

Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient

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Abstract: Height and lateral growth, biomass distribution, leaf morphology, and crown architecture were studied in yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), and beech (*Fagus grandifolia* Ehrh.) seedlings growing under 1–50% of above-canopy light in a sugar maple stand, in Quebec. All three species showed increasing growth with increasing light, but growth of yellow birch was higher and more responsive than that of sugar maple and beech. All three species showed typical sun–shade morphological responses, such as decreasing specific leaf area and leaf area ratio, and increasing leaf area index, with increasing light availability. Sugar maple was morphologically more plastic than the other species. It showed variations in biomass allocation to leaves and branches, a decrease in branch length to seedling height ratio, and a marked increase in the ratio of leaf area to stem length. Although our results clearly demonstrate the ability of these three species to modify several of their morphological features in response to variations in light, they do not show a clear relationship between species shade tolerance and morphological response to light variations. We suggest that species-specific developmental patterns may act as important constraints to morphological acclimation to light variation.

Résumé : La croissance latérale et en hauteur, la distribution de la biomasse, la morphologie foliaire et l'architecture de la cime ont été étudiées chez des semis de bouleau jaune (*Betula alleghaniensis* Britton), d'érable à sucre (*Acer saccharum* Marsh.) et de hêtre (*Fagus grandifolia* Ehrh.) qui croissaient dans des conditions de luminosité variant de 1 à 50% de la lumière incidente dans un peuplement d'érable à sucre au Québec. Chez les trois espèces, la croissance augmentait à mesure qu'il y avait plus de lumière mais la croissance du bouleau jaune était plus forte et réagissait davantage comparativement à celle de l'érable à sucre et du hêtre. Les trois espèces avaient des réactions morphologiques typiques de conditions de lumière et d'ombrage telles qu'une diminution de la surface foliaire spécifique et du ratio de la surface foliaire, ainsi qu'une augmentation de l'indice de surface foliaire, à mesure que la quantité de lumière augmentait. L'érable à sucre était plus plastique que les autres espèces. Cette essence exhibait des variations dans l'allocation de la biomasse vers les feuilles et les branches, une diminution du rapport entre la longueur des branches et la hauteur des semis, ainsi qu'une augmentation marquée dans le rapport entre la surface foliaire et la longueur de la tige. Même si nos résultats démontrent clairement la capacité de ces trois espèces à modifier plusieurs de leurs caractéristiques morphologiques en réaction à des variations de la luminosité, ils ne suggèrent aucune relation précise entre la tolérance à l'ombre de ces espèces et leurs réactions morphologiques aux variations de la luminosité. Nous croyons que les patrons de développement spécifiques à ces espèces peuvent occasionner d'importantes contraintes pour leur acclimation aux variations de la luminosité.

[Traduit par la Rédaction]

Introduction

In the temperate deciduous forests of eastern North America, small-scale disturbances such as relatively small canopy gaps have been shown to play an important role in forest dynamics (Runkle 1985). These canopy gaps can be created by a variety of natural causes (e.g., branch falls, ice storm damage, individual tree death, etc.) or by silvicultural interven-

tions (Runkle 1991; Coates and Burton 1997). Canopy openings increase light levels and affect other characteristics of the environment (Collins et al. 1985). The response of tree species to the variations in environmental conditions, including light availability, that result from canopy gap formation differs between species (Bazzaz 1979), and these interspecific differences have significant implications for forest dynamics (Canham and Marks 1985; Canham 1989).

Species-specific patterns of extension growth are important to tree seedlings, because it is through extension growth that seedlings exploit available space, forage for higher light microsites, and possibly overtop surrounding vegetation (Caldwell 1987; King 1994; Küppers 1994; Givnish 1995). Mechanisms that underlie species-specific growth response to variation in light availability include leaf-level physiological and morphological acclimation, as well as plant-level acclimation, such as changes in biomass distribution and

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crown architecture (Kitajima 1994; Sipe and Bazzaz 1994). The importance of crown morphological characteristics that determine the pattern of light interception by leaves in the canopy has been investigated in a number of recent studies (Kohyama 1987; Canham 1988, 1989; Küppers 1989, 1994; King 1994; Givnish 1995). Changes in crown morphology have been shown to play an important role in the acclimation capacity of species to different light environments, and crown morphological plasticity was found to be especially important to shade-tolerant species (Canham 1988, 1989).

In this study, we investigated the response of extension growth, biomass distribution, leaf morphology, and crown architecture to a gradient of light conditions in naturally regenerating seedlings of three sympatric hardwood species: yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), and American beech (*Fagus grandifolia* Ehrh.). These species are the major overstory components of the sugar maple – yellow birch – beech forest type, and they differ in shade tolerance. Yellow birch is generally classified as mid-tolerant (Baker 1949). Its establishment is favored by an opening in the canopy coupled with soil disturbance (Erdmann 1990). Sugar maple and beech are both very tolerant of shade (Baker 1949), beech more so than sugar maple (Kobe et al. 1995). They can both survive for many years under a closed canopy as advance regeneration and are able to sustain multiple episodes of growth suppression (Canham 1985, 1990).

The objectives of this study are (i) to compare the extension growth responses of naturally established yellow birch, sugar maple, and beech seedlings growing under a range of natural light conditions; (ii) to determine the most important morphological characteristics that differentiate yellow birch, sugar maple, and beech seedlings; and (iii) to compare the morphological responses of seedlings of these three species to variations in light conditions.

In this study, the gradient of natural light conditions was obtained by selecting seedlings under a range of canopy openness. Other environmental factors such as light spectral quality, density of surrounding vegetation, water and nutrient availability, and microclimate (e.g., air temperature) often vary among microsites with differing canopy openness and light regimes (Collins et al. 1985). Therefore, the growth and morphological responses observed in this study across the gradient of natural light conditions reflect the cumulative effects of all those factors.

Methods

Study site and seedlings

This study was conducted in a sugar maple – yellow birch – beech stand in the Duchesnay Experimental Forest (46°55'N, 71°40'W), near Québec, Canada. The stand was located on a moderate, south-facing slope (5–10°) at an elevation of approximately 250 m. The humus was a moder, with a humo-ferric podzol soil underlain with well-drained glacial till. Mean annual precipitation was 1200 mm, and mean daily temperature ranged from –13°C in January to 18°C in July (Environment Canada 1982).

The overstory was dominated by sugar maple, beech, and yellow birch (60, 20 and 15% of merchantable volume, respectively) (Majcen and Richard 1991). American yew (*Taxus canadensis* Marsh.), mooseberry (*Viburnum alnifolium* Marsh.), and striped maple (*Acer pensylvanicum* L.) were found in the understory. Pin

cherry (*Prunus pensylvanica* L.f.), red-berried elder (*Sambucus pubens* Michx.), and red raspberry (*Rubus idaeus* L.) were present under some canopy gaps.

Part of the stand (approximately 15 ha) was subjected to a selection cut of hardwood species in the fall of 1989. Approximately 30% of the basal area was harvested through a mix of single- and multiple-tree selection, leaving a residual basal area of approximately 17.5 m²·ha⁻¹ (Majcen and Richard 1991). In this area of the study site, canopy gaps ranged in size from approximately 50 to 300 m².

In May 1993 we randomly selected yellow birch, sugar maple, and beech seedlings growing in gaps (total $n = 30$ per species) as well as under a closed canopy (total $n = 15$ per species). Selected seedlings measured between 0.5 and 2 m in height, had no obvious morphological defects due to previous injury, and were dominant compared with the surrounding understory vegetation. To improve the completeness of the data set, another set of yellow birch, sugar maple, and beech seedlings (total $n = 15$ per species) was sampled in 1995. These seedlings were selected along transect lines established in the selectively logged area of the stand, and we used the same selection criteria as described above. Considering the size of the seedlings we studied (0.5–2 m at the time of measurements) and the crown development that had occurred over 4–6 years since gap formation, we assumed that the morphological characteristics of the seedlings were mostly the result of crown development that had occurred under the new understory conditions created since the cut.

Light measurements

The percentage of above-canopy light (photosynthetic photon flux density (PPFD) 400–700 nm) reaching the top of each seedling was used to describe the light environment of each individual and can be viewed as an index of the overall understory growing conditions of each seedling. Light measurements were taken under completely overcast sky conditions following the method described in Parent and Messier (1996). Results obtained by Messier and Puttonen (1995a), and Parent and Messier (1996) have shown that %PPFD measured at any time during the day under overcast sky conditions is representative of the mean daily %PPFD reaching a point in the understory for both clear and overcast conditions.

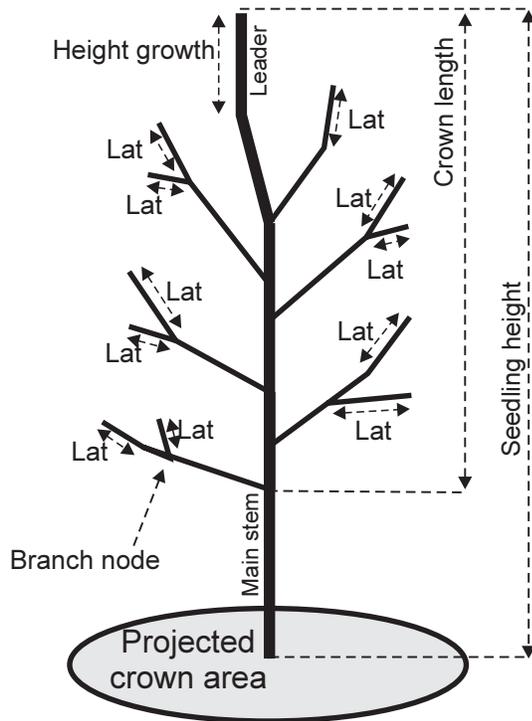
Light measurements were taken in July and August of 1993 and 1995 between 08:00 and 17:00 eastern standard time. Above-canopy PPFD was measured with a point quantum sensor (LI-190SA, LICOR, Lincoln, Neb.) installed 3 m above the ground in an open area located 0.5 km away from the study site. This sensor was linked to a datalogger (LI-1000, LICOR, Lincoln, Neb.), which recorded 1-min averages of readings taken every 5 s. A second point quantum sensor was used to measure PPFD above each seedling. The time of each measurement was recorded and %PPFD for each seedling was calculated as a percentage of above-canopy PPFD.

Growth, biomass, and morphological measurements

The total height, crown length, average crown diameter, projected crown area, and stem diameter at the root collar were measured in the field for each seedling. The base of the crown was defined as the lowest leaf-bearing branch (Fig. 1). The average crown diameter was calculated as the mean of two perpendicular diameter measurements, one of which was the maximum crown diameter.

Seedlings were harvested at the end of August (1993 or 1995) and brought to the laboratory. We assumed that the annual extension growth would be completed by that time for the three study species (Marks 1975; Bicknell 1982). The current-year (1993 or 1995) extension growth of the leader and of all lateral shoots were measured using bud scars to separate successive growth increments.

Fig. 1. Schematic representation of a seedling, and some of the measured variables. Height growth was measured on the leader, defined as the shoot reaching the highest point in the crown. Lateral growth was measured on each lateral shoot ending (Lat). Main branches are those that originate from the main stem (this seedling would have six main branches). The total length of branches is the length of all woody structures except the main stem. A branch node was defined as any intersection point between more than two branch segments (this seedling would have 11 branch nodes). See Methods for more information.



The leader was defined as the shoot that reached the highest point of the crown (Fig. 1). All other shoots were referred to as lateral branches (Fig. 1). In the measurement of extension growth, we did not correct for the departure of shoot angle from vertical (for the leader) or from horizontal (for the lateral shoots). Lateral extension growth was averaged for all lateral shoots to calculate the mean lateral growth. Only the current-year growth results were analysed, because we found in another study that although absolute growth rates vary from year to year, no difference in the ranking of the species occurs among years (J.P. Ricard and C. Messier, unpublished manuscript). We recorded the number of branches that originated from the main stem and the number of branch nodes (Fig. 1). The length of the main stem (measured from the root collar to the tip of the leader) and the length of all branches were measured. All woody structures were then dried at 65°C for 5 days and weighed.

The number of leaves was recorded for each seedling. All leaves were dried at 65°C for 3 days and weighed, except for a subsample of 40 randomly chosen leaves per seedling (or less when the number of leaves of a seedling was <40; the minimum number of leaves was 18) that was kept in the freezer for subsequent measurements of leaf area, petiole length and specific leaf area (SLA). The mean leaf area and mean petiole length of each seedling were obtained by analysing a digitized image of the subsample of leaves with the MacFolia software package (Régent Instruments Inc., Québec, Que.). The subsample of leaves was then dried and weighed. Each seedling's SLA was calculated from the subsample as the ratio of leaf area to leaf dry weight. The total leaf area per

seedling was estimated from the product of the SLA and the dry weight of all leaves, while the total petiole length per seedling was estimated from the product of the mean individual petiole length and the total number of leaves.

A number of ratios were calculated from the above-mentioned variables. The ratio of height growth to mean lateral growth was calculated, as well as percentages of aboveground dry weight in leaves, branches, and main stem. Leaf display was described by the leaf area index (LAI; total leaf area/projected crown area), the leaf area ratio (LAR; total leaf area/aboveground biomass), and an index of efficiency of leaf display (ELD), which was defined as the ratio of total leaf area to total length of branches and main stem (Canham 1988; Lei and Lechowicz 1990). The importance of petioles as leaf-support structure was assessed by calculating the percentage of the total length of leaf-support structure in petioles (total petiole length/total length of petioles, branches, and main stem \times 100). Crown shape was described by the ratio of crown length to mean crown diameter (RCLD). We also calculated the ratio of total branch length to seedling height (RBLH), and the ratio of seedling height to stem diameter at root collar.

Statistical analysis

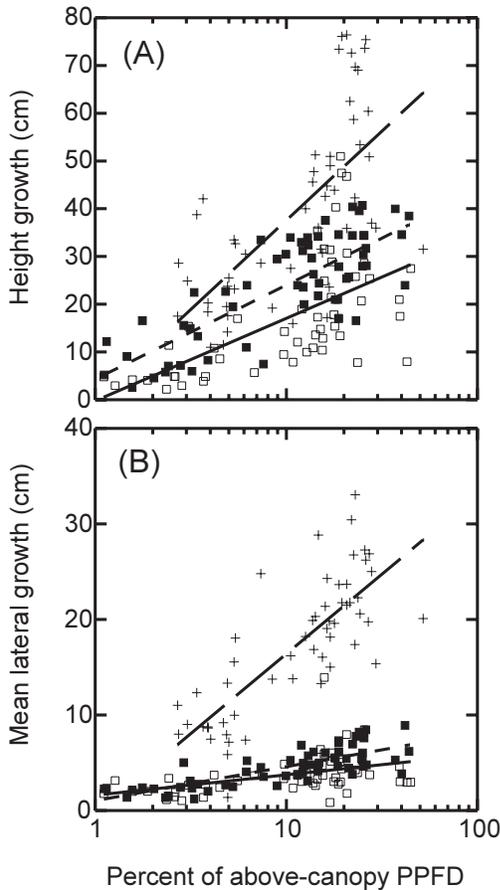
The response of growth, biomass distribution, and morphological variables to variation in light availability was investigated for each species using linear regression analysis. The independent variable, %PPFD, was transformed to its natural logarithm when necessary to meet the conditions of normality and homoscedasticity. Differences in slope coefficients between species were tested by examining the significance of the interaction term between species and light availability, using the general linear model procedure of SYSTAT, version 7.0. When the slopes were not found to be significantly different between species, we tested for further differences among species using analysis of covariance (with species as the main factor and light availability as the covariate). Unless otherwise indicated, probability values <0.05 were considered significant. All statistical analyses were conducted using SYSTAT, version 7.0.

Results

Height and lateral growth

All three species showed increases in height growth (Fig. 2A) and mean lateral growth (Fig. 2B) in response to increased %PPFD. The effect of light on growth differed between species (height growth: $P = 0.001$; mean lateral growth: $P < 0.001$). Yellow birch showed the most pronounced increases in both height and lateral growth (Fig. 2). The effect of %PPFD on height growth did not differ significantly between sugar maple and beech ($P = 0.518$). Therefore, differences in height growth between sugar maple and beech were further tested by analysis of covariance (with \ln PPFD as the covariate). Height growth was found to be significantly higher in beech than in sugar maple ($P < 0.001$). The ratio of height growth to mean lateral growth did not vary with %PPFD in yellow birch ($R^2 = 0.034$, $P = 0.181$) and beech ($R^2 = 0.010$, $P = 0.454$). However, a weak positive relationship was found for sugar maple ($y = 1.73 \ln \text{PPFD} + 1.26$, $R^2 = 0.090$, $P = 0.031$; data not shown), which indicates that, for sugar maple, height growth increased more rapidly than mean lateral growth with increasing %PPFD.

Fig. 2. Scatterplots and fitted regression lines of (A) height growth for yellow birch ($y = 16.21 \ln x + 0.25$, $R^2 = 0.431$, $P < 0.001$), sugar maple ($y = 7.51 \ln x - 0.23$, $R^2 = 0.358$, $P < 0.001$), and beech ($y = 8.56 \ln x + 4.31$, $R^2 = 0.623$, $P < 0.001$), and (B) mean lateral growth for yellow birch ($y = 7.25 \ln x - 0.29$, $R^2 = 0.610$, $P < 0.001$), sugar maple ($y = 0.92 \ln x + 1.60$, $R^2 = 0.172$, $P = 0.002$), and beech ($y = 1.54 \ln x + 1.05$, $R^2 = 0.605$, $P < 0.001$) on the percentage of above-canopy PPFD. Yellow birch (crosses and long-dashed broken line), sugar maple (open squares and solid line), beech (solid squares and short-dashed broken line).



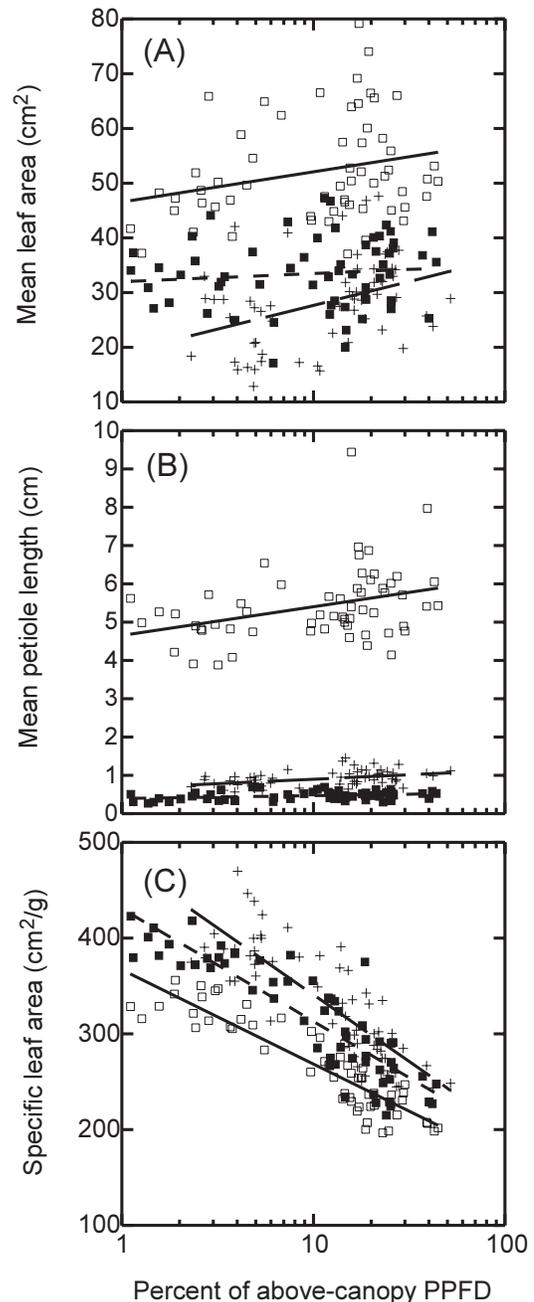
Biomass distribution

Only sugar maple showed a variation in biomass distribution with increasing light. A weak positive relationship was found with the percentage of foliar biomass ($y = 1.90 \ln \text{PPFD} + 23.68$, $R^2 = 0.111$, $P = 0.011$), while a weak negative relationship was found with the percentage of branch biomass ($y = -2.44 \ln \text{PPFD} + 19.12$, $R^2 = 0.156$, $P = 0.004$). No light-related variation was found in the percentage of biomass in the main stem for any of the three species (yellow birch: $P = 0.943$; sugar maple: $P = 0.492$; beech: $P = 0.127$; data not shown).

Leaf characteristics

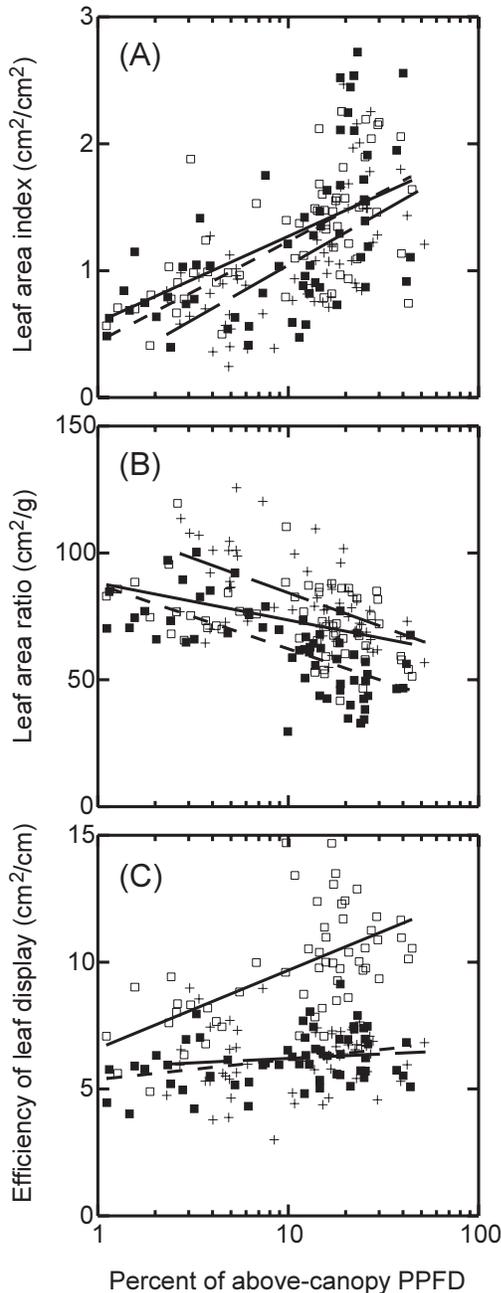
Leaf area increased with increasing %PPFD in yellow birch and sugar maple (Fig. 3A) but did not vary in beech ($P = 0.429$). There was, however, much variability in the data (Fig. 3A), and the relationship observed for sugar ma-

Fig. 3. Scatterplots and fitted regression lines of (A) mean leaf area for yellow birch ($y = 3.78 \ln x + 18.96$, $R^2 = 0.145$, $P = 0.003$), sugar maple ($y = 2.40 \ln x + 46.56$, $R^2 = 0.064$, $P = 0.053$), and beech ($y = 0.67 \ln x + 31.98$, $R^2 = 0.011$, $P = 0.429$); (B) mean petiole length for yellow birch ($y = 0.10 \ln x + 0.67$, $R^2 = 0.161$, $P = 0.001$), sugar maple ($y = 0.33 \ln x + 4.65$, $R^2 = 0.118$, $P = 0.008$), and beech ($y = 0.03 \ln x + 0.40$, $R^2 = 0.100$, $P = 0.014$); and (C) specific leaf area for yellow birch ($y = -60.64 \ln x + 480.41$, $R^2 = 0.686$, $P < 0.001$), sugar maple ($y = -42.80 \ln x + 366.99$, $R^2 = 0.815$, $P < 0.001$), and beech ($y = -51.22 \ln x + 430.83$, $R^2 = 0.771$, $P < 0.001$) on the percentage of above-canopy PPFD. Symbols and line styles are as in Fig. 2.



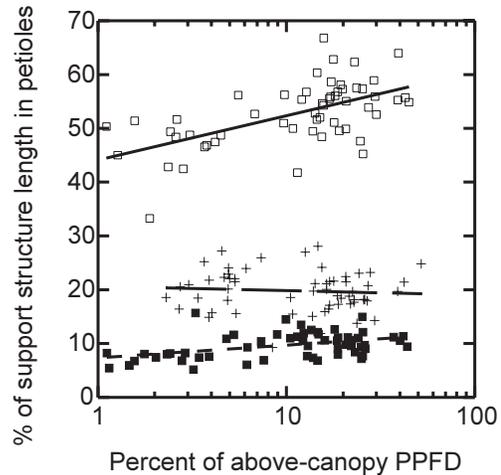
ple was only marginally significant ($P = 0.053$). Petiole length increased slightly with increasing light in all three study species (Fig. 3B). Slopes differed between species

Fig. 4. Scatterplots and fitted regression lines of (A) leaf area index for yellow birch ($y = 0.372 \ln x + 0.187$, $R^2 = 0.382$, $P < 0.001$), sugar maple ($y = 0.295 \ln x + 0.591$, $R^2 = 0.380$, $P < 0.001$), and beech ($y = 0.344 \ln x + 0.439$, $R^2 = 0.329$, $P < 0.001$); (B) leaf area ratio for yellow birch ($y = -11.81 \ln x + 111.49$, $R^2 = 0.315$, $P < 0.001$), sugar maple ($y = -6.34 \ln x + 88.17$, $R^2 = 0.181$, $P = 0.001$), and beech ($y = -11.03 \ln x + 87.62$, $R^2 = 0.448$, $P < 0.001$); and (C) efficiency of leaf display for yellow birch ($y = 0.155 \ln x + 5.848$, $R^2 = 0.011$, $P = 0.435$), sugar maple ($y = 1.341 \ln x + 6.586$, $R^2 = 0.361$, $P < 0.001$), and beech ($y = 0.348 \ln x + 5.373$, $R^2 = 0.110$, $P = 0.011$) on the percentage of above-canopy PPFD. Symbols and line styles are as in Fig. 2.



($P = 0.009$) with beech having a more modest increase in petiole length than the other two. SLA showed a strong negative response to increasing light in all species (Fig. 3C).

Fig. 5. Scatterplot and fitted regression lines of the percentage of leaf-support structure length in petioles for yellow birch ($y = -0.350 \ln x + 20.638$, $R^2 = 0.006$, $P = 0.571$), sugar maple ($y = 3.589 \ln x + 44.069$, $R^2 = 0.343$, $P < 0.001$), and beech ($y = 1.024 \ln x + 7.336$, $R^2 = 0.184$, $P = 0.001$) on the percentage of above-canopy PPFD. Symbols and line styles are as in Fig. 2.

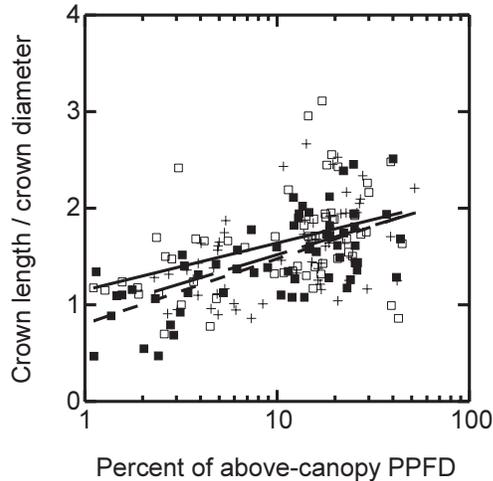


The slope of the regression lines differed between species ($P = 0.011$), the difference being significant between birch and maple only (birch vs. maple: $P = 0.003$; birch vs. beech: $P = 0.145$; maple vs. beech: $P = 0.071$). The number of leaves in the crown did not vary with %PPFD for any of the species (yellow birch: $P = 0.788$; sugar maple: $P = 0.574$; beech: $P = 0.161$; data not shown).

Leaf display, branching pattern, and crown architecture

LAI increased (Fig. 4A), while LAR decreased (Fig. 4B), with increasing light in all three species. For both LAI and LAR, there was no difference in slope between species (LAI: $P = 0.665$; LAR: $P = 0.092$). Actual LAI values did not differ between species ($P = 0.205$). LAR values differed between species ($P < 0.001$), however, with yellow birch having the highest mean LAR (82.2 ± 2.2 , mean \pm SE), followed by sugar maple (73.1 ± 1.9), and then beech (62.3 ± 2.2) (birch vs. maple: $P = 0.006$; birch vs. beech: $P < 0.001$; maple vs. beech: $P = 0.001$; Tukey's test). ELD increased markedly with increasing light for sugar maple, while the increase in ELD was much less pronounced for beech and not significant at all for yellow birch (Fig. 4C). The percentage of the leaf-support structure length in petioles increased with increasing light in both sugar maple ($P < 0.001$) and beech ($P = 0.001$), but not in yellow birch ($P = 0.571$) (Fig. 5). The increase in the percentage of the leaf-support structure length in petioles was significantly more pronounced in sugar maple than in beech ($P = 0.001$). The percentage of the leaf-support structure length in petiole also varied markedly between species, from 15 to 20% in beech and yellow birch to more than 40% in sugar maple (Fig. 5). RBLH decreased with increasing light in sugar maple ($y = -0.37 \ln \text{PPFD} + 2.61$, $R^2 = 0.165$, $P = 0.003$) but did not vary for yellow birch ($P = 0.640$) or beech ($P = 0.268$) (data not shown). The number of branch nodes did not vary as a function of light for any of the species, although beech had a much

Fig. 6. Scatterplot and fitted regression lines of the ratio of crown length to crown diameter (RCLD) for yellow birch ($y = 0.262 \ln x + 0.918$, $R^2 = 0.226$, $P < 0.001$), sugar maple ($y = 0.212 \ln x + 1.151$, $R^2 = 0.173$, $P = 0.001$), and beech ($y = 0.293 \ln x + 0.803$, $R^2 = 0.438$, $P < 0.001$) on the percentage of above-canopy PPFD. Symbols and line styles are as in Fig. 2.



higher number of branch nodes (45 ± 3) than the other two (yellow birch: 19 ± 1 ; sugar maple: 15 ± 1) (birch vs. maple: $P = 0.300$; birch vs. beech and maple vs. beech: $P < 0.001$; Tukey's test). The number of branches also did not vary with %PPFD for any of the species (data not shown), but differed between species ($P = 0.009$), with beech having a higher number of branches (13.9 ± 0.5) than yellow birch (9.9 ± 0.4) and sugar maple (9.5 ± 0.5) (birch vs. maple: $P = 0.840$; birch vs. beech and maple vs. beech: $P < 0.001$; Tukey's test). RCLD increased with increasing light in all species (Fig. 6), with no difference in slope between species ($P = 0.545$). The seedling height to stem diameter at the root collar ratio did not vary with light for any of the species (data not shown), but differed between species ($P < 0.001$); yellow birch (147.8 ± 4.3 , mean \pm SE) had a higher ratio than either sugar maple (122.8 ± 3.4) or beech (122.5 ± 2.8) (birch vs. maple and birch vs. beech: $P < 0.001$; maple vs. beech: $P = 0.999$; Tukey's test).

Discussion

Interspecific differences in growth patterns

The main characteristic that distinguished the mid-tolerant yellow birch from the more shade-tolerant sugar maple and beech was its opportunistic pattern of extension growth. Although all three species showed increased extension growth in response to increased %PPFD, both the height and the lateral growth of yellow birch were higher and more responsive to increased %PPFD than in sugar maple and beech. Yellow birch also had a higher ratio of height to stem diameter at the root collar than the other two species. This growth strategy is associated with an indeterminate growth pattern (Marks 1975; Bicknell 1982) and appears well adapted for the exploitation of the temporarily higher light levels found under canopy openings. Under canopy gaps, a growth strategy that favors height increment helps to enable seedlings to reach and maintain a dominant position relative to their

neighbors and to reach the overstory before gap closure occurs (Hibbs 1982; Runkle and Yetter 1987).

Not only did yellow birch have higher growth rates than sugar maple and beech under relatively high %PPFD, but also under the most shaded conditions. High growth rates in both sun and shade have also been reported for yellow birch by Logan (1965), Bellefleur and LaRocque (1983), and Walters et al. (1993). This tendency of sustained height growth in shade may be characteristic of less shade-tolerant species, which may lack the ability to temporarily suppress their growth, and may reflect a light-seeking strategy for species adapted to the exploitation of high-resource environments (Walters et al. 1993). However, species that maintain high growth rates in shade have been shown to incur higher rates of mortality (Kitajima 1994; Kobe et al. 1995). It has been suggested that a high growth rate in shade occurs as a trade-off with resource allocation to attributes favoring long-term survival, such as allocation to root growth (Logan 1965; Marks 1975; Walters et al. 1993), stem diameter, wood density, starch reserves, and defensive compounds (Kitajima 1994; Pacala et al. 1994; Walters and Reich 1996). For instance, Logan (1965) observed that yellow birch maintained higher height growth rates than sugar maple under both high and low light conditions (from 100 to 13% of full sunlight) but had, in shade, a much lower biomass allocation to roots than sugar maple. As well, results reported in Kobe et al. (1995) and in Pacala et al. (1996) indicate that the probability of mortality under low light is higher in yellow birch than in sugar maple and beech. In contrast to yellow birch, the more conservative growth patterns of sugar maple and beech may enhance survival in shade by minimizing costs associated with the maintenance of woody structures and by allowing increased allocation to attributes that favor long-term survival in shaded conditions. Since yellow birch had a higher height growth rate than the more tolerant sugar maple and beech under all light conditions, our results suggest that shade tolerance is not based on the ability of shade-tolerant species to outgrow less tolerant competitors under shady conditions.

In shady conditions, a growth pattern that favors lateral crown expansion might be advantageous in enabling seedlings to minimize self-shading and to forage for higher light microsites along horizontal gradients of light availability (Canham 1988; Givnish 1988, 1995; Poulson and Platt 1996). In this study, all three species had lower ratios of crown length to crown diameter in shade compared with higher light conditions, indicating that crowns were proportionally more broad in shade than in higher light. Such results are in agreement with predictions made by Horn (1971) and Givnish (1988). A positive relationship between the ratio of height growth to lateral growth and light has been observed in many studies (Klinka et al. 1992; Parent and Messier 1995; Chen et al. 1996). However, in this study, only sugar maple showed an increase in its ratio of height growth to lateral growth with increasing %PPFD, and the relationship was weak. One possible reason why this ratio did not vary in yellow birch and beech, although light-related variations in crown length to crown diameter ratio were observed, is that branch angles varied across light conditions in these two species (observed in beech by Canham 1988). Light-related variations in this ratio might also be more

obvious in coniferous species (Klinka et al. 1992; Parent and Messier 1995; Chen et al. 1996) than in deciduous ones, the latter having more complex crown architectures.

While marked differences in extension growth patterns often exist between intolerant (or mid-tolerant) and shade-tolerant species (as observed here between yellow birch and the other two species), more subtle differences between shade-tolerant species have been shown to have potentially important implications in explaining species coexistence (Canham 1988, 1989; Peters et al. 1995; Poulson and Platt 1996). Canham (1988) and Poulson and Platt (1996) observed that sugar maple seedlings had lower height growth rates than beech seedlings under a closed canopy but responded more strongly to an increase in light and outgrew beech in small gaps. Our results, however, do not indicate that sugar maple has the ability to outgrow beech under light conditions up to 50% PPFD. Height growth of sugar maple and beech responded similarly to increasing light (the slopes were the same), and height growth of beech was higher than that of sugar maple under all light conditions. Higher growth rates in beech as compared with sugar maple under light conditions typical to small canopy gaps have also been reported by Cypher and Boucher (1982) and Bellefleur and Villeneuve (1984). Although it is not known why the observed growth responses of sugar maple and beech in this study differed from results reported elsewhere (Canham 1988, 1989; Peters et al. 1995; Poulson and Platt 1996), our results, as well as those of Cypher and Boucher (1982) and Bellefleur and Villeneuve (1984), indicate that the growth response (and ranking of growth response) of sugar maple and beech do vary between sites. Therefore, one should be careful in making generalizations about the growth response of these two species to increased light availability.

Morphological response to variation in light availability

Yellow birch, sugar maple, and beech showed typical sun–shade responses to variations in light availability for a number of morphological characters. First, we observed a strong negative relationship between SLA and %PPFD. This leaf-level morphological response to variation in light availability has been observed in many other studies (e.g., Loach 1970; Bazzaz 1979; Popma and Bongers 1988; Klinka et al. 1992; Walters et al. 1993; Wang et al. 1994; Messier and Puttonen 1995b; Chen et al. 1996). A higher SLA in shade is believed to increase the efficiency of light interception by maximizing the leaf area displayed per unit of leaf biomass. We also observed a negative relationship between LAR and %PPFD, in agreement with results obtained elsewhere (e.g., Loach 1970; Popma and Bongers 1988; Walters et al. 1993). A higher LAR in shade also contributes towards maximizing light interception in low light conditions. Finally, we observed increases in LAI and RCLD with increasing light, which indicates that the crowns of seedlings growing under relatively high %PPFD were more vertically oriented (higher RCLD) and had more foliage overlap (higher LAI) than those of seedlings growing in shade; this result is in agreement with predictions made by Horn (1971) that a more vertically oriented and multilayered crown would maximize light interception under high light conditions, while a more horizontal display and monolayered crown would be favored in shade.

Although all three species showed some morphological variations in response to increasing %PPFD, sugar maple was more plastic than the other two species in its pattern of leaf display and crown structure, a high morphological plasticity that has also been observed by Canham (1988). Light-related variations in biomass allocation to leaves and branches, and in RBLH, were observed in maple but not in birch and beech. Also, ELD increased markedly with increasing light in sugar maple but remained more or less constant in yellow birch and beech. The light responses of ELD observed for sugar maple and beech are in agreement with results reported by Canham (1988). The observed lower RBLH under high light conditions in maple might contribute an explanation to the increase in ELD observed in maple with increasing %PPFD. The decrease in RBLH observed in sugar maple with increasing %PPFD might be compensated by the increase in mean petiole length. To our knowledge, the relative contribution of petioles as leaf-support structures has been quantified for the first time in the present study and was shown to be much higher in sugar maple than in the other two species. The reliance on petioles as leaf-support structures in maple appears to be advantageous in that it could minimize the metabolic costs associated with production and maintenance of branches (Givnish 1988) and reduce mutual shading (Takenaka 1997). In species with large leaves and long petioles, like sugar maple, shoots can be shorter and more widely spaced to achieve a given degree of leaf overlap (White 1983). Support of leaves by long petioles also provides sugar maple with a highly plastic means of displaying its leaves in space, since petiole length and orientation are determined each year. In contrast to petioles, once growth of a branch is completed in a given direction, a tree cannot reverse the process unless the branch is shed.

While sugar maple has large opposite leaves with long petioles, yellow birch and beech have relatively small alternate leaves with short petioles. Species with small leaves and short petioles must have either a relatively higher order of branching (beech) or relatively longer shoots (yellow birch) to support their leaves (White 1983). Such requirements may pose a constraint on the reduction of branch length in these two species. In yellow birch and beech, the denser leaf distributions (higher LAI), and the narrower crowns (higher RCLD) observed under high light conditions occurred without changes in ELD and without variations in the RBLH. In yellow birch and beech, the higher LAI and RCLD observed under higher light conditions may have resulted from an increase in branch angles from horizontal (observed in beech by Canham 1988).

Although the observed differences were most obvious between sugar maple and the other two study species, yellow birch and beech also differed from one another in a number of their morphological features. In yellow birch, total lateral growth was high and partitioned among relatively few lateral branches so that mean lateral growth was much higher than in the other two species. In beech, total lateral growth was partitioned among a large number of shoot endings, and branch nodes were more numerous than in the other two species. The long lateral shoots of yellow birch (see mean lateral growth) and the ramified branching pattern of beech (i.e., high number of branch nodes) may be necessary for leaf display in species with short petioles (White 1983).

Although some studies have suggested that there is a relationship between shade tolerance and crown-level morphological plasticity to light variation, with shade-tolerant species generally being more plastic than less tolerant ones (Canham 1988; Chen et al. 1996), our results do not indicate any such relationship. In fact, yellow birch and beech, the two study species at the opposite ends of the shade tolerance gradient, differed the least among the three study species. Our results suggest that genetically inherent species-specific developmental constraints, such as leaf size and shape, petiole length, phyllotaxy, and branching pattern, may act as important constraints to morphological acclimation to light variation. We suggest that such constraints need to be considered in future studies of morphological plasticity in relation to variations in light availability.

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