Growing-Space Relationships in Young Even-Aged Northern Hardwood Stands Based on Individual-Tree and Plot-Level Measurements

David Ray, Ruth D. Yanai, Ralph D. Nyland, and Terry R. McConnell

ABSTRACT

The amount of growing space occupied by trees of given sizes and species is traditionally assessed on a plot basis, using observations from groups of trees growing within an area of fixed size. Our study combines individual-tree with plot-based observations of upper-canopy trees representing a range of shade tolerance (*Fagus grandifolia* ≥ *Acer saccharum* > *Betula alleghaniensis* ≥ *Fraxinus americana*) in three young, fully stocked, even-aged northern hardwood stands. The amount of canopy growing space used by a stem of given size was described by the ratios of crown projection area and crown surface area to stem basal area. These variables were related to species, stand, and relative basal area using analysis of covariance. Both ratios were generally highest in the youngest (19 years) stand, intermediate in the mid-aged stand (24 years), and lowest in the oldest stand (29 years). A few differences were detected among species, with shade-tolerants having larger ratios. Allometric models were used in conjunction with plot density data to estimate canopy cover at the stand level. Considerable crown overlap was indicated among upper-canopy trees in all three stands. Estimates from tree-centered plots suggested that crowns occupied 1.81 ± 0.02 times the ground area in the youngest stand and 1.45 ± 0.03 times in the mid-aged and oldest stands; when corrected for sampling bias, these ratios were at least 1.30 and 0.96, respectively. Combining individual-tree with plot-level measurements afforded a comprehensive assessment of trends in growing-space occupancy not possible using either technique alone.

Keywords: allometry, crown projection area, crown surface area, even-aged, growing space, northern hardwoods, shade tolerance, stand dynamics

The allometric relationship between crown size and stem diameter has received considerable attention because of the effect of crown dimensions on stocking (Minkler and Gingrich 1970, Lamson 1987), stem increment (Cole and Lorimer 1994, Webster and Lorimer 2003), and tree leaf area (Tucker et al. 1993, Valentine et al. 1994). The crown-competition factor introduced by Krajicek et al. (1961) used the relationship between the crown width and stem diameter of open-grown trees as an index of stocking in forest stands. This approach was later incorporated into Gingrich's (1967) stocking guide for upland hardwoods in the Central States to define the minimum stem densities for full site occupancy, i.e., the B-line.

Measurements taken on densely populated, fixed-area plots have traditionally been used to establish the upper limits of stem density, allowing the estimation of stocking or relative density. Examples include Reineke's (1933) stand density index, the tree-area-ratio approach of Chisman and Schumacher (1940), and the self-thinning trajectory by Drew and Flewelling (1979). An average crown projection area can also be calculated by dividing the ground area by the stem density. However, this approach assumes that total crown cover is 100% and that crowns do not overlap. Inferences about stocking based on crown projection areas obtained from crown-width models (e.g., Hemery et al. 2005) are likewise compromised

by assumptions about spacing and crown overlap. Measuring both stem density and crown area in the same stands (*sensu* Lorimer et al. 1988) allows these assumptions to be tested.

Shade tolerance has been proposed as a predictor of maximum stand density, but with mixed results. Daniel et al. (1979, p. 298) conclude that stands composed of shade-tolerant species, primarily conifers, support higher densities than shade intolerants at full stocking, whereas the opposite trend has been documented in mixed-species stands in the Allegheny hardwood (Roach 1977, Stout and Nyland 1986) and upland central hardwood types (Minkler and Gingrich 1970). Species-specific regression models that predict crown width from stem diameter provide further evidence of such a relationship (Minkler and Gingrich 1970, Lamson 1987, Gering and May 1995). In contrast, other studies have found no such link based on plot measurements (Zeide 1985) or observation of individual trees (Bragg 2001, Hemery et al. 2005).

Large differences in tree allometry have been demonstrated among species or functional groups and among trees of different size and age, particularly in the context of diverse species assemblages (Poorter et al. 2006, Aiba and Nakashizuka 2009). One such relationship that is of particular interest to stocking assessment in forestry involves the tendency for the ratio of crown width to stem diameter to decline as trees increase in size (Assmann 1970, Hemery

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This article uses metric units; the applicable conversion factor are: millimeter (mm): 1 mm = 0.039 in.; centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; square meters (m^2): 1 m^2 = 10.8 ft^2; kilometers (km): 1 km = 0.6 mi; hectares (ha): 1 ha = 2.47 ao.

et al. 2005). This relationship is visible in a wide range of species-specific crown-width models (e.g., Bragg 2001, Bechtold 2003) when the resulting crown-width to stem diameter ratios are plotted against dbh. Similar trends emerge from the canopy cover estimates for mixed northern hardwoods presented by Leak et al. (1987, Appendix Tables 17–19) and are supported by size-density relationships portrayed by traditional density management diagrams (Reineke 1933, Drew and Flewelling 1979), i.e., those assuming a self-thinning exponent close to 1.6. By contrast, if self-thinning were directly proportional to basal area (BA), the exponent would be 2, suggesting that stand BA remains constant at full stocking. A declining ratio between crown and stem size is consistent with a self-thinning exponent that is less than 2.

The ranking of species by shade tolerance in relation to growing space requirements may change as stand development progresses. In a recent comparison of size-density relationships across numerous species, Lhotka and Loewenstein (2008) reported multiple self-thinning trajectories and noted that comparisons of growing-space utilization among species may be valid only for a given stage of stand development, i.e., at a common average stand diameter. Some evidence indicates shade-tolerance characteristics are most strongly expressed when trees are young (Kneeshaw et al. 2006), suggesting that differences in crown-stem allometry associated with shade tolerance might also be highest early in stand development.

Our study was designed to investigate species differences in growing-space occupancy at the individual-tree level and to combine those results with observations of groups of trees measured on larger plots. To do so, we sampled three young even-aged northern hardwood stands in the stem-exclusion stage of stand development. We hypothesized a positive relationship between crown-stem allometry and species shade-tolerance characteristics, where more shade-tolerant species occupy more growing space per unit stem diameter. We also hypothesized that the ratio of crown size to stem size would decline with stand age or average tree size independent of species.

Methods

Study Site

These data were collected from three Adirondack northern hardwood stands established by shelterwood-method seed cutting at the Huntington Wildlife Forest near Newcomb, New York (44′E 00″N, 74′E 13″W). The climate is cool, moist, and continental; average annual precipitation is ~1,010 mm, and the mean annual temperature is 4.4°C (Shepard et al. 1989). The study stands were located on gently to modestly sloping terrain. Soils at all three sites are Spodosols in the Beckett series. These are deep, moderately well drained, strongly acid, and moderately coarse-textured soils with a fragipan.

Prior to seed cutting, the stands supported well developed northern hardwood communities 200–300 years in age dominated by sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.), with lesser amounts of yellow birch (*Betula alleghaniensis* Britton), white ash (*Fraxinus americana* L.), and black cherry (*Prunus serotina* Ehrh.). Dense American beech understories were controlled by mist-blowing of herbicide followed by individual stem injection of larger unmerchantable American beech trees (Sage 1987). The mist-blowing treatment was not selective and greatly reduced advance regeneration and trees up to approximately 5 m tall of all species (Sage 1987). Controlled hunting reduced local deer populations from 10 down to 5 deer km^{-2}, a level deemed necessary for securing desirable reproduction in this region (Kelty and Nyland

1981, Sage et al. 2003). Shelterwood seed cutting left primarily sawtimber-sized sugar maple trees at a wide spacing (20–50% canopy cover) in all the stands.

Data were collected for this study when these stands had developed for 19 (youngest stand), 24 (mid-aged stand), and 29 (oldest stand) years following seed cutting. At this time, 9, 20, and 19 years had elapsed since the final overstory removal in each stand. Species composition of the reproduction was similar in all three stands, with varying proportions of yellow birch and sugar maple and lesser amounts of American beech and white ash (Ray et al. 1999). The older stands had widely scattered individuals of black cherry and quaking aspen (*Populus tremuloides* Michx.), with crowns extending above the general level of the main canopy. Scattered pin cherry (*Prunus pennsylvanica* L.f.) were still of this stature in the youngest stand (19 years) but had begun to die off in the older ones (24 and 29 years).

Site quality was quite similar among the three stands included in this study. We used Carmean et al.'s (1989) site index (SI) curves (base age, 50); SI was highest for white ash (22.3 ± 0.1 m) and lowest for American beech (18.4 ± 0.3 m) ($n = 30$ trees/stand). Sugar maple and yellow birch were virtually identical at 21.1 ± 0.2 m. The largest range in SI values for an individual species was 1.1 m for American beech, being highest in the mid-aged stand and lowest in the oldest. The average range in SI values determined across stands for the other species was 0.6 ± 0.1 m.

Sampling Design and Crown Measures

A systematic grid consisting of 40 sample points was established in each stand at an approximate spacing of 30 m (4 lines and 10 points/line). The closest qualifying stem to each grid point (always less than half the distance to adjacent points) of any of the four study species, American beech, sugar maple, yellow birch, and white ash, was considered for inclusion in the sample. Candidate trees had to occupy an upper-canopy position (dominant or codominant crown class) and have no detectable top damage as evidenced by prominent forking along the main stem. Ten upper-canopy trees of each species were sampled in each stand (4 species × 10 individuals × 3 stands = 120 sample trees). We gave priority to candidate trees that provided the most spatially dispersed sample of the target species, but in a few instances it was necessary to select two trees of a given species at the same grid point to meet the sampling requirement for a stand. Tree ring counts made at ground level were used to confirm that all sample trees became established following seed cutting, not from older advance regeneration that escaped the herbicide treatments. Fourteen (12%) of the initially selected trees exceeded the stand-specific minimum age limit and were replaced with alternates.

The dbh was measured before each tree was felled. Sample trees were then cut at ground level, and total height and height to the base of the live crown (the lowest major branch supporting live foliage) were measured along the main stem. The crown portion was then separated from the main stem just below the base of the live crown, stood upright so the branches were displayed naturally, and secured with ropes to surrounding trees. Horizontal and vertical crown dimensions were then measured along eight equally spaced radii. The horizontal distance and corresponding height to live foliage (BLC_{FOL}) were determined using a telescoping height pole and carpenter's level.

Table 1. Characteristics of the sample including stem counts by canopy position on the circular plots centered on the sampled trees. Values are mean (standard error) based on 40 plots per stand.

Stand age (years)	Plot size (ha)	Dominant and codominant (upper canopy)	Intermediate and overtopped	Upper-canopy proportion (dominant + codominant/total)
		. . . .(Stem count).		
19	0.0013	3.8 (0.24)	7.3 (0.51)	0.35
24	0.0040	7.6 (0.47)	16.0 (1.15)	0.32
29	0.0040	5.5 (0.38)	15.4 (1.38)	0.26

Crown-Stem Allometry

Two measures were selected to describe the crowns of the individual sample trees. Crown projection area (CPA) was determined by summing the areas of the eight pie-shaped sections:

$$\text{CPA} = \sum_{i=1}^{8} \frac{\pi r_i^2}{8}, \tag{1}$$

where r is crown radius in meters. Foliated crown surface area (CSA) was estimated by assuming a paraboloid shape for the crown area above BLC_{FOL}, to approximate the photosynthetically active surface or foliar shell, *sensu* Mitchell (1975), and then summing the sections, as for CPA:

$$\text{CSA} = \sum_{i=1}^{8} \frac{\left[\left(\frac{2\pi r_i}{12 l_i^2} \right) \left(\frac{2r_i^2}{4} + 4l_i^2 \right)^{1.5} - \left(\frac{2r_i^3}{8} \right) \right]}{8}, \tag{2}$$

where l is the length of crown section supporting live foliage, also in meters.

The resulting crown measures were used as numerators in growing-space ratios having stem BA as the denominator. Whereas CPA/BA represents the amount of horizontal ground area occupied by a stem of given size, CSA/BA represents the total amount of crown surface area associated with that same stem.

Plot-Based Measures

To quantify the competitive environment of the sample trees, we measured dbh and assigned a crown class (dominant, codominant, intermediate, or overtopped) to all trees ≥2.5-cm dbh on 2-m-radius (age 19 years) and 3.6-m-radius (ages 24 and 29 years) circular plots centered on the sample trees. These plots were small enough to limit sampling to the proximate main-canopy competitors of each sample tree. Larger plots were used in the older stands because of increased distance between stems as self-thinning progressed and the distance between individual trees increased (Table 1).

To describe local crowding, we used relative basal area (RBA), which is the ratio of BA on a given plot in a given stand to the maximum BA observed across all plots in that stand. This measure has the advantage of being independent of stand BA and stem density, which differed systematically across the stands of different ages. RBA indexes crowding across stands similarly to a stocking guide, where older stands with larger trees support higher BA than younger stands at A-line stocking, yet have similar levels of crowding. The stands were too young, except for the oldest, to use existing stocking diagrams (Roach 1977, Leak et al. 1987).

The Model

A general linear modeling framework was used to carry out an analysis of covariance relating crown-stem allometry (CPA/BA or CSA/BA) to stand, species and their interaction, with plot RBA describing local crowding. Species and stand were treated as class variables in this analysis. A log-transformation was applied to the dependent variables to normalize the residuals and satisfy assumptions of the analysis. Tukey's means-separation procedure was used to evaluate significant differences associated with main effects and interactions; all tests were evaluated at the $\alpha = 0.05$ level.

Estimating Crown Overlap

Parameter estimates from the stand- and species-specific CPA/BA models were used to calculate the CPA of all upper-canopy trees on the 120 sample-tree-centered circular plots. The four study species accounted for ~85% of all upper-canopy stems (both in terms of BA and stem counts) across all plots. To estimate CPA for the remaining ~15% (all hardwoods, primarily aspen, red maple (*Acer rubrum* L.), and pin cherry (*Prunus pensylvanica* L.), we fit a pooled model of the form ln(CPA/BA) = stand + RBA to the entire data set. Crown overlap was estimated by summing the predicted CPA of all upper-canopy trees on a plot and dividing by the plot area. Analysis of covariance was used to test for differences in estimated crown overlap among stands with RBA as a covariate; pairwise comparisons were carried out using a Tukey procedure.

Using tree-centered plots instead of random or systematically located plots yields an overestimate of crown overlap among upper-canopy trees similar to including one extra tree per plot, for randomly selected trees. The simplest proof of this relationship applies to Poisson distributions of tree density (Appendix A). We used a correction based on the observed variance in tree density in each of the three stands (Appendix A). Note that this correction applies to plots centered on randomly selected trees, whereas our trees were selected to be near systematically selected grid points. For this reason, the true density is lower than the uncorrected values but higher than the bias-corrected values. We present both values but base the significance tests on the uncorrected densities.

Results

Tree and Stand Characteristics

Differences in tree-level attributes were consistent with expectations for even-aged stands at different times following regeneration cutting, as reported previously for these sites (Nyland et al. 2004). For example, the total height of upper-canopy stems in the 19-year-old stand was 70% of that in the 29-year-old stand ($P < 0.001$). Similarly, the average dbh in the youngest stand was 60% of that in the oldest stand ($P < 0.001$). Differences in live-crown ratio were statistically significant ($P < 0.001$) but small in magnitude. Both

Table 2. Summary of conditions on the 40 tree-centered plots in each stand (stems ≥ 2.54 cm dbh). Values are means (standard error) and range for basal area (BA), which was used to determine the competition variable, relative basal area (RBA).

Stand age (years)	BA minimum	BA maximum	BA	Stems/ha	QMD (cm)
	. . . . (m²/ha)				
19	5.6	40.8	18.6 (1.1)[a]	8,773 (518)[a]	5.2 (0.1)[a]
24	7.4	41.8	21.5 (0.9)[a,b]	5,993 (343)[b]	6.9 (0.2)[b]
29	12.7	48.7	24.5 (1.1)[b]	5,189 (392)[b]	8.1 (0.3)[c]

[a,b,c] Letters indicate significant differences at $\alpha = 0.05$.
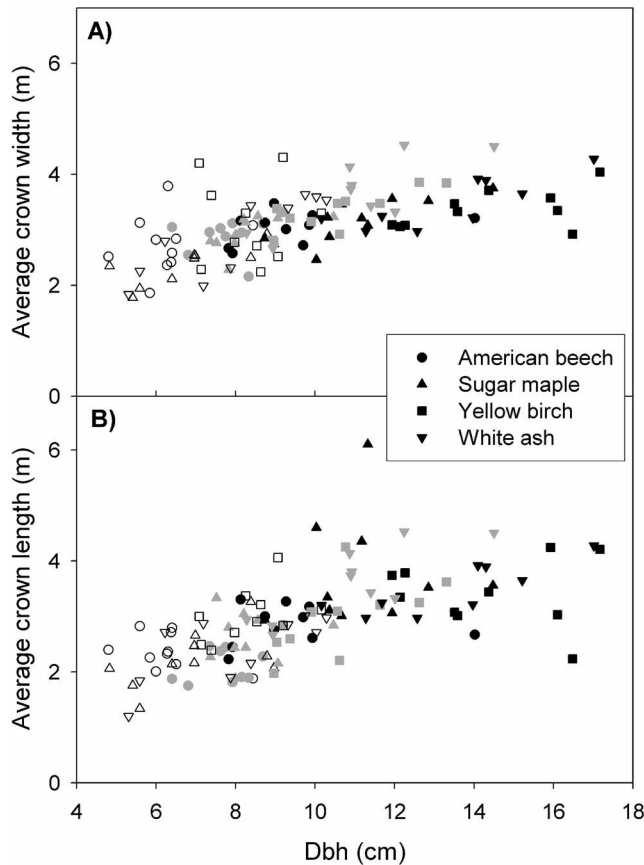QMD, average stand diameter.

Figure 1. Relationship between stem diameter and crown width (A) and crown length (B) for four northern hardwood species in three even-aged stands. Open symbols indicate trees in the youngest stand (19 years), gray symbols indicate mid-aged trees (24 years), and black symbols indicate the oldest trees (29 years). The shape of the symbols is consistent for a species across stands.

As expected, crown dimensions, both width and length, increased with increasing stem diameter (Figure 1). On average, these crowns tended to be slightly wider than they were long, yielding a ratio of 1.13 for width to length, determined across all trees in the sample. The largest-diameter upper-canopy stems of each species in the younger stand were as large as or larger than the smallest ones in the mid-aged stand. The same was true for the mid-aged and oldest stands.

An abundance of stems in the intermediate and overtopped crown classes is indicative of height differentiation and crowded growing conditions. Averaged across stands, $67 \pm 2\%$ of all stems and $36 \pm 1\%$ of BA (total stems ≥ 2.5-cm dbh) occurred in these lower crown classes. The proportion of upper-canopy stems was highest in the youngest and lowest in the oldest stand (Table 1). That our sample was drawn from fully stocked stands is important for relating individual-tree growing-space measurements with those made at the plot level. Evidence that these stands were fully stocked is provided by the fact that the oldest stand had conditions consistent with the A-line of Leak et al.'s (1987) stocking guide for northern hardwoods, and exceeded the A-line for 60% beech-birch-maple on Roach's (1977) guide for Allegheny hardwoods, which is most compositionally similar to our stands. Although neither the youngest nor mid-aged stand had a BA or stem density described by either of these guides, extrapolating those A-lines to fit our stands suggests that they were also fully stocked.

Crown-Stem Allometry

The ANCOVA models accounted for 67% (CPA/BA) and 57% (CSA/BA) of the total variation in the growing-space ratios based on stand, species, and RBA (Table 3). The largest mean-square value was recorded for the stand variable in both models (Table 3). The mean-separation procedure indicated that CPA/BA was 15% higher in the youngest stand than in the mid-aged stand and 31% higher in the mid-aged than in the oldest stand (Figure 2A).

The significance of species in the CPA/BA model was due to shade-tolerant beech exhibiting a higher ratio than the other study species (Figure 2B). On average, beech had 33% more CPA for a stem of given BA than sugar maple, yellow birch, or white ash.

For CSA/BA, yellow birch exhibited a significantly lower ratio in each of the progressively older stands. Similarly, beech had a lower CSA/BA in the oldest stand than in the youngest stand (Figure 2C). Neither the CSA/BA of sugar maple nor that of white ash differed among stands, resulting in a significant interaction between stand and species in the CSA/BA model.

Beech had a higher CSA/BA ratio than white ash (the least shade-tolerant species) in the youngest and mid-aged stands, and it also had a higher ratio than shade-intermediate yellow birch in the oldest stand (Figure 2C). Shade-tolerant sugar maple had a higher CSA/BA than yellow birch in the oldest stand.

measures of crown size (CPA and CSA) increased with stand age ($P < 0.001$). For CPA, the means separation procedure indicated a difference between the youngest (6.8 ± 0.5 m²) and the two older stands (8.8 ± 0.4 and 9.1 ± 0.3 m²), whereas CSA increased significantly between the youngest (14.0 ± 0.7 m²) and mid-aged stands (16.9 ± 0.9), as well as between the mid-aged and oldest stands (21.1 ± 1.0 m²).

Conditions on the tree-centered plots indicated stem densities were lowest in the oldest and mid-aged stands and highest in the youngest stand (Table 2). Total BA was higher in the oldest stand than the youngest stand, whereas quadratic mean stand diameter (QMD) was larger in the oldest than the mid-aged stand and larger in the mid-aged than youngest stand.

Table 3. ANCOVA table showing statistics associated with variables used to model growing-space ratios (crown projection area/basal area [CPA/BA] and crown surface area/basal area [CSA/BA]). The relative BA of upper-canopy competitors provided the covariate.

Growing-space ratio	Source	df	Mean square	P
ln(CPA/BA) ($R^2 = 0.670$)				
	Stand	2	3.503	<0.001
	Species	3	1.287	<0.001
	Stand × species	6	0.090	0.21
	Relative BA	1	1.430	<0.001
	Error	107	0.063	
ln(CSA/BA) ($R^2 = 0.573$)				
	Stand	2	2.699	<0.001
	Species	3	1.051	<0.001
	Stand × species	6	0.207	0.02
	Relative BA	1	0.650	0.008
	Error	107		

Table 4. Regression coefficients obtained from the ANCOVA model for the crown projection area/basal area (CPA/BA) by species (Table 2) not including the insignificant stand × species interaction term. A general (not species-specific) model was developed to apply to hardwood species for which crown measurements were not available. The model form is ln(CPA/BA) = intercept + stand (stand coefficient) + species (species coefficient) + RBA (relative basal area coefficient).

	Coefficient	
Model parameter	ln(CPA/BA)	ln(CPA/BA)
Intercept	7.361	7.392
Stand age (years)		
19	0.206	0.204
24	0.137	0.139
29	0	0
Species		
American beech	0.299	0
Sugar maple	−0.016	0
Yellow birch	0	0
White ash	−0.109	0
RBA	−0.628	−0.684

The ratio between crown and stem size was smaller under more crowded conditions for both CPA/BA and CSA/BA (Table 3). Local crowding, indicated by RBA, was a significant covariate in both models. Examination of the P values and mean squares associated with the independent variables suggest that RBA accounted for a higher proportion of the variability in the CPA/BA model than in the CSA/BA model.

Canopy Cover and Crown Overlap

Scaling the individual-tree CPAs up to the plot level indicated considerable crown overlap (crown area/ground area) among upper-canopy stems in these developing northern hardwood stands (Figure 3). Total canopy cover was strongly related to the stand ($P < 0.001$) and plot RBA ($P < 0.001$) variables according to the model ($R^2 = 0.88$). We calculated crown overlap to be 17% lower in the mid-aged (1.54 ± 0.04) and oldest (1.47 ± 0.03) stands than in the youngest stand (1.80 ± 0.03) ($P < 0.001$), based on the stem densities from the tree-centered plots. Despite inclusion of the RBA term in the CPA/BA models used to estimate individual tree CPA (Table 4), local crowding was still highly significant in the full model ($P < 0.001$); crown overlap was higher on plots with high RBAs. In other words, crowns were smaller under crowded conditions, but not as much smaller as predicted by dividing the ground area by the number of stems.

We calculated crown overlap using our tree-centered plots to estimate the density of dominant and codominant trees, but this will overestimate stand-level stem density (Appendix A). The bias was lowest in the mid-aged stand (+23%), intermediate in the youngest stand (+28%), and highest for the oldest stand (+34%). Applying these stand-specific correction factors (Appendix A) yields more modest estimates of crown overlap among upper-canopy stems, ranging from a high of 1.30 in the youngest stand to a low of 0.96 in the oldest stand (Figure 3). The true crown overlap probably lies between these two estimates, as the bias correction assumes that our plots were centered on randomly selected trees (which would tend to overrepresent areas of high density). Note also that our calculation omits the canopies of intermediate and overtopped trees. In fact, approximately 70% of total stems ≥ 1 in. dbh on the tree-centered plots were classified as intermediate and overtopped (Table 1).

Discussion
Putting the Sample in Context

Despite representing only a short segment of an entire developmental sequence for an even-aged northern hardwood community, the sampled stands followed the trajectory described earlier for stem count, BA, and average tree size (Oliver and Larson 1996, Nyland 2001). The data set was limited to young even-aged stands, where the oldest (age 29) at QMD = 8.1 cm, had only recently developed to the point where it could be located on the stocking guide commonly used for this forest type (Leak et al. 1987). That stand was approximately midway to the point where a traditional commercial thinning might be undertaken (age 50–60), and perhaps a third of the way through an even-aged sawtimber rotation (age 90–100) for sites of similar quality.

Limiting the sample to this age range had certain advantages. It allowed us to take precise measurements of the vertical and horizontal crown dimensions of trees in upper-canopy positions (dominant and codominant crown classes). Tree crowns in subcanopy positions may become relatively flat-topped (O'Connell and Kelty 1994), stem taper may increase with wind exposure (Jacobs 1954), and strata may differ in the effect of crown abrasion (Rudnicki et al. 2004). Studying young stands and trees in the main canopy circumvented these problems. We sought to identify differences in crown-stem allometry related to stand age and shade tolerance.

That our sample lacked any true shade-intolerant species constrained our ability to test the influence of shade tolerance on crown-stem allometry. The dominance of more shade-tolerant species is characteristic of northern hardwood stands in this region. The shade-intolerant species in our stands were either short-lived and
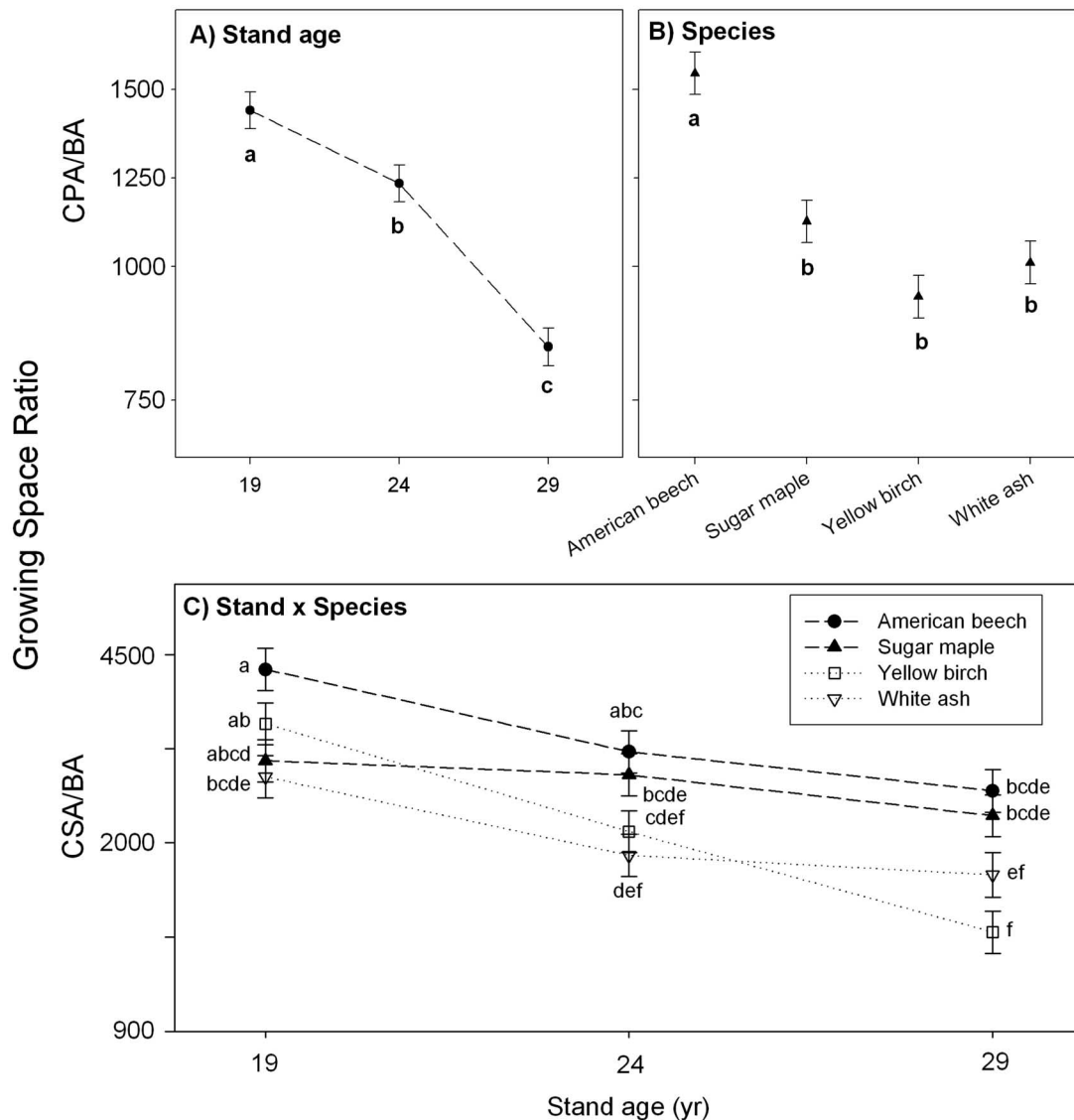
Figure 2. Adjusted least-squares means and standard errors for the growing-space ratios based on CPA (CPA/BA) (A and B) and foliated surface area (CSA/BA) (C) in relation to species and stand age. Results of a Tukey pairwise mean-separation procedure (different letters indicate significance at the $\alpha = 0.05$ level).

dying (pin cherry) or were present at low densities and not represented in consistent amounts in all three stands (black cherry, aspen, paper birch).

Drivers of Growing-Space Ratios for Individual Trees

We found both growing-space ratios (CPA/BA and CSA/BA) to be highest in the youngest stand and lowest in the oldest stand. These results suggest that stem cross-sectional area increases at a faster rate than crown area early in the stem-exclusion stage of stand development. Consistent with this interpretation, in Great Britain the ratio between crown and stem diameter for 10 broadleaf species decreased with tree size up to an average stem diameter of approximately 30 cm (Hemery et al. 2005). Assmann (1970, p. 109) reported a similar trend on the basis of long-term observation of European beech, and crown-width equations for a wide range of broadleaf species in the eastern United States portray a similar relationship (Bragg 2001, Bechtold 2003).

Although certain species differed in crown-stem allometry according to our analysis (Figure 2A), the link to shade tolerance was

not compelling. Prior stocking analyses (Roach 1977, Stout and Nyland 1986) and crown-width models (Lamson 1987) from similar forests led us to hypothesize that these ratios would be higher for more shade-tolerant species because they tended to have fewer stems per hectare at full stocking and larger crown widths for a given dbh. The only consistent difference we found was between beech and all other species for CPA/BA, where this very shade-tolerant species did occupy more growing space relative to stem diameter. Although the separation of beech from sugar maple was unexpected, some research suggests that beech is more shade tolerant (Canham 1988, Takahashi and Lechowicz 2008), and data presented by Leak et al. (1987, Appendix Tables 17 and 19) also support this assertion. Similarly, the few significant differences detected in the relationship between shade tolerance and CSA/BA conformed to the hypothesis that the ratio would be higher for the more shade-tolerant species.

Although our data did not indicate a strong relationship between growing-space ratios and shade tolerance based on these relatively young northern hardwood stands, of the few significant differences that were found, none contradicted predictions based on prior
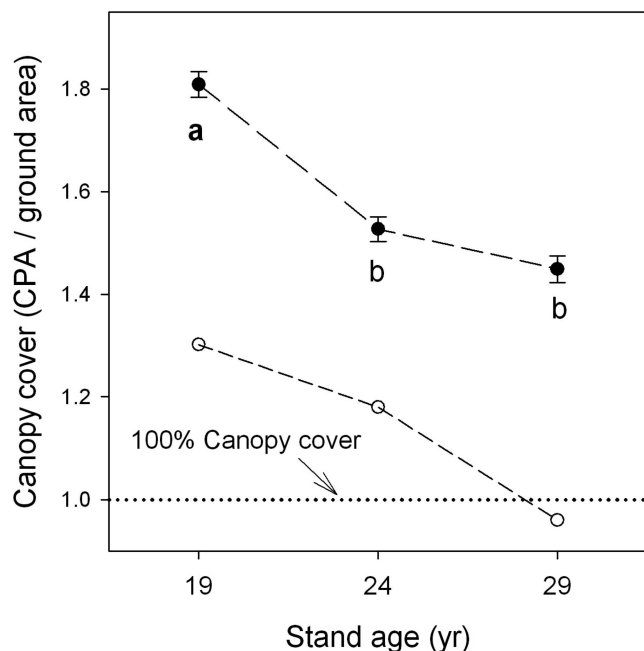
Figure 3. Least-squares means and standard errors (solid symbols) for canopy cover contributed by upper-canopy stems (dominant and codominant crown classes) defined as the sum of CPA of canopy-dominant trees on the tree-centered plots divided by the corresponding ground area. The open symbols are the values corrected for sampling bias associated with using tree-centered plots (Appendix A). Both estimates exclude the crowns of intermediate and overtopped trees, which would increase the total canopy coverage.

stocking analyses (Roach 1977, Stout and Nyland 1986) or crown width models (Lamson 1987). By contrast, when evaluated across monospecific stands exhibiting a range of shade tolerance, the shade-tolerant species appeared to occupy less growing space (Daniel et al. 1979, p. 295). This general observation includes conifer species, however, which have a crown architecture different from that of broadleaf species. Canopy stratification in even-aged mixed-species stands (Oliver and Larson 1996, Smith et al. 1997) and the potential for canopy position (or light environment) to influence crown architecture (O'Connell and Kelty 1994, Canham 1988, Osada et al. 2004) may help explain this apparent contradiction.

Working with southern pines, Zeide (1985) reported that the crowns of less shade-tolerant species were most sensitive to competition. Examination of the RBA parameter used to adjust for differences in plot density in our crown-allometry models generally supports this view (data not shown). Both the magnitude and significance of those terms implied a greater effect of crowding on crown size for the shade-intermediate species, particularly white ash. The crown-width models presented by Bragg (2001) for sugar maple, yellow birch, and white ash are consistent with ours in terms of species sensitivity to crowding. Bragg's study did not include American beech.

Our stands were not stratified by species, and our sample was restricted to trees within the main-canopy layer. Differentiation of individual trees by crown class, as opposed to stratification of the species into canopy layers, was the most common developmental pathway reported by Guldin and Lorimer (1985) among the compositionally diverse even-aged northern hardwood communities

they studied, suggesting that intrastrata competition may be most important in shaping crown-stem allometry in this forest type. That no interaction was detected between our local-crowding covariate and the species factor for either growing-space ratio suggests that the crown-stem allometry of these four species was similarly affected by competition. Likewise, Bragg (2001) found no relationship between species shade tolerance and the model parameter used to adjust diameter-based crown-width regression models for differences in local crowding among the 24 species he sampled.

Growing-Space Dynamics at the Plot Level

Two aspects of the plot-based assessment were striking: the overall high level of canopy cover and the apparent decline in those values over the relatively short 10-year age difference represented by these stands (Figure 3). Similarly, Ford and Deans (1978) reported high crown overlap in a densely stocked young conifer stand, where as much as three-quarters of the ground area was occupied by more than one tree crown. The tables of canopy cover by species group and size class presented by Leak et al. (1987) also conform to the trend we observed. That crown overlap declines with stand development has been reported previously for conifer forests (Zeide 1985, Cade 1997).

The phenomenon of crown shyness or disengagement provides one possible explanation for the declining growing-space ratios observed here; in this phenomenon, branch mortality due to crown-crown interactions increases as trees become taller and sway more in the wind (Putz et al. 1984, Long and Smith 1992), particularly in dense stands (Rudnicki et al. 2004). Whereas crown expansion is directly constrained by proximate competitors, diameter growth need not be similarly affected. Relatively deeper crowns, increased efficiency of better-illuminated foliage, or crown densification could offset reduced CPA in relation to diameter increment. In addition, mortality increases in importance as stand development progresses, such that crown expansion less effectively fills the larger gaps formed in older stands (Zeide 2005). Though both explanations likely have a role in the development and persistence of canopy gaps in even-aged forest stands, the declining ratio between crown area and stem cross-sectional area observed in our young stands seems more consistent with crown abrasion or mortality of shaded branch tips. We observed lower foliage density on the periphery of the sampled crowns, where branches were overlapping with neighboring trees. Also, the canopy gaps created by removing the sample trees appeared considerably smaller than the crown spread actually measured, particularly in the youngest stand. Unfortunately, we did not measure gap dimensions to formally test this assertion.

Plot-level BA of main-canopy stems was 39% higher in the oldest compared with the youngest stand. A lesser degree of canopy cover and higher BA at the plot level in older stands is consistent with the dimensional analysis of individual trees (Figure 2). That crowns in the youngest stand occupied relatively more growing space is apparently associated with a short period of considerable crown overlap among main-canopy stems. The short-lived period of peak leaf area observed soon after canopy closure (Reynolds and Ford 2005) may be associated with this trajectory in crown overlap. Alternatively, the apparent reduction in crown overlap among main-canopy trees may be at least partially offset by trees in lower crown positions as differentiation into crown classes progresses with stand development (Table 1).

Summary and Management Implications

Earlier research suggested that the shade-tolerant species in compositionally similar mixed-hardwood forests tend to occupy more growing space for a stem of given size than co-occurring shade intolerants (Roach 1977, Stout and Nyland 1986, Lamson 1987). We found only a few species differences in the crown-stem allometry of upper-canopy trees in fully stocked young even-aged northern hardwood stands, which did not contradict these predictions.

The tendency for older, larger trees to have smaller crown-stem ratios than younger, smaller trees is also supported by findings from previous work (Assmann 1970, Leak et al. 1987, Hemery et al. 2005). By combining individual tree measurements with plot density information, we found considerable overlap among the crowns of upper-canopy stems in these young stands. Crown overlap was reduced in the older stands, consistent with temporal trends in leaf area reported previously, where the longer-term carrying capacity may be briefly overshot in fully stocked, rapidly developing even-aged stands (Long and Smith 1992, Reynolds and Ford 2005).

Historically, density management has not been a common practice in young northern hardwood stands. Moderate thinning provides little benefit to diameter growth because of rapid rates of crown expansion and canopy reclosure (Heitzman and Nyland 1991). Aggressive thinning carries a risk of lengthening the retention of lower branches, reducing bole quality. Manual pruning of these branches (Schlesinger and Shigo 1989) has not been considered cost-effective for traditional management goals. Emerging markets for woody biomass may present novel opportunities to thin young hardwood stands, but further study will be required to determine whether such treatments are compatible with long-term management for quality sawtimber.

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Appendix: Estimating Bias in Density Estimates from Tree-Centered Plots

In this appendix, we quantify the bias that results when the density of trees is estimated using plots centered on randomly selected trees rather than plots centered on randomly or systematically selected points. In this study, plots were centered on trees that were close to systematic grid points. The bias introduced by centering plots on these trees is smaller than the bias described here for randomly selected trees, which would tend to oversample densely populated areas.

In a closed-canopy forest, the locations of dominant stems are likely to be independent (Poisson) or negatively correlated (dispersed) rather than positively correlated (clumped). The average density on tree-centered plots, ν, overestimates the true density, μ, by approximately σ^2/μ for a broad class of cases in which the locations of trees are independent or negatively correlated. We used this correction, using the measured variance σ^2 in each of our three stands. The proof for the case of independently distributed trees follows.

Assume that tree locations are represented by the points of a translation-invariant Poisson point process in the plane. Translation invariance implies that the intensity measure is a multiple of the usual two-dimensional area measure. (The intensity measure of a point process is the expected number of points in a given set. For background on point processes, see Moller and Waagepetersen [2004].) The multiplier, μ, which represents the mean density of trees per unit area, is the parameter of interest. Let N be the number of trees in a unit area plot R centered at a point chosen at random. The parameter μ is the expected value of N in any unit area, regardless of its shape. We shall use a circle.

Let ν be the expected number of trees in a unit area circular plot centered at a tree chosen at random. We shall prove

$$\nu = \mu + 1. \tag{A1}$$

by translation invariance, we may assume that R is the unit circle centered at the origin.

Let B_ε denote the small circle of area ε also centered at the origin. Let P_n denote the conditional probability given that $N = n$. Conditional on the event $\{N = n\}$, the locations, $X_1, X_2, \ldots, X_n$, of the trees in R are independent and uniformly distributed on R.

Then we have

$$n\varepsilon - n^2\varepsilon^2 \le P_n\left(\bigcup_{j=1}^{n}\{X_j \in B_\varepsilon\}\right) \le n\varepsilon. \tag{A2}$$

The right-hand inequality is just a union bound and holds without any assumptions on the joint distribution of tree locations. To obtain the left-hand inequality, take complements and use independence to show that the middle member of Equation A2 is equal to $1 - (1 - \varepsilon)^n$. This and Taylor's formula easily yield the left-hand inequality in Equation A2.

Let A denote the event in the middle member of Equation A2. Then by Bayes' formula, $P(N = n \, A)$ is equal to

$$\frac{P_n(A)f(n)}{\sum_k P_k(A)f(k)}, \tag{A3}$$

where f denotes the (Poisson) probability function of N. Use the left-hand inequality in Equation A2 in the numerator and the right-hand inequality in Equation A2 in the denominator to obtain $P(N = n \, A) \ge (n - n^2\varepsilon)f(n)/\mu$. Multiply both sides by n and sum on n from 1 to infinity to obtain $E(N\,A) \ge E(N^2)/\mu - \varepsilon E(N^3)$. Letting ε tend to zero, we obtain $\nu \ge \mu + \sigma^2/\mu = \mu + 1$, since the variance σ^2 is equal to the mean for the Poisson distribution. The opposite inequality is proved similarly, using the left side of Equation A2 in the denominator of Equation A3 and the right side of Equation A2 in the numerator of Equation A3.

The solution for the Poisson distribution is a special case of the bias σ^2/μ for the Poisson distribution $\sigma^2 = \mu$. The more general case pertains to tree distributions that are negatively correlated as well as independent (the Poisson case) (McConnell).