Sapling growth as a function of resources in a north temperate forest

STEPHEN W. PACALA[1]
Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, U.S.A.
CHARLES D. CANHAM
Institute of Ecosystem Studies, Millbrook, NY 12545, U.S.A.
AND
JOHN A. SILANDER, JR., AND RICHARD K. KOBE
Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs, CT 06269-3042, U.S.A.

Received November 16, 1993
Accepted April 28, 1994

PACALA, S.W., CANHAM, C.D., SILANDER, J.A., JR., and KOBE, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. Can. J. For. Res. **24**: 2172–2183.

Radial and height growth are characterized for saplings of 10 dominant tree species in a transition oak – northern hardwoods forest in southern New England. Growth of saplings in the field is regressed against measures of whole-season light availability, soil moisture, and sapling size. Statistical tests show strong effects of light availability on growth, but no significant effects of soil moisture. Comparison of the light-dependent growth functions for the 10 species revealed three apparent interspecific trade-offs. (*i*) Species growing quickly at high light tended to grow slowly at low light and vice versa. The order of species from fast growing at high light to fast growing at low light did not correspond to traditional classifications of shade tolerance, and variation along this axis was approximately continuous. (*ii*) There was substantial variation off the species continuum defined in *i*. At any point along the continuum from fast growth at high light to fast growth at low light, some species grew faster than others, and these faster growing species had lower survivorship during periods of suppression than the slower growing species. (*iii*) Height growth at high light was inversely related to survivorship when suppressed. This variation was again continuous (species did not cluster into discrete categories), but the order of the species did correspond closely to a traditional ordering of shade tolerance. There was little correspondence between our estimated growth functions and the growth functions assumed in the JABOWA–FORET class of forest simulation models. These results raise serious concerns about the current practice of assigning growth functions to species in simulation models using traditional classifications of shade tolerance.

PACALA, S.W., CANHAM, C.D., SILANDER, J.A., JR., et KOBE, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. Can. J. For. Res. **24** : 2172–2183.

L'étude de la croissance radiale et en hauteur des gaules de 10 essences prédominantes dans la chênaie à feuillus nordiques est réalisée au sud de la Nouvelle Angleterre. La croissance des gaules est analysée en fonction de leur taille, de la lumière disponible et de l'humidité du sol. Les effets de la lumière disponible sur la croissance sont significatifs, mais ceux de l'humidité du sol ne le sont pas. La comparaison de la croissance des 10 essences en fonction de la lumière révèle trois comportements. (*i*) Les espèces à croissance rapide en pleine lumière poussent lentement à faible lumière et vice versa. En fonction de leur croissance, les essences se dispersent de façon continue sur l'axe ombre–soleil. Leur dispersion ne correspond pas aux classifications traditionnelles de la tolérence à l'ombre. (*ii*) La croissance varie considérablement le long de l'axe ombre–soleil. À une position donnée sur l'axe, certaines essences poussent plus vite que d'autres et leur survie est plus faible durant les périodes d'oppression que celle des espèces à croissance lente. (*iii*) La croissance en hauteur en pleine lumière est inversement proportionnelle à la survie en période d'oppression. La variation de la croissance en hauteur est également continue (non en catégories) le long de l'axe ombre–soleil, mais l'ordre des espèces correspond étroitement à une classification traditionnelle de la tolérance à l'ombre. Il y a peu de ressemblance entre nos fonctions de croissance et les fonctions hypothétiques dans les modèles de simulation JABOWA–FORET. L'ensemble de ces résultats soulève de sérieuses inquiétudes sur l'utilisation des classes traditionnelles de tolérance à l'ombre pour représenter la croissance de diverses espèces forestières dans les modèles de simulation.

[Traduit par la Rédaction]

Introduction

Interspecific variation in shade tolerance is widely cited as a primary cause of secondary succession (Baker 1949; Kramer and Kozlowski 1960; Horn 1971; Farquhar and von Caemmerer 1982; Bazzaz 1979; Shugart 1984; Spurr and Barnes 1980; Glitzenstein et al. 1986; Clark and Clark 1992). Foresters typically categorize tree species into two to five classes of shade tolerance (e.g., Baker 1949; Burns and Honkala 1990; Whitmore 1989; Swaine and Whitmore 1988), using information on radial and height growth, survivorship, and crown and bole allometry (Spurr and Barnes 1980). The incongruence of different classification schemes (see Kobe et al. 1993) probably reflects the application of different criteria, spatial and temporal variation within tree species, and error: "we have only the slightest knowledge of what is meant by shade tolerance" (Baker 1949). The traditional division into discrete classes of shade tolerance is generally recognized as arbitrary (Spurr and Barnes 1980) and does not necessarily reflect actual clustering of species with similar characteristics. Several recent studies provide evidence that tree species' responses to variation in light fall along a multidimensional continuum of shade tolerance, rather than clustering into discrete categories (e.g., Brokaw and Scheiner 1989; Martinez-Ramos et al. 1989; Canham 1988*a*, 1989; Clark and Clark 1992; Kobe et al. 1993).

[1]Author to whom all correspondence should be addressed.

Printed in Canada / Imprimé au Canada

The most widely studied models of forest dynamics rely extensively on published classifications of shade tolerance (Shugart 1984; Botkin 1992). We refer to these models as JABOWA–FORET models because they are derivatives of JABOWA (Botkin et al. 1972) and its offspring FORET (Shugart and West 1977). JABOWA–FORET models are able to reproduce an extensive list of phenomena, including observed patterns of secondary succession and community structure, geographical patterns of zonation, long-term responses of forest composition to past climatic change, and age and size structure (see the review in Shugart 1984). The models are currently used as "community modules" in forest ecosystem models (e.g., Pastor and Post 1988) and to predict the responses of forests to forecasted greenhouse warming (reviewed in Pacala and Hurtt 1992).

JABOWA–FORET models were designed to be parameterized using information already in the published literature; hence the reliance on published categorizations of shade tolerance. This feature has enabled the rapid development of JABOWA–FORET models for an enormous diversity of forests, but given the imprecision of the traditional concept of shade tolerance, it also raises questions about the mechanistic underpinnings of the models. Do these models embody a mechanistic understanding of forest dynamics or do they simply mimic the right behavior for substantially wrong reasons?

The notion of shade tolerance is used in JABOWA–FORET models to parameterize the species-specific responses of tree growth to light availability. The "growth submodel" for species i has the following form:

$$[1] \quad w = f_i(r)p_i(L)$$

where w is the width of an annual radial increment (growth ring), $f_i(r)$ is a species-specific function of radius r, and $p_i(L)$ is a species-specific "growth modifying function" describing the effects of light availability (L) on radial growth. In most current versions, the right-hand side of [1] is also multiplied by other growth-modifying functions describing the effects of factors such as water and nitrogen availability.

The direct way to estimate the right-hand side of [1] is to regress ring width against radius and light level, but this is not the standard practice in JABOWA–FORET models because of the lack of suitable published data. Instead, a function for $p_i(L)$ is simply assigned to each shade-tolerance class. These functions are chosen to be consistent with the finding that leaves of shade-tolerant species tend to have higher photosynthetic rates at low light levels and lower photosynthetic rates at high levels than shade-tolerant species (see Shugart 1984). For example, in JABOWA and FORET there are two such functions, one assigned to all species classified as shade tolerants in published tables and one assigned to all shade intolerants (Fig. 1). Thus, it is assumed that published shade-tolerance classifications predict the response of photosynthesis to light and that the functional response of whole-tree growth to light is congruent with the leaf-level photosynthetic response.

To estimate the $f_i(r)$, a complex procedure is used that relies on three kinds of information published by foresters (see Shugart 1984): (*i*) quadratic regressions of height against diameter for each species, (*ii*) published values for the maximum age and diameter attained by a species, and (*iii*) a constant of proportionality (multiplying the right-hand side of [1]) calculated from maximum age, diameter, and height or obtained from data on the growth of monospecific stands. Note that this procedure relies on statistical outliers (sizes and ages of the oldest and largest trees ever observed) to parameterize the growth of saplings and average adults. Moreover, the notion of maximum age and size is itself problematic for organisms with indeterminate life-span and growth.

Because of these and other concerns, we designed a forest model (SORTIE) from components that could be estimated directly from data collected in the field, and we collected the necessary data for the 10 dominant tree species on a site in northwestern Connecticut (Pacala et al. 1993; Canham et al. 1994; Kobe et al. 1993; Ribbens et al. 1994). In this paper, we report the observed dependencies of radial and height growth on size (radius) and on light and water availability. We focus primarily on the growth of seedlings and saplings (individuals <8 m tall) because a tree's success at reaching the canopy is largely determined by its performance as a sapling (Canham 1988*b*; Clark and Clark 1992). As expected, we show that growth is strongly influenced by light availability. The 10 species segregate along a continuum of growth responses to light with at least two dimensions; the species do not cluster into relatively discrete categories. Also, there are a number of surprises, including species typically classified as intolerant that grow relatively quickly under low light levels and species typically classified as tolerant that grow relatively slowly at low light levels and quickly at high light levels. In general, the estimated growth functions poorly match their counterparts assumed in JABOWA–FORET models. We show that the growth responses can be reconciled with traditional notions of shade tolerance if we integrate measurements of light-dependent growth, architecture, and mortality (mortality information from Kobe et al. 1994).

In contrast with light, we observed no relationship between water availability and sapling growth. We do not interpret this result as evidence that water is unlimiting, but rather that the saplings experienced more variation in light than in water availability. Finally, although nitrogen is thought to be a limiting resource in northeastern forests (e.g., Rastetter et al. 1991), variation in nitrogen mineralization is independent of variation in light levels within our study sites (A.C. Finzi, C.D. Canham, and S.W. Pacala, to be published). A separate study of the effects of nitrogen availability on growth is underway and will be reported elsewhere.

Methods

Study sites and tree species

The study sites are located in and around Great Mountain Forest in northwestern Connecticut (42°00′N, 73°15′W) at elevations of 350–550 m. All sites are second-growth stands that were logged 80–150 years ago. Soils are sandy, acidic Spodsols on glacial till derived from mica schist bedrock.

Forests in the region are dominated by a mix of species characterizing the conifer–hardwood forests of northern New England and the oak forests of southern New England. The 10 species discussed in this paper include all the dominant and major subdominant species found in mid- and late-successional stands. The species are (in roughly decreasing order of a traditional classification of shade tolerance; Baker 1949): *Fagus grandifolia* Ehrh. (American beech, FAGR), *Tsuga canadensis* (L.) Carr. (eastern hemlock, TSCA), *Acer saccharum* Marsh. (sugar maple, ACSA), *Acer rubrum* L. (red maple, ACRU), *Betula alleghaniensis* Britton (yellow birch, BEAL), *Pinus strobus* L. (white pine, PIST), *Quercus rubra* L. (red oak, QURU), *Quercus alba* L. (white

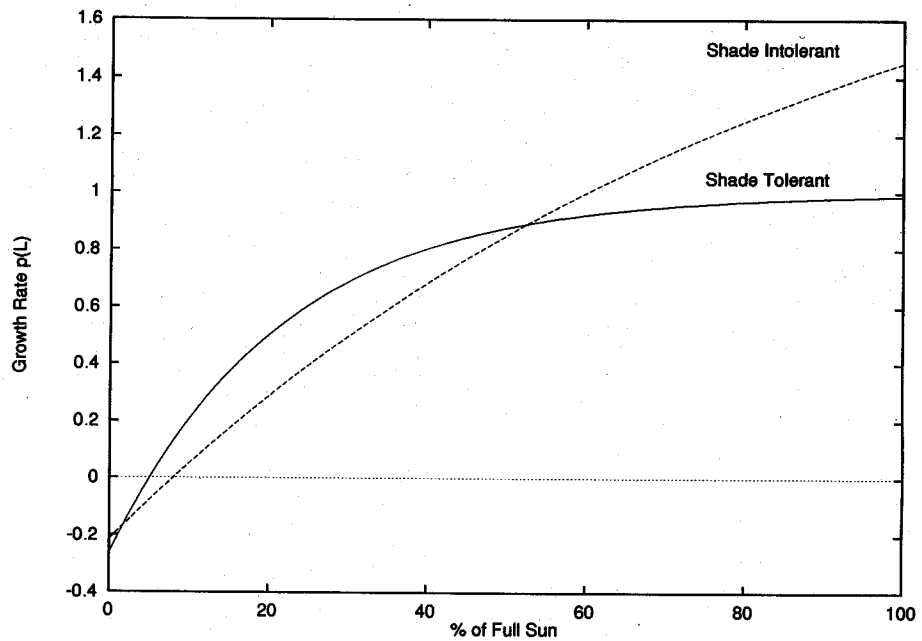

FIG. 1. The "growth modifying functions" in the JABOWA and FORET models ($p_i(L)$ in model [1]).

oak, QUAL), *Prunus serotina* Ehrh. (black cherry, PRSE), and *Fraxinus americana* L. (white ash, FRAM). Note that this list excludes the true early successional fugitive species in this type of forest, including *Prunus pensylvanica* L.f. (pin cherry), *Betula papyrifera* Marsh. (paper birch), and *Betula populifolia* Marsh. (grey birch).

Data collection

Growth rates

We harvested a total of 641 saplings ranging in radius (10 cm from the ground) from 2 to 50 mm and in height from 15 to 750 cm. Saplings were chosen to span the range of overstory density in Great Mountain Forest, from closed canopy to large natural and man-made disturbances. The sample size per species ranged from 49 to 100. Saplings were tagged in early summer and harvested late in the fall (after leaf fall in late October and November). At the time of harvest, we recorded the height of each sapling and the length of extension growth during the preceding growing season on the largest apical stems (up to three stems per plant if available), and we removed a section of stem at a height of 10 cm. We later measured the widths of each of the five most recent annual growth increments using an ocular micrometer. In this paper we report only results obtained for the most recent growth ring. Inclusion of the earlier four rings yielded poorer statistical fits, perhaps because we lacked light measurements for these years. We also do not present data on extension growth because these were inconsistent with our height–diameter data (see below). Together, the extension and radial growth data implied that height should increase with diameter from two to three times faster than observed, perhaps because winter dieback of terminal leaders or browsing by deer substantially reduces effective height growth in Great Mountain Forest. The samples for FAGR, TSCA, ACRU, BEAL, and ACSA were collected in 1990 and 1991, for FRAM and PIST in 1991, and for QURU, QUAL and PRSE in 1991 and 1992.

Light availability

To assess light availability, we took a fish-eye photograph above each sapling in midsummer preceding harvest. We then computed an index of whole growing season light availability (GLI, following Canham 1988*a*) from each photograph. This index integrates the seasonal and diurnal movements of the sun, the mix of diffuse and beam radiation, and the spatial distribution of canopy openness into a single index in units of percent of full sun. We have confirmed with arrays of quantum sensors that this index is correlated, with a slope not significantly different from 1, with total photosynthetically active radiation under closed and open canopies, and in gaps (Canham 1988*a*; Canham et al. 1994).

Soil moisture

To assess water availability, we measured soil moisture for a subsample of approximately 50 individuals of each species; for FAGR, TSCA, ACSA, ACRU, and BEAL in 1990 and for PRSE, QURU, QUAL, PIST, and FRAM in 1991. In 1990, measurements were gravimetric and taken from a single soil sample at the base of each harvested sapling in September (yielding water content as a percent of total soil mass). In 1991, we used a time domain reflectometer to measure soil moisture (percent of volume) at the base of each harvested individual on three dates during the growing season. We report results for the average of these three dates. Although crude, we have shown that these methods are able to detect gradients of soil moisture within gaps (driest near the north edge because of the angle of the sun), differences between gaps and closed canopy, and temporal changes in soil moisture (C.D. Canham, A. Finzi, and S.W. Pacala, to be published).

Height–diameter relationships

Finally, to predict height growth from radial growth, we measured heights and diameters (10 cm above the ground) of approximately 60 individuals per species (range from 47 to 125) for all species except QUAL. These individuals ranged from 25 cm tall to canopy height and were not part of the harvested samples used to measure the dependence of radial growth on light and water availability. All individuals were growing in forest stands or in gaps rather than as completely isolated individuals because we were interested in predicting the outcome of competition among saplings, and open-grown

TABLE 1. Parameter estimates of the radial growth model

Species	A	S	R^2	N	θ	L^*
QURU	0.266±0.080	0.022±0.011	0.56	71	0.99	0.01
QUAL	0.171±0.032	0.036±0.030	0.69	71	0.94	0.03
FRAM	0.226±0.088	0.025±0.008	0.52	63	1.03	−0.01
PIST	0.230±0.048	0.019±0.007	0.78	60	0.91	−0.04
ACRU	0.167±0.064	0.027±0.014	0.24	49	0.73	−0.05
PRSE	0.249±0.069	0.064±0.029	0.59	110	0.77	0.01
BEAL	0.169±0.047	0.137±0.071	0.44	49	1.21	−0.06
ACSA	0.125±0.029	0.159±0.077	0.23	54	1.00	−0.03
TSCA	0.229±0.037	0.051±0.022	0.50	53	0.71	−0.03
FAGR	0.152±0.035	0.075±0.052	0.53	55	0.76	0.01

NOTE: A and S, parameters of model [2] ± 95% confidence limits; R^2, refers to model [2] only; N, sample size; θ, refers to model [2] with modification *iii*; L^*, refers to model [2] with modification *ii*.

trees have allometries different from trees under competition. Heights were measured with a 7-m pole if possible and by triangulation (clinometer and measuring tape) otherwise.

Regression analysis

Radial growth as a function of light

In this paper, effects of light on growth are summarized by the following regression equation:

$$[2]\quad w = rp(L) + \varepsilon$$

where

$$p(L) = \frac{AL}{\frac{A}{S} + L}$$

$$\varepsilon \sim N(0,\ C[rp(L)]^D)$$

Here, w is the ring width of an individual with radius r and light level L. The effect of light on growth is the Michaelis Menton function $p(L)$, where A is the asymptotic relative growth rate (w/r) under high light and S is the slope at zero light. Note that the proportionality of w and r implies geometric growth. Observed ring widths are assumed to be normally distributed about the mean ($rp(L)$) with variance $C[rp(L)]^D$. The variance is given as a power function of the predicted mean to handle species-specific heteroscedasticity in the data. We estimated A, S, C, and D for each species using maximum likelihood and a simulated annealing algorithm (Szymura and Barton 1986), and asymptotic sampling distributions for these estimates by inverting the information matrix (Mood et al. 1974).

In addition, we fit a large number of variants of [2] to the data for the following reasons: (*i*) to evaluate the strength of the dependence of growth on light, we replaced $p(L)$ by the constant A; (*ii*) to allow a nonzero intercept, as in Fig. 1, we replaced $p(L)$ by $AL/(A/S + L) - I$ if $L \geq L^*$ and $P(L) = 0$ if $L < L^*$, where $I = AL^*/(A/S + L^*)$; (*iii*) to allow departures from geometric growth, we replaced r by r^θ, the logistic function $r(1 - r\phi)$, and several sigmoid functions; (*iv*) to investigate effects of soil moisture, we replaced $p(L)$ by a Michaelis Menton function of water availability ($AH/(A/S + H)$, where H is soil moisture), a two-resource Michaelis Menton function implying joint limitation by light and water ($AHL/[A/S + L)(A/V + H)]$, where V is a constant), and the function $[AL/(A/S + L)] + VH$ (to detect simple linear dependence of the residuals of eq. 2 on soil moisture; (*v*) to investigate an alternative functional form for the light response, we replaced $p(L)$ by the exponential Michaelis Menton function $A(1 - e^{-SL/A})$; and (*vi*) to determine if patterns of heteroscedasticity were species specific, we replaced D by 0, 1, and 2 (thus assuming equal dependence of the variance on the mean for all species). Also, in each of *i–v*, we replaced the expression $rAL/(A/S + L)$ in the variance $C[rAL/(A/S + L)]^D$ by the appropriate predicted mean ring width.

We compared results obtained from eq. 2 and the above alternatives using likelihood ratio tests (Edwards 1992). Thus, we formally tested the hypothesis that sapling growth depends on light (comparison of [2] with *i*), that radial growth is positive only at sufficiently high light levels (comparison of [2] with *ii*), that sapling growth is geometric (comparison of [2] with *iii*), that growth depends on soil moisture (comparison of the first function in *iv* with *i* and the second two functions in *iv* with [2]), and that heteroscedasticity is species specific (comparison of *vi* with [2]). Each of these tests involved a single degree of freedom because each compared regression functions with and without a single additional free parameter (Edwards 1992). However, because the hypotheses were tested repeatedly for 10 different species, we adjusted the significance threshold for 10 comparisons. To achieve a significance level of α (e.g., $\alpha = 0.05$), we used the one-half χ^2-value corresponding to the threshold $1 - (1 - \alpha)^{0.1}$ (see Edwards 1992).

Relationship between height and diameter

The relationship between height and diameter is given by the exponential Michaelis Menton regression function:

$$[3]\quad H = \alpha(1 - e^{-(\beta/\alpha)2r}) + \varepsilon$$

where

$$\varepsilon \sim N(0,\delta[\alpha(1 - e^{-(\beta/\alpha)2r})^\gamma])$$

Here, H is the height (m) of an individual with radius r (cm), α is the asymptotic height, β is the slope at radius zero, and δ and γ govern the dependence of the variance on the mean (necessary because of species-specific heteroscedasticity). We also tried the hyperbolic Michaelis Menton function, $\alpha 2r/(\alpha/\beta + 2r)$, in place of the predicted mean in [3], but this provided generally poorer fits. As with [2] we estimated the parameters in [3] with maximum likelihood and simulated annealing, and asymptotic sampling distributions by inverting the information matrix.

Adjusted values of A *and* S *assuming a reference allometry*

The outcome of competition for light probably depends more on height than on radial growth. Interspecific comparisons of light-dependent growth in height are complicated by the fact that height growth is summarized by four

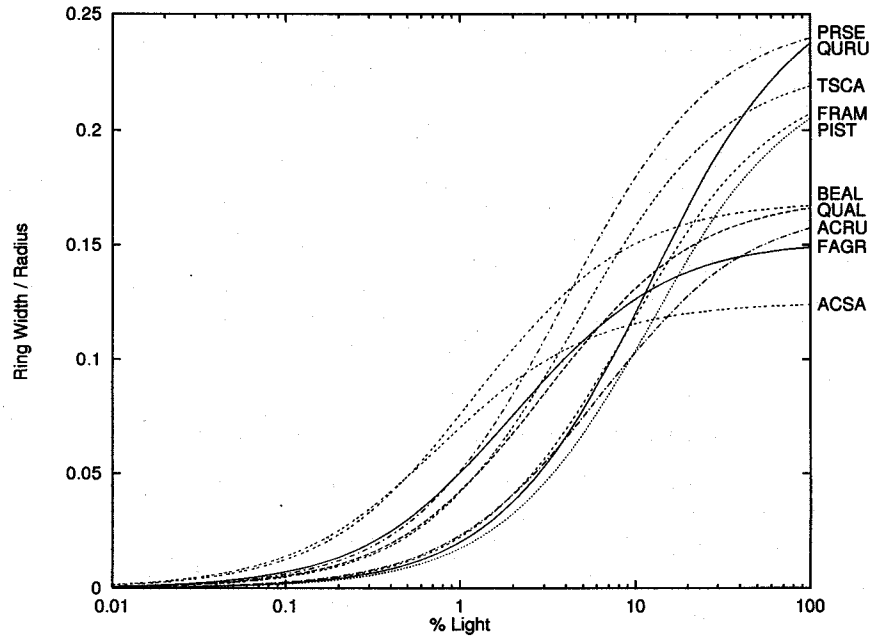

FIG. 2. Estimated radial growth functions for 10 tree species (model [2], using parameter values in Table 1).

estimated parameters for each species (A, S, α, and β), whereas radial growth is summarized by only two (A and S). For this reason, we produced models of height growth with only two species-specific parameters as follows. We first used [2] and [3] to compute, for each species, the length of time necessary to grow from the seedling stage (r = 1 mm) to 5 m in height at a low light level representative of conditions in Great Mountain Forest (L = 1%) and in full sun (L = 100%). These times are labeled t_1 and t_{100}, respectively. We then assumed an average "reference allometry" common to all species, α = 30.0 and β = 1.7, and calculated new species-specific values for A and S that yielded the same values of t_1 and t_{100}. We refer to these new values of A and S as adjusted values. Thus, if one species has a larger adjusted value of A than another, then, in full sun, it will be the first to reach 5 m in height. This is not necessarily true of the unadjusted A values, because the species with the larger unadjusted value could be shorter for a given radius than the species with the smaller unadjusted value (in which case it could reach 5 m in height more slowly even with faster radial growth). We also computed adjusted values of A and S for growth to 3, 7, and 10 m in height, but these yielded results similar to those presented in this paper. In addition, similar results were obtained if we used 30% of full sun as the high light level (rather than 100%) when computing the adjusted values. This is important because 30% is more typical of light levels in a forest gap than is 100%. Although we did not sample open-grown saplings, measured light levels exceeded 30% in part of the sample for every species. Finally, no adjusted values were calculated for QUAL because we lacked height–diameter data for this species.

Results

Radial growth model

Estimates of A *and* S *from model [2]*

The results of the regression analysis of the radial growth model are presented in Table 1 and Figs. 2–5. The estimates plotted in Fig. 3*a* show some evidence of an interspecific trade-off between the abilities to grow at high and low light (a trade-off between A and S). Note that the estimates appear to be negatively correlated, progressing from ACSA (high S and low A) to QURU (low S and high A), and show no evidence of clustering into discrete shade-tolerance classes. The estimates also exhibit substantial variation in the orthogonal direction; points for BEAL and PRSE are farther from the origin than are points for FAGR, AGRU, and PIST (growth rate at all light levels increases with distance from the origin). Thus, the continuum appears to have two dimensions, making any ordering of the species along a single shade-tolerance axis problematic.

Moreover, several of the estimates are seemingly at odds with traditional assignments of shade tolerance. For example, BEAL has an extremely high low-light growth rate (large S) and a relatively low high-light growth rate (low A), despite its traditional classification as a relatively intolerant species. In contrast, the late-successional shade-tolerant TSCA has a high A and an intermediate to low S. On the other hand, species such as ACSA, PIST, FRAM, QURU, and PRSE have estimates in accord with conventional wisdom (high S and low A for ACSA and the reverse for PIST, FRAM, QURU, and PRSE).

Note that the above patterns are generally supported by the confidence intervals in Table 1 and Fig. 3*b*. The considerable uncertainty of each estimate is offset by the interspecific differences among the estimates. However, other apparent differences among the estimates are overwhelmed by the sizes of the confidence regions. Thus, we cannot conclude that ACSA is more shade tolerant than FAGR or that ACRU has a lower high-light growth rate than PIST or FRAM.

Goodness of fit

Values of R^2 (Table 1) show that the calibrated models explain an average of 51% of the variance in radial growth. It is important to understand that our regression method does not maximize R^2. Maximization of R^2 is not the appropriate regression criterion because the variance of ε in [2] is not a constant (a constant variance would imply homoscedasticity). Although the model explains more than half the variance for most species, the two maple species have R^2-values

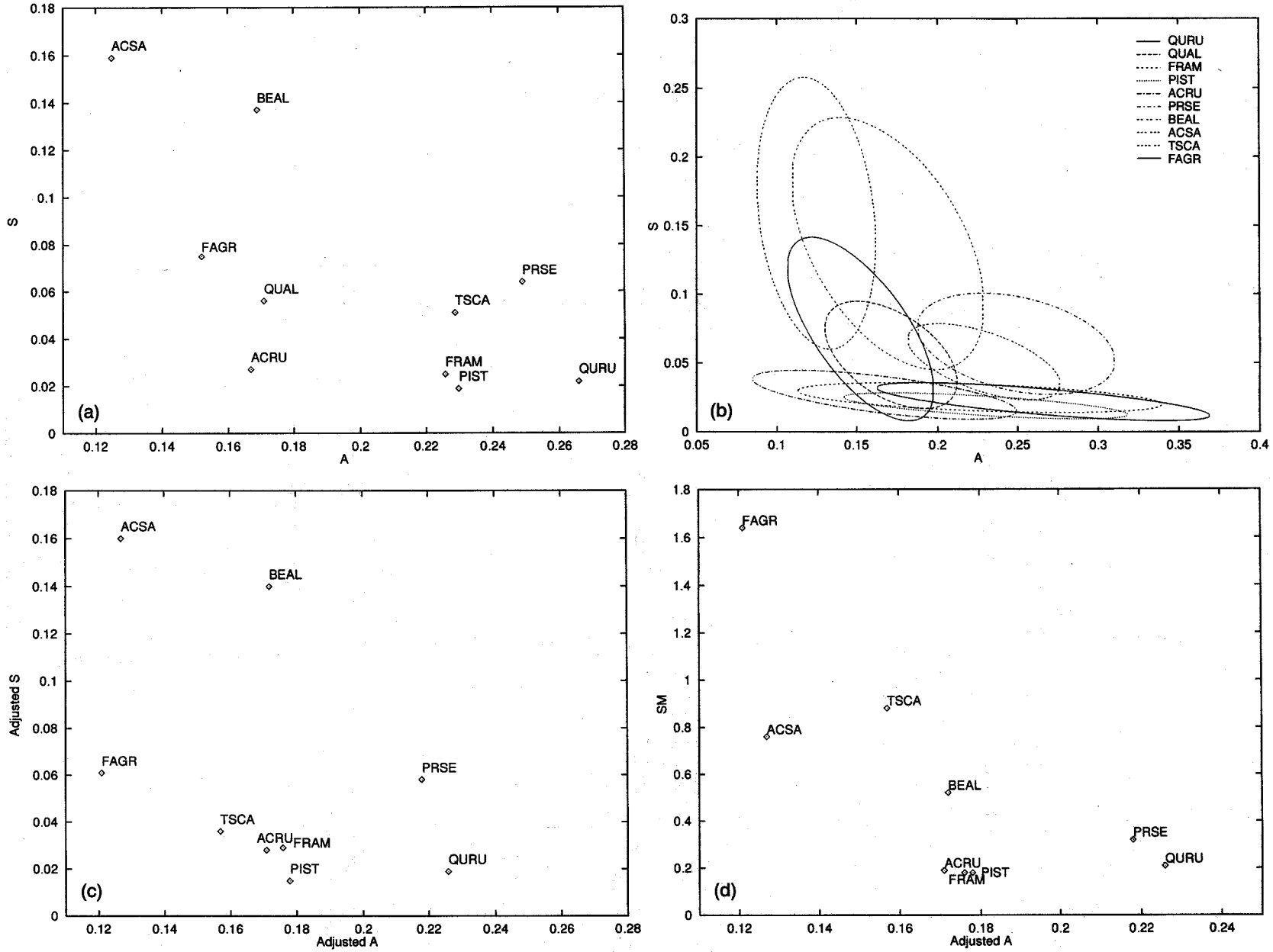

FIG. 3. Estimates of parameters governing the response of growth to light. (*a*) Radial growth at low versus high light (*S* vs. *A* from model [2] and Table 1). (*b*) Bivariate 95% confidence intervals for the estimates in Fig. 3*a*. The diamonds in Fig. 3*a* show the centers of the ellipses in Fig. 3*b* and are thus useful in identifying which species corresponds to each ellipse. (*c*) Height growth at low versus high light (adjusted *S* vs. adjusted *A* (see text for the definitions of these)). (*d*) Low-light survivorship versus high-light height growth (*SM* vs. adjusted *A* (*M* is from the mortality function described in the section entitled The integration of patterns of growth-dependent mortality)).

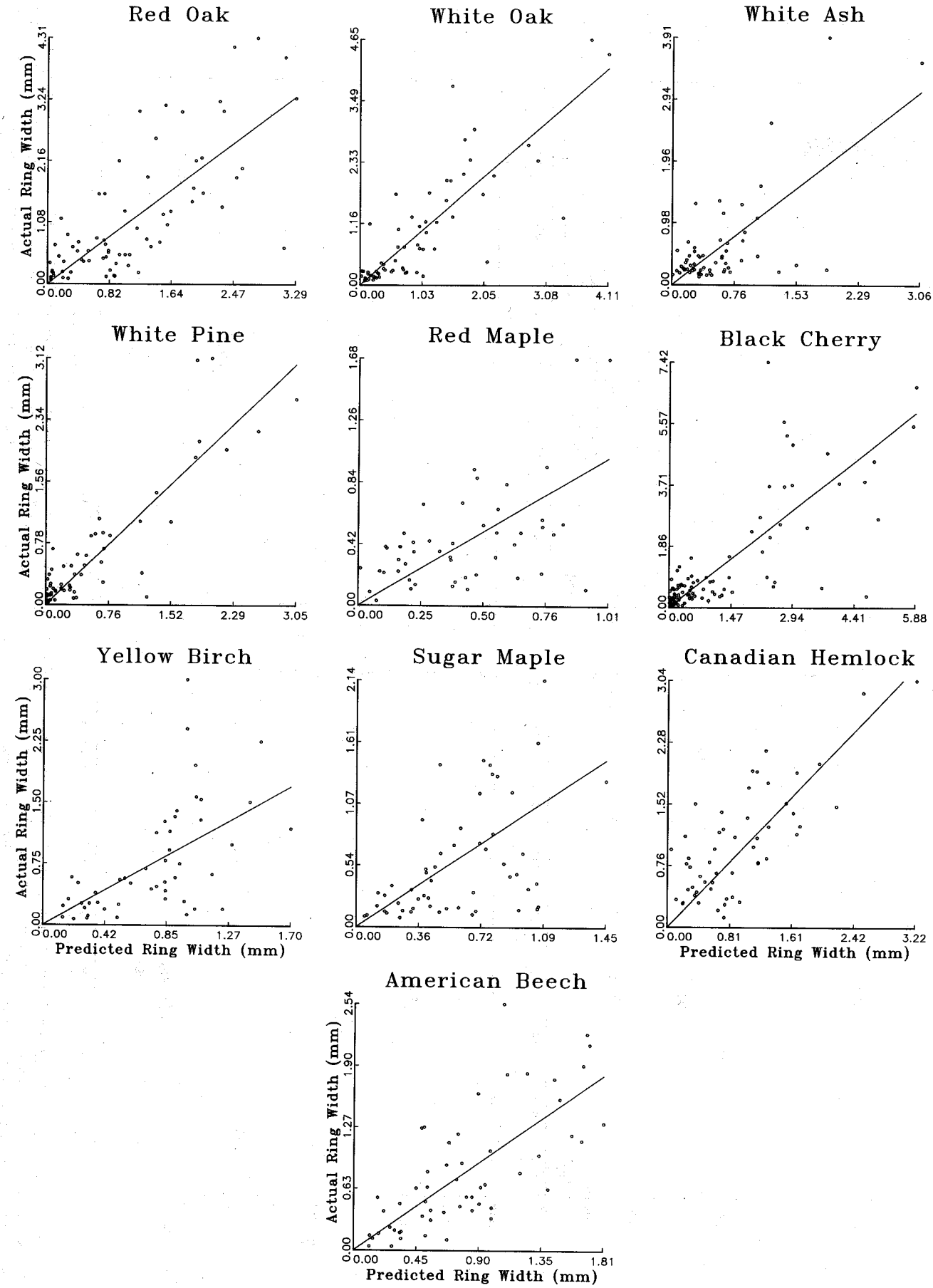

FIG. 4. Observed radial growth versus growth predicted by model [2] and parameter values in Table 1.

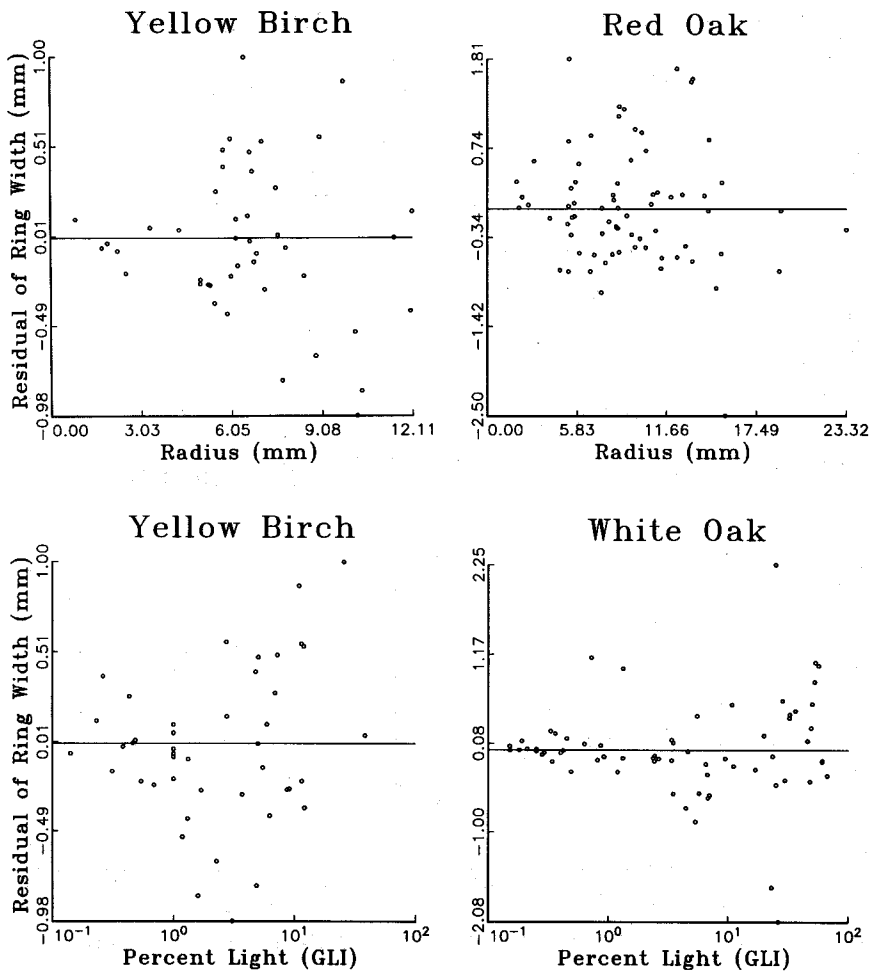

FIG. 5. Representative plots showing the balance of residuals in the radial growth model [2] with respect to the two independent variables r and L.

of only approximately one-fourth. Possible sources of residual variation include disease, herbivory, unmeasured resources (e.g., nitrogen), genetic variation, and microclimate. Also, the data in Fig. 4 and the examples in Fig. 5 show that the residuals are well balanced with respect to both independent variables (r and L).

Regression models other than [2] and effects of soil moisture

In this section, we discuss the modifications of [2] described as points *i–vi* under Regression analysis (Radial growth as a function of light) in the Methods section.

(*i*) Effects of light on radial growth were statistically highly significant for all 10 species. The regression model with only radius as an independent variable was significantly worse than [2] in all cases (likelihood ratio tests, 1 df, $p < 0.001$ for all species).

(*ii*) Saplings continue to grow in diameter (albeit slowly) at very low light levels (<0.1%). Estimates of the x-intercept L^* were very close to zero (last column of Table 1), and the model with this extra parameter was not significantly better than [2] for any species (likelihood ratio tests, 1 df, largest difference in log-likelihoods was 0.77 (ACRU) and the 0.05 significance threshold is 3.93).

(*iii*) No departure from geometric growth was statistically significant for any species. For example, estimates of θ (Table 1) cluster around 1, implying approximate geometric growth. Inclusion of this extra parameter was not justified statistically (likelihood ratio tests, 1 df, the largest difference in log-likelihoods was 2.11 (PRSE, all others ≤1.03) despite a 0.05 significance threshold of 3.93).

(*iv*) We observed no statistically significant effects of soil moisture on growth. In no case could the inclusion of a parameter allowing effects of soil moisture be justified statistically (at the 0.05 level, likelihood ratio tests, 1 df). Figure 6 contains four representative plots illustrating the lack of any correlation between residuals from the model [2] and soil moisture.

(*v*) The exponential Michaelis Menton function provided generally lower likelihoods than [2] (log-likelihoods lower by <1.0 for two species, >1.0 and <2.0 for three species, >2.0 and <3.0 for two species, >3.0 and <4.0 for one species, and higher by <0.2 for the remaining two species). Thus, we focus exclusively on model [2].

(*vi*) Likelihood ratio tests (1 df) showed that the model assuming constant residual variance ($D = 0$) was significantly worse (0.05 level) for 8 of 10 species, significantly worse for 4 of 10 when $D = 1$, and significantly worse for 7 of 10 when $D = 2$. Note the species-specific heteroscedasticity evident in Fig. 4.

Comparison of [2] to radial growth models in JABOWA–FORET

The models JABOWA and FORET include a complex dependence of growth on radius (see Shugart 1984). However, near the lower size limit for saplings in these models (137 cm

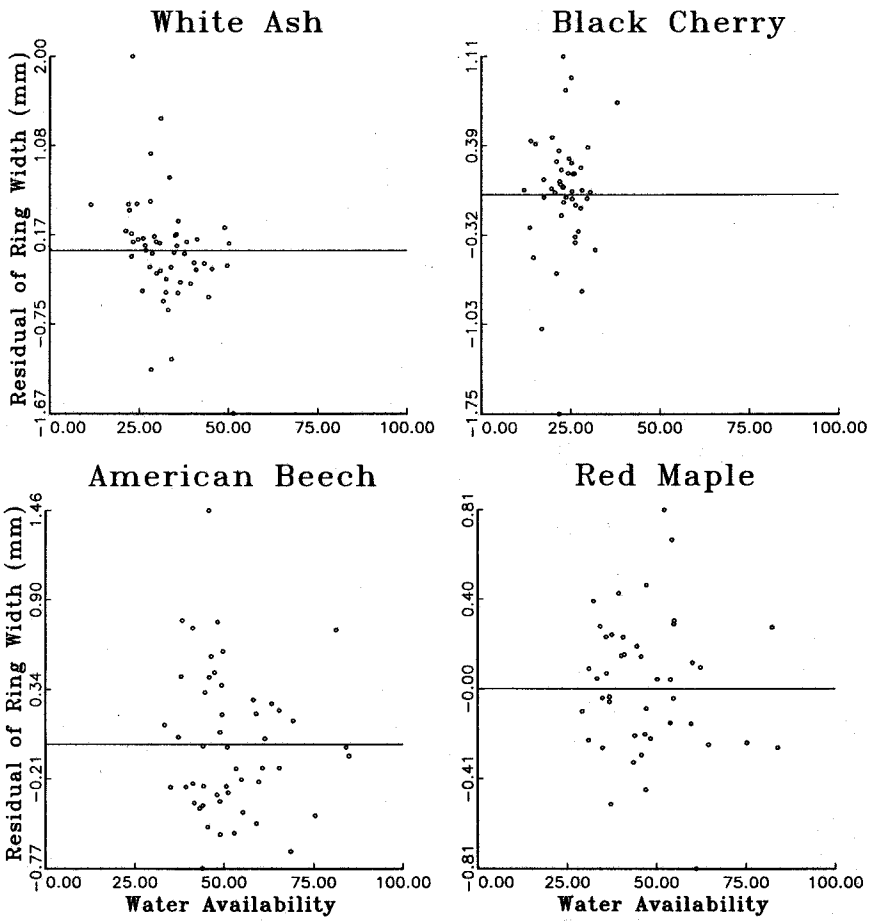

FIG. 6. Representative plots showing the residuals of the radial growth model [2] as a function of soil moisture.

tall), radial growth takes a simple form. Relative radial growth rate (w/r) is then proportional to a function of light level. In other words, $f_i(r)$ in [1] is then simply given by a constant, G_i, times r. Because this is precisely the same mathematical form as [2], we can compare [2] with the models of light-dependent growth assumed in JABOWA and FORET.

Figure 7 shows the relative growth functions assumed in FORET and JABOWA for the 8 of our 10 species included in FORET and the 5 of our 10 species included in JABOWA. To facilitate comparison with our results, the functions in Fig. 7 are adjusted to the thermal climate of our sites. JABOWA–FORET models include a simple way to adjust the constant G, by the number of degree-days greater than 40°F (4.4°C). Other than this adjustment, the parameter values and functional forms are precisely as reported in Shugart (1984).

Even so, care must be taken when comparing our results (Fig. 2) with those in Fig. 7, because some JABOWA–FORET models include effects of nutrients and water (which would multiply the curves by constants that depend on current levels of nutrients and water), and because radial growth is predicted at breast height (137 cm) in JABOWA–FORET and at 10 cm in [2]. Thus, one must not place too much emphasis on the scale of the vertical axis in Fig. 7.

Nonetheless, the lack of correspondence is striking between the curves estimated from field data in Fig. 2 and the curves assumed by JABOWA–FORET models in Fig. 7. In particular, although all curves in Fig. 7 predict zero growth at light levels of either ≤5% or ≤8% of full sun, our results indicate that all species grow radially at least one-half their maximum potential rates when in 8% sunlight.

TABLE 2. Height–diameter relationships

Species	α	β	R^2	N
QURU	33.6±3.1	1.26±0.07	0.98	93
FRAM	32.4±2.5	1.69±0.13	0.96	77
PIST	38.4±7.4	1.00±0.09	0.97	55
ACRU	25.7±2.4	1.89±0.11	0.97	47
PRSE	30.8±2.1	1.35±0.11	0.98	125
BEAL	23.2±2.2	1.89±0.15	0.96	48
ACSA	24.8±2.9	1.87±0.11	0.93	55
TSCA	29.6±8.9	0.73±0.06	0.92	50
FAGR	34.6±7.1	1.06±0.06	0.96	51

NOTE: α and β, parameters of model [3] ± 95% confidence limits.

Height–diameter relationships

Estimates and confidence intervals for α and β in [3] are found in Table 2. Note that saplings of the two conifer species and FAGR are shorter, for a given radius, than are saplings of the remaining species (see values of β). The high values of R^2 imply that most within-species variation in height–diameter relationship is caused by differences between trees growing with and without neighbors; recall that our sample contained no open-grown trees.

Adjusted estimates of A *and* S

A comparison of the adjusted values of A and S (Fig. 3*c*) shows that patterns of height growth vary, like patterns of radial growth (Fig. 3*a*), in two dimensions. First, species that grow quickly in low light tend to grow slowly in high

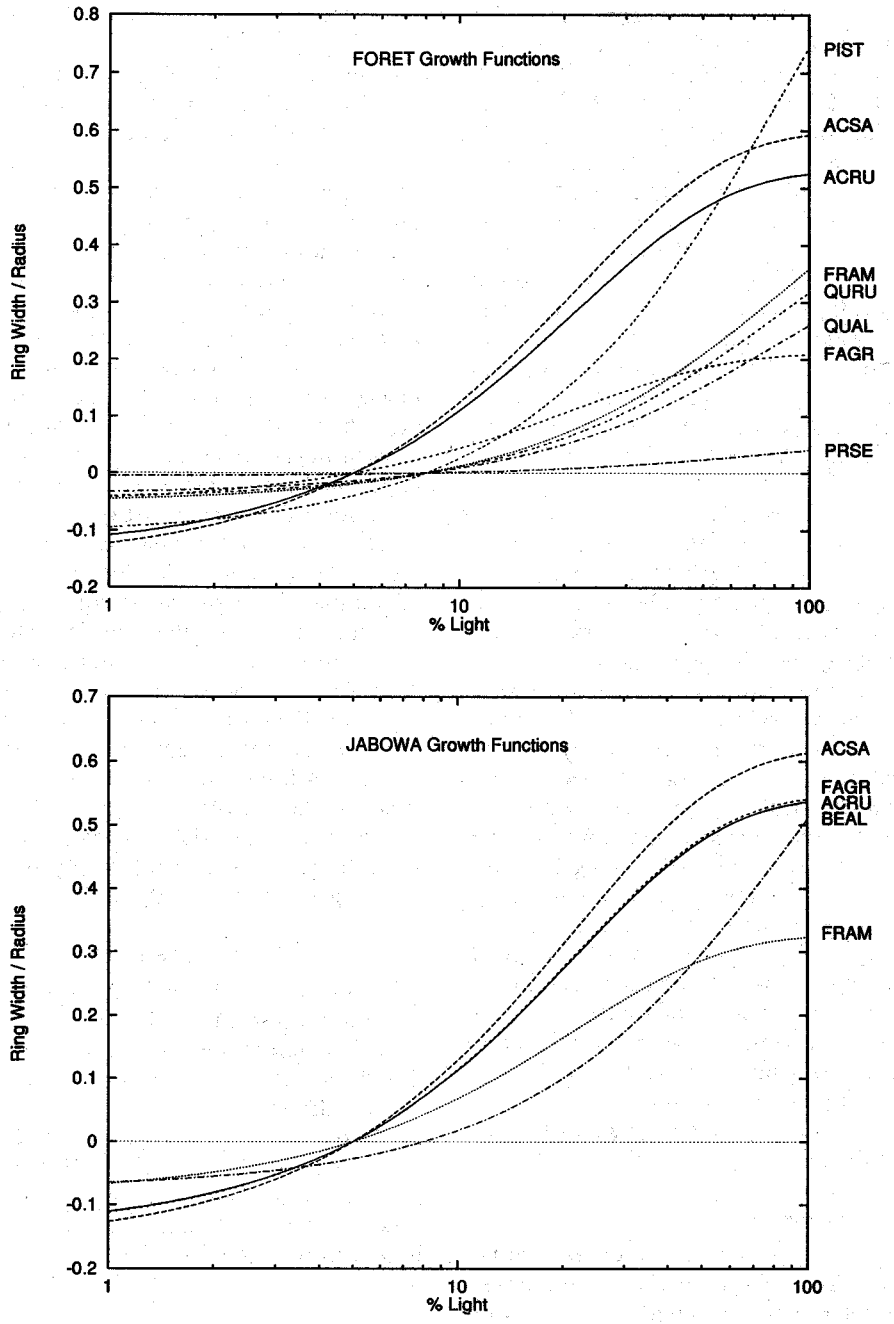

FIG. 7. Radial growth functions from the FORET (*a*) and JABOWA (*b*) models, as reported in Shugart (1984).

light (compare ACSA and FAGR with QURU and PIST). Second, some species tend to grow generally faster than others. Note that the adjusted values are arrayed along two negatively sloping arcs, converging at QURU, and that the arc containing ACSA, BEAL, and PRSE is farther from the origin (indicating faster growth at low and high light) than is the arc containing FAGR, TSCA, ACRU, FRAM, and PIST. This apparent clustering into two arcs does not correspond to any traditional shade-tolerance classification; each arc contains both early and late successional species.

Also observe that the positions of FAGR and TSCA in Fig. 3*c* are shifted to the left of their positions in Fig. 3*a*. These species tend to have "squat" stems (low values of β) and so reach 5 m in height more slowly than their radial growth rates alone would imply. Thus, the squat stem architecture of FAGR and TSCA places ACSA, BEAL, TSCA, and FAGR together in the upper left-hand portion of Fig. 3*c*, the "traditional" location of shade-tolerant species despite the traditional classification of BEAL as a relatively intolerant species (see Fig. 7*b*). It is interesting that these are the four most abundant species in undisturbed old growth in this region (Hough and Forbes 1943; Nichols 1913; Potzger 1946). All of the old-growth species show relatively slow high-light growth in height and fast low-light growth in height, including the gap-phase species BEAL.

The integration of patterns of growth-dependent mortality

Kobe et al. (1994) estimated a series of models relating a sapling's probability of mortality to its growth history. A simple one-parameter mortality model is as follows: probability of mortality = $e^{-Mw'}$, where M is a constant and w' is the average radial growth (ring width) over the past 5 years

(see Kobe et al. 1994 for further information including methods of estimation). Estimates of *M* are as follows: ACSA 4.8, BEAL 3.8, PRSE 5.0, FAGR 21.9, TSCA 17.3, ACRU 7.2, PIST 9.4, FRAM 5.1, AND QURU 9.6. Thus, the fast-growing species on the outer arc in Fig. 3*c* are less able to tolerate slow growth (have lower values of *M*) than are the slow-growing species on the inner arc. JABOWA–FORET models typically assign the same model of growth-dependent mortality to each species (Shugart 1984; Kobe et al. 1993).

The above mortality model and [2] may be combined to produce a model of light-dependent survivorship. Because, under conditions of low light (*L* near zero), the probability of mortality is approximately *MSrL*, we can use *MS* as an index of low-light survivorship. Note that *MS* is analogous to *S*, our measure of low-light growth. Just as *S* is the slope of the low-light growth rate *SrL*, *MS* is the slope of the low-light mortality rate *MSrL*.

Figure 3*d* contains a plot of our index of high-light height growth (adjusted *A*) against our index of low-light survivorship (*MS*). The figure thus integrates information on radial growth, allometry, and mortality. The plot shows a striking interspecific trade-off in the ability to overtop within a gap (relatively fast height growth in high light indicated by large adjusted *A*) and the ability to survive periods under closed canopy (relatively high survivorship at low light indicated by large *MS*). Estimates are arrayed approximately along a one-dimensional continuum in Fig. 3*d*; there is less scatter in the orthogonal direction than in Figs. 3*a* and 3*c*. The species again show no tendency to cluster into discrete categories of shade tolerance, and their order along the continuum does correspond closely to traditional assignments of shade tolerance. Note that the order of the species from the upper left to the lower right of the figure is nearly identical with the traditional ordering of shade tolerance given in the Methods section. This result implies that traditional concepts of shade tolerance correspond to integrated strategies of performance (e.g., integrating growth, mortality, and allometry) and provides further evidence of the problems inherent in using traditional assignments of shade tolerance to parameterize models of growth.

Discussion

Our analysis of the data implies five principal results. First, sapling growth in Great Mountain Forest increases with light availability, but is not correlated with levels of soil moisture. The absence of significant effects of water may be interpreted either as evidence that water was unlimiting or as evidence that the amount of within-species variation in water availability was insufficient to allow the detection of water limitation. Obviously, this issue could be resolved by sampling across a broader range of sites or by experimentally manipulating water availability.

Second, sapling growth to 8 m in height is approximately geometric, and positive radial growth occurs even at very low light levels. A sapling attains fully one-half of its maximal rate of radial growth at between 1% (for ACSA) and 8% (for QURU) of full sun.

Third, the growth responses of the 10 species segregate along a continuum. There is some evidence of a trade-off between growth rate at high versus low light. Species such as QURU, PIST, and FRAM have the fast radial growth at high light and slow growth at low light, whereas species such as ACSA and FAGR have the reverse. However, there is also evidence of variation in the orthogonal direction; BEAL and ACRU have approximately the same high-light growth rates but BEAL grows more than five times faster at low light. Moreover, this orthogonal variation appears to be correlated with a sapling's ability to survive periods of slow growth. Thus, the species along the "fast-growing" arc in Fig. 3*c* have higher mortality when suppressed (lower estimates of *M*) than the species along the "slow-growing" arc. An allocational hypothesis might explain this pattern. Species in the slow-growing arc may allocate more photosynthate to attributes that promote survivorship in the understory (i.e., carbohydrate stores accumulated during favorable periods or defensive compounds), whereas species in the fast-growing arc may allocate resources primarily to new growth. Finally, some of the patterns of radial and height growth depart from conventional wisdom. BEAL, with its large low-light growth rate, is the most conspicuous example.

Fourth, a comparison between our estimates and the growth functions assumed in JABOWA–FORET models does not support the current practice of calibrating forest models on the basis of published classifications of shade tolerance.

Fifth, there is an interspecific trade-off between a species' ability to overtop under conditions of high light (adjusted A in Fig. 3*d*) and its ability to survive at low light (MS in Fig. 3*d*). The order of the species along this continuum corresponds closely to traditional assignments of shade tolerance. If the continuum in Fig. 3*d* is generalizable to other tree species, then it offers the possibility of streamlined estimation of forest models. For example, one might obtain a reasonable estimate of MS simply by measuring the rate of height growth at high light.

Acknowledgements

We thank the Childs family for their generous hospitality and for the use of the facilities at Great Mountain Forest. We also thank the National Science Foundation (BSR-8918616), the Department of Energy (DE-FG02-90ER60933), and NASA for funding the project. We are especially grateful to our project manager Diane Burbank and to graduate students J. Hill, A. Finzi, and E. Ribbens. Finally, we thank the numerous undergraduate assistants who worked long hours in the forest and laboratory. This study is a contribution to the program of the Institute of Ecosystem Studies.

Baker, F.S. 1949. A revised tolerance table. J. For. **47**: 179–181.

Bazzaz, F.A. 1979. The physiological ecology of plant succession. Ann. Rev. Ecol. Syst. **10**: 351–371.

Botkin, D.B. 1992. Forest dynamics: an ecological model. Oxford University Press. Oxford, U.K.

Botkin, D.B., Janak, J.F., and Wallis, J.R. 1972. Rationale, limitations and assumptions of a northeastern forest simulator. IBM J. Res. Dev. **16**: 106–116.

Brokaw, N.V.L., and Scheiner, S.M. 1989. Species composition in gaps and structure of a tropical forest. Ecology, **70**: 538–541.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. U.S. Dep. Agric. Agric. Handb. 654.

Canham, C.D. 1988*a*. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology, **69**: 786–795.

Canham, C.D. 1988*b*. An index for understory light levels in and around canopy gaps. Ecology, **69**: 1634–1638.

Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. Ecology, **70**: 548–550.

Canham, D.C., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in

forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. **24**: 337–349.

Clark, D.A., and Clark, D.B. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecol. Monogr. **62**: 315–344.

Edwards, A.W.F. 1992. Likelihood. Expanded edition. Cambridge University Press, New York.

Farquhar, G.D., and von Caemmerer, S. 1982. Modeling photosynthetic response to environmental conditions. Encyl. Plant Physiol. New Ser. **2**: 549–587.

Glitzenstein, J.S., Harcombe, P.A., and Streng, D.R. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. Ecol. Monogr. **56**: 243–258.

Horn, H.S. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, N.J.

Hough, A.F., and Forbes, R.D. 1943. The ecology and silvics of forests in the high plateaus of Pennsylvania. Ecol. Monogr. **13**: 301–320.

Kobe, R., Pacala, S.W., Silander, J.A., Jr., and Canham, C.D. 1994. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. In press.

Kramer, P.J., and Kozlowski, T.T. 1960. The physiology of trees. McGraw-Hill, New York.

Martinez-Ramos, M., Alvarez-Buylla, E., and Sarukhan, J. 1989. Tree demography and gap dynamics in a tropical rain forest. Ecology, **70**: 555–558.

Mood, A.M., Graybill, F.A., and Boes, D.C. 1974. Introduction to the theory of statistics. McGraw-Hill, New York.

Nichols, G.E. 1913. The vegetation of Connecticut. II. Virgin forest. Torreya, **13**: 191–215.

Pacala, S.W., and Hurtt, G.C. 1992. Population dynamic consequences of climate change for terrestrial vegetation. *In* Biotic interactions and global change. *Edited by* P. Kareiva, R. Huey, and J. Kingsolver. Sinauer, Sunderland, Mass. pp. 57–74.

Pacala, S.W., Canham, C.D., and Silander, J.A., Jr. 1993. Forest models defined by field measurements: I. the design of a northeastern forest simulator. Can. J. For. Res. **23**: 1980–1988.

Pastor, J., and Post, W.M. 1988. Response of northern forest to CO_2-induced climate change. Nature (London), **334**: 55–58.

Potzger, J.E. 1946. Phytosociology of the primeval forest in central-northern Wisconsin and upper Michigan, and a brief post-glacial history of the lake forest formation. Ecol. Monogr. **16**: 211–250.

Rastetter, E.B., Ryan, M.G., Shaver, G.R., Melillo, J.M., Nadelhoffer, K.J., Hobbie, J.E., and Aber, J.D. 1991. A general biogeochemical model describing the responses of C and N cycles in terrestrial ecosystems to changes in CO_2, climate and N deposition. Tree Physiol. **9**: 101–126.

Ribbens, E., Pacala, S.W., and Silander, J.A., Jr. 1994. Recruitment in northern hardwood forests: a method for calibrating models that describe patterns of tree seedling dispersal. Ecology, **75**(6): 1794–1806.

Shugart, H.H. 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York.

Shugart, H.H., and West, D.C. 1977. Development of an Appalachian deciduous forest model and its application to assessment of the impact of chestnut blight. J. Environ. Manage. **5**: 161–179.

Spurr, S.H., and Barnes, B.V. 1980. Forest ecology. 3rd ed. John Wiley & Sons, New York.

Swaine, M.D., and Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio, **75**: 81–86.

Szymura, J.M., and Barton, N.H. 1986. Genetic analysis of a hybrid zone between the fire-bellied toads near Cracow in southern Poland. Evolution, **40**(6): 1141–1159.

Whitmore, T.C. 1989. Canopy gaps and the two major groups of forest trees. Ecology, **70**: 536–538.