

SAPLING BIOMASS ALLOCATION AND GROWTH IN THE UNDERSTORY OF A DECIDUOUS HARDWOOD FOREST¹

E. H. DELUCIA,^{2,3} T. W. SIPE,⁴ J. HERRICK,⁵ AND H. MAHERALI²

²Department of Plant Biology, University of Illinois, Urbana, Illinois 61801;

⁴Department of Biology, Franklin and Marshall University, Lancaster, Pennsylvania 17601; and

⁵Department of Biology, West Virginia University, Morgantown, West Virginia 26506

Above- and belowground tissues of co-occurring saplings (0.1–1 m height) of *Acer saccharum* Marsh. (very shade tolerant), *Acer rubrum* L. (shade tolerant), *Fraxinus americana* L. (intermediate shade tolerant), and *Prunus serotina* Ehrh. (shade intolerant) were harvested from a forest understory to test the hypothesis that the pattern of biomass allocation varied predictably with shade-tolerance rank. The placement and length of branches along the main axis were consistent with the formation of a monolayer of foliage for the tolerant and intermediate species. Other morphological characteristics did not vary predictably with shade-tolerance rank. The maintenance of high specific leaf area (SLA; leaf area/leaf mass) and leaf area ratio (LAR; leaf area/sapling mass) is considered important for growth under extreme shade, yet these traits were not clearly related to the shade-tolerance rank of these species. *Fraxinus americana*, an intermediate species, had the highest LAR and growth rate in the understory, and with the exception of *P. serotina*, the very shade-tolerant *A. saccharum* had the lowest LAR. *Prunus serotina* maintained a large starch-rich tap root and shoot dieback was common, yielding the largest root/shoot ratio for these species. The observed allocation patterns were not similar to the long-standing expectation for the phenotypic response of juvenile trees to shade, but were consistent with three hypothetical “growth strategies” in the understory: (1) the low SLA and LAR of *A. saccharum* may provide a measure of defense against herbivores and pathogens and thus promote persistence in the understory, (2) the high SLA for *F. americana* and high LAR for *F. americana* and *A. rubrum* may enable these species to achieve high growth rates in shade, and (3) the large carbohydrate stores of *P. serotina* may poise this species for opportunistic growth following disturbance. The relative importance of resistance to herbivores and pathogens vs. the maintenance of high growth rates may be important in evaluating the patterns of biomass allocation in the understory.

Key words: *Acer*; *Fraxinus*; light environment; nitrogen; *Prunus*; root/shoot ratio; shade tolerance; starch.

Differential growth and survival of understory saplings cause changes in species composition during forest succession and strongly influence the response of mature forests to disturbance. A number of structural and physiological traits contribute to persistence in the deep shade of the forest understory; these traits (Bazzaz, 1979; Givnish, 1988) and certain aspects of sapling demography have been used to loosely define shade tolerance (Baker, 1949; Graham, 1954). Among structural attributes, the maintenance of high leaf area per unit leaf mass (specific leaf area; SLA), high leaf area per unit sapling mass (leaf area ratio; LAR), and low root/shoot mass ratio is believed to maximize growth in light-limited habitats and thus confer shade tolerance (Horn, 1971; Givnish, 1988; Abrams and Kubiske, 1990).

Although the importance of these traits is evident when individuals of a single species are grown in contrasting irradiances (Boardman, 1977; Givnish, 1988), the interpretation of the results from interspecific comparisons can be ambiguous. For example, Kitajima (1994) and Vee-

nedaal et al. (1996) found that in contrast to the prediction above, SLA decreased and root/shoot ratio increased with increasing shade tolerance among seedlings of several new- and old-world tropical tree species. As an explanation for similar discrepancies among maple species, Lei and Lechowicz (1990) proposed that shade-tolerant species expressed structural traits that were “adaptive” for adults but not necessarily for saplings. An alternative explanation involves a shift in the current paradigm about shade tolerance.

The prevailing model of shade tolerance is based on carbon economy and asserts that structural and physiological traits that maximize the net rate of carbon gain are adaptive in the understory (Givnish, 1988). In contrast to this model, Walters et al. (1993) recognized that phenotypic responses to shade, while potentially maximizing growth, may not promote survival. The potential for an inverse relationship between growth rate and survival is supported by recent interspecific comparisons of seedlings and saplings in forest understories (Kitajima, 1994; Pacala et al., 1994; Kobe et al., 1995; Kobe, 1996). Some of the structural attributes that may contribute to slow growth but also increase survival of shade-tolerant species include low SLA and high wood density. These traits may promote survival by conferring resistance to herbivory and pathogens (Coley, Bryant, and Chapin, 1985; Kitajima, 1994).

Most studies of juvenile tree growth and survival in the field have focused on shoot growth only (Canham and Marks, 1985). In such cases, it is impossible to know

¹ Manuscript received 19 May 1997; revision accepted 28 October 1997.

The authors thank the staff of Harvard Forest for logistical support. Special thanks go to Drs. F. A. Bazzaz and David R. Foster for providing a stimulating and supportive sabbatical for EHD and TWS, who were supported by the Charles Bullard Fund for Forest Research at Harvard Forest.

³ Author for correspondence: Department of Plant Biology, University of Illinois, 265 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801 (phone: 217 333 6177, FAX: 217 244 7246, e-mail: delucia@uiuc.edu).

whether increases in shoot mass parallel or occur at the expense of root growth. Though low irradiance is a major limiting factor in the understory, it is not the only limiting resource. Belowground competition for water and nutrients in moist forests has received surprisingly little attention since the early demonstrations by Toumey and Kienholz (1931) and Korstian and Coile (1938) that such competition may be significant. Survival in the shade may require allocation to roots at levels that slow shoot growth.

Shade tolerance as a descriptor of ecological performance has escaped rigorous quantitative definition. An emerging view offers a continuum of "strategies" for understory performance; natural selection may favor attributes that promote growth in the shade for some species, attributes that promote long-term survival for others or attributes that poise a species for an exploitive response to a canopy gap.

In this paper we describe the patterns of above- and belowground biomass allocation for saplings of four hardwood tree species that vary in their traditional classification of shade tolerance. Although our inferences are limited by the small number of species examined, our objective was to determine whether patterns of allocation were related to traditional tolerance rank. We expected that access to light and soil resources may vary with sapling size. Because of the logistical problems associated with selecting comparably sized saplings of different species and the size-dependent biases inherent in comparisons of simple ratios, our interspecific comparisons are based on allometric relationships generated within a species for saplings that ranged from <0.1 m to >1 m in height. Tissue nitrogen and starch concentrations were also measured. Size-dependent variation in these components may provide insight into access to soil resources and sapling carbon balance.

The patterns of biomass, nitrogen, and starch allocation were examined for saplings of sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), and black cherry (*Prunus serotina* Ehrh.) growing in close proximity under a relatively uniform canopy. Based on traditional shade-tolerance rankings (Baker, 1949; Spurr and Barnes, 1980), these species represent a continuum with sugar maple and red maple classified as very shade tolerant and tolerant, and ash and cherry classified as intermediate and intolerant, respectively.

METHODS

Site and species—Red maple (*Acer rubrum*), sugar maple (*A. saccharum*), white ash (*Fraxinus americana*), and black cherry (*Prunus serotina*) saplings were selected in the understory of a young second-growth hardwood forest in central Massachusetts (Harvard Forest: 42°30'N, 72° 15'W). This location was chosen because of its relatively continuous canopy and because of the abundance of saplings of each species. Red oak (*Quercus rubra* L.) and red maple were the dominant overstory species, followed by yellow birch (*Betula lenta* L.), sugar maple, paper birch (*B. papyrifera* Marsh.), beech (*Fagus grandifolia* Ehrh.), and hemlock (*Tsuga canadensis* (L.) Carr.). Mean (± 1 SD) leaf-area index (LAI) in July was 4.05 ± 0.15 m²/m² ($N = 20$, LI-2000 canopy analyzer, LI-COR, Lincoln, NE). Assuming an extinction coefficient of 0.5, this LAI corresponds to a gap-light index, as defined by Canham (1988), of 9.14. The soil, a Gloucester stony loam, is de-

rived from granitic glacial till and is coarse, prone to drought, and relatively infertile.

Light measurements—Daily integrated photosynthetically active radiation was measured for four consecutive days above each sapling with diazo-paper integrating light sensors (Friend, 1961; Sullivan and Mix, 1983). Each sensor was made from 15 layers of diazo paper (Azon number 4516 nonerasable diazo sepia paper, Azon Corp., Johnson City, NY) sandwiched between two layers of cardboard. The top layer of cardboard had a 7-mm diameter hole. A log-linear calibration relating the degree of exposure of each layer of diazo paper to incident photosynthetically active irradiance (400–700 nm), as measured with a quantum sensor (LI-185B, LI-COR), was constructed in the understory near where the sensors were to be deployed. Therefore, the calibration curve was constructed under the range of irradiances and light quality experienced by the saplings. Each sensor was placed in a small water-tight "jeweler's" bag and one sensor was mounted directly above each sapling. Sensors were placed and collected at dusk to minimize systematic sampling error in irradiance. The light data were used as a covariant in analyzing the size dependence of growth and, because saplings were randomly selected, provided an estimate of the horizontal variance of irradiance in the understory.

To quantify the spatial variation in irradiance that might be experienced by a small sapling in the understory, we constructed four three-dimensional frames (1.5 m on a side) that suspend an array of 125 evenly spaced diazo light sensors. Each cube was constructed of small-diameter PVC (polyvinyl chloride) pipe strung with fishing line and provided a three-dimensional array (horizontal "layers" and vertical "slices") of light sensors at 25-cm intervals starting at the forest floor. Thus, each cube encompassed a measuring volume of 1.95 m³. To capture the range of conditions in the understory, cubes were placed directly under a large red oak, a large white ash, and on the north side of the crown of a large hemlock. A fourth cube was placed under a mixed canopy of hardwood species. The light sensors (125 sensors/cube) were left out for 24 h on a clear day. Leaf area index at five locations above each cube was measured with a canopy analyzer.

Sapling harvests and growth rates—Two-year-old or older saplings of each species, in ten height classes up to 1 m (5–8 individuals/height class), were randomly selected. If inspection of the root collar revealed that a sapling was a sprout or if the main stem had recently died back it was rejected and another sapling was chosen. The initial sample size decreased as it became apparent that some sprouts escaped our initial culling.

Height and basal diameter were measured on each sapling prior to harvest. We determined that the horizontal extent of the root system was within an area circumscribed by a radius of twice the height of each sapling and rooting depth did not exceed 25 cm. Based on these observations, intact saplings with complete root systems were excavated, placed in large plastic bags, and transported to our field laboratory. At the laboratory soil was carefully washed from the roots. The cumulative length of all branches and the total length of the main stem axis, in addition to total projected leaf area (model 3100, LI-COR), were measured; subsequently, tissues were dried in a forced-convection oven at 60°C until a constant mass was attained. A small section of the base of the stem from each sapling was removed for determining age. After drying and weighing the component tissues were ground to 60 mesh with a Wiley mill for determination of chemical components.

Sapling biomass was log-linearly related to age (data not shown). Relative growth rate was therefore calculated as the slope of the natural log of total plant dry mass vs. sapling age. The growth rate of the main axis (length growth) was linearly related to total stem length, and mean annual length increment for the last 3 yr was calculated as the mean increment growth divided by total length ($\times 100$).

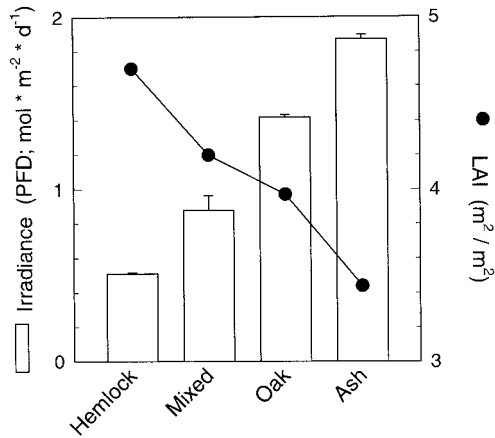


Fig. 1. Integrated photosynthetically active irradiance (PAR; 400–700 nm) and leaf area index (LAI) measured under four canopy locations in a hardwood forest. Mean irradiance (± 1 SD) was measured at 125 locations in a 1.95-m³ volume under each of four canopy types. LAI was measured at 1-m height in five locations above each irradiance-sampling matrix. Error bars for LAI (± 1 SD) are smaller than the symbols.

Tissue chemistry—A subsample of saplings from each size class ($N = 20$ individuals/species) were randomly selected for measurement of leaf, stem, taproot, and small root starch and nitrogen concentration. The taproot was defined as the main root axis, and the rest of the root system was classified as small root. Starch and soluble sugar contents of oven-dried ground samples were determined as glucose equivalents using ethanol and perchloric acid extractions according to Tissue and Wright (1995). Because it took several hours to dissect and process large saplings, we consider our estimates of soluble sugar and leaf starch concentrations unreliable and do not present these data. Total N content was determined by CHN analysis (Model NA 1500, Carlo Erba, Milan, Italy).

Statistical analyses—Because the assumptions of parametric tests were violated, comparisons of mean incident irradiance among horizontal layers and vertical slices within each light cube were tested with a Kruskal Wallis one-way ANOVA. Comparisons of mean irradiance and leaf area index (log transformed) between cubes were done with a parametric ANOVA.

Allometric relationships among plant components (e.g., leaf area vs. total mass) for each species were calculated with logarithmic or linear least-squares regressions. Regression models were compared across species using covariance analysis, where a species by size interaction ($P < 0.05$) indicated a significant difference among slopes (Steele and Torrie, 1980). The intercepts for each species were not tested if slope coefficients were significantly different among species. For direct comparison of species, the regression models were used to calculate the pattern of biomass allocation for a theoretical sapling with a dry mass of 50 g. All species comparisons by component and component comparisons within a species were made with two-way ANOVA and Bonferroni-adjusted post hoc tests. When appropriate, variables that changed with size (e.g., N and starch concentration) were natural-log transformed to meet the assumption of the ANOVA. Statistical analyses were conducted with SYSTAT (version 5.2).

RESULTS

Light environment—Daily integrated irradiance for 1.95-m³ volumes at different positions in the understory, calculated as the average of all light sensors within a cube, was correlated with local leaf area index and varied

TABLE 1. Architecture of tree saplings in the understory of a hardwood forest. The form of the equations (linear or logarithmic), “y” intercepts (b_0), and slopes (b_1) are illustrated for each pair of variables. The units for length and mass are cm and g, respectively.

	b_0	b_1	r^2	N
Height = $b_0 + b_1$ (stem length)**				
<i>Acer rubrum</i>	1.02	0.90*	0.95	58
<i>Acer saccharum</i>	1.30	0.87*	0.93	46
<i>Fraxinus americana</i>	-0.08	0.95*	0.98	43
<i>Prunus serotina</i>	9.37#	0.64*	0.75	59
Branch number = $b_0 + b_1$ (stem length)**				
<i>Acer rubrum</i>	-0.89#	0.08*	0.77	44
<i>Acer saccharum</i>	-1.21#	0.08*	0.59	57
<i>Fraxinus americana</i>	-1.41*	0.07*	0.60	59
<i>Prunus serotina</i>	-0.62	0.12*	0.88	47
ln(cumulative branch length) = $b_0 + b_1$ (stem length)**				
<i>Acer rubrum</i>	0.62#	0.04*	0.64	26
<i>Acer saccharum</i>	0.69	0.04*	0.75	35
<i>Fraxinus americana</i>	0.46	0.03#	0.42	21
<i>Prunus serotina</i>	2.47*	0.02*	0.58	39
ln(height) = $b_0 + b_1$ ln(total mass)**				
<i>Acer rubrum</i>	2.69*	0.51*	0.89	44
<i>Acer saccharum</i>	2.67*	0.50*	0.92	58
<i>Fraxinus americana</i>	2.56*	0.50*	0.88	61
<i>Prunus serotina</i>	2.45*	0.48*	0.81	47

* Intercept or regression coefficient is different from 0 at $P < 0.001$.

Intercept or regression coefficient is different from 0 at $P < 0.05$.

** Regression coefficients among species were significantly different at $P < 0.01$.

directly with overstory composition (Fig. 1). Ash produced a relatively sparse canopy with a LAI of 3.4 and a correspondingly high daily irradiance. At the other extreme, the LAI near hemlock was >4.7 , resulting in a threefold reduction in irradiance compared to ash.

There was significant variation in incident irradiance within the 1.95-m³ cubes, and this variation was greater for the vertical than for the horizontal plane (data not shown). The average value of integrated irradiance among vertical slices was statistically different ($P < 0.05$) for all cubes, but was only different between horizontal layers for cubes under hemlock and the mixed canopy. Under hemlock integrated irradiance increased from 0.4 mol·m⁻²·d⁻¹ at the forest floor to 0.6 mol·m⁻²·d⁻¹ at 1 m. The ranges of irradiance under the mixed, oak, and ash canopies were 0.8–0.9, 1.3–1.6, and 1.5–2.1 mol·m⁻²·d⁻¹, respectively. This vertical variation was a function of the distribution and abundance of the relatively sparse understory vegetation. The horizontal variation was from 8 to 15% (calculated for east-west and north-south orientations) compared to 15–27% variation between vertical slices.

For all species, the range in irradiance above the randomly selected saplings was considerably greater than the vertical and horizontal variation in irradiance measured within light cubes.

Aboveground architecture and whole-plant biomass allocation—Differences in aboveground architecture were greatest between white ash and black cherry (Table 1). Because of its curved main axis, cherry required more total stem length and stem mass to achieve a given height than the other three species. Ash produced the most erect stem as indicated by an almost direct correspondence be-

TABLE 2. Component biomass allocation of tree saplings in the understory of a hardwood forest. The linear regression model, "y" intercepts (b_0), and slopes (b_1) are illustrated for each pair of variables. The units for mass and area are g and cm^2 , respectively.

	b_0	b_1	r^2	N
Above ground allocation				
Leaf mass = $b_0 + b_1$ (stem mass)**				
<i>Acer rubrum</i>	0.28#	0.42*	0.94	44
<i>Acer saccharum</i>	0.23#	0.31*	0.89	58
<i>Fraxinus americana</i>	0.26	0.35*	0.85	61
<i>Prunus serotina</i>	0.85*	0.25*	0.86	48
Leaf area = $b_0 + b_1$ (stem mass)**				
<i>Acer rubrum</i>	65.48#	96.12*	0.94	44
<i>Acer saccharum</i>	89.91#	86.63*	0.87	58
<i>Fraxinus americana</i>	80.60	139.49*	0.86	61
<i>Prunus serotina</i>	277.44*	69.81*	0.83	48
Leaf area = $b_0 + b_1$ (stem cross-sectional area)**				
<i>Acer rubrum</i>	-174.28#	27.11*	0.78	41
<i>Acer saccharum</i>	70.04	16.47*	0.64	56
<i>Fraxinus americana</i>	-104.53	25.58*	0.74	59
<i>Prunus serotina</i>	118.30	30.00*	0.69	45
Belowground allocation				
Taproot mass = $b_0 + b_1$ (total root mass)**				
<i>Acer rubrum</i>	-0.09	0.72*	0.95	44
<i>Acer saccharum</i>	-0.14	0.70*	0.95	58
<i>Fraxinus americana</i>	0.19	0.60*	0.91	61
<i>Prunus serotina</i>	-2.54#	0.88*	0.97	48

* Intercept or regression coefficient is different from 0 at $P < 0.001$.

Intercept or regression coefficient is different from 0 at $P < 0.05$.

** Regression coefficients among species were significantly different at $P < 0.01$.

tween height and stem length (slope = 0.95), but red maple produced the greatest height with the lowest investment in stem biomass. Cherry produced substantially more branches per unit of stem length than the other species, but they were relatively short. As a result, the total branch length per unit stem length was greater for the maples and for ash than for cherry.

The ratio of leaf area or leaf mass to stem mass (branches plus stem) may relate to the metabolic cost of providing support for the photosynthetic tissues. The slope of the relationship between leaf and stem mass was lower for black cherry than for the other species (Table 2). Despite a large "y" intercept, black cherry also produced substantially less leaf area for a given investment in stem mass than the other species. Because of its high ratio of leaf area/mass (specific leaf area, discussed below), ash had the greatest leaf area per unit stem mass, whereas red maple had the greatest leaf mass per unit stem mass.

There was a significant log-linear decrease in specific leaf area (leaf area in square centimetres/leaf mass in grams) with total plant biomass for sugar maple ($r = -0.57$, $P < 0.001$) and red maple ($r = -0.49$, $P < 0.001$). In both cases, however, the variance was high and the corresponding coefficients of determination were low (data not shown). The mean (± 1 SD) SLAs for white ash, sugar maple, black cherry, and red maple, were 381.5 ± 46.2 , 313.4 ± 28.6 , 298.5 ± 35.0 , and 239.5 ± 28.6 cm^2/g , respectively. The post hoc test indicated that the SLAs for sugar maple and white ash were not significantly different, whereas the SLA for white ash was significantly greater than the SLA for red maple. The

SLA for red maple was significantly lower than for the other three species.

The area of pith and the area from the vascular cambium outward were subtracted from the total cross-sectional area of the base of the stem to yield the stem cross-sectional area in Table 2. Assuming the remaining area in these small saplings was all functional xylem, the slope of the relationship between leaf area and stem cross-sectional area represents the leaf/sapwood area ratio. Leaf/sapwood area ratio varied by almost twofold with sugar maple and black cherry having the smallest and largest values, respectively (16.47 vs. 30.00 cm^2/cm^2).

There was significant variation in the apportionment of biomass to small root and tap root among these species (Table 2). It should be noted that this was a coarse distinction, as all biomass not associated with the taproot was classified as small root. Thus, small root in this study represents ephemeral roots plus smaller woody branch roots. Below ground, 60% of the total root mass was in the taproot for ash compared to 88% for cherry. The maples were intermediate between ash and cherry with 70–72% of total root mass invested in the taproot.

The ratio of leaf area/total sapling mass (leaf area ratio; LAR) represents the proportional investment in assimilatory surface area. This ratio, represented by the slope of the regression between leaf and total sapling mass (Table 3), was considerably lower for cherry than for the other three species. Ash had the highest leaf area/sapling mass ratio, followed by red maple and sugar maple. Cherry also had lowest proportion of its total mass allocated to stem or to all aboveground tissues combined. Total shoot mass (leaves + branches + stem) was linearly related total sapling mass and represented only 28% of total sapling mass for cherry compared to 40% or greater for the other species. The relatively small investment in aboveground mass for cherry was caused by a disproportionately large investment in the taproot (Table 3, Fig. 2).

The percentage of total biomass in the different above- and belowground compartments was calculated for theoretical 50-g saplings of each species using the species-specific regressions in the tables. The proportional investment in the taproot was striking for cherry (Fig. 2). This species allocated >50% of total mass to the taproot compared to <33% for the other three species. This large investment in tap root was at the expense of leaf and stem mass. The theoretical 50-g black cherry sapling invested ~8% of total mass in leaves compared to 13–21% for the other species. Red maple had the greatest investment in leaf and branch mass, and ash had the greatest proportional investment in stem biomass. The investment in small root mass was from 9.2 to 16.8% (Fig. 2).

Tissue chemistry—Starch and nitrogen concentrations (percentage of dry mass) of component tissues represent carbon storage and potential metabolic activity, respectively. These variables were analyzed for size-dependent variation and for differences among components within a species and across species for a given component.

Across species the highest concentration of N was in leaves followed by small roots (Fig. 3). There were no significant differences in N% between stems and taproots for any species. The N concentration approached 2% for

TABLE 3. Whole-plant biomass allocation for tree saplings in the understory of a hardwood forest. The linear regression model, “y” intercepts (b_0), and slopes (b_1) are illustrated for each pair of variables. The units for area and mass are cm^2 and g, respectively.

	b_0	b_1	r^2		b_0	b_1	r^2	N
Leaf mass = $b_0 + b_1$ (total mass)**				Branch mass = $b_0 + b_1$ (total mass)**				
<i>Acer rubrum</i>	0.04	0.21*	0.95	<i>Acer rubrum</i>	-0.56*	0.13*	0.82	44
<i>Acer saccharum</i>	0.13	0.13*	0.87	<i>Acer saccharum</i>	-0.17#	0.06*	0.84	58
<i>Fraxinus americana</i>	-0.02	0.16*	0.88	<i>Fraxinus americana</i>	-0.24#	0.05*	0.66	61
<i>Prunus serotina</i>	1.06#	0.07*	0.68	<i>Prunus serotina</i>	-0.14	0.07*	0.83	48
Leaf area = $b_0 + b_1$ (total mass)**				Total shoot mass = $b_0 + b_1$ (total mass)**				
<i>Acer rubrum</i>	11.48	46.57*	0.95	<i>Acer rubrum</i>	-0.52*	0.48*	0.99	44
<i>Acer saccharum</i>	61.75	35.04*	0.86	<i>Acer saccharum</i>	-0.28	0.40*	0.97	58
<i>Fraxinus americana</i>	-25.04	61.24*	0.88	<i>Fraxinus americana</i>	-0.57*	0.42*	0.95	61
<i>Prunus serotina</i>	331.63#	19.03*	0.66	<i>Prunus serotina</i>	0.56	0.28*	0.84	48
Stem mass = $b_0 + b_1$ (total mass)**				Leaf area = $b_0 + b_1$ (small root mass)				
<i>Acer rubrum</i>	0.05	0.34*	0.97	<i>Acer rubrum</i>	49.65	367.10*	0.64	44
<i>Acer saccharum</i>	-0.11	0.34*	0.97	<i>Acer saccharum</i>	106.15#	198.67*	0.73	58
<i>Fraxinus americana</i>	-0.33	0.37*	0.94	<i>Fraxinus americana</i>	104.13	297.24*	0.77	61
<i>Prunus serotina</i>	0.70	0.21*	0.83	<i>Prunus serotina</i>	267.05#	136.06*	0.59	48

* Intercept or regression coefficient is different from 0 at $P < 0.001$.
 # Intercept or regression coefficient is different from 0 at $P < 0.05$.
 ** Regression coefficients among species were significantly different at $P < 0.01$.

leaves of ash and cherry and was significantly greater for leaves of these species than for the two maple species ($P < 0.05$). The N concentration in small roots of ash was greater than cherry and similar to the other two species. Leaf nitrogen concentration increased in direct proportion to total leaf biomass for cherry ($r = 0.70$, $P < 0.001$), ash ($r = 0.88$, $P < 0.001$), and sugar maple ($r = 0.65$, $P = 0.002$) (data not shown). Taproot and small root N concentration increased with increasing mass of these tissues for ash (tap root: $r = 0.70$, $P < 0.001$; small root: $r = 0.54$, $P = 0.014$), but small root N concentration decreased with increasing small root mass for cherry ($r = 0.70$, $P = 0.003$). The only species to show a positive correlation between average nitrogen concentration for the entire sapling and total sapling biomass was red maple ($r = 0.66$, $P = 0.015$).

With the exception of cherry, which had an exceptionally high starch concentration in small roots (~17%), the highest starch concentrations were in the taproots (Fig. 3). Starch concentrations were approximately equal for stems and small roots of red maple, sugar maple, and ash, and ranged between 6 and 9%.

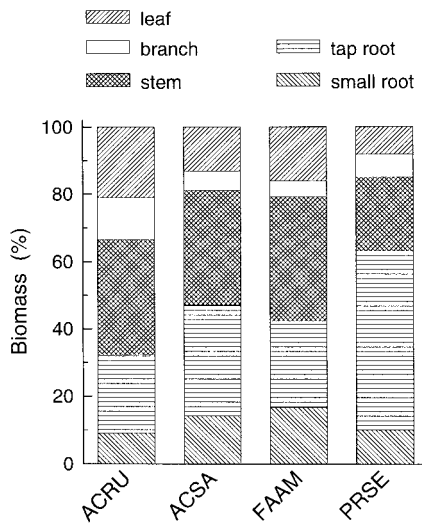


Fig. 2. Percentage allocation of biomass to leaf, branch, stem, taproot, and small root for a theoretical 50-g sapling of red maple (*Acer rubrum*, ACRU), sugar maple (*Acer saccharum*, ACSA), white ash (*Fraxinus americana*, FAAM), and black cherry (*Prunus serotina*, PRSE). Biomass allocation was calculated from the allometric relationships in Tables 2 and 3.

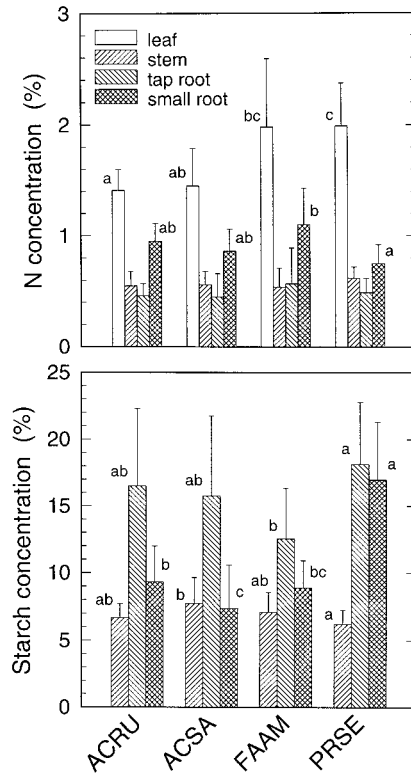


Fig. 3. Total nitrogen and starch concentration for leaf (N only), stem, taproot, and small root of red maple (*Acer rubrum*, ACRU), sugar maple (*Acer saccharum*, ACSA), white ash (*Fraxinus americana*, FAAM), and black cherry (*Prunus serotina*, PRSE). Each bar represents the mean, and the error bar is 1 SD ($N = 20$). Bars with different letters represent tissues that are significantly different ($P < 0.05$) between species. Size-related differences in N and starch are reported in the Results.

TABLE 4. Growth rate and incident daily irradiance for tree saplings in the understory of a hardwood forest.

Species	Length increment (%)	Relative growth rate (%)	Incident irradiance (mol·m ⁻² ·d ⁻¹)
<i>Acer rubrum</i>	11.6 (0.4) c	13.0 (4.7) ^a	2.03 (0.75)
<i>Acer saccharum</i>	6.1 (4.2) a	14.9 (3.5)	1.73 (0.65)
<i>Fraxinus americana</i>	27.3 (6.1) abc	29.5 (3.1)	1.73 (0.63)
<i>Prunus serotina</i>	11.1 (7.6) b	19.5 (4.5)	1.97 (0.65)

Note: The values for length increment are means \pm 1 SD for individual saplings of each species. Means followed by different letters are significantly different at $P < 0.001$. Relative growth rate (RGR; g·g⁻¹·yr⁻¹) was calculated as the slope of ln(sapling biomass) vs. age (from ring counts), and the error term is the standard error for the regression. There was significant variance among species in RGR as indicated by analysis of covariance ($P < 0.05$). The values for length increment and RGR are expressed as percentage increases per year. There was a marginally significant difference ($P < 0.1$) in mean (\pm SD) daily irradiance among species. A multiple range test was not performed for this variable.

^a Standard error for the regression.

decreased with increasing stem mass for ash ($r = -0.47$, $P = 0.054$), sugar maple ($r = -0.67$, $P = 0.009$), and red maple ($r = -0.52$, $P = 0.07$) but did not vary with increasing biomass of stems or small roots.

Growth rates and sapling-specific light environment—Growth rates were expressed as length increment and as relative growth rate (biomass increment; Table 4). Of the four species examined in this study ash had the greatest length increment and relative growth rate. The relative growth rate of 29.5% indicates a biomass increment of 0.295 g·g⁻¹·yr⁻¹. Cherry had the lowest relative growth rate, and sugar maple had the lowest rate of height growth. Neither measure of growth (length increment or RGR) for any species varied significantly with integrated incident daily irradiance measured during mid-summer.

Because incident irradiance was measured for each sapling, primarily to use as a covariant in statistical comparisons among species, we were able to compare the light environment in which the different species grew. There was a marginally significant difference in light environment ($P < 0.10$), with red maple and cherry growing in slightly brighter microsites than sugar maple and ash (Table 4).

DISCUSSION

Incident irradiance was measured in the understory at two spatial scales. Each "light sensor cube" captured the vertical and horizontal variation in irradiance that would be experienced by a small sapling; at a larger scale, the cubes were positioned under different canopy species thereby capturing the horizontal variation in the forest. The horizontal variance of instantaneous irradiance over the scale of an individual sapling can be high (Oberbauer et al., 1988). For example, Chazdon (1988) and Baldocchi and Collineau (1994) demonstrated that the instantaneous values recorded for sensors as close as 0.1–0.5 m can be uncorrelated. Because of this variation, different portions of a sapling simultaneously experience different irradiances, leaf temperature, and leaf-to-air vapor pressure deficit (LAVPD), raising important questions about

the degree of physiological integration in individual saplings. We report variation of up to 15% in daily integrated irradiance over similar horizontal scales. Through its effect on the growth and carbon balance of individual branches, this variation may modify the aboveground architecture of saplings.

As reported by Canham and Burbank (1994), incident irradiance varied predictably below the crowns of different species. Leaf area index was highest and irradiance was lowest under hemlock and the opposite was true for ash (Fig. 1). The variation in LAI is inversely correlated with the traditional shade-tolerance rank for large trees and is controlled more by the depth of the crown than by lateral spread of the canopy individuals (Canham and Burbank, 1994).

The phenotypic responses of trees to changes in light availability and theoretical arguments based on optimization of resource acquisition have produced a number of predictions about the "adaptive" architecture and allocation patterns for shade-tolerant species (Canham and Marks, 1985). Horn (1971) proposed that the construction of a monolayer of foliage, which would minimize self-shading and thus maximize light interception per unit leaf area, would be advantageous in the understory. Based on our data this prediction appears to be robust.

Although we did not quantify the three-dimensional arrangement of foliage, our measurements of branch length per unit stem length support Horn's hypothesis. Black cherry, the least shade-tolerant species, maintained the greatest number of branches per unit length of the main stem, as indicated by the slope of the regression between branch number and stem length (Table 1), but the branches were relatively short and dispersed evenly along the main axis. Branch length increased logarithmically with increasing stem length for all species, and the slope of this relationship was twice as large for the shade-tolerant maples as for the intolerant black cherry (Table 1). Sugar maple, red maple, and ash held their branches and foliage near the top of the stem and, in combination with the production of longer branches, maintained a monolayer of foliage. Consistent with these observations, Canham (1988) found that shade-tolerant sugar maple and beech increased lateral growth relative to height growth in darker microsites in the understory, thereby reducing self-shading. The greater probability of harvesting transient sunflecks afforded by greater lateral branch spread in the heterogeneous radiation environment of the understory (Oberbauer et al., 1988) may partially offset the investment in resources associated with branch construction, maintenance, and assimilate transport.

An unusual feature of cherry was that the main axis grew in a gentle arc rather than perfectly erect. As a result of this arc, cherry required greater stem length (Table 1) and biomass to achieve a given height relative to the other species. Shade-intolerant woody plants produce lower density wood than their more tolerant counterparts (Augsburger, 1984; Lei and Lechowicz, 1990). The wood densities reported for adults of our species are 0.47, 0.49, 0.55, and 0.56 g/cm³ (measured at 12% moisture content) for black cherry, red maple, white ash, and sugar maple, respectively (Forest Service, 1987). For cherry, lower density may have produced weaker wood less able to sustain erect growth. Cherry also is prone to extreme

bending under the mass of snow or ice, resulting in leader loss (Burns and Honkala, 1990).

Optimizing leaf display with respect to the carbon investment in constructing and maintaining leaves, stems, and roots could potentially increase carbon assimilation for understory saplings. This optimization can be achieved by constructing leaves with a high specific leaf area (SLA; leaf area per unit mass) and by constructing saplings with high leaf area ratios (LAR; leaf area per unit whole-plant mass). Increasing SLA is an almost universal phenotypic response to shade (Loach, 1970; Popma and Bongers, 1988; Walters, Kruger, and Reich, 1993). The SLA for shade-grown individuals of hardwood trees, for example, is approximately twice the value of sun-grown individuals of the same species, regardless of the degree of shade tolerance (Abrams and Kubiske, 1990). This relationship may not extend to interspecific comparisons.

For 27 northern hardwood tree species growing in the shaded understory, Abrams and Kubiske (1990) found that, on average, SLA increased with increasing shade-tolerance rank; the class average for intolerant species was 265 cm²/g compared to 394 cm²/g for shade-tolerant species. Our species did not conform to this trend. White ash, a species of intermediate tolerance, had higher SLA than the other three species, and the average SLA of the most shade-tolerant species, sugar maple, was within 5% of the SLA for the least shade-tolerant species, black cherry. Interpretation of the functional significance of SLA is further confounded by the results of a survey of 13 tropical tree seedlings. In this survey Kitajima (1994) found that, unlike Abrams and Kubiske (1990), SLA was inversely correlated with the degree of shade tolerance. Moreover, no relationship between SLA and tolerance rank was found between canopy trees in a hardwood forest (Bassow and Bazzaz, 1997). The potentially competing demands of building a leaf that maximizes light interception per unit carbon investment (high SLA) vs. building a thick, tough leaf that resists herbivory (low SLA) may explain this apparent conflict (Coley, Bryant, and Chapin, 1985; Kitajima, 1994; Coley and Barone, 1996).

Our data also did not support the prediction that the proportional investment in leaf area, expressed as the leaf area ratio (LAR), was correlated with shade tolerance. Leaf area was linearly related to total plant mass for all species (Table 3). Using these relationships to calculate the leaf area for a theoretical understory sapling weighing 50 g (dry mass), cherry had a leaf area of 1283 cm² compared to 1800 cm² or greater for the other species. Cherry conformed to our expectation. The leaf area for saplings of comparable mass for the other three species, however, was inversely related to the traditional shade-tolerance ranking. From most to least shade tolerant, the predicted leaf areas were: 1814 (sugar maple), 2340 (red maple), and 3037 cm² (white ash).

We measured nitrogen concentration (N%) as a proxy for physiological capacity, since nitrogen concentration is highly correlated with maximum photosynthetic rate (Field, Merino, and Mooney, 1983) and with the respiration rates of woody tissues (Ryan et al., 1996). Cherry and ash had significantly higher leaf N% than the two maples. This is consistent with higher photosynthetic ca-

capacity associated with shade-intolerant species (Fredrickson et al., 1996; Wallace and Dunn, 1980; Walters, Kruger, and Reich, 1993). Although coefficients of determination were quite low, nitrogen concentration increased with increasing total leaf mass for cherry, ash, and sugar maple, and the average N concentration for the whole sapling increased with increasing sapling mass for red maple. These increases may reflect an enhanced capacity to acquire N with increasing size. This may occur through two quite different mechanisms. Since incident irradiance increased modestly with height, presumably leading to enhanced photosynthesis, the additional carbon gain realized by taller saplings may facilitate uptake and reduction of N. Alternatively, N concentrations may rise with whole plant mass if increased allocation to root systems allows saplings to forage more widely, support greater mycorrhizal activity, and thereby out compete neighbors for limiting nutrients.

The high starch concentration in the tap roots of these small saplings suggests that these species actively store carbohydrates even in the light-limited understory. It appears that cherry stores starch in small roots in addition to the tap root (Fig. 3). There were weak negative correlations of starch concentration with increasing stem mass in the two maple species and ash but when all tissues were averaged there was no relationship between starch concentration and sapling mass. Leaf area increased linearly with sapling mass for all species (Table 3) thereby keeping the supply and utilization of carbohydrates in balance as sapling mass increased.

The inconsistencies in relating SLA and LAR to the traditional shade-tolerance rankings may arise because these rankings, with their emphasis on light as a driving variable, are too narrowly defined. Light availability, at least at the levels typically measured in a dense understory, is unquestionably the primary physical factor influencing growth, but a myriad of biotic interactions influence the patterns of biomass allocation (Canham et al., 1996) and survival. Resistance to herbivory and pathogens may be powerful selective pressures in the understory, imposing their own influence on plant structure (Coley, Bryant, and Chapin, 1985; Kitajima, 1994). A broader interpretation of "shade tolerance" that extends the strict carbon economy paradigm by embracing the role of biotic factors may be necessary to adequately interpret the patterns of biomass allocation of these species.

The patterns of biomass allocation observed in this study are consistent with three general growth strategies in the understory: one that promotes persistence, one that maximizes growth in the understory, and one that promotes the maintenance of a high potential for exploiting canopy gaps. Sugar maple and to some extent red maple represent this first strategy. Consistent with its low photosynthetic capacity (Walters, Kruger, and Reich, 1993; Naidu, 1996), sugar maple had the lowest rates of height growth and the second lowest rate of biomass increment in this study (Sipe and Bazzaz, 1995). It reaches the canopy through longevity, typically retaining a subordinate position even in newly formed canopy gaps (Canham, 1985). Traits that minimize the risk of mortality may be paramount for this species. Low SLA and LAR contribute to its low growth rates (Poorter, Remkes, and Lambers, 1990; King, 1991) but may confer resistance to her-

bivory, pathogens (Hoffland et al., 1996), and transient water limitations. This supposition is supported by the observation that sugar maple is not highly susceptible to insect injury (Burns and Honkala, 1990).

In contrast to the maples, ash, traditionally defined as intermediate shade tolerant, had higher LAR and SLA than the more tolerant maples. These traits may have contributed directly to the comparatively high rates of height and biomass growth for this species in the understory (Table 4). High LAR and SLA may, however, increase its susceptibility to browsing and disease, which is notably high for this species (Burns and Honkala, 1990).

Cherry had the lowest LAR and SLA, traits consistent with its rank as a shade-intolerant species. This species was unusual in its large investment in root biomass, particularly in taproot. Total shoot mass was linearly related to total mass with a slope of 0.40–0.48 for the maples and ash compared to 0.28 for cherry. Using these regression equations, the root/shoot ratio for hypothetical 50-g saplings of the maples and ash were between 1.2 and 1.5 compared to 2.6 for cherry. There were very few cherry saplings greater than 1.5 m tall in this forest, and many of these saplings showed evidence of repeated stem dieback and browsing. The construction of this large taproot may be related to these disturbances in this species—with each instance of dieback or browsing the taproot continues to increase in size relative to the shoot resulting in a large root/shoot ratio. The large storage capacity provided by this taproot may poise this species for rapid growth once a canopy gap forms but may contribute to its low relative growth rates in the understory.

The benefits of phenotypic responses to low irradiance, such as increases in specific leaf area (SLA) and leaf area ratio (LAR), may not be adaptive for late-successional hardwood saplings that persist for long periods in the understory. The species in this study may represent three distinct growth strategies. The high LAR and SLA of white ash, coupled with its erect growth form, enable white ash to maintain high growth rates in the understory. Compared to ash, the lower SLA and LAR of the two maple species may confer resistance to herbivory at the potential cost of reduced growth rates. These traits may improve the probability of surviving for extended periods in the understory. The large stores of carbohydrates in the taproot of cherry, and the pattern of growth and dieback, may poise this species for rapid (exploitive) growth following a canopy disturbance. Persistence may be reduced, however, by the development of a very large root/shoot ratio for this species. The traditional notion of shade tolerance is more complicated than is often presented. A more complete interpretation of the patterns of biomass allocation of trees in the understory may emerge by considering factors that influence the ability to cope with herbivores and pathogens and competition for soil resources.

LITERATURE CITED

ABRAMS, M. D., AND M. E. KUBISKE. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade tolerance rank. *Forest Ecology and Management* 31: 245–253.

AUGSPURGER, C. K. 1984. Seedling survival of tropical tree species:

interactions of dispersal distance, light gaps, and pathogens. *Ecology* 65: 1705–1712.

BAKER, F. S. 1949. A revised tolerance table. *Journal of Forestry* 47: 179–181.

BALDOCCHI, D., AND S. COLLINEAU. 1994. The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. In M. M. Caldwell and R. W. Pearcy [eds.], *Exploitation of environmental heterogeneity by plants*, 21–71, Academic Press, London.

BASSOW, S. L., AND F. A. BAZZAZ. 1997. Intra- and inter-specific variation in canopy photosynthesis in a mixed deciduous forest. *Oecologia* 109: 507–515.

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

BOARDMAN, N. K. 1977. Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology* 28: 355–377.

BURNS, R. M., AND B. H. HONKALA. 1990. *Silvics of North America*, volume 2. Hardwoods. Agriculture Handbook 654, Forest Service, United States Department of Agriculture, Washington, DC.

CANHAM, C. D. 1985. Suppression and release during canopy recruitment of *Acer saccharum*. *Bulletin of the Torrey Botanical Club* 112: 134–145.

———. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69: 786–795.

———, AND D. H. BURBANK. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research* 24: 337–349.

———, AND P. L. MARKS. 1985. The response of woody plants to disturbance: patterns of establishment and growth. In S. T. A. Pickett and P. S. White [eds.], *The ecology of natural disturbance and patch dynamics*, 119–217. Academic Press, Orlando, FL.

———, A. R. BERKOWITZ, V. R. KELLY, G. M. LOVETT, S. V. OLLINGER, AND J. SCHNURR. 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Canadian Journal of Forest Research* 26: 1521–1530.

CHAZDON, R. L. 1988. Sunflecks and their importance to forest understory plants. *Advances in Ecological Research* 18: 1–63.

COLEY, P. D., AND J. A. BARONE. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27: 305–335.

———, J. P. BRYANT, AND F. S. CHAPIN, III. 1985. Resource availability and plant anti-herbivore defense. *Science* 230: 895–899.

FIELD, C., J. MERINO, AND H. A. MOONEY. 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. *Oecologia* 60: 382–389.

FRIEND, D. T. C. 1961. A simple method of measuring integrated light values in the field. *Ecology* 42: 577–580.

FOREST SERVICE. 1987. *Wood handbook: wood as an engineering material*. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture. Revised 1987. Agriculture Handbook Number 72.

FREDRICKSEN, T. S., K. C. STEINER, J. M. SKELLY, B. J. JOYCE, T. E. KOLB, K. B. KOUTERICK, AND J. A. FERDINAND. 1996. Diel and seasonal patterns of leaf gas exchange and xylem water potential of different-sized *Prunus serotina* Ehrh. trees. *Forest Science* 42: 359–365.

GIVNISH, T. J. 1988. Adaptation to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiology* 15: 63–92.

GRAHAM, S. A. 1954. Scoring tolerance of forest trees. Michigan Forestry Note 4. University of Michigan, Ann Arbor, MI.

HOFFLAND, E., G. J. NIEMANN, J. A. VANPELT, J. B. M. PUREVEEN, G. B. EIJKEL, J. J. BOON, AND H. LAMBERS. 1996. Relative growth rate correlates negatively with pathogen resistance. *Plant, Cell and Environment* 19: 1281–1290.

HORN, H. S. 1971. *The adaptive geometry of trees*. Princeton University Press, Princeton, NJ.

KING, D. A. 1991. Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. *Functional Ecology* 5: 485–492.

KITAJIMA, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98: 419–428.

KOBE, R. K. 1996. Intraspecific variation in sapling mortality and

- growth predicts geographic variation in forest composition. *Ecological Monographs* 66: 181–201.
- , S. W. PACALA, J. A. SILANDER, JR., AND C. D. CANHAM. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* 5: 517–532.
- KORSTIAN, C. F., AND T. S. COILE. 1938. Plant competition in forest stands. Duke University School of Forestry Bulletin 3, 123 pp.
- LEI, T. T., AND M. J. LECHOWICZ. 1990. Shade adaptation and shade tolerance in saplings of three *Acer* species from eastern North America. *Oecologia* 84: 224–228.
- LOACH, K. 1970. Shade tolerance in tree seedlings. II. Growth analysis of plants raised under artificial shade. *New Phytologist* 69: 273–286.
- NAIDU, S. L. 1996. Coordination of physiological and morphological acclimation of shade-grown tree saplings to late-season canopy gap formation. Ph.D. dissertation, University of Illinois, Urbana, IL.
- OBERBAUER, S. F., D. B. CLARK, D. A. CLARK, AND M. QUESADA. 1988. Crown light environments of saplings of two species of rain forest emergent trees. *Oecologia* 75: 201–212.
- PACALA, S. W., C. D. CANHAM, J. A. SILANDER, JR., AND R. K. KOBE. 1994. Sapling growth as a function of resources in a northern temperate forest. *Canadian Journal of Forest Research* 24: 2172–2183.
- POORTER, H., C. REMKES, AND H. LAMBERS. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiology* 94: 621–627.
- POPMA, J., AND F. BONGERS. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* 75: 625–632.
- RYAN, M. G., R. M. HUBBARD, S. PONGRACIC, R. J. RAISON, AND R. E. MCMURTRIE. 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiology* 16: 333–343.
- SPE, T. W., AND F. A. BAZZAZ. 1995. Gap partitioning among maples (*Acer*) in central New England: survival and growth. *Ecology* 76: 1587–1602.
- SPURR, S. H., AND B. V. BARNES. 1980. Forest ecology, 3rd ed. John Wiley & Sons, New York, NY.
- STEELE, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics—a biometrical approach. McGraw-Hill, New York, NY.
- SULLIVAN, T. J., AND M. C. MIX. 1983. A simple and inexpensive method for measuring integrated light energy. *Environmental Science and Technology* 17: 127–128.
- TISSUE, D. T., AND S. J. WRIGHT. 1995. Effect of seasonal water availability on phenology and the annual carbohydrate cycle of tropical forest shrubs. *Functional Ecology* 9: 518–527.
- TOUMEY, J. W., AND R. KIENHOLZ. 1931. Trenched plots under forest canopies. Yale University School of Forestry Bulletin 30.
- VEENENDAAL, E. M., M. D. SWAINE, R. T. LECHA, M. F. WALSH, I. K. ABBRESE, AND K. OWUSU-APRIYIE. 1996. Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology* 10: 501–511.
- WALLACE, L. L., AND E. L. DUNN. 1980. comparative photosynthesis of three gap phase successional tree species. *Oecologia* 45: 331–340.
- WALTERS, M. B., E. L. KRUGER, AND P. B. REICH. 1993. Growth, biomass distribution and CO₂ exchange of northern hardwood seedlings in high and low light: relationship with successional status and shade tolerance. *Oecologia* 94: 4–16.