Tree growth prediction using size and exposed crown area

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Abstract: We address the relationships between tree growth rate and growing environment for 21 co-occurring species. Tree growth rates are obtained from mapped plots at the Coweeta Long-Term Ecological Research site in the southern Appalachian Mountains. We employ high-resolution aerial photography to assess the light environment for trees growing in these plots, using exposed crown area (ECA) as a surrogate for light interception. The relationship between growth and ECA is compared with two other growth predictors: tree size and shade-tolerance classification. We find that ECA is an excellent predictor of tree growth (average $R^2 = 0.69$ for nine species). When ECA is combined with tree size, growth rate prediction is improved (average $R^2 = 0.76$). Tree size alone is also a strong predictor of tree growth (average $R^2 = 0.68$). Shade-tolerance classification, by contrast, is a poor predictor of tree growth.

Résumé : Les auteurs ont examiné les relations entre le taux de croissance des arbres et leur environnement pour 21 espèces qui croissent ensemble. Le taux de croissance des arbres provient de parcelles cartographiées sur le site de Coweeta Long-Term Ecological Research dans le sud des Appalaches. Ils ont utilisé la photographie aérienne à haute résolution pour évaluer l'environnement lumineux des arbres qui croissent dans ces parcelles en ayant recours à la superficie exposée de la cime (SEC) comme substitut pour l'interception de la lumière. La relation entre la croissance et la SEC est comparée à d'autres prédicteurs de la croissance : la dimension de l'arbre et la classe de tolérance à l'ombre. Leurs résultats montrent que la SEC est un excellent prédicteur de la croissance (R^2 moyen = 0,69 pour neuf espèces). Lorsque la SEC est combinée à la dimension des arbres, la prédiction du taux de croissance est améliorée (R^2 moyen = 0,76). La dimension des arbres est aussi un bon prédicteur de la croissance des arbres (R^2 moyen = 0,68). La classe de tolérance à l'ombre par contre est un mauvais prédicteur de la croissance des arbres.

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Introduction

Interspecific differences in tree growth rate play a key role in controlling forest dynamics and composition (Peet and Christensen 1980; Huston and Smith 1987; Clark and Clark 1992). Species differences result from responses to resources that are difficult to measure and quantify for large individuals. Trees growing near one another compete for resources, which affects growth and mortality rates. Plants compete for light, water, nutrients, and physical space, but the relationship between these resources and tree growth is rarely quantified. For instance, only one field study provides regressions of tree growth as a function of nitrogen availability (Mitchell and Chandler 1939). Several recent studies include regressions linking tree growth to resource availability, but only for seedlings and saplings (Kobe et al. 1995; Finzi and Canham 2000; Messier and Nikinmaa 2000; Dünisch et al. 2002; Kobe et al. 2002; Lin et al. 2002). For adult trees, regressions linking growth and resource availability are nearly nonexistent (Clark et al. 1999). Here we present regressions describing growth as a function of light interception for large trees, and we compare this approach with two commonly used predictors of tree growth: tree size and shade-tolerance classification.

In the absence of resource-based regressions, foresters and ecologists often summarize complex inter- and intra-specific tree growth patterns with coarse descriptors such as drought- and shade-tolerance classification (Bazzaz 1979). These classifications are incorporated into the growth functions in most forest simulation models (Botkin 1993). However, Pacala et al. (1994) demonstrated that saplings in a Connecticut forest exhibit a range of growth responses to light availability. Related modeling efforts (Pacala et al. 1996) suggest that species-specific light–growth–mortality relationships determine the outcome of forest simulation models.

In addition to tolerance classifications, tree size (typically reported using diameter at breast height or basal area as a proxy measurement) is commonly used to predict tree growth. The expected growth rate of a tree changes with age and size. Correlations between size and growth rate arise both from internal, physiological causes (Gower et al. 1996) and because increasing size affects a tree's ability to acquire resources.

In this paper, we use low-altitude, high-resolution imagery to compare growth rates of large trees with the amount of light they intercept. Exposed crown area (ECA), measured from aerial photos, is used as a surrogate for light interception. When combined with a measure of tree size (we use both stem diameter and basal area at breast height), ECA can be used to examine the complex relationship between the ability of a tree to command resources (which increases

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Table 1. Relative contribution of 21 taxa to the composition of our five study plots.

Species	Mean DBH (cm)	No. of trees	% of total stems	% of total basal area
Acer rubrum	8.9	450	27.3	9.3
Acer pensylvanicum	4.5	140	8.5	0.7
Acer saccharum	11.2	39	2.3	1.3
Betula alleghaniensis	13.3	75	4.5	3.5
Betula lenta	20.1	63	3.8	6.7
Carya glabra	18.4	77	4.7	6.8
Cornus florida	6.9	52	3.1	0.6
Fraxinus americana	15.8	30	1.8	2.0
Liriodendron tulipifera	23.8	60	3.6	8.9
Magnolia fraseri	3.6	47	2.9	0.2
Nyssa sylvatica	9.8	130	7.9	3.3
Oxydendrum arboreum	15.2	109	6.6	6.6
Pinus rigida	28.0	28	1.7	5.7
Quercus alba	25.7	6	0.4	1.0
Quercus coccinea	27.5	20	2.1	4.0
Quercus prinus	23.8	141	8.6	20.9
Quercus rubra	30.4	46	2.8	11.1
Quercus velutina	15.7	29	1.8	1.9
Robinia pseudo-acacia	18	23	1.4	2.0
Tilia americana	18.2	35	2.1	3.0
Tsuga canadensis	6.5	49	3.0	0.5

with size) and the amount of tissue that must be supported (which also increases with size). We extend the basic approach of Hix and Lorimer (1990), who assessed ECA from the ground. Because ECA can be difficult to estimate from below in dense stands with overlapping crowns, we used air-photo rather than ground-based estimates of ECA.

ECA is a crude measure of light availability. For example, a small tree with a 10-m^2 crown growing isolated in a field will have an ECA of 10 m^2. A larger tree, with a 100-m^2 crown, growing in the shade of taller neighbors may also have an ECA of 10 m^2. Certainly, however, the two trees experience very different light environments. To separate the effects of tree size and ECA, we first use regressions that compare the utility of stem size and ECA as predictors of growth rate. The two factors are considered both separately and together. We then compare growth rate with a ratio of ECA/stem basal area. This ratio indicates a tree's ratio of energy availability / energy demand.

Herwitz et al. (2000) used air photos to link ECA and survivorship, but lacked detailed growth records. Here, growth rates are regressed against both ECA-based estimates of light interception and more readily obtained predictors of tree growth. Our objective is to provide improved data for growth prediction in stands where trees compete for light.

Materials and methods

Our analysis of tree growth consisted of two parts. First, we examined interspecific differences in growth rate. Second, we determined the extent to which (1) ECA-based estimates of light interception, (2) stem size, and (3) shade-tolerance classification explain growth.

Study area

Data were obtained from five 80 m × 80 m permanent plots at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains (35°03′N, 83°27′W). Annual temperatures average 13 °C, and annual precipitation averages 220 cm (Swift et al. 1988). The two upper elevation plots receive approximately 24% more precipitation but are approximately 3.3 °C colder than the three lower elevation plots. Soils are primarily Ultisols and Inceptisols (Velbel 1988). The five plots are located in four distinct forest types along an elevation gradient: xeric oak–pine, cove hardwood, mixed oak, and northern hardwood forests. The plots are in two watersheds that have served as control watersheds throughout the history of watershed experiments at Coweeta (Swank and Crossley 1988).

Our study plots are located in second-growth forests established after clearing by logging and the chestnut blight early in the 20th century. *Quercus prinus* and *Quercus rubra* are the most dominant canopy species (Table 1). *Acer rubrum* is the most common understory tree in all but our highest plot, and all plots have large evergreen shrub patches, *Rhododendron maximum* or *Kalmia latifolia*, in the understory. Tree species with small mean diameters at breast height (DBH) (Table 1) tend to be late successional and dominate the understory. Species with large mean DBH tend to be early successional, shade intolerant, and uncommon in the understory.

Obtaining growth rates

Our growth analysis is based on five permanent mapped plots remeasured using DBH tapes over a total of 2–5 years. A Total Station (Topcon Corporation, Paramus, New Jersey) was used to survey a 10 m × 10 m *x*, *y*, and *z* grid overlay for each 80 m × 80 m plot (thus each plot was subdivided into 64 grid cells). Coordinates for individual trees were then determined within each grid cell. Only trees >2 m tall were measured. Growth rates were determined as average change in DBH per year. For some subsequent analyses, DBH and diameter growth rates were converted to basal area (BA) and basal area increment (BAI). These conversions served to make the ratio of ECA/BA a straightforward area–area comparison.

Growth as a function of species

To determine how growth varied among species, we used analysis of variance (ANOVA; all statistical analyses were performed using SPLUS, Insightful Corp., Seattle, Washington). To homogenize variances, growth rates were transformed by raising the diameter growth rate of each tree to the 0.25 power. Initial analysis of all trees using ANOVA indicated highly significant effects of species on diameter growth, even after accounting for plot effects. To test if these effects are independent of size, we conducted additional ANOVAs comparing growth rate to plot and species for trees 5–15 cm DBH and trees 20–40 cm DBH. Trees less than 15 cm DBH tend to be in the understory, whereas trees greater than 20 cm DBH usually have crowns in the canopy or subcanopy (P.H. Wyckoff and J.S. Clark, personal observation). To assess pairwise differences for species within these two size classes, we used the Tukey–Kramer multiple comparison method, which is designed for unequal group sizes. Significance was determined using Tukey's honestly significant differences at the 95% confidence level.

Determining exposed crown area

To assess the light environment of trees growing in the five plots, we measured ECA for each tree using aerial photography. ECA is the area of a tree's canopy not overtopped by any other tree, and thus serves as a surrogate measure of light interception.

To obtain low-elevation, high-resolution photographs of the five 80 m × 80 m plots, we employed a helicopter (Helivision, Concord, North Carolina) and camera crew (Wendall Wagner Photography, Greensboro, North Carolina) in October 1997. To aid location from the air, plots were marked with 122-cm-diameter red balloons. Because these balloons blew around in the wind, they could not be used as fixed points for subsequent photo rectification. To aid rectification, white plastic garbage bags (dimensions: 61 cm × 71 cm) were nailed to the ground on our 10-m grid at known *x*, *y*, and *z* survey coordinates. A Hasselblad 200 series camera with an 80-mm lens was used to take photographs of each plot from a height of 150–280 m above the ground.

Images from 5.5 cm × 5.5 cm color transparency film were digitized at resolutions of 2400 dpi and 3200 dpi for analysis. Enlargements were made of two photos from each plot for ground-truthing and locating canopies on tree maps. Like Key at al. (2001), we found that fall color made individual canopies easy to delineate.

We imported the digitized photos into Imagine (ERDAS, Inc., Atlanta, Georgia) for rectification. Rectification was done using first- and second-degree nearest neighbor resampling algorithms. Resampling was based on *x* and *y* coordinates of ground control points (gcps). Gcps included white plastic garbage bags visible in the photos, as well as other points whose location could be determined in the field. These additional gcps were primarily litter traps, placed in the gradient plots as part of another study. We used a Total Station to determine the *x*, *y*, and *z* coordinates of these additional gcps relative to the 10 m × 10 m plot grid.

Rectified images with acceptable error were only obtained from two plots (total RMS error was less than 0.4 m for each photograph used). In the other plots, few gcps were visible, making rectification impossible. We imported the rectified images into Arc/Info (Environmental Systems Research Institute, Inc., Redlands, California) and outlined ECA for each tree visible in an image. Trees near the edges of images were avoided because, even in rectified images, edge trees were viewed at oblique angles.

Two factors served to limit the utility of our ECA measurements. First, we were unable to obtain proper stereo-pairing of our aerial photos, and thus could not determine the relative heights of trees. This meant that we could only visualize canopies in two dimensions rather than in three dimensions, and thus could not fully determine the impact of shading by neighbors. Second, we did not obtain total crown area for our sample trees, so we know the absolute amount of exposed crown area, but not the ratio of exposed crown: total crown. As a rough substitute for crown size measurements, we use stem size in the analysis below.

Growth as a function of exposed crown area and diameter

We compared ECA with growth rate using several regression models. These analyses included all trees growing in the central areas of our rectified photos. Understory trees have negligible ECA and were assigned ECA values of 1 m^2 (zero values for ECA would preclude log transformation during statistical analysis). Measured ECA values ranged from 3 to 188 m^2. To examine the relationship between ECA and stem basal area as predictors of BAI growth, we analyzed both predictors separately and then in a combined model. We determined that a log transformation was necessary to linearize the relationship among the three variables. The resulting combined model, with fitted parameters β_0, β_1, and β_2, and experimental error ε, relates growth to ECA and diameter of tree *i*:

$$[1] \qquad \log g_i = \beta_0 + \beta_1 \log a_i + \beta_2 \log bi + \varepsilon_i$$

where *g* is growth rate (cm^2 BAI/year), *a* is ECA (m^2), and *b* is stem size (cm^2 BA). Parameters were fit by minimizing the sum of squared residuals, and ε values were assumed to be normally distributed.

We next examined a ratio of ECA/BA, *R*, as a tool for predicting growth increment. *R* can be seen as an index of a tree's ratio of area of light exposure (energy supply) to size (energy demand). BAI was regressed against *R* (without log transformation) and then again with log transformed *R* as an additional variable in eq. 1.

Growth as a function of diameter and shade tolerance

Shade-tolerance classifications for the 21 most abundant species in our five plots were gathered from available literature (Baker 1949; Wenger 1984; Burns and Honkala 1990). Tree species were divided into five tolerance classes, ranging from "very tolerant" to "very intolerant". Linear regression

Table 2. Growth rates by species and species comparisons for trees 5–15 cm in diameter at breast height.

Species	Shade tolerance	Mean growth (cm/year)	SD
Magnolia fraseri	Intermediate	0.368	0.178a
Tsuga Canadensis	Very tolerant	0.342	0.182a
Acer pensylvanicum	Very tolerant	0.262	0.159ab
Quercus velutina	Intermediate	0.200	0.194bc
Acer rubrum	Tolerant	0.178	0.148bc
Tilia Americana	Tolerant	0.174	0.118bcd
Acer saccharum	Very tolerant	0.162	0.195bcd
Oxydendrum arboreum	Tolerant	0.141	0.167bcd
Nyssa sylvatica	Intolerant	0.120	0.095cd
Quercus prinus	Intermediate	0.109	0.114cd
Betula lenta	Intermediate	0.102	0.196cd
Fraxinus Americana	Intermediate	0.086	0.047cd
Liriodendron tulipifera	Intolerant	0.084	0.048cd
Carya glabra	Intolerant	0.081	0.064cd
Betula alleghaniensis	Intermediate	0.069	0.064de
Cornus florida	Very tolerant	0.030	0.039e

Note: Only species represented by eight or more individuals are listed. Species denoted with the same letters, a–e, are not significantly different at $\alpha = 0.05$.

Table 3. Pairwise species comparisons for trees 20–40 cm in diameter at breast height.

Species	Shade tolerance	Mean growth (cm/year)	SD
Fraxinus americana	Intermediate	0.613	0.091a
Quercus coccinea	Intermediate	0.434	0.307ab
Acer rubrum	Tolerant	0.368	0.184ab
Quercus rubra	Intermediate	0.351	0.129abc
Pinus rigida	Intolerant	0.327	0.173abc
Betula alleghaniensis	Intermediate	0.326	0.174bc
Carya glabra	Intolerant	0.299	0.321bc
Quercus prinus	Intermediate	0.299	0.176bc
Liriodendron tulipifera	Intolerant	0.288	0.196bc
Oxydendrum arboreum	Tolerant	0.259	0.141bc
Betula lenta	Intermediate	0.258	0.221bc
Robinia pseudo-acacia	Very intolerant	0.213	0.168bc
Nyssa sylvatica	Intolerant	0.129	0.151bc

Note: Only species represented by eight or more individuals are listed. Species denoted with the same letters, a–e, are not significantly different at $\alpha = 0.05$.

was used to compare shade-tolerance classification with diameter growth for both understory and canopy trees of each species. We omitted *Cornus florida* from this analysis because, although considered very shade tolerant, its growth in the understory at Coweeta is low because of dogwood anthracnose disease.

Results

Interspecific variation in growth

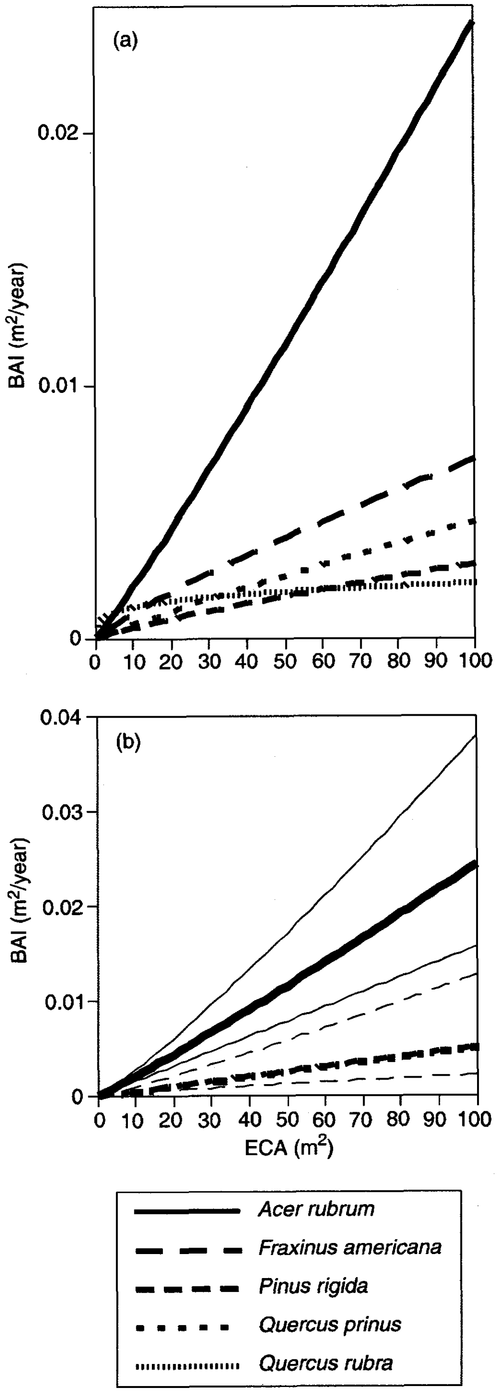
Diameter growth rates are reported for the 21 most abundant tree species (1649 individual trees) in Table 1. Analysis of variance indicates that stand type and species are strongly related to growth rate for both understory (5–15 cm diameter DBH) and canopy (20–40 cm DBH) size trees. Species effects remain significant even after accounting for the effect of plot ($F_{[20,468]} = 8.76$, $p < 0.001$ for understory trees, Table 2; $F_{[17,274]} = 3.26$, $p < 0.0001$ for canopy trees, Table 3). In the understory, the most rapidly growing species grows more than an order of magnitude faster than the slowest species (Table 2). Interspecific differences are substantially less pronounced in the canopy (Table 3).

Growth as a function of light and diameter

Figure 1 shows one of the low-level aerial photos used to relate growth and light interception via ECA. After rectifying photos and measuring ECA for properly rectified, undistorted trees, our ECA data set consisted of 580 individual trees, allowing for analysis of nine species. Species exhibit differing BAI growth rates at a given value of ECA (Figs. 2 and 3). The amount of the variation in growth rate explained by these light interception functions is large for some species (R^2 up to 0.88, Table 4; parameter values reported in Ta-

Fig. 1. Example of the aerial photos used to estimate exposed crown area.

Fig. 2. (*a*) Exposed crown area (ECA) versus annual basal area increment (BAI) growth for five species. (*b*) ECA versus BAI for *Acer rubrum* (thick solid line) and *Carya glabra* (thick broken lines). Bracketing thin lines indicate one standard deviation for the parameters in eq. 1.



ble 5). Although most species exhibit similar ECA–growth relationships (Fig. 2*a*), confidence intervals do not overlap at high levels of exposed crown area for *Acer rubrum* and the other species (Fig. 2*b*).

BA also explains much of the variance seen in BAI growth (R^2 up to 0.72, Table 4), and there is a strong correlation between ECA and BA. In fact, judged by R^2, BA is a better predictor of growth than ECA for five of nine species. Combining ECA and BA leads to at least a marginally better prediction of growth (in terms of R^2) than either variable alone for all species. For the average species, ECA explains 69% of the variation in growth, BA explains 68%, and a combined model explains 76% (Table 4). In an extreme case, ECA explains 46% of the variance in growth for *Quercus rubra*, and DBH explains 33%, but combining the two variables explains 77% (Table 4). In the combined model, the ECA term is significant for three of nine species, while the BA term is significant for four of nine. *Quercus rubra* is the only species for which both ECA and BA are significant variables ($p < 0.05$) in the combined model (Table 5; Fig. 3). Because growth asymptotes or even declines for very large individuals of some species, some terms in the combined model are negative.

Regressions indicate that *R*, the ratio of ECA to BA, is a poor predictor of BAI (Table 6). For *Acer rubrum*, the regression suggests a nonsensical realtionship whereby growth decreases as light increases. For the other eight species, growth increases as *R* increases, but the percentage of growth variance explained is low, and regressions are only significant for two species. In only one case, *Betula alleghaniensis*, does the inclusion of *R* significantly improve a model formulation that already includes ECA (data not shown).

Growth as a function of shade-tolerance classification

There is a weak relationship between understory diameter growth rates and a species' shade-tolerance classification (simple least squares linear regression, $R^2 = 0.36$; $p = 0.01$). *Magnolia fraseri* and *Quercus velutina* grew rapidly in the understory, despite being classified as merely "intermediate" in shade tolerance. For canopy-sized trees, shade-tolerance

Fig. 3. The interactive impact of exposed crown area (ECA) and basal area (BA) on basal area increment (BAI) for *Quercus rubra*.

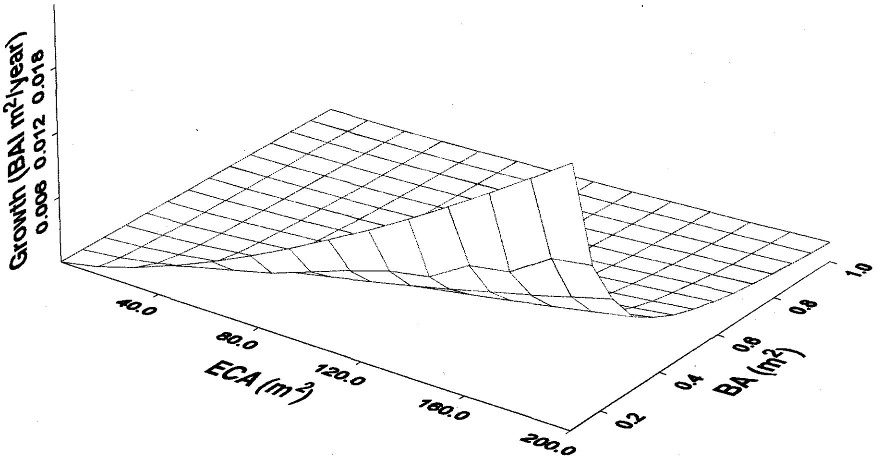


Table 4. Amount of variance explained by regressing basal area growth against exposed crown area (ECA), basal area (BA), and a combined model (eq. 1).

	ECA		BA		Combined	
Species (sample size)	R^2	p	R^2	p	R^2	p
Acer rubrum (107)	0.70	<0.001	0.80	<0.001	0.80	<0.001
Betula allleghaniensis (37)	0.74	<0.001	0.81	<0.001	0.82	<0.001
Carya glabra (17)	0.76	<0.001	0.78	<0.001	0.79	<0.001
Fraxinus americana (20)	0.87	<0.001	0.79	<0.001	0.87	<0.001
Oxydendrum arboreum (14)	0.88	<0.001	0.90	<0.001	0.92	<0.001
Pinus rigida (21)	0.52	<0.001	0.48	0.001	0.52	0.002
Quercus prinus (14)	0.63	0.001	0.54	0.003	0.66	0.003
Quercus rubra (8)	0.46	0.06	0.33	0.13	0.77	0.02
Tilia Americana (20)	0.67	<0.001	0.68	<0.001	0.69	<0.001

classification does not explain variation in growth (regression NS).

Discussion

Our analysis yields three principal results. First, species differences are among the most important predictors of diameter growth in large trees. However, interspecific differences in growth rate are strongest in the understory, and within-species variance also declines when moving from the understory to the canopy. Second, we find that a traditional metric, shade-tolerance classification is a relatively weak predictor of growth. Third, we find that both ECA and stem BA explain much of the variance in growth rates for a given species. Combining the two predictors yields improvement over either predictor alone.

Species effects on tree growth

Species differences account for much of the variation in tree growth, but differences in average diameter growth rate for the fastest and slowest growing species are much more pronounced in the understory than in the canopy (Tables 2 and 3). This latter result may reflect highly variable resource availability in the early life stages. Even within a species, heterogeneity in growth rates is more pronounced in the understory than in the canopy. For the typical species, the standard deviation in growth rate was 90% of the mean growth rate for understory trees (Table 2), but only 65% of the mean for canopy sized individuals (Table 3).

Shade-tolerance classifications are a poor predictor of tree growth

The classic shade-tolerance classifications correlate with understory growth rate across species ($R^2 = 0.36$, $p = 0.01$), but they are not informative for individual species. For example, two tolerance classifications, "very intolerant" and "intermediate", have within-group growth rate variation greater than the predicted growth rate difference between the average "very intolerant" and the average "very tolerant" species. For canopy trees, shade-tolerance classification shows no relationship to growth rate. Thus, these crude classifications offer no predictive power for large trees. This analysis illustrates the problems inherent in growth-prediction algorithms based on crude tolerance classifications that are still used in many forest simulation models (Pacala and Hurtt 1993).

Size and resource effects on tree growth

Both of our measures of an individual tree's ability to command resources, size (BA) and light interception (ECA), are strong predictors of growth rate. Individuals of most species exhibit a large growth increase when moving from dark

Table 5. Parameter estimates and standard errors (SE) for eq. 1.

	ECA		BA		Combined		
	β_2	β_1	β_0	β_1	β_0	β_1	β_2
Species	Intercept (SE)	ECA (SE)	Intercept (SE)	BA (SE)	Intercept (SE)	BA (SE)	ECA (SE)
Acer rubrum	–8.69(0.12)	1.08(0.07)*	–3.02(0.33)	0.95(0.05)*	–2.31(0.91)	1.08(0.15)*	–0.15(0.18)
Betula allleghaniensis	–8.86(0.17)	0.72(0.07)*	–3.94(0.37)	1.03(0.08)*	–3.21(1.53)	1.19(0.32)*	–0.12(0.23)
Carya glabra	–9.82(0.25)	0.99(0.14)*	–3.53(0.86)	1.10(0.15)*	–5.83(2.67)	0.70(0.47)	0.39(0.42)
Fraxinus americana	–8.77(0.19)	0.83(0.08)*	–3.51(0.59)	1.04(0.13)*	–8.43(1.65)	0.07(0.32)	0.78(0.25)*
Oxydendrum arboreum	–9.31(0.19)	0.82(0.09)*	–3.53(0.44)	1.11(0.11)*	–5.92(1.54)	0.66(0.29)*	0.36(0.22)
Pinus rigida	–9.55(0.63)	0.81(0.21)*	–3.93(0.76)	1.09(0.27)*	–10.09(4.89)	–0.11(0.98)	1.00(0.78)
Quercus prinus	–9.47(0.34)	0.89(0.19)*	–4.63(1.12)	0.84(0.23)*	–13.83(4.70)	–0.77(0.83)	1.62(0.81)*
Quercus rubra	–7.18(0.39)	0.23(0.10)*	–5.96(0.26)	0.19(0.11)	–13.63(2.50)	–1.12(0.43)*	1.38(0.45)*
Tilia americana	–8.11(0.19)	0.52(0.09)*	–5.2(0.46)	0.57(0.09)*	–6.36(1.80)	0.34(0.35)	0.22(0.33)

Note: All intercept parameters are significant ($p < 0.05$). Other significant parameters are marked with asterisks. ECA, exposed crown area; BA, basal area.

Table 6. Amount of variance explained by regressing basal area growth against the ratio of exposed crown area (ECA, m^2)/basal area (BA, m^2).

Species	R^2	p
Acer rubrum[a]	—	—
Betula allleghaniensis	0.37	<0.001
Carya glabra	0.22	0.06
Fraxinus americana	0.70	<0.001
Oxydendrum arboreum	0.12	0.23
Pinus rigida	0.33	0.008
Quercus prinus	0.25	0.07
Quercus rubra	0.20	0.26
Tilia americana	0.02	0.57

[a] Model fit not consistent with a biological interpretation; suggests that increased ECA/BA ratio (energy capture / energy demand) leads to decreased growth.

understory conditions (our 5–15 cm DBH group) to high light canopy growth conditions (our 20–40 cm DBH group) (Tables 2 and 4). This leads to a strong correlation between BA and ECA. For trees of similar size, however, variation in ECA adds information not captured by the more readily measured BA. Although R, the ratio of ECA/BA, does not explain growth as well as either ECA or BA alone, it does correlate positively with growth (Table 6). For eight of nine species, as this ratio of energy capture to energy demand increases, growth increases as well. For many of the nine species, R is only weakly correlated with tree size.

ECA alone accounts for approximately the same amount of variation in growth rate (average $R^2 = 0.69$) as diameter alone ($R^2 = 0.68$). Combining the two variables results in a substantial improvement over either variable considered singly (average $R^2 = 0.76$), although ECA adds significantly to a model that already includes BA for only three species. There is a definite, and expected, interaction between ECA and BA: trees that have a small size (small DBH) grow faster at a given amount of exposed crown area than do larger trees (Table 6). Of our nine species, *Quercus rubra* best demonstrates this interaction (Fig. 3).

Studies of tree physiology lead to an expected pattern of whole-plant response to light (Givnish 1988). For large trees, however, such expectations are based on studies at the leaf level, scaled-up to predict whole-plant response. The measurements presented here are more direct and independent of leaf-level measurements. Growth response to increasing ECA is, perhaps surprisingly, more pronounced for shade-tolerant *Acer rubrum* than for intolerant *Pinus rigida* (Fig. 3). Tolerant *Acer rubrum*, a species whose importance has increased substantially in recent years throughout the Eastern United States, grows faster than our other species at all values of ECA (Fig. 2). There are other tree species at our sites that probably grow faster than *A. rubrum* at some values of ECA (*Magnolia fraseri* for example, Table 2), but for whom ECA–growth relationships could not be estimated because of inadequate sample size.

ANOVA results indicate large differences in growth rate among species (Tables 2 and 3), but with the exception of *Acer rubrum*, our nine species exhibit similar growth responses to increasing ECA (Fig. 2). How can these seemingly contradictory results be explained? It is likely that within our plots, different species experience different average light environments. Thus species could have very different growth rates, even while sharing similar ECA–growth relationships. It is also possible, however, that were we to increase our sample sizes, statistically significant differences among species would emerge in ECA–growth relationships.

It is not unreasonable for a reader to look at the predictive power provided by growth functions including ECA (Table 4), compare them with functions based only on BA, and conclude that the extra effort required to assess ECA is not worthwhile. As noted, however, functions that included ECA were better than functions based on diameter alone, in some cases substantially (examples: *Fraxinus americana*, *Quercus prinus*, and *Quercus rubra*, Table 4). In addition, the utility of the ECA measurements reported here is limited by the fact that we were unable to obtain relative heights or total crown area for our trees. When ECA is combined with those additional parameters, prior studies suggest that growth rate prediction may be substantially enhanced (Hix and Lorimer 1990; Herwitz et al. 1998, 2000).

Despite the limitations of the present study, we feel that we have demonstrated that assessment of individual tree light conditions with low altitude, high-resolution aerial photography is a potentially important new tool. The 1990s saw a concerted effort by ecologists to establish the relationship between light and whole-plant growth for seedlings and saplings. However, only Hix and Lorimer (1990) and Herwitz et al. (2000) have studied large trees. Other studies of whole-tree response to light have not included trees larger than 5 cm DBH, but results here suggest that species respond to light at diameters far larger than 5 cm. As knowledge of whole-plant response to light increases, it will allow for increased subtlety in forest models and more accurate and reliable predictions of future forest composition.

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