Growth and Canopy Architecture of Shade-Tolerant Trees: Response to Canopy Gaps

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GROWTH AND CANOPY ARCHITECTURE OF SHADE-TOLERANT TREES: RESPONSE TO CANOPY GAPS[1]

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Abstract. Patterns of aboveground growth, branching, and leaf display were examined in saplings of *Acer saccharum* Marsh. (sugar maple) and *Fagus grandifolia* Ehrh. (beech) to determine (1) the responses of aboveground growth rates to variation in forest light regimes and (2) the importance of branching and leaf display patterns to the ability of saplings of these two species to respond to changes in forest light regimes produced by canopy gaps.

For both species, rates of height growth, lateral growth, and the production of new shoots in even the low gap light levels created by small canopy gaps (15–75 m^2) were as much as an order of magnitude greater than growth rates of saplings beneath closed canopies. However, saplings of both species showed little response to further increases in gap light levels. The strong response of maple saplings to low gap light levels was correlated with an increase in sapling leaf area index and the efficiency of leaf display (measured as leaf area per unit length or surface area of branches). In beech, the more modest response to low light levels in small gaps and the higher growth rates than maple beneath a closed canopy were paralleled by a lack of significant increase in beech leaf area indices in small gaps and a higher efficiency of leaf display beneath a closed canopy than in small gaps.

Thus, the magnitude of the response of these two species to small canopy gaps is correlated with their degree of plasticity in patterns of branching and leaf display. Both species can be considered small-gap specialists in the sense that their combinations of shade tolerance, growth responses, and canopy architecture make them particularly successful at exploiting small canopy gaps. However, the two species differ in their placement on a gradient in the degree to which woody plants respond to canopy disturbances.

Key words: aboveground growth; Acer saccharum; *branching patterns; canopy gaps;* Fagus grandifolia; *leaf display; morphological plasticity; northern hardwood forests; shade tolerance.*

INTRODUCTION

Canopy gaps are characterized by temporary increases in the availability of light (March and Skeen 1976, Canham 1984, Chazdon and Fetcher 1984) and potentially water and nutrients (Minckler et al. 1973, Vitousek and Denslow 1986). The importance of rapid growth rates for the exploitation of canopy openings by gap-phase and shade-intolerant tree species has been widely discussed (Marks 1975, Runkle 1981, Hibbs 1982, Canham and Marks 1985). However, the traits that maximize the response of a seedling or sapling to increased levels of light beneath a gap differ markedly from the traits that enable a shade-tolerant species to persist beneath a closed canopy (e.g., Larcher 1969, Bazzaz 1979). While much of the recent research on plant response to variation in forest light regimes has focused on the photosynthetic responses of leaves (e.g., Wallace and Dunn 1980, Fetcher et al. 1983, Pearcy 1983), net whole-plant carbon gain will also depend on a wide range of morphological traits that determine the pattern of interception of light by leaves and the magnitude of maintenance respiration by roots and shoots. In general, the changes in growth form and leaf display that allow a plant to exploit high light regimes can be expected to have correspondingly high metabolic demands for the maintenance respiration of leaves and branches (Horn 1971, Canham and Marks 1985). Thus, the magnitude of the response of a shade-tolerant sapling to a canopy gap can be expected to depend not only on the magnitude of the increase in resource availability, but also on the ability of the plant to modify physiological and morphological traits that determine the efficiency of use of higher resource levels present in canopy gaps. While the degree of acclimation of various physiological processes may be greatest in species that colonize open habitats (e.g., Bazzaz 1979, Bazzaz and Carlson 1982), there still may be considerable selective pressure for architectural plasticity in shade-tolerant tree species.

The principal objectives of this study were (1) to determine how the patterns of aboveground growth of shade-tolerant trees vary across a range of forest light regimes and (2) to investigate how variation in canopy architecture influences the response of shade-tolerant

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trees to variation in forest light regimes. While it appears likely that large gaps alter the availability of both soil moisture and nutrients, the current study considered only the effects of canopy gaps on the availability of light.

METHODS

Selection of study sites, gaps, and saplings

The study was conducted in old-growth northern hardwood forests in the western and central Adirondack Mountains of New York. These forests occupy upland sites at elevations of 350–950 m (Heimburger 1934, Young 1934, Roman 1980). Old-growth stands in the region are dominated by mixtures of the four major shade-tolerant tree species: *Acer saccharum* Marsh. (sugar maple), *Fagus grandifolia* Ehrh. (beech), *Picea rubens* Sarg. (red spruce), and *Tsuga canadensis* (L.) Carr. (eastern hemlock). Two of these species, sugar maple and beech, were chosen for study.

The specific stands chosen for study had canopies containing both sugar maple and beech, with one of the two species as the most abundant canopy tree. Gap and understory beech saplings were collected from stands in the Five Ponds Wilderness Area in Herkimer County, New York (44°05′ N, 74°55′ W). The stands were located on the north and west slopes of Partlow Mountain, and had no recorded history of logging, although some high grading of softwood species may have occurred prior to 1900 (Roman 1980). Sugar maple saplings were collected from stands along Little Sucker Brook and on Gooseberry Mountain in the Huntington Wildlife Research Forest in Essex County, New York (44°00′ N, 74°15′ W). The stand along Little Sucker Brook has not been logged by the present owners (Syracuse University), but was included in a selective cut of softwood species (probably *Picea rubens* and *Tsuga canadensis*) during the 1920s (R. Sage, *personal communication*). The stand on Gooseberry Mountain was subjected to a light selective cut of hardwood species (principally sugar maple) in 1966–1967. Saplings collected from the Gooseberry Mountain stand included individuals found in old openings created by logging. Canopy gaps created by the selective logging did not differ in any recognizable way from naturally occurring gaps (particularly after 15 yr). Stands in both regions were on moderate slopes (0°–20°) and were underlain by deep, well-drained, loamy soils derived from glacial till (Becket-Peru association [Typic and Aquic Haplorthods] and the Potsdam-Crary association [Typic and Aquic Fragiorthods]).

Stands in which distinct gaps could be identified within an otherwise intact canopy of relatively uniform height (20–30 m) were systematically searched for gaps between 5 and 15 yr old. A maximum gap age of 15 yr allowed me to limit sampling to relatively small saplings (<4 m height), whereas a minimum age of 5 yr allowed time for saplings to respond to an opening. Approximate gap age was estimated from observations of the state of decay of fallen canopy trees, with occasional calibration from datable scars left on neighboring trees by the fall of a canopy tree. Actual gap sizes ranged from ≈ 15 to 500 m^2, resulting from the death of 1–5 canopy trees. In order to minimize the effects of competition between neighboring saplings and focus on the potential growth of dominant individuals under different light regimes, only dominant saplings within the selected gaps were chosen for measurement.

Additional saplings of each of the species were collected from beneath closed canopies for comparisons with saplings growing in gaps. The sugar maple saplings were collected from 10 m radius circular quadrats centered at a series of randomly located points in the Little Sucker Brook stand. Beech saplings were collected from randomly located circular plots along transects through an approximately 1-ha stand at the foot of Partlow Mountain in the Five Ponds Wilderness Area. In both cases, points were excluded from sampling if any gaps larger than ≈ 10 m^2 were visible above a point. Open-grown saplings of both species were collected from recent clearcuts in the Huntington Forest. As in the case of saplings collected from gaps, sampling was limited to individuals between 1 and 4 m in height that were not significantly shaded by neighboring saplings.

Sapling measurements

Height growth was calculated from measurements of the elongation and angle (from horizontal) of the terminal leader for the past 5 yr of growth. Mean rates of lateral growth of the crown were determined by measuring the previous 5 yr of extension growth and branch angles on lateral branches that extended out to the perimeter of the crown (Canham 1984).

The mean and total lengths of new shoots were estimated by counting all of the terminal, leaf-bearing shoots and measuring the length of the current year's growth on either a random sample (consisting of 10, 20, or 40% of the branches) or a complete sample, depending on overall sapling size. The same sample of leaf-bearing shoots was used for measurements of the mean number of leaves per shoot and total leaf area per shoot (LI-COR model LI-3000 Leaf Area Meter). Sapling leaf area index (*LAI*) was computed by dividing the estimated total sapling leaf area by a measurement of the horizontal, cross-sectional area of the crown (Canham 1984).

Measurements of the shoot systems of saplings were designed to provide information on both the quantity of metabolically active shoots (using branch length and surface area) and the pattern of branching (using branch bifurcation ratios). The branches of each sapling were ordered following Strahler (1957) for calculation of branch bifurcation ratios. In this scheme, each terminal, unbranched segment of a branch is considered a first-order segment. When two segments of equal order join, the resulting segment is assigned the next higher order (Strahler 1957). Steingraeber (1980) has argued that the bifurcation ratio of first- to second-order branches (R_{12}) is most appropriate for comparisons of leaf display. However, most studies of bifurcation ratios use an average ratio for all branch orders (R_B) calculated using Motomura's formula (Whitney 1976). For comparison with these earlier studies, both ratios were calculated. All branch segments of second order or higher were measured for total length, basal diameter, and terminal diameter. These measurements, when combined with the measurements of length and average diameter recorded for the sample of first-order shoots, were used to estimate the total length and surface area of the shoot system. Each first-order branch segment was assumed to be an untapered cylinder. The surface area of second and higher order branches was calculated from a logarithmic taper model (Canham 1984).

Ratios of leaf area to branch surface area and length were used as indices of the efficiency of leaf display in the two species. The allometric relationships between total leaf area and stem surface area and length were essentially linear for sugar maple (Canham 1984). Thus, in any particular light regime, the ratio of total leaf area to stem surface area or length was independent of sapling size over the range of sapling sizes observed in this study (1–4 m in height for all saplings except 1–10 m for understory sugar maple saplings). This makes it possible to compare average ratios for groups of saplings without problems of differences in the mean size of saplings in each group. The allometric exponent for leaf area vs. total stem surface area of beech saplings in gaps was slightly but significantly <1.0, indicating that the ratio of leaf area to stem surface area declined slightly with increasing sapling size (Canham 1984). As a result, comparisons between leaf/shoot surface area ratios were affected by the larger mean size of the saplings from the gaps. If the surface area of the main bole was omitted in the calculation of total stem surface area, the resulting allometric relationship for branch surface area (i.e., total stem surface area minus the surface area of the main bole) was linear. Thus, the ratio of leaf area to branch surface area was used for beech saplings to avoid the influence of sapling size.

In order to test for the influence of suppression prior to release in a gap on the subsequent response to changes in understory light regimes, the history of suppression and release was determined for each sapling by measuring annual ringwidths along one radius of the main stem (using a disk cut at a height of 0.5 m). Both species showed significant differences between current radial growth rates of saplings under closed canopies and saplings in even very small gaps (Canham 1984, 1985). These differences were used to specify a threshold growth rate that identified a period of release (0.5 mm/yr in sugar maple and 0.4 mm/yr in beech). A period of suppression was defined as a period of three or more years of growth below the threshold, in which there were no periods of three or more years of growth rates greater than the threshold.

The root systems of beech saplings were excavated to determine, if possible, whether a sapling was of seed or sprout origin. With the exception of a barely significant difference in shoot growth rates there were no significant differences in any of the growth rates or morphological parameters for saplings of seed vs. sprout origin (Canham 1984). Therefore, results are presented with saplings of both origins pooled.

Calculation of a gap light index

Large seasonal changes in the amount of direct beam radiation received through a gap severely limit the usefulness of instantaneous or even integrated daily measurements of photosynthetically active radiation (PAR) as indices of seasonal total light levels at points in or near gaps. Moreover, gap size is not necessarily a good index of the amount of light received by individual saplings within a gap because there is significant spatial variation within a gap in the total amount of radiation received over the course of a season (Canham 1984). There are, however, several reasonably predictable relationships between the geometry (size and shape) of a canopy gap and the transmission of diffuse and direct PAR to a point within the gap (Canham 1984). A gap light index (*GLI*) that specifies the percent of seasonal total PAR that is transmitted through a canopy gap to a specific point in the understory can be calculated as:

$$\begin{aligned} GLI = (& [\%SKY \cdot (1 - \%SUN)] \\ & + (\{KT + [\%SKY \cdot (1 - KT)]\} \cdot \%SUN)) \cdot 100, \end{aligned}$$

where $\%SKY$ is the percent of the sky hemisphere visible in the gap, KT is a mean seasonal atmospheric transmission coefficient, and $\%SUN$ is the percent of seasonal total PAR received while the sun is within the outline of the gap (Canham 1984). Values of the index range from 0%, when there is no identifiable gap above a point, to 100% in the open. Mean monthly values of KT are available for major weather stations from meteorological records (i.e., Knapp et al. 1980). In the field, the geometry of the gap was recorded by measuring the angle (from horizontal) from the leader of a sapling to the edge of the gap in the eight principal compass directions and any additional directions required to describe the outline of the gap in polar coordinates. The terms $\%SKY$ and $\%SUN$ were then calculated solely from the measurements of gap geometry using a computer program that determines the times during a predefined growing season when the sun was within the outline of the gap (Canham 1984). Details of the derivation and calculation of the gap light index used for this study are given in Canham (1984). A more general derivation of the index is given in Canham (1988).

The gap light index was tested in the stand along Little Sucker Brook (Canham 1984). Integrated total light levels, measured using quantum sensors (LI-COR,

TABLE 1. Aboveground growth of sugar maple and beech saplings beneath closed canopies and in low gap light levels. Data are means ± standard error of the mean. All branch angles are in degrees from horizontal.

	Sugar maple		Beech	
	Closed canopy	Low gap light levels	Closed canopy	Low gap light levels
Sample size	25	7	11	11
Height growth (cm/yr)	2.78 ± 0.538	28.7*** ± 3.13	5.24 ± 1.35	12.5* ± 2.37
Leader angle (°)	34.9 ± 3.78	61.6** ± 5.85	30.6 ± 7.39	42.4^{NS} ± 3.62
Lateral growth (cm/yr)	2.8 ± 0.321	12.1*** ± 1.59	6.2 ± 0.572	11.4** ± 1.26
Lateral branch angle (°)	26.9 ± 2.47	28.4^{NS} ± 2.71	13.4 ± 2.05	3.4** ± 1.84
Length of new shoots (cm)	1.63 ± 0.102	4.87** ± 0.724	2.65 ± 0.518	5.24** ± 0.539
Relative shoot growth (%/yr)†	14.9 ± 1.22	58.3** ± 8.28	27.4 ± 5.69	50.3** ± 5.49

* $P < .05$, ** $P < .01$, *** $P < .001$, NS = $P > .05$; separate-variance t tests comparing closed canopy and gap saplings within each species.

† Relative shoot growth is the total length of new shoots produced annually as a percent of the total length of shoots present at the beginning of the growing season.

Incorporated), for periods of 1–3 d at 15 points in and around gaps were compared with gap light index values calculated from measurements of gap geometry. For the 15 points, the regression of percent transmission of open-site radiation (%T) vs. the gap light index (GLI) was

$$\%T = 2.438 + 1.177 \cdot GLI \qquad (r^2 = 76.8\%).$$

The intercept of the equation was slightly lower than the mean percent transmission of PAR to five additional, randomly chosen points beneath closed canopies (mean = 3.93%, range = 2.80–4.80%, $t = 3.82$, $P < .05$), although the slope was not significantly different from 1.0 ($t = 1.032$, $P > .20$). Thus, the percent of open-site PAR received in the understory for these 20 points was approximately equal to the percent transmission by a closed canopy plus the value of GLI calculated on the basis of gap geometry. The gap light index therefore provides a relative index of the amount of light reaching a sapling through a gap over the course of the growing season.

Data analysis

The growth and morphology of saplings beneath closed canopies were compared with those of saplings collected from the lowest light levels created by small gaps. This approach was dictated by the significance of the distinction between a closed canopy and even a small gap for studies of canopy dynamics, as well as by a preliminary analysis of the data. In particular, for many of the growth and morphological variables, the major response to the full range of light regimes (from full shade to full sun) occurred as a threshold response at the transition between a closed canopy and even the lowest gap light levels. For these reasons, understory saplings were compared with saplings collected within small single-tree gaps (15–75 m^2) at points that received no direct sunlight through the gap opening over the course of the growing season. For variables where there was also interest in a comparison between open-grown saplings and saplings in gaps, a group of saplings with the highest gap light indices (mean $GLI = 25.8\%$ for sugar maple and 21.1% for beech) was chosen for comparison with open-grown saplings. The second major set of questions addressed interactions between light levels, canopy architecture, and growth of saplings collected from specifically within the range of light levels created by canopy gaps. Regression and partial correlation analysis (Nie et al. 1980) were used to identify relationships between these sets of variables.

RESULTS

Growth

Sugar maple saplings in the low light levels of the smallest canopy gaps (mean $GLI = 3.6\%$) had significantly greater growth rates than saplings beneath a closed canopy (Table 1). Height growth of maple saplings in gaps was correlated with aspects of sapling size, growth history, and morphology, i.e., height growth = 13.56 (crown radius) + 6.18 (R_B) − 9.72 (suppression), $R^2 = 30.6\%$, where suppression was coded as an indicator variable (0 = no suppression, 1 = suppression prior to release in the current gap), and R_B was a branch bifurcation ratio (see Methods: Sapling Measurements). After accounting for the effects of these variables, height growth was not correlated with the gap light index. The average (± SE) height growth of all 29 saplings collected from gaps was 35.5 ± 1.55 cm/yr. In contrast to height growth, lateral growth of maple saplings was significantly correlated with the gap light index ($r = 0.62$), although the trend appears to level off at GLI values >20% (Fig. 1). Lateral branch angles were constant over the entire range of gap light levels ($\bar{X} \pm \text{SE} = 28.7° \pm 1.7°$). The relationship between the total length of new shoots produced in a year and the total length of the shoot system for maple saplings collected from gaps was essentially linear, with an estimated allometric exponent of 0.93 (95% CI = 0.79–1.11), indicating a constant relative shoot growth rate over the range of sapling sizes. Partial correlation analysis indicated that relative shoot growth was weakly correlated with gap light level (as measured by %SKY), the percent of a sapling's lifetime that it had not been

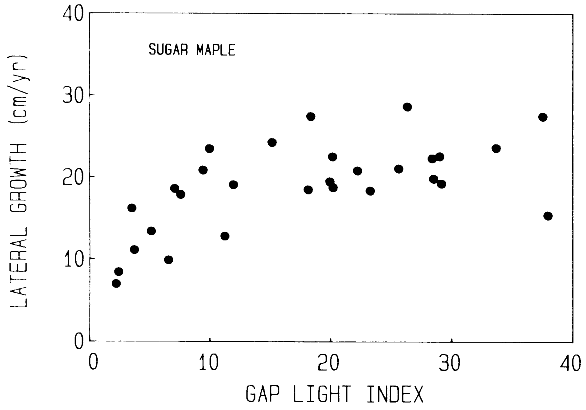

FIG. 1. Lateral growth of sugar maple saplings collected from a range of gap light levels.

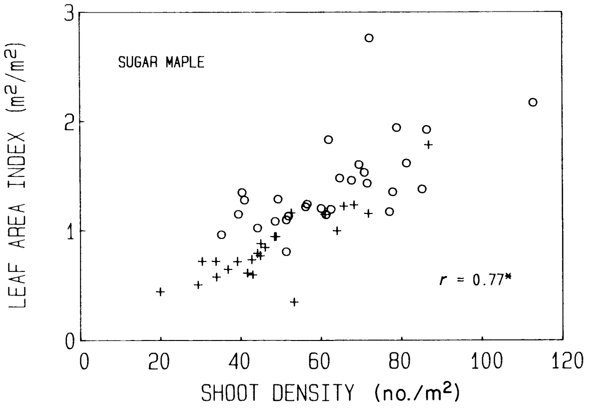

FIG. 2. Relationship between leaf area index and shoot density for sugar maple saplings collected from beneath closed canopies (+) and from a range of gap light levels (○).

suppressed, and the ratio of leaf to branch surface area (partial correlation coefficients = 0.47, 0.43, and 0.75, respectively, after controlling for each of the other variables).

Growth of beech saplings in low gap light levels (mean $GLI = 2.9\%$) was also significantly greater than growth in the understory (Table 1), although the magnitude of the difference was much smaller than for sugar maple. As in sugar maple, height growth was not significantly correlated with gap light levels. The average (± SE) height growth rate of all 32 beech saplings from gaps was 15.2 ± 1.6 cm/yr, less than half the average growth rate for maple. Height growth of beech saplings was not correlated with any of the measured aspects of growth history or with any of the calculated indices of leaf display and branching patterns. Saplings of sprout origin did not differ significantly from saplings of seed origin in either height growth or leader angle. With increasing gap light levels, beech lateral growth rates increased ($r = 0.47$ for lateral growth vs. *GLI*, $P < .05$) even though lateral branch angles became more vertical ($r = 0.65$, $P < .05$). Of the four aspects of gap light levels that were computed for each sapling (*GLI*, %*SKY*, %*SUN*, and the number of days during the growing season when the sun was above the gap horizon) the last two had the highest correlation with lateral growth rates ($r = 0.47$, 0.25, 0.54, and 0.57, respectively; coefficients > 0.35 are significant at $P < .05$). Although all four of the light indices are correlated with each other to some degree, the last two terms are most closely related to the amounts of direct beam radiation received by saplings. In contrast, lateral growth was not significantly correlated with %*SKY*, which is most closely related to penetration of diffuse sky radiation through a gap. The results suggest that both branch angles and net growth rates of lateral branches in beech responded most strongly to periods of direct sunlight, while showing little response to variation in the amount of diffuse radiation that penetrated through the gaps. In contrast to sugar maple, there were no partial correlations between relative shoot growth rates and any of the measured aspects of gap light levels, growth history, or sapling morphology.

Leaf display and branching patterns

Leaf area indices (*LAI*) of maple saplings were significantly greater in low gap light levels than beneath a closed canopy (Table 2). However, beech showed no differences between the *LAI* of saplings beneath a closed

TABLE 2. Components of leaf display in sugar maple saplings. Data are means ± standard error of the mean.

	Closed canopy	Canopy gaps Low gap light levels	 All gap light levels†	 High gap light levels	Open grown
Sample size	25	7	29	10	6
Leaf area index (m^2/m^2)	0.872 ± 0.060	1.37* ± 0.148	1.41 ± 0.075	1.53*** ± 0.178	4.73 ± 0.696
Leaf size (cm^2)	48.4 ± 1.76	51.4^{NS} ± 2.65	52.3 ± 1.76	51.04^{NS} ± 3.61	54.3 ± 2.33
No. of leaves per shoot	3.88 ± 0.138	4.22^{NS} ± 0.128	4.37 ± 0.079	4.51^{NS} ± 0.145	4.76 ± 0.115
Shoot density (no./m^2)§	47.7‡ ±3.03	64.4^{NS} ± 9.88	63.1‡ ± 3.21	66.4* ± 5.10	187.4 ± 30.9

* $P < .05$, *** $P < .001$, NS = $P > .05$; separate-variance t tests comparing closed-canopy saplings with saplings in low gap light levels, and saplings in high gap light levels with open-grown saplings.

† The figures for all gap light levels are given for reference, since there were no significant correlations between any aspect of leaf display and the gap light index.

‡ The difference between saplings beneath a closed canopy and saplings from all gap light levels was significant at $P < .05$.

§ Density of leaf-bearing shoots per unit cross-sectional area of the crown.

TABLE 3. Components of leaf display in beech saplings. Data are means ± standard error of the mean.

	Closed canopy	Canopy gaps			Open grown
		Low gap light levels	All gap light levels†	High gap light levels	
Sample size	11	11	32	8	9
Leaf area index (m^2/m^2)	0.890 ± 0.060	0.853^{NS} ± 0.070	0.990 ± 0.053	1.11*** ± 0.150	2.32 ± 0.255
Leaf size (cm^2)	33.0 ± 1.81	33.3^{NS} ± 2.55	33.6 ± 1.55	35.9^{NS} ± 4.08	31.7 ± 2.12
No. of leaves per shoot	2.59 ± 0.211	3.06^{NS} ± 0.236	3.29 ± 0.197	3.44^{NS} ± 0.380	3.36 ± 0.123
Shoot density (no./m^2)‡	109.4 ± 8.21	87.9* ± 6.02	99.1 ± 6.24	96.7*** ± 10.4	219.2 ± 19.7

* $P < .05$, *** $P < .001$, NS = $P > .05$; separate-variance t tests comparing closed-canopy saplings with saplings in low gap light levels, and saplings in high gap light regimes with open-grown saplings.

† The figures for all gap light levels are given for reference, since there were no significant correlations between any aspect of leaf display and the gap light index.

‡ Density of leaf-bearing shoots per unit cross-sectional area of the crown.

canopy and of saplings in low gap light levels (or even between closed-canopy saplings and the mean *LAI* of all gap saplings) (Table 3). There was a weak but significant correlation between *LAI* and %*SKY* ($r = 0.380$, $P < .05$) for maple saplings in gaps, but there were no significant correlations between gap light levels and any aspect of leaf display in beech; nor did leaf display vary with the origin of beech saplings. It is worth noting that for both species, variation in *LAI* over the full range of light conditions can be attributed almost entirely to differences in shoot density, rather than to differences in leaf size or in the number of leaves per shoot (e.g., Fig. 2 and Tables 2 and 3). The high leaf area indices of open-grown saplings of both species were the result of very high densities of leaf-bearing shoots within the crown. These high shoot densities were, in part, a consequence of the steeper branch angles and the columnar shapes of the crowns of both species when growing in the open (C. D. Canham, *personal observations*).

On the basis of the ratios of leaf area to branch surface area and length, maple saplings in low gap light levels had significantly higher efficiencies of leaf display than saplings beneath closed canopies (Table 4). In contrast, beech had a higher efficiency of leaf display beneath closed canopies than in gaps, regardless of gap light level. The efficiency of leaf display was not correlated with the gap light index for either species.

The observed patterns of variation in sapling *LAI* were closely paralleled by variation in branch bifurcation ratios (Table 5). My results for sugar maple saplings confirm the general results of Steingraeber et al. (1979) that there are significant differences in bifurcation ratios of maple saplings from different light regimes. However, the differences were found even in the comparison of saplings from closed canopies and low gap light levels and thus can not be interpreted simply in terms of differences between open-site and closed-canopy light regimes as in Steingraeber et al. (1979) and Whitney (1976). There was no correlation between bifurcation ratios (either R_B or R_{12}) and the gap light index for either species. Within the sample of 25 maple saplings collected from beneath closed canopies, saplings with lower bifurcation ratios did not

TABLE 4. Efficiency of leaf display: ratios of leaf surface area to stem surface area (L/S) and leaf surface area to stem length (L/SL) in sugar maple and beech, and the ratio of leaf surface area to branch (total stem minus bole) surface area (L/B) in beech saplings. Data are means ± standard error of the mean.

	Closed canopy	Canopy gaps	
		Low gap light levels	All gap light levels†
Sugar maple			
Sample size	25	7	29
L/S	4.61 ± 0.159	6.60** ± 0.384	6.53 ± 0.194
L/SL (cm^2/cm)	8.28 ± 0.330	11.27*** ± 0.281	11.75 ± 0.320
Beech			
Sample size	11	11	32
L/S	5.96 ± 0.345	5.40^{NS} ± 0.408	5.31 ± 0.197
L/SL (cm^2/cm)	6.12 ± 0.204	5.99^{NS} ± 0.330	6.10 ± 0.183
L/B	8.32 ± 0.341	7.04* ± 0.467	6.61 ± 0.296

* $P < .05$, ** $P < .01$, *** $P < .001$, NS = $P > .05$; separate-variance t tests comparing understory saplings and saplings in low gap light levels.

† The figures for all gap light levels are given for reference, since there were no significant correlations with the gap light index.

TABLE 5. Bifurcation ratios for sugar maple and beech saplings across a range of light regimes. R_B is Motomura's formula (Whitney 1976) for the average bifurcation ratio of the entire shoot system. R_{12} is the ratio of first-order (leaf-bearing) to second-order branches.

		Canopy gaps			
	Closed canopy	Low gap light levels	All gap light levels†	High gap light levels	Open grown
Sugar maple					
Sample size	25	7	29	10	6
R_B	3.78 ± 0.101	4.91* ± 0.167	5.17 ± 0.126	5.35^{NS} ± 0.266	5.08 ± 0.288
R_{12}	3.78 ± 0.117	5.21* ± 0.214	5.43 ± 0.123	5.58^{NS} ± 0.240	5.44 ± 0.553
Beech					
Sample size	11	11	32	8	9
R_B	3.91 ± 0.102	3.72^{NS} ± 0.102	3.80 ± 0.694	3.78* ± 0.096	4.14 ± 0.106
R_{12}	4.05 ± 0.138	3.88^{NS} ± 0.137	3.94 ± 0.083	3.91^{NS} ± 0.110	4.18 ± 0.129

* $P < .05$, NS = $P > .05$; separate-variance t tests comparing understory saplings and saplings in low gap light levels, and comparing open-grown saplings and saplings from high gap light levels.

† The figures for all gap light levels are given for reference, since there were no correlations between the gap light index and bifurcation ratios in either species.

have higher ratios of leaf area to branch length as predicted by the arguments of Leopold (1971) and Whitney (1976).

DISCUSSION

Canopy architecture and the utilization of gap light regimes

The ability of maple saplings in low gap light levels to increase leaf area indices without proportional increases in the total length or surface area of shoots suggests that saplings were capable of increasing the fraction of incident radiation intercepted by leaves without a significant increase in the metabolic costs of producing and maintaining branches to support those leaves. It seems likely that this variation in leaf display was an important component of the strong increases in aboveground growth rates for maple saplings in low gap light levels. In contrast, the more modest response to low gap light levels by beech, and the higher growth rates than sugar maple when growing beneath a closed canopy, were paralleled by a lack of variation in leaf area indices and a higher efficiency of leaf display beneath a closed canopy than in low gap light levels.

Observations by Steingraeber et al. (1979) of low bifurcation ratios for maple saplings in deep shade and high ratios in open-grown saplings were consistent with arguments by Leopold (1971) and Whitney (1976) that a branch system with a high bifurcation ratio should be more efficient (in terms of the amount of stem tissue required to display a given area of leaves) for the columnar crowns characteristic of high light levels, while low bifurcation ratios should be more efficient for the planar leaf display often found in low light levels. However, since leaf display in saplings from both the understory and low gap light levels occurred largely on nearly horizontal branches (Table 1), the arguments of Leopold (1971) and Whitney (1976) relating variation in bifurcation ratios to variation in crown shape can not be used to explain my results.

Nonetheless, the variation in bifurcation ratios exhibited by sugar maple in this study does appear to be an important component of the observed difference in efficiency of leaf display, albeit in a much simpler way than envisioned by earlier arguments. Specifically, the increase in LAI for maples in low gap light levels occurred simply as a result of the release of lateral buds, producing numerous short lateral branches. This resulted in an increase in both shoot density (Table 2) and branch bifurcation ratios (Table 5). Although these lateral branches are not true spur shoots, their mean length was very low (Table 1) while the leaf area displayed per shoot was relatively high (≈188 cm^2; Table 2). Thus, there was a significant increase in LAI with only a slight increase in the surface area or length of branches. This pattern of branching provides an ecologically significant yet developmentally simple form of plasticity in canopy architecture.

Although sugar maple leaf display responded significantly to even the lowest gap light levels, leaf display in both species showed no further response to the entire range of gap light levels sampled. This was true even for saplings that could have received direct sunlight through a gap on every day of the growing season. This lack of response to high light levels in large gaps may have been due to the relatively short duration of direct sunlight on any given day even in the large gaps. The mean length of time that the sun was above the gap horizon (averaged over only those days on which the sun was at least briefly above the gap horizon) was in all cases <30% of total day length. Moreover, the actual amount of the sky visible in a gap was never >15% of the sky hemisphere (Canham 1984). Thus, on cloudy days (i.e., when atmospheric transmission was <50%), light levels for saplings in gaps would have been considerably less than one half of full sunlight even when the sun was above the gap horizon.

Saplings of both species are capable of responding to open environments with much higher leaf area indices than were observed for saplings in gaps (Tables 2 and 3). However, there appear to be several factors that limit the effectiveness of high leaf area indices for shade-tolerant saplings in large gaps. During periods of full sunlight, saplings with high leaf area indices can maintain a high average illumination on a large total leaf area through a combination of high leaf angles (from horizontal) (McMillen and McClendon 1975), spacing between leaves (Horn 1971), and clustering of leaves on branches (Kira et al. 1969). However, all of these mechanisms would produce significant self-shading of some fraction of total leaf area for the remaining 70% or more of the day when the sun was below the horizon of a gap.

The morphological plasticity described in this study for sugar maple can be contrasted with the relatively limited degree of physiological plasticity observed in this species (Bazzaz and Carlson 1982). Penning de Vries (1975) has suggested that a major factor in the ability of plants to physiologically acclimate to changes in light levels is a high turnover rate for enzymes in leaves. However, one of the consequences of a high protein turnover rate is often a high maintenance respiration rate (Penning de Vries 1975). This suggests that the low levels of physiological acclimation observed in shade-tolerant species (e.g., Logan and Krotkov 1968, Bazzaz and Carlson 1982) may be due to an incompatibility between acclimation responses and the low maintenance respiration rates necessary for shade tolerance in woody plants. In contrast, morphological and developmental plasticity of the sort described for sugar maple, in this as well as other studies (e.g., Steingraeber et al. 1979), may be more compatible with shade tolerance because it may not involve metabolic costs analagous to those potentially associated with physiological acclimation.

Aboveground growth rates and the dynamics of sugar maple and beech

There have been a number of attempts to predict actual patterns of gap-phase or tree-by-tree replacement for northern hardwood tree species (e.g., Barden 1979, 1980, Woods 1979). In many gaps there is little question about the identity of the saplings that will eventually fill the gap, because of an overwhelming size advantage achieved prior to the formation of the gap (e.g., Barden 1979). While the height growth rates of beech saplings beneath closed canopies may not be rapid enough to allow canopy recruitment in the absence of an opening, they should contribute to an advantage in height over adjacent sugar maple saplings during prolonged periods when there are no gaps nearby in the canopy. In contrast, the relative abundance and height of understory maple saplings can be expected to increase during periods when canopy gaps are frequently or consistently present somewhere in the canopy above an area of the forest floor. The results of this study suggest the simple hypothesis that the relative abundance of canopy beech trees will increase during periods with low rates of canopy disturbance, while the abundance of sugar maple will increase following periods with higher rates of gap formation. It should be pointed out that the effects of gap frequency on the dynamics of these two species represent a distinctly nonequilibrial influence on the dynamics of two of the species that have traditionally been identified as archetypal components of old-growth forests in the northeastern United States.

While height growth and relative shoot growth in sugar maple and beech showed little response to increases above even very low gap light levels, lateral growth rates of both species were significantly correlated with the gap light index. This underscores the potential significance of lateral growth by saplings of shade-tolerant trees. Measurements and simulations of gap light regimes indicate that there can be significant spatial variation in seasonal total light levels beneath gaps (Canham 1988). Thus, lateral growth of 1–2 m can result in significant increases in the amount of light received by a branch over the course of a growing season. It is not unusual to see saplings on the edge of a gap with most of their leaves displayed on long branches that extend toward the gap. Lateral growth can, in effect, act as a means of locating more favorable microenvironments within the understory. A more significant consequence of high lateral growth rates, particularly in large gaps, may be the shading of smaller saplings of less shade-tolerant tree species that become established following gap formation.

It is possible to recognize two hypothetical extremes for the role of shade tolerance in the process of canopy recruitment in trees. At one extreme a sapling may be capable of slow but gradual growth under a closed canopy, without significant response to periodic openings in the canopy. At the other extreme, shade tolerance may function principally as a mechanism for persistence in the understory, without significant net growth underneath a closed canopy. In this strategy, periods of appreciable net growth occur only during periods of release caused by an opening in the canopy. There are limits to the degree to which any woody plant can minimize net growth of secondary structures. Neither beech nor sugar maple produces true spur shoots, and the maintenance of leaf display requires relatively continuous production of new shoot material. Both mean new shoot lengths and relative shoot growth of closed-canopy saplings were higher in beech, a species with very short petioles, than in sugar maple, in which the overlap of leaves on shoots with very short internodes is partially avoided through the benefits of relatively long, flexible petioles.

These two hypothetical patterns of growth represent the endpoints of a gradient in the degree to which shade-tolerant species respond to the pulses of light and other resources created by the death of overstory trees. While both maple and beech showed significant responses to low light levels present in small canopy gaps, they differed in their placement along the gradient. Beech saplings had only a modest response to the low gap light levels and had higher efficiencies of leaf display beneath a closed canopy than in gaps. Sugar maple, in contrast, had a much stronger response to low gap light levels in small canopy gaps, and saplings had higher efficiencies of leaf display in gaps than in the understory. Differentiation of the responses of shade-tolerant tree species along this gradient represents an extension of the partitioning of gap microenvironments by traditionally defined gap-phase species (Denslow 1980). Although the two species differ in the magnitude of their response and apparent dependence on gaps, both species can be considered small-gap specialists in the sense that their combinations of shade tolerance and growth responses make them particularly successful at exploiting small canopy gaps. In this regard, there is very little basis for a functional distinction between these two shade-tolerant species and the more traditionally defined gap-phase species.

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LITERATURE CITED

Barden, L. S. 1979. Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the southern Appalachians, Tennessee. Oecologia (Berlin) **44**:141–142.

———. 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. Oikos **35**:16–19.

Bazzaz, F. A. 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics **10**: 351–371.

Bazzaz, F. A., and R. W. Carlson. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. Oecologia (Berlin) **54**:313–316.

Canham, C. D. 1984. Canopy recruitment in shade tolerant trees: the response of *Acer saccharum* and *Fagus grandifolia* to canopy openings. Dissertation. Cornell University, Ithaca, New York, USA.

———. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. Bulletin of the Torrey Botanical Club **112**:134–145.

———. 1988. An index for understory light levels in and around canopy gaps. Ecology **69**, *in press*.

Canham, C. D., and P. L. Marks. 1985. The response of woody plants to disturbance: patterns of establishment and growth. Pages 197–216 *in* S. T. A. Pickett and P. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.

Chazdon, R. L., and N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. Journal of Ecology **72**:553–564.

Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. Biotropica (Supplement):47–55.

Fetcher, N., B. R. Strain, and S. F. Oberbauer. 1983. Effects of light regime on the growth, leaf morphology and water relations of seedlings of two species of tropical trees. Oecologia (Berlin) **58**:314–319.

Heimburger, C. C. 1934. Forest-type studies in the Adirondack region. New York State Agricultural Experiment Station Memoirs, Number **165**.

Hibbs, D. E. 1982. Gap dynamics in a hemlock–hardwood forest. Canadian Journal of Forest Research **12**:522–527.

Horn, H. S. 1971. The adaptive geometry of trees. Monographs in Population Biology, Number 3. Princeton University Press, Princeton, New Jersey, USA.

Kira, T., K. Shinozaki, and K. Hozumi. 1969. Structure of forest canopies as related to their primary productivity. Plant and Cell Physiology **10**:129–142.

Knapp, C. L., T. L. Stoffel, and S. D. Whitaker. 1980. Insolation data manual: long term monthly averages of solar radiation, temperature, degree-days and global KT for 248 National Weather Service stations. Solar Energy Research Institute, Washington, D.C., USA.

Larcher, W. 1969. The effects of environmental and physiological variables on the carbon dioxide gas exchange of trees. Photosynthetica **3**:167–198.

Leopold, L. B. 1971. Trees and streams: the efficiency of branching patterns. Journal of Theoretical Biology **31**:339–354.

Logan, K. T., and G. Krotkov. 1968. Adaptations of the photosynthetic mechanism of sugar maple (*Acer saccharum*) seedlings grown in various light intensities. Physiologia Plantarum **22**:104–116.

March, W. J., and J. N. Skeen. 1976. Global radiation beneath the canopy and in a clearing of a suburban hardwood forest. Agricultural Meteorology **16**:321–327.

Marks, P. L. 1975. On the relation between extension growth and successional status of deciduous trees of the northeastern United States. Bulletin of the Torrey Botanical Club **102**:172–177.

McMillen, G. G., and J. H. McClendon. 1975. Leaf angle: an adaptive feature of sun and shade leaves. Annals of Botany (London) **140**:437–442.

Minckler, L. S., J. D. Woerheide, and R. C. Schlesinger. 1973. Light, soil moisture and tree reproduction in hardwood forest openings. United States Forest Service Research Paper **NC-89**.

Nie, N. H., C. H. Hull, M. N. Franklin, J. G. Jenkins, K. I. Sours, M. J. Norusis, and V. Beadle. 1980. SCSS: a user's guide to the SCSS conversational system. McGraw-Hill, New York, New York, USA.

Pearcy, R. W. 1983. The light environment and growth of C_3 and C_4 tree species in the understory of a Hawaiian forest. Oecology (Berlin) **58**:19–25.

Penning de Vries, F. W. T. 1975. The cost of maintenance processes in plant cells. Annals of Botany **39**:77–92.

Roman, J. R. 1980. Vegetation–environment relations in virgin, middle elevation forests in the Adirondack Mountains, New York. Dissertation. State University of New

York, College of Environmental Sciences and Forestry, Syracuse, New York, USA.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology **62**:1041–1051.

Steingraeber, D. A. 1980. The analysis of branching patterns in trees. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.

Steingraeber, D. A., L. J. Kascht, and D. H. Franck. 1979. Variation of shoot morphology and bifurcation ratio in sugar maple (*Acer saccharum*) saplings. American Journal of Botany **66**:441–445.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union **38**:913–920.

Vitousek, P. M., and J. S. Denslow. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. Journal of Ecology **74**:1167–1178.

Wallace, L. L., and E. L. Dunn. 1980. Comparative photosynthesis of three gap phase successional tree species. Oecologia (Berlin) **45**:331–340.

Whitney, G. G. 1976. The bifurcation ratio as an indicator of adaptive strategy in woody plant species. Bulletin of the Torrey Botanical Club **103**:67–72.

Woods, K. D. 1979. Reciprocal replacement and the maintenance of codominance in a beech–maple forest. Oikos **33**: 31–39.

Young, V. A. 1934. Plant distribution as influenced by soil heterogeneity in the Cranberry Lake region. Ecology **15**: 154–196.