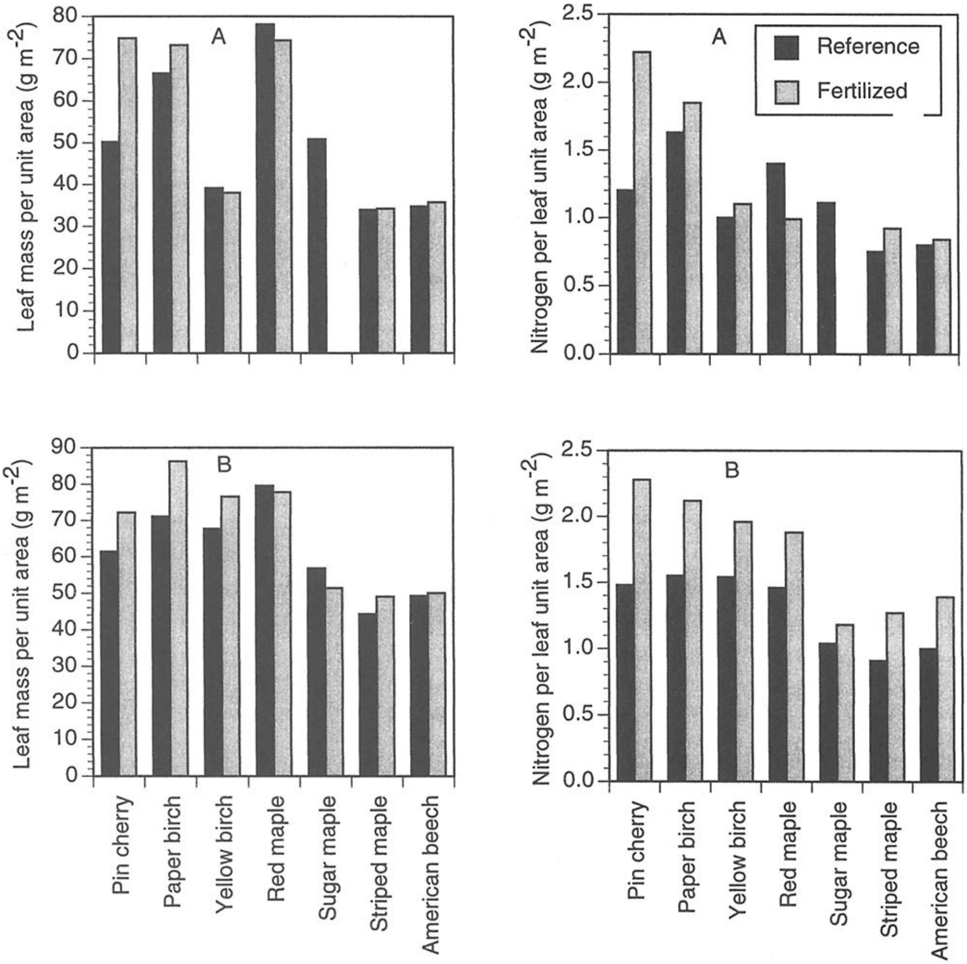

FIG. 1.—Whole-canopy average leaf mass per unit area and area-based N concentration for seven tree species growing in reference and fertilized plots of A, a 19-y old and B, a 25-y-old northern hardwood stand in central New Hampshire. Whole-canopy averages were computed by weighting average values for each height increment in the canopy by the proportion of leaf area in each layer

differences in LMA between fertilized and reference plots were not statistically significant, there was a consistent trend towards higher leaf-area-weighted average LMA for the intolerant species (pin cherry and paper birch) in the fertilized plots (Fig. 1). These averages were computed by weighting the average LMA values for each height increment by the proportion of leaf area in that height increment for each particular species. These weighted averages are based on very large sample sizes (300 to 700 leaves); that is, 20–30 leaves per canopy layer, several canopy layers per tree and several replicate sample trees per plot. Fertilization significantly ($P < 0.05$) increased the LMA of shade foliage of pin cherry and paper birch in the young stand and both birch species in the older stand (Fig. 2). In contrast LMA of sun foliage was not consistently or significantly affected by fertilization.

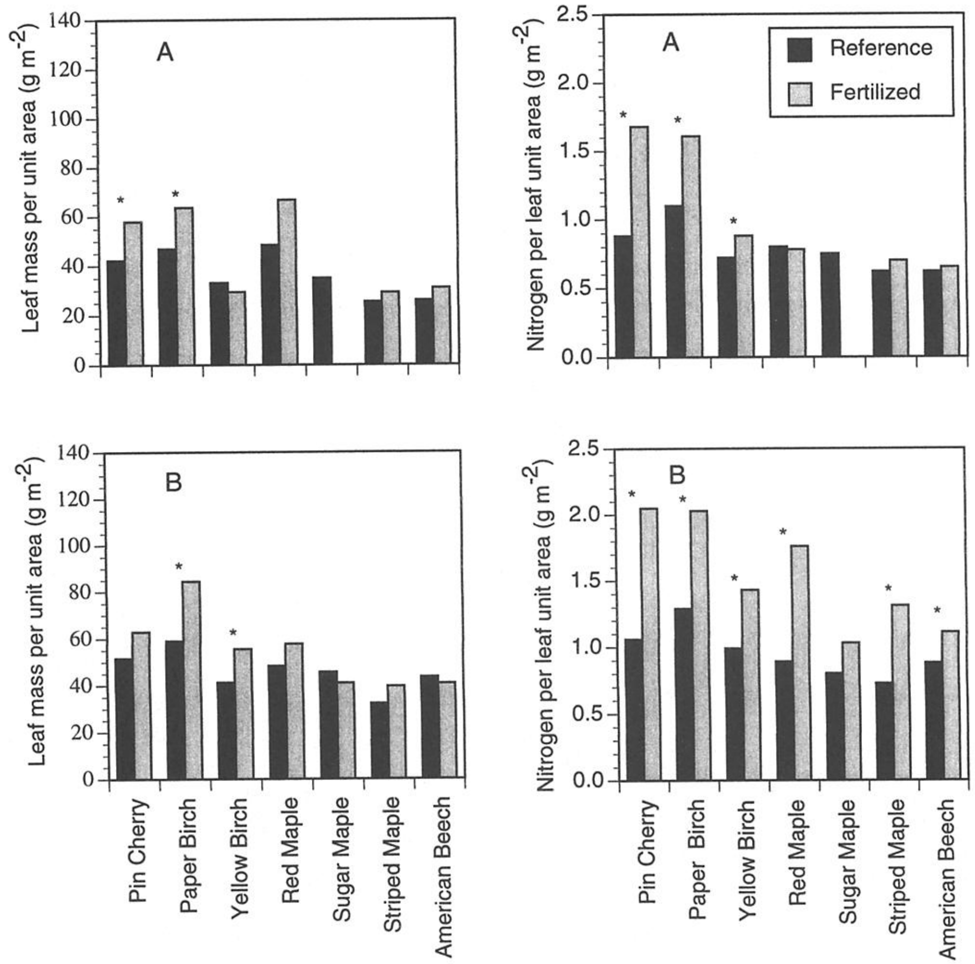

FIG. 2.—Leaf mass per unit area and area-based N concentration for more shaded foliage (<20% of maximum light availability or lowest canopy layers for pin cherry) of seven tree species growing in reference and fertilized plots of A, a 19-y-old and B, a 25-y-old northern hardwood stand in central New Hampshire. Asterisks denote significant ($P < 0.05$) differences between control and fertilized plots

The effects of fertilization on the slope of the LMA-PAR relationship varied among species and stands. In particular, in the older stand the slopes for yellow birch, sugar maple and American beech increased significantly ($P < 0.05$) in response to fertilization; those for red maple and striped maple were not significantly different (Table 2). In the younger stand no significant differences were observed.

*Foliar nitrogen.*—Nitrogen concentration (mass-based) increased significantly with height in the canopy in the reference plots only for pin cherry (older stand) and red maple (younger stand; data not shown). Fertilization resulted in significant increases of foliar N concentrations for most species, the only exceptions being red maple and beech in the

TABLE 3.—Intercepts and slopes of linear regressions between estimated light availability (MJ $m^{-2}$ $d^{-1}$) and area-based nitrogen concentration (g $m^{-2}$) in the two study sites in central New Hampshire. Within columns, slopes appended by the same letter are not significantly different ($P > 0.10$). Significant differences in the slopes between reference and fertilized plots for a species are indicated by asterisks (*)

| | Reference | | | Fertilized | |
|---|---|---|---|---|---|
| Species | Intercept | Slope | | Intercept | Slope |
| A. 19-year-old forest | | | | | |
| Pin cherry | 0.66 | $0.098^{a}$ | | ns[1] | ns |
| Paper birch | 0.88 | $0.164^{ab}$ | | 1.31 | $0.174^{a}$ |
| Yellow birch | 0.53 | $0.184^{ab}$ | | ns | ns |
| Red maple | 0.55 | $0.181^{ab}$ | | ns | ns |
| Sugar maple | 0.60 | $0.246^{ab}$ | | na[2] | na |
| American beech | 0.36 | $0.263^{b}$ | | ns | ns |
| Striped maple | 0.40 | $0.190^{ab}$ | | 0.54 | $0.257^{a}$ |
| B. 25-year-old forest | | | | | |
| Pin cherry | 0.90 | $0.104^{a}$ | | ns | ns |
| Paper birch | 1.20 | $0.085^{a}$ | | 1.77 | $0.115^{a}$ |
| Yellow birch | 0.82 | $0.136^{a}$ | * | 1.33 | $0.179^{ab}$ |
| Red maple | 0.74 | $0.144^{a}$ | | 1.22 | $0.316^{bc}$ |
| Sugar maple | 0.65 | $0.188^{a}$ | * | 0.64 | $0.480^{bc}$ |
| American beech | 0.69 | $0.133^{a}$ | * | 0.79 | $0.290^{bc}$ |
| Striped maple | 0.44 | $0.246^{b}$ | | 0.72 | $0.468^{c}$ |

[1] ns—not significant ($P > 0.05$)

[2] na—not available

younger stand (data not shown); foliar N of red maple in the young fertilized plot was exceptionally low (Table 1). For paper birch, yellow birch and striped maple fertilization resulted in highly significant ($P < 0.01$) slopes of the N concentration (mass-based) vs. height regression in both stands, as concentrations increased more in the upper than lower canopy foliage. This effect did not occur for the other species.

In the reference plots slopes of the regressions between area-based N concentration (N area) and estimated light availability were highly significant ($P < 0.01$) for all species (Table 3). The rankings of slopes among species were comparable to those for LMA, but few of the between-species differences were statistically significant. Fertilization resulted in significant increases in N area for pin cherry in the young stand and pin cherry and paper birch in the older stand. This effect resulted mostly from the response of shade foliage; in fact, N area increased significantly for shade foliage of most of the species (Fig. 2), whereas N area of sun foliage was not significantly different between reference and fertilized plots.

In the older stand fertilization significantly increased the slope of the N area vs. light regression for four species (yellow birch, sugar maple, beech, striped maple; Table 3). The more shade tolerant species generally exhibited significantly higher slopes of this regression in the fertilized plots in the older stand. In contrast, in the fertilized plot of the young stand the N area vs. light regression was significant only for two species (paper birch and striped maple).

## DISCUSSION

Our goal was to elucidate how foliar characteristics of forest trees are connected with the pattern and process of stand development following large-scale disturbance. Previous research has demonstrated that several leaf traits may vary systematically through the canopy of individual trees in response to differences in light availability. Particularly prominent are increases in LMA and N-area with increasing height in the canopy of both temperate (Hollinger, 1989; Ellsworth and Reich, 1993) and tropical forests (Medina and Klinge, 1983). These plastic responses of foliage to variation in light availability may maximize whole-canopy carbon gain of individual trees by optimizing photosynthetic capacity (Jurik, 1986) and the distribution of limited amounts of nitrogen (DeJong and Doyle, 1985; Hirose and Werger, 1987), and they may be controlled both physiologically and ontogenetically (Traw and Ackerly, 1995). Our results support and extend the observation of Goulet and Bellefleur (1986) that foliage plasticity is related functionally to shade tolerance: this relationship holds across a group of seven species growing in early successional stands and applies to N-area as well as LMA. That is, we observed that the slope of regressions of LMA and N-area against estimated light availability generally were lower for shade intolerant than tolerant species (Table 2), indicating greater plasticity in the tolerant species.

This interpretation of the patterns needs to be qualified by three observations. First, a confounding taxonomic effect may contribute to the pattern, as the intermediate tolerant red maple followed the pattern of its more tolerant congeners (sugar maple and striped maple), whereas yellow birch, also an intermediate species, followed the pattern of its intolerant congener (paper birch). It is also notable that a summary of recent studies has suggested that the shade tolerance of red maple is relatively high (Abrams, 1998). A wider survey of other genera that contain species of differing tolerance could address possible taxonomic relationships. Second, if the mode of origin of individuals influences foliage plasticity, it might be confounding that the birches and pin cherry usually reproduce from seed whereas beech, striped maple and red maple commonly arise by vegetative sprouting following disturbance in these northern hardwood forests (Hughes, 1986). A systematic comparison between individuals of seed and sprout origin would be needed to evaluate this explanation. Finally, the overall design of this study limits the generality of inferences that can be drawn from the results because the treatment was replicated in only two sites. This limitation was unavoidable because of the large number of samples required to characterize LMA (*e.g.*, this study included about 10,000 measurements of LMA).

The high foliage plasticity of striped maple (Table 2) fits the life history of this species and illustrates the important role of plasticity for a species that experiences a highly variable light environment. Striped maple is a common understory tree that survives as suppressed seedlings for up to 20 y but grows rapidly in response to canopy disturbance (Hibbs *et al.*, 1980). Modulation of leaf morphology would seem to coincide with this combination of shade tolerance and rapid growth. Wilson and Fischer (1977) observed that striped maple first produces a pair of shade leaves on every shoot, but that subsequent leaf pairs are only produced in a high light environment. Although individual striped maple leaves exhibit little physiological plasticity (Jurik *et al.*, 1988), high morphological plasticity probably contributes to an effective strategy for striped maple in the understory of northern hardwood forests.

Some of the unexplained variation in the regressions between light availability and LMA or N area probably resulted from our approach to estimating light availability for different canopy layers. Undoubtedly, the spatial variability of light availability in each canopy layer is high and our estimates could exhibit systematic bias across species because of self-shading within individual tree crowns. As detailed by Fahey *et al.* (1998), the relative positions in the canopy of the different species were affected by the fertilization treatment. Also, the effects of variation in branch and leaf angles, leaf thickness and pigmentation may reduce the accuracy of the light estimates by influencing the reflection and transmission of radiation through the canopy and, consequently, the effective light extinction coefficient (Canham *et al.,* 1994). Unfortunately, direct measurements of the light environment for the large samples needed in this sort of study were not possible.

Fertilization resulted in significant increases in LAI in both stands and, consequently, greater attenuation of light. Hence, it was surprising that the canopy average LMA of the intolerant species, pin cherry and paper birch, was higher in the fertilized plots (Fig. 1). The base of the live crown of these species (only) was about 2 m higher in the fertilized than the reference plots in both stands, a value that corresponds with the overall differences in canopy height (Table 1). The increase in canopy average LMA resulted from significantly higher LMA of shaded foliage in the fertilized plots (Fig. 2), suggesting that in the reference plots LMA of shaded foliage was constrained by limited availability of nutrients to allocate to lower leaves. As pointed out by DeJong and Doyle (1985), the light environment of lower foliage of trees is characterized by shorter intervals of high light rather than simply continuously low light. The effect of fertilization was to markedly increase the area-based N concentration of this shaded foliage (Fig. 2), permitting higher photosynthesis rates (Ellsworth and Reich, 1993). Thus, increased N availability may allow intolerant species to allocate larger amounts of N to shaded foliage with the effects on LMA resulting from consequent potential for high photosynthetic rates in the shifting light environment lower in the canopy.

In contrast, nutritional constraints on more shade tolerant species are fundamentally different; canopy-average LMA of these species did not respond to fertilization (Fig. 1). This observation might reflect the higher total LAI in these plots, as well as the greater canopy dominance of the intolerant species, especially pin cherry (Fahey *et al.,* 1998). Moreover, in the older stand fertilization caused an increase of the plastic response of both LMA and N area to differences in light availability through the canopy in the tolerant species (Table 2). Although the fertilized plots and the reference plots were sampled in different years, previous measurements in these sites indicated that foliar nitrogen concentration did not differ significantly across four years of measurement and LMA between two years (Fahey *et al.,* 1998). Climatic conditions also were similar in both years.

Although further study of the contrasting patterns of response of LMA and N area to fertilization between intolerant and tolerant northern hardwood species is needed, our results indicate that the shade tolerance of trees influences both the plasticity of leaf characteristics as well as the effects of nutrient limitation on those characteristics. Of particular interest would be comparative measurements in reference and fertilized treatments of: (1) photosynthetic light response curves of foliage from different canopy positions; (2) light environment within the crowns of individual trees; and (3) allocation of foliar N between pigments and carboxylation enzymes. These measurements would improve understanding of the mechanistic basis of nutritional effects on the outcome of interspecific competition in mixed species forest stands (Fahey *et al.,* 1998).

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