Juvenile Tree Survivorship as a Component of Shade Tolerance

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JUVENILE TREE SURVIVORSHIP AS A COMPONENT OF SHADE TOLERANCE[1]

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Abstract. With a view toward understanding species-specific differences in juvenile tree mortality and the community-level implications of these differences, we characterized juvenile survivorship of 10 dominant tree species of oak transition–northern hardwood forests using species-specific mathematical models. The mortality models predict a sapling's probability of dying as a function of its recent growth history. These models and species-specific growth functions (published elsewhere), characterize a species' shade tolerance. Combined growth and mortality models express a sapling's probability of mortality as a function of light availability. We describe the statistical bases and the field methods used to calibrate the mortality models.

We examined inter- and intraspecific variation in juvenile mortality across three sites: Great Mountain Forest (low pH, nutrient poor soils) in northwestern Connecticut, a calcareous bedrock region (neutral pH, nutrient rich soils) also in northwestern Connecticut, and a site in central-western Michigan (low pH, nutrient poor soils).

Interspecific differences in juvenile mortality have profound effects on community dynamics and composition; the importance of these effects is demonstrated through a spatially explicit simulator of forest dynamics (SORTIE). The 10 species we examined occupy a continuum of survivorship levels at 1% of full sun.

There was surprisingly little intraspecific variation in mortality functions for sugar maple, American beech, eastern hemlock, and white ash between the Great Mountain and Michigan sites. However, there was a striking increase in survivorship for sugar maple in the calcareous site. Differences in survivorship among the sites are correlated with soil pH and presumably nutrient availability.

Growth rates in high-light and low-light survivorship are inversely correlated across species; as level of shade tolerance increases, a species grows more slowly in high light and exhibits increased survivorship under low light. Our results indicate that interspecific differences in sapling mortality are critical components of forest community dynamics.

Key words: Connecticut; forest dynamics; forest succession; growth; JABOWA-FORET; juvenile trees; mortality; saplings; shade tolerance; SORTIE; temperate forests.

INTRODUCTION

The consensus among foresters and plant ecologists is that forest succession is driven largely by interspecific differences in shade tolerance: slow-growing shade-tolerant trees replace relatively shade-intolerant colonizers in the absence of major disturbance (Spurr and Barnes 1980, Shugart 1984, Glitzenstein et al. 1986). While many studies have focussed on physiological adaptation to low light (e.g., Bazzaz 1979), there have been relatively few studies that have quantified shade tolerance from empirically derived functions that link light availability, growth, and survivorship.

We propose that shade tolerance can be quantitatively defined using functions that predict growth from local light levels and predict mortality from growth. In this paper, we examine mortality as one component of shade tolerance and discuss growth to the extent that it predicts mortality. Growth as a component of shade tolerance is treated in full detail elsewhere (Pacala et al. 1994).

In predicting mortality from growth, we are assuming that growth is an integrated measure of whole-plant carbon balance, which ultimately determines mortality (Givnish 1988). Fast growing individuals within a species (and within sites of equal growth potential) should have higher survivorship than slow growing individuals. This same assumption is implicit in numerous other studies that predict tree mortality from growth (Monserud 1976, Buchman 1983, Buchman and Lentz 1984, Hamilton 1986, 1990). Because sapling carbon balance is often light limited (GMF: Pacala et al 1994; La Selva: Clark and Clark 1992), examining mortality as a function of light is important to understanding demographic and community processes in terms of re-

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source availability (e.g., shade tolerance). However, light and carbon balance are not perfectly correlated (e.g., variation can be introduced by nutrient availability and herbivory) and there can be additional error in the relationship between total carbon balance and growth (because plants allocate carbon to a wide range of pools). In general, such error can lead to biased predictions (see Walters and Ludwig (1981) on stock–recruitment relationships of fisheries). In Appendix A, we evaluate our methods in relation to these sources of error and demonstrate that the reported interspecific differences in low-light mortality are several times greater than the bias resulting from even the most extreme scenarios of error.

We focus on sapling mortality and growth because the ability of juvenile stages to survive and grow in low-light environments is critical to understanding succession. Many researchers have suggested the importance of juvenile mortality to plant community dynamics (e.g., Leak 1970, Good and Good 1972, Harcombe and Marks 1978, Lorimer 1981, 1984, Hibbs 1983, Peet 1984, Glitzenstein et al. 1986, Connell 1989, Schupp et al. 1989). Clark and Clark (1992) showed that canopy recruitment in a wet tropical forest is primarily influenced by the relative growth and mortality of saplings <4 cm in diameter. Sensitivity analyses in demographic studies of tree populations have shown that juvenile mortality influences the finite rate of increase more than either mature-tree mortality or fecundity (Hartshorn 1972, Pinero et al. 1984). Juvenile mortality clearly has an important influence on population and community dynamics.

Nevertheless, this is one of the few studies (of which we are aware) that model interspecific differences in juvenile mortality over a range of growth rates and light conditions. It is critical to understand these interspecific differences in juvenile growth and survivorship because they are major driving forces of forest succession.

METHODS

Species and sites

We calibrated mortality predictors for juveniles of ten major tree species, spanning a range of presumed shade tolerances (Baker 1949), in transition oak–northern hardwood forests of eastern North America (Table 1).

We sampled saplings from three distinct areas to examine regional and environmental variation in the mortality predictors. Great Mountain Forest (GMF) in Norfolk, Connecticut, was our primary field site for a large-scale project characterizing forest community dynamics, which included development of these mortality models. The acidic soils at GMF are derived from shallow deposits of glacial till and underlying schist and gneiss bedrock. Appropriate field sites for black cherry (*Prunus serotina*), white oak (*Quercus alba*), and red

oak (*Q. rubra*), were not located at GMF; for these species we sampled from similar sites at Skiff Mountain Wildlife Reserve in Ellsworth, Connecticut (black cherry), and Meshomasic State Forest in Glastonbury, Connecticut (northern red and white oak). To examine the influence of soil fertility on mortality processes, we also sampled sugar maple and white ash saplings from more nutrient-rich, limestone-derived soils in the Blackberry River valley in North Canaan, Connecticut. Finally we examined a subset of species on deep glacial sand plains near Ludington, Michigan, near the western edge of the range of this community type. In each of these areas, a single study stand was selected for each species.

The most important criterion in choosing study sites within these areas was sufficiently wide variation in light levels to produce a wide range in growth rates. The size and boundaries of each study site were determined by including at least 30 "recently dead" saplings (defined in next section).

Field sampling

From each study site we determined the numbers of live and recently dead saplings and collected a random sample of stems of live individuals and a random sample (or the complete population) of recently dead stems. We tallied the number of live and recently dead saplings of the focal species along belt transects. From the same transects, 30–60 living individuals were randomly harvested. The entire population of recently dead individuals (30–60 stems) within site boundaries was harvested. At the GMF white ash site, we randomly sampled 42 of the 60 recently dead individuals present.

We defined a "sapling" as any individual >25 cm in height that did not have foliage reaching the canopy of the stand. Thus the upper limit of the definition varied among sites and was established at 6, 8, or 10 cm dbh (diameter at breast height), depending upon local canopy height. Most trees in our samples were <4–5 m in height.

We determined "recently dead" individuals by leaf retention and twig suppleness features of individuals that we estimated to have been dead for <30 mo. We calibrated our field standards against the characteristics of at least 10 individuals of each species, selected from a range of sizes (0.5 to 5 cm diameter) that we had killed and left in the field. We checked the characteristics of the sacrificed saplings after 10, 22, and 33 mo. At 22 mo, all individuals continued to fit our criteria of recently dead (R. K. Kobe, *unpublished data*). At 33 mo, individuals of all species, except for hemlock, failed to fit our recently dead criteria. Thus our criteria included saplings that had been dead for 22 to 33 mo, a range that includes our original estimate of 30 mo. Hemlock's mortality is overestimated because all hemlock saplings continued to fit the criteria after 33 mo. However, hemlock's low estimated mortality constrains the extent of our overestimate to a few percentage

TABLE 1. Mortality function parameter estimates and two confidence intervals (CIs) for all species and sites addressed in this study. CIs from inverting the likelihood ratio test (95%) are given in roman type; bootstrapped CIs (96%) are given in italics.

Species	Site*	A (95% CI) (96% CI)	B (95% CI) (96% CI)
White ash (*Fraxinus americana*)	GMF	0.999 (0.72–1) (*0.77–1.0*)	5.15 (3.77–6.69) (*3.66–7.05*)
	Calcareous	0.998 (0.66–1) (*0.66–0.99*)	8.39 (6.44–11.04) (*5.67–11.09*)
	Michigan	0.55 (0.28–0.87) (*0.15–0.99*)	4.58 (2.68–7.01) (*0.67–8.1*)
Sugar maple (*Acer saccharum*)	GMF	0.998 (0.83–1) (*0.99–1.0*)	4.79 (3.9–5.92) (*4.0–5.92*)
	Calcareous	0.148 (0.093–0.22) (*0.078–0.32*)	0.52 (0–1.22) (*0–2.25*)
	Michigan	0.999 (0.65–1) (*0.74–0.99*)	6.26 (4.98–7.84) (*5.04–8.82*)
American beech (*Fagus grandifolia*)	GMF	0.014 (0.005–0.029) (*0.006–0.06*)	0.2 (0–3.6) (*0.025–6.58*)
	Michigan	0.12 (0.055–0.208) (*0.052–0.196*)	0.002 (0–0.54) (*0.001–0.047*)
Yellow birch (*Betula lutea*)	GMF	0.555 (0.4–0.72) (*0.24–0.99*)	2.67 (2.12–3.38) (*1.2–4.52*)
	Michigan	0.995 (0.59–1) (*0.51–0-99*)	5.99 (4.65–7.52) (*4.43–7.25*)
Red maple (*Acer rubrum*)	GMF	0.99 (0.78–1.0) (*0.74–1.0*)	6.64 (5.63–7.79) (*5.37–7.67*)
Eastern hemlock (*Tsuga canadensis*)	GMF	0.077 (0.031–0.15) (*0.024–0.215*)	5.97 (3.37–9.17) (*2.2–11.93*)
Black cherry (*Prunus serotina*)	Ellsworth	0.998 (0.74–1.0) (*0.76–1.0*)	4.85 (3.48–6.84) (*3.45–7.46*)
White oak (*Quercus alba*)	Meshomasic	0.82 (0.58–1.0) (*0.56–0.998*)	3.78 (2.51–5.33) (*2.51–5.33*)
Northern red oak (*Quercus rubra*)	Meshomasic	0.985 (0.58–1.0) (*0.41–0.99*)	9.38 (7.14–12.28) (*5.66–13.12*)
White pine (*Pinus strobus*)	GMF	0.268 (0.14–0.43) (*0.06–0.76*)	4.67 (2.86–6.91) (*0.59–10.05*)

* GMF = Great Mountain Forest; with the exception of the Michigan site, all study areas were in Connecticut.

points. Because recently dead saplings had died within an estimated 30 mo, our functions characterize probability of mortality for an ≈ 30-mo period.

Radial growth: measurement and use as a predictor variable

We removed a stem cross section at 10-cm height from every selected live and recently dead sapling. We measured the widths of at least the 10 most recent annual rings of each sapling stem section (both recently dead and live samples) along a representative radius (the radius bisecting the angle formed by the longest and shortest radii of the cross section). We measured the radial growth rings using an ocular micrometer and computer-assisted mechanical stage, which provides resolution to 0.01 mm. Measurement error associated

with this technique is negligible (R. K. Kobe, *unpublished data*).

The arithmetic average of the five most recent years of radial growth was used to predict mortality. We had an a priori reason to use a 5-yr interval because the forest simulator SORTIE is based on this time interval. To check the use of 5 yr, we tried different time intervals to predict mortality. For all species, using the arithmetic average growth over an interval of the most recent 2–7 yr resulted in the highest likelihoods. Parameter estimates based on the five most recent years of radial growth were within the support limits (Edwards 1992) of parameter estimates obtained from other growth intervals associated with higher likelihoods.

We evaluated the contribution of stem size to the prediction of mortality, following the precedent of most models of mature tree mortality that include diameter (Buchman 1983, Buchman and Lentz 1984, Hamilton 1986, 1990). Size influences mortality indirectly by affecting radial growth. For example, we substituted W/R^z in the place of average growth rate in Eqs. 7 and 8, where W is the average ring width, R is the stem radius, and z is an estimated constant that scales the contribution of R to predicting mortality. This formulation resulted in estimates of z not significantly different from zero at the $P < 0.05$ level for each of the species (likelihood ratio tests, 1 df). Thus in this formulation, stem size does not directly influence mortality. However, size does influence survival indirectly. Sapling radial growth rate is positively dependent upon stem size (Pacala et al. 1994), thus larger saplings grow faster (at a given light level) and are less likely to die. This indirect effect is accounted for in the simulation model of forest dynamics SORTIE (see details on SORTIE in Methods: Simulations using SORTIE and in Pacala et al. 1993).

Parameter estimation

Our goal was to estimate species-specific parameters for functions that predict a sapling's probability of mortality based on growth (g). These functions, represented by $m(g)$, specify mortality probability for a 2.5-yr period, the upper time limit of our field definition of "recently dead."

We derived a maximum likelihood function to estimate the parameters of $m(g)$ for each species. Recall from the earlier section on field methods that we collected a sample of live stems and a sample of recently dead stems, and counted the numbers of live and dead stems on the plot with transects. All three of these components enter the likelihood function.

Growth rates of surviving individuals and growth rates prior to death are conditional density functions. Recall that stems were chosen for radial growth measurements conditioned upon their status of being dead or live. Let the probability density function of all growth rates in a site be $h(g)$. Then the density function of growth rates of individuals prior to death is:

$$Y_D(g \mid \text{death}) = \frac{h(g)m(g)}{\displaystyle\int_0^\infty m(g)h(g)\,dg}. \quad (1)$$

In words, the density function of prior growth rates given mortality is equal to the product of the probabilities of growth and mortality normalized by the expectation of mortality. Similarly, the density function for live individuals is:

$$Y_L(g \mid \text{survivorship}) = \frac{h(g)[1 - m(g)]}{\displaystyle\int_0^\infty [1 - m(g)]h(g)\,dg}. \quad (2)$$

Let the expectation of probability of mortality (denominator of Eq. 1) be represented by $\bar{U}$.

We also counted the numbers of live and dead stems at each site to provide empirical data on the expectation of mortality ($\bar{U}$). The probability that D dead saplings are found in a transect of N total individuals without respect to order is a series of Bernoulli trials (live or dead):

$$(\bar{U}^D)(1 - \bar{U})^{N-D}. \quad (3)$$

The likelihood is a function of the parameters of the underlying models $h(g)$ and $m(g)$ and for this data set is:

$$L = (\bar{U}^D)(1 - \bar{U})^{N-D} \cdot \prod_{i=1}^{\text{no. dead}} \frac{h(g_i)m(g_i)}{\bar{U}}$$

$$\cdot \prod_{i=1}^{\text{no. live}} \frac{[1 - m(g_i)]h(g_i)}{1 - \bar{U}}. \quad (4)$$

In words, Eq. 4 is: (the likelihood of obtaining the data set) = (the probability of encountering D dead saplings and $N - D$ live saplings without respect to order) × (the product of the probability densities that a dead individual had growth history g_i prior to its death) × (the product of the probability densities that a live individual had growth history g_i). Note in Eq. 4 that D and $N - D$ represent transect counts of dead and live individuals while "no. dead" and "no. live" are the number of stems collected to develop the growth densities.

We used a gamma density function to specify $h(g)$ because it provides good fits to the data. The density of growth rates at a site is:

$$h(g_i) = \frac{\left(\dfrac{\alpha}{\beta}\right)^\alpha g_i^{\alpha-1} e^{-\alpha/\beta g_i}}{\Gamma(\alpha)}. \quad (5)$$

The gamma density function is controlled by two parameters: α influences the density's peak and β controls spread.

We tried several functional forms for $m(g)$. A negative exponential function provided the best fit to the data and easy to interpret parameters:

$$m(g) = P(\text{mortality/growth}) = Ae^{-Bg}, \qquad (6)$$

where: $0 < A < 1$ and $B > 0$, $m(g)$ is the probability of mortality given growth, and g is recent growth history. The parameters A and B are estimated for each species.

One of the alternative functional forms for $m(g)$ was:

$$m(g) = P(\text{mortality} \mid \text{growth}) = e^{-Sg^V}, \qquad (7)$$

where S and V are estimated parameters. In this formulation, $m(g)$ approaches a value of one when growth equals zero. Eq. 7 resulted in likelihoods within the support limits of Eq. 6. We used Eq. 6 because its parameters are more easily interpreted than those of Eq. 7.

The maximum likelihood analysis that we used provides estimates and support limits for the parameters of the mortality function $m(g)$ and the density of growth rates $h(g)$. The parameter search algorithm is based on Metropolis et al. (1953) and finds the set of parameter values (A, B, α, and β) that yields the highest likelihood (using Eq. 4).

Support regions

We used three methods to explore uncertainty in parameter estimates: (1) bootstrapping, (2) likelihood ratio tests, and (3) the information matrix. Bootstrapping (subsampling with replacement) was performed for 100 iterations, developing 100 sets of parameter estimates using Eq. 4. The central 96 values for each parameter correspond to the 96% confidence interval (Table 1). Univariate support regions (95%) were obtained by inverting the likelihood ratio test (Edwards 1992) (Table 1). The support regions developed from bootstrapping and the likelihood ratio test were generally in close agreement, suggesting that the chosen functions were appropriate and the sample sizes adequate. Bivariate support regions were obtained from the information matrix (Edwards 1992; Pacala et al., *in press*).

Mortality as a function of light

In Eq. 6, mortality is predicted as a function of direct measurements of growth. Examining survivorship as a function of light availability provides a resource-based measure for comparing survivorship among species.

We examined mortality as a function of light availability by linking mortality as a function of growth (Eq. 6) with species-specific models characterizing growth as a function of light availability (Eq. 8) that we developed in a separate study (for details see Pacala et al. 1994). In this section, we summarize our approach in developing growth models and then describe how the two models were combined with error propagation.

We focussed on variation in light availability as the predictor variable for growth. Sample sizes per species ranged from 49 to 110 individuals stratified across a range of light environments. We quantified the light environment around each chosen sapling using hemi-

spherical canopy photos to compute the gap light index (GLI) (Canham 1988b). GLI specifies the percentage of direct and diffuse photosynthetically active radiation (PAR) reaching any particular point, based upon small holes in canopy cover. Calculations of GLI values take into account solar tracks and angles over the course of the growing season and thus provide an estimate of light availability integrated over the growing season. GLI values are a better predictor of plant performance than instantaneous measures of light and are highly correlated with direct measurements of seasonal PAR ($r = 0.93$) (Canham 1988b); but they are not correlated with N mineralization rates or with water availability (Pacala et al. 1994).

Light intensity (GLI) explained more than 50% of the variation in growth for 7 of the 10 species. The total range in variation explained by GLI was 23–78%. The following model characterizing radial growth in terms of GLI provided the best fit of several different models:

$$\Delta R = R \cdot f(\text{GLI}) + \theta, \qquad \text{if } \theta > -R \cdot f(\text{GLI});$$

$$\Delta R = 0, \qquad \text{if } \theta \le -R \cdot f(\text{GLI});$$

where

$$f(\text{GLI}) = \frac{P_1 \cdot \text{GLI}}{\dfrac{P_1}{P_2} + \text{GLI}}; \qquad (8)$$

where R is stem radius, ΔR is the change in stem radius, GLI is the Gap Light Index, and θ is a normally distributed random variable with zero mean and variance (σ^2) $= C[R \cdot f(\text{GLI})]^D$. The asymptotic or light saturated growth (P_1), the slope at zero or low light growth (P_2), and the two variance parameters (C and D) were estimated with maximum likelihood techniques.

To examine mortality as a function of light, growth over the most recent 5 yr was predicted from light availability for a stem of 1-cm radius (Eq. 8) and then mortality predicted from the resulting growth (Eq. 6). To develop confidence intervals for the prediction of mortality as a function of light, we propagated error through the models. Growth, when predicted as a function of light (Eq. 8), is a random variable because θ is a random variable. We must account for the randomness of θ when calculating the expected mortality. This is complicated by the fact that we require five consecutive ring widths to predict mortality. We assumed that an individual "draws" a single value of θ that lasts at least 5 yr. Thus residual errors are assumed to be temporally correlated within an individual, which increases variation in the 5-yr average growth at any given light level. Note that this results in statistically conservative estimates. In contrast, assuming negatively correlated error from year to year would result in much less variation in growth, closely approximating the mean prediction of growth over a 5-yr period. With the statis-

FIG. 1. Probabilities of mortality (in a 2.5-yr period) as functions of radial growth for the 10 tree species sampled from Great Mountain Forest (GMF) in northwestern Connecticut. Beech and hemlock exhibit low mortality across all growth rates. Red maple and red oak respond to higher growth rates with rapid declines in mortality.
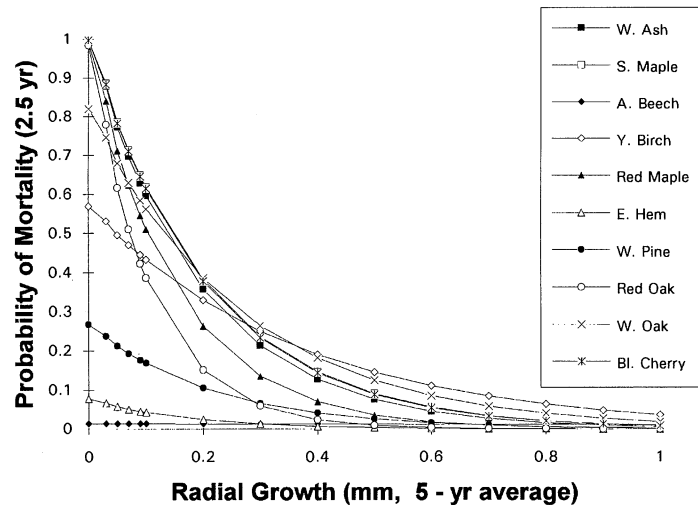
tically conservative assumption, the expected mortality for a given value of GLI is:

$$(1 - \phi)A + \phi \int_{-f(\text{GLI}) \cdot R_0}^{\infty} \frac{1}{\sqrt{2\pi}\sigma} \cdot e^{-\theta^2/2\sigma^2}$$

$$\cdot Ae^{-B \cdot \frac{r_0 \left[\sum_{i=0}^{5} (1 + f(\text{GLI}))^i \theta^{5-i} \right] - r_0}{5}} d\theta,$$

where

$$\phi = \int_{-f(\text{GLI}) \cdot R_0}^{\infty} \frac{1}{\sqrt{2\pi}\sigma} \cdot e^{-\theta^2/2\sigma^2} \, d\theta. \quad (9)$$

Furthermore, we propagated sampling error into these models by calculating the expectation of mortality using 100 sets of bootstrapped parameter values for Eqs. 6 and 8. For a given light level, the 96 central expectations of mortality (Eq. 9) correspond to the 96% confidence interval of the prediction of mortality as a function of light.

Simulations using SORTIE

SORTIE is a spatially explicit model of forest dynamics based upon the life history attributes of individual trees (see Pacala et al. 1993 for details). The basic elements of SORTIE are species-specific submodels that predict a tree's growth, survival, recruitment (i.e., fecundity, dispersal, and seedling establishment), and submodels that predict the local availability of resources (currently light availability, with planned extensions to nitrogen and water). Growth predictors are mechanistically based on resources and mortality is predicted from growth. Recruitment of seedlings is a function of distance to and size of parent trees (Ribbens et al. 1994). The species-specific resource submodel is based on canopy tree alterations of understory light regimes (Canham et al. 1994), which in turn predict growth. Tests of the model indicate that it accurately predicts the dynamics and species composition

of transition northern hardwood forests for a range of specified conditions (Nichols 1913, Hough and Forbes 1943, Potzger 1946, Pacala et al. 1993).

We used SORTIE simulations to examine the importance of species-specific mortality functions on community dynamics and structure. We ran one set of simulations assigning species-specific mortality functions and another set assigning identical mortality functions to all species. In the simulations using the same mortality function, we assigned a high (white ash), moderate (yellow birch), and low mortality (beech) function to all species and replicated each simulation three times with different random number seeds.

RESULTS

Our formulation of the mortality model allows for a range of outcomes in characterizing the mortality component of shade tolerance (Figs. 1and 2, Table 1). The A parameter is a species' probability of mortality as its growth rate or local light level approaches the limit of zero. Thus A can be interpreted as mortality probability under low growth or in very low light. The B parameter relates a species' survivorship to growth rate; a high B value means that there is a rapid decrease in probability of mortality as growth increases. Thus, B can be interpreted as sensitivity to shading (in so far as growth is a function of light).

These parameters are a quantitative measure of the mortality component of shade tolerance. Species with low A parameters have lower probabilities of mortality across a range of growth rates and light environments and thus can be considered very shade tolerant. At Great Mountain Forest (GMF), beech and hemlock both exhibit relatively low probabilities of mortality for all observed growth rates (Figs. 1 and 2). Beech mortality bears no relationship to growth, perhaps because saplings are predominantly root sprouts at GMF and could be receiving carbon subsidies from parent trees. Given slow growth, red oak and red maple experience high
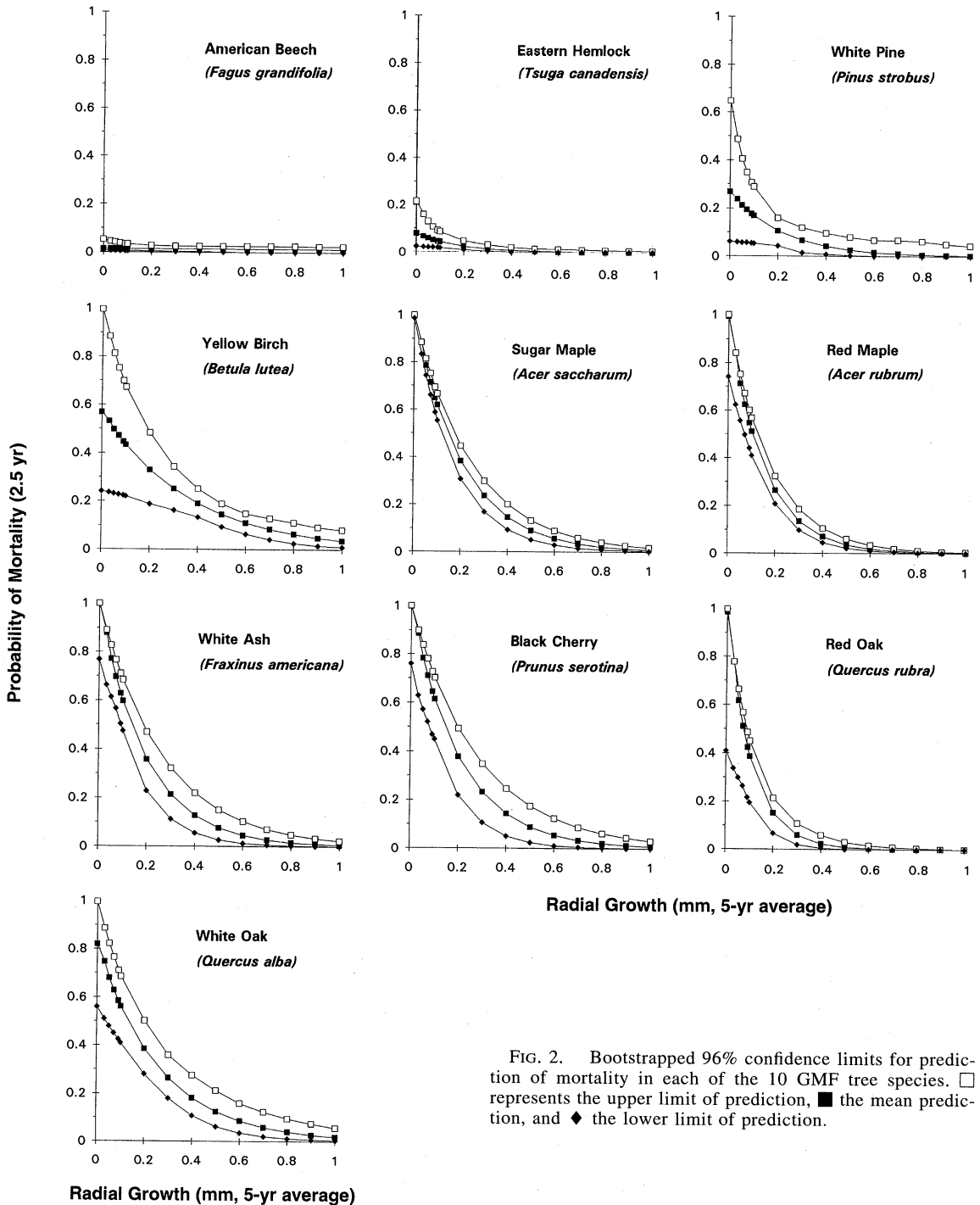
FIG. 2. Bootstrapped 96% confidence limits for prediction of mortality in each of the 10 GMF tree species. □ represents the upper limit of prediction, ■ the mean prediction, and ◆ the lower limit of prediction.

Radial Growth (mm, 5-yr average)

mortality, but slight increases in growth coincide with large increases in survivorship.

Mortality functions based on local light availability rather than growth allow for resource-based interspecific comparisons. Growth as a function of GLI (Gap Light Index, =% full sun) is species specific and thus is not a uniform standard. In other words, under equiv-alent light availability, species show significant differences in annual radial growth (Fig. 3).

For the populations studied at GMF for which we have developed growth models, we can express mortality as a function of GLI. Fig. 4 shows mortality as a function of light availability based upon mean growth responses at each light level. In other words, Fig. 4
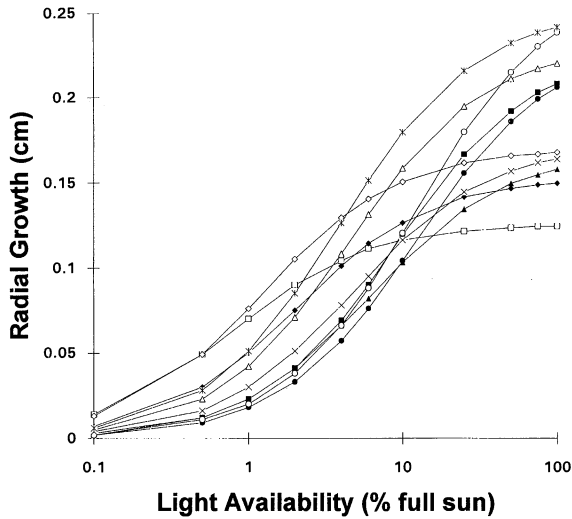
FIG. 3. Radial growth as a function of light for saplings of the 10 GMF tree species. Symbols for species as in Fig. 1. Parameter estimates from Pacala et al. (1994).

shows how the "mean" plant will respond to light availability in terms of survivorship; population-level variation in growth estimates is not incorporated here. Confidence intervals (96%) that incorporate all sources of error show some differentiation among species for mortality predictions at 1% GLI (Fig. 5), however, there is considerable overlap among some species. Recall from the methods that these intervals are statistically conservative.

To assess the ability to discern interspecific differences in low-light mortality, we compared randomly drawn pairs of mortality expectations for 1% GLI (Table 2). If the sets of mortality predictions cannot be
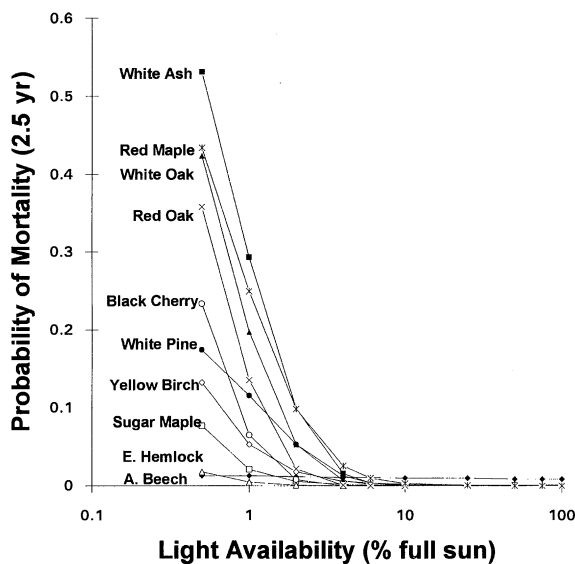
FIG. 4. Mortality as a function of light intensity for a 2.5-yr period using mean growth responses at each light level.
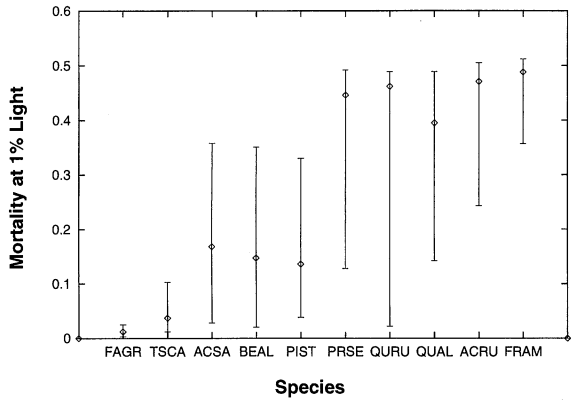
FIG. 5. The expectation of mortality (i.e., incorporating error in growth) at 1% of full sun for the 10 species sampled from GMF in Norfolk, Connecticut. Each range corresponds to the 96% confidence interval (incorporating sampling error) around the prediction of mortality. Species codes are taken from the Latin names, e.g., QUAL = *Quercus alba* (white oak).

discriminated between any two species, then each of the two species will have higher mortality in ≈50% of comparisons. We found differences in low-light mortality between most pairs of species, even when sampling error and error associated with growth predictions were taken into account. In 27 of the possible 45 pairwise comparisons among species, one species had greater mortality at least 95% of the time. Beech had higher survivorship under low light than all other species. Bivariate support regions (95%) of the parameters (for mortality = $f(g)$) show that the GMF species tend to segregate in parameter space along a continuum (Fig. 6).

We found surprisingly little evidence of geographic variation in mortality responses for beech, yellow birch, sugar maple, and ash. In the Michigan forest tract, beech mortality was relatively low and independent of growth rate (Fig. 7). The mortality patterns of beech, sugar maple, ash, and yellow birch (Fig. 7)

TABLE 2. Discrimination among tree species* in terms of probability of mortality at low light (1% of full sun). The entries are the percentage of randomly drawn pairs of comparisons when the column species had higher mortality predictions than the row species. The predictions of mortality incorporated variation in growth and sampling error. Boldface entries are ≥95%.

	TSCA	ACSA	BEAL	PIST	PRSE	QURU	QUAL	ACRU	FRAM
FAGR	99	**100**	99	**100**	**100**	**100**	**100**	**100**	**100**
TSCA		94	**95**	**95**	99	**95**	**100**	99	**100**
ACSA			44	37	**96**	86	**98**	**97**	**100**
BEAL				43	**97**	86	**96**	**96**	**100**
PIST					94	90	**96**	**96**	**100**
PRSE						45	32	65	80
QURU							42	68	88
QUAL								80	91
ACRU									68

* Coded by the first two letters of each word in their Latin names, e.g., ACRU = *Acer rubrum*.
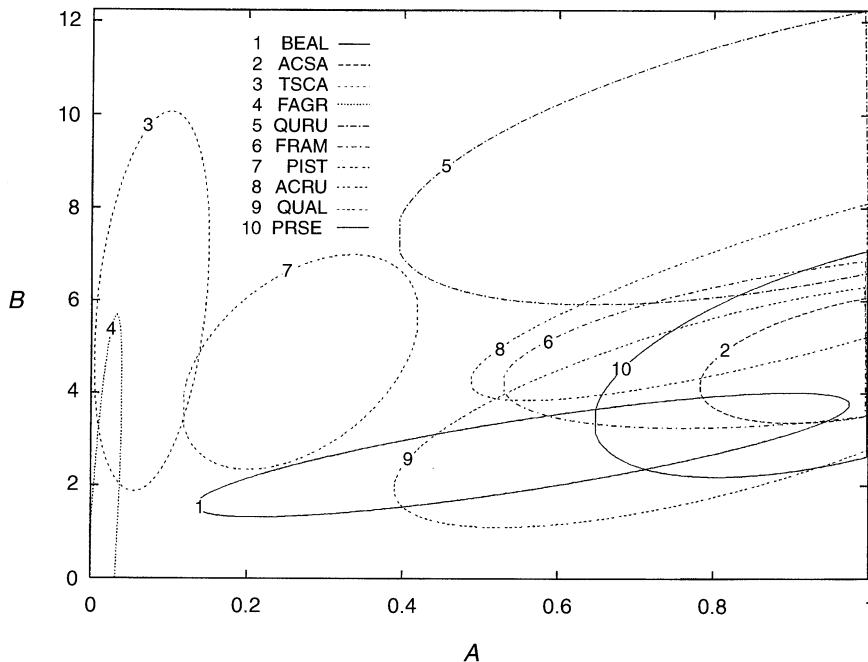
FIG. 6.   Bivariate 95% confidence regions of the mortality function parameters for saplings of the 10 species sampled at Great Mountain Forest. Species codes as in Fig. 5. The species tend to segregate in parameter space.

ranked in the same general order at the Michigan and GMF sites.

We also sampled sugar maple and ash saplings from a calcareous bedrock region in northwestern Connect-icut to compare survivorship across different soil types (Fig. 7). Based on mortality models as functions of growth, sugar maple, in particular, showed a substantial shift there towards increased survivorship at low growth rates in comparison to the GMF and MI pop-ulations (Fig. 7).

Low-light survivorship and high-light height growth are inversely correlated along an axis and define the level of shade tolerance for the GMF species (Fig. 8, top panel) (the only site that has been characterized with both growth and mortality models). As ability to persist under low light increases, height growth under high light decreases (allometric equations relating di-ameter and height reported in Pacala et al. 1994). What is especially significant about this axis is that the spe-cies order according to their successional status. Ash, along with white pine and red maple, have high mor-tality at low light and fast growth at high light; in contrast, beech has low rates of low-light mortality and slow growth in high-light environments. It is important to note that species do not order according to succes-sional status when viewed in terms of low- and high-light growth abilities (Fig. 8, bottom panel). This is an explicit assumption of other models of shade tolerance and forest simulators (e.g., Shugart 1984).

We ran SORTIE simulations (Pacala et al. 1993) with and without species-specific mortality predictors to ex-

amine the importance of species differences in mor-tality on the dynamics and structure of the community. Our test criterion was dominance by beech and hemlock after 1000 yr of succession; these species comprise >85% of the biomass in old growth forests on sites similar to GMF (Nichols 1913, Hough and Forbes 1943, Potzger 1946, Pacala et al. 1993).

Simulations that incorporated species-specific mor-tality functions (as developed from field data from GMF) resulted in a forest dominated by beech and hem-lock, with a minor presence of other species (Fig. 9A). Assigning the same mortality function to all species (i.e., when the simulations are driven by species-spe-cific growth and recruitment functions only), fails to predict the old-growth dominance of beech and hem-lock. If all species are assigned high (Fig. 9B), mod-erate (Fig. 9C), or low (Fig. 9D) mortality functions, yellow birch dominates due to its wide dispersal and high growth rate at light levels <10% full sun.

It is important to note that the *only* SORTIE simu-lation to predict the old-growth dominance of hemlock and beech was the simulation that incorporated inter-specific differences in juvenile mortality. Thus predic-tions of the simulator are sensitive to species-specific differences in mortality.

DISCUSSION

Shade tolerance has been central to the conceptual basis of forest ecology. However, there has been little effort to characterize shade tolerance quantitatively, through a combination of juvenile growth and survival.

GMF   **MICHIGAN**   **CALCAREOUS**
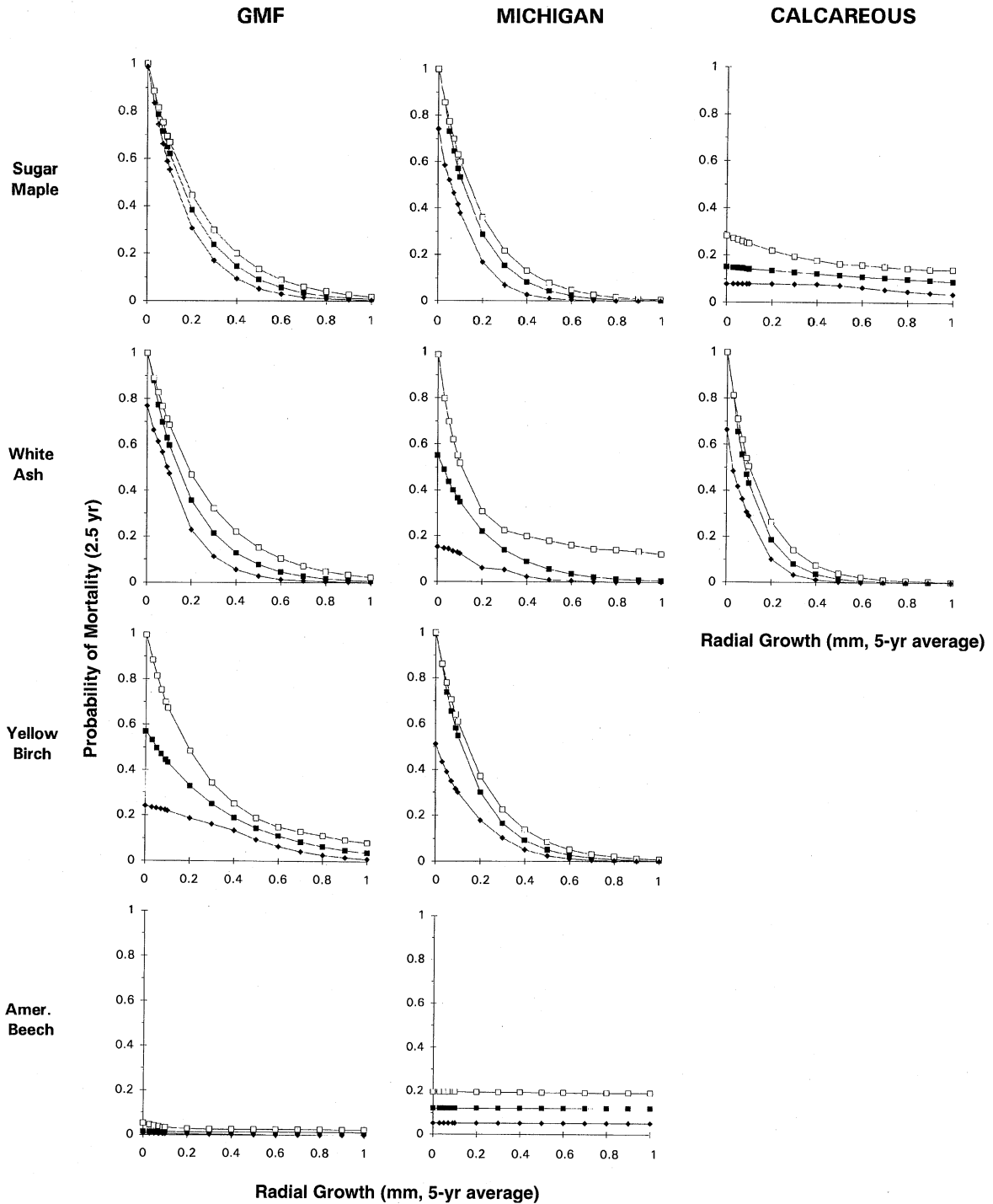
FIG. 7. Intraspecific variation in mortality functions (96% confidence limits) at three different sites. Probabilities of mortality (in a 2.5-yr period) as functions of growth for multiple samples of sugar maple, white ash, yellow birch, and American beech. Symbols as in Fig. 2.

Functions characterizing survivorship and growth offer the advantage of specifying level of shade tolerance on a continuum, rather than a few discrete classes (e.g., Baker 1949, Shugart 1984).

Our results are compatible with the view that shade-tolerant saplings are able to withstand periods of suppressed growth (Canham 1985, 1989, 1990) and that shade-intolerant species die when suppressed. The ten
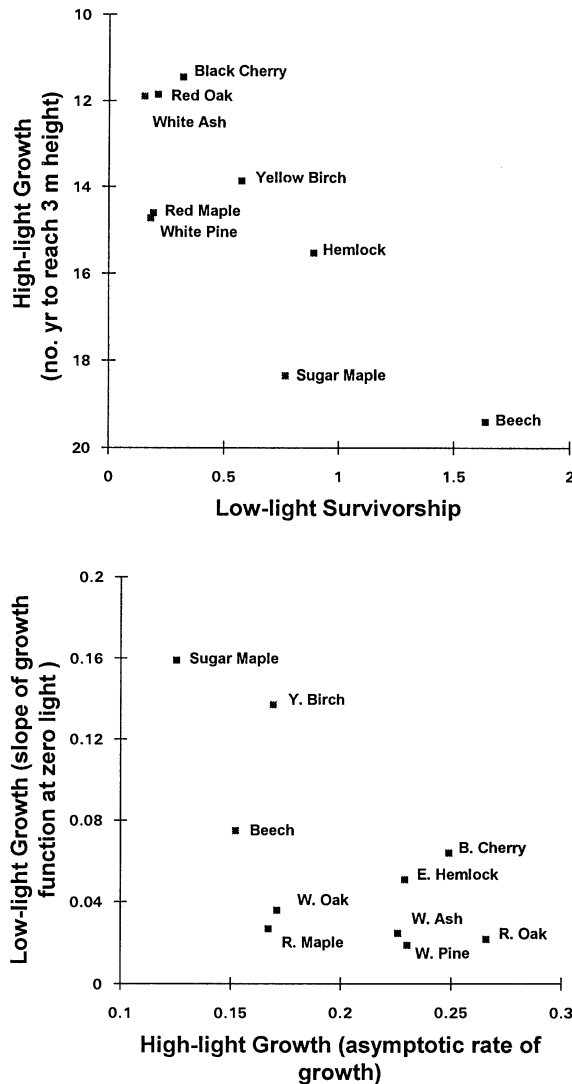
FIG. 8. The trade-offs associated with shade tolerance. Top panel: the two dimensions of shade tolerance trade off in a linear fashion. The x axis, or low-light survivorship, is calculated from the slope of the growth function at zero light and the decay parameter (B) of a simplified mortality predictor ($P[m] = e - B$ [growth]). The y axis represents the number of years necessary for a seedling to reach 3 m in height at full sunlight. Note that the species order in terms of tolerance rank. Bottom panel: high-light vs. low-light growth as applied to the species we examined at GMF. The x axis is the asymptotic rate of growth. The y axis is the slope of the growth function at zero light. The species do not order according to level of shade tolerance along the axis of this trade-off. Note that JABOWA–FORET models of forest dynamics (as reviewed by Shugart 1984) assume high-light and low-light growth abilities correspond to successional status.

FIG. 9. Proportion of basal area per species for 1000-yr SORTIE simulations based upon Great Mountain Forest parameter estimates. (A) Species-specific mortality. (B) High mortality: all species assigned white ash function. (C) Moderate mortality: all species assigned yellow birch function. (D) Low mortality: all species assigned beech function.

species we examined occupy a full range of survivorship levels at 1% full sun (Table 2). Similarly, Augspurger (1984) found a range of low-light survivorship for 18 species of tropical tree seedlings. It would be difficult to classify our species into two groups of "ecological consequence," (i.e., "pioneer" and "non-pioneer") as Whitmore (1989) and Swain and Whitmore (1988) propose for tropical trees.

Geographic and environmental variation in mortality

There was surprisingly little variation in mortality functions for the same set of species sampled at both GMF and the Michigan forest site. These sites are widely separated geographically, and differ in climate, length of the growing season, precipitation (135 cm/yr in Connecticut vs. 76 cm/yr in Michigan), and soil depth. Both sites have nutrient-poor and acid soils of similar pH (Connecticut: 4.0–5.0 [R. K. Kobe, *unpublished data*]; Michigan: 4.5–5.5 [Mason County, Michigan, Soil Conservation Service, *personal communication*]). Thus it appears that mortality responses in these species are relatively insensitive to these climatic differences.

However, differences in soils (and by extension nutrient availability) appear to have marked effects on survivorship in some species. Sugar maple exhibits lower mortality in the calcareous soils of northwestern Connecticut than at GMF or the Michigan site. One

study of which we are aware has shown that soil nutrient status can directly influence low-light survivorship. *Impatiens parviflora* has higher survivorship in shaded microsites under high nitrogen supplies (Peace and Grubb 1982). Furthermore, there is ample evidence that distribution of mature sugar maple trees is influenced by soil attributes; for example, Leak (1978, 1982) has shown that sugar maple is more dominant on fine tills and enriched soils than on coarse-grained glacial tills. Thus, higher sugar maple sapling survivorship in the calcareous vs. acidic soils may be the mechanism of sugar maple's canopy and understory dominance in the calcareous soils in comparison to GMF (R. K. Kobe, *personal observation*). White ash also has higher survivorship on the calcareous soils than at GMF and sites with similar soils (e.g., Leak 1978, Reschke 1990).

Several researchers (e.g., Spurr and Barnes 1980, Lorimer 1983) have acknowledged but have not explicitly demonstrated the environmental lability of shade tolerance. The variation in shade tolerance across environments points to the problems associated with using rigidly fixed tolerance classifications (e.g., Baker 1949). Lability in shade tolerance could explain the considerable disagreement on tolerance classifications of certain species (Baker 1949).

Comparison to previous characterizations of shade tolerance

Augspurger (1984) and Hett and Loucks (1970) developed indices of shade tolerance based on the slope of regressions fit to the proportion of seedlings dying under low-light conditions as a function of time. These studies provide a quantitative measure of shade tolerance, but fail to link survivorship to variation in light availability.

Other models of tree mortality focus on mature trees (Buchman 1983, Buchman and Lentz 1984, Hamilton 1990) and do not explicitly examine shade tolerance in juveniles. For example, Buchman and co-workers examined mortality in 19 species, but have no representatives of individuals <2.54 cm dbh in 12 of those species. An additional 3 species have <20 individuals. Models of mature-tree mortality have been adapted to smaller size classes. Hamilton (1990) modified a model by incorporating the reciprocal of dbh into the predictor, which results in mortality approaching infinity as dbh approaches zero. This model can not be applied realistically to very small stems because stand establishment becomes impossible, as Hamilton (1990) acknowledges. In addition, the large number of parameters used in many of these models generally provides good statistical fits to data but obscures biological meaning of the parameters (e.g., Buchman's (1983) model has seven parameters).

The mortality of individual trees is a major component of widely used JABOWA-FORET forest simulators (Shugart 1984), but these simulators do not incorporate species-specific differences in mortality (Shugart 1984). Differences in shade tolerance are modelled by assuming a trade-off between high- and low-light growth; shade-tolerant species are assumed to grow relatively faster in low light and slower in high light in comparison to shade-intolerant species. In JABOWA-FORET simulators, species are assigned to one of two (three in some versions of the simulator) growth modifying functions following tolerance classifications of Baker (1949) and Fowells (1965). This does have indirect implications for tree mortality, because mortality is linked to growth.

Shugart's (1984) comprehensive review of JABOWA-FORET simulators describes the mortality subroutine as follows: all individuals have an "intrinsic mortality" that is inversely related to the estimated maximum age ("agemax") for a given species and mortality is scaled arbitrarily by the "percentage of a cohort under optimal growth conditions" assumed to reach agemax. For example, if 2% of a cohort is assumed to reach agemax, the annual probability of mortality is 4.0/agemax (e.g., annual probability of mortality = 0.04 if agemax = 100). In addition, the "intrinsic mortality" is augmented to an annual mortality rate of 0.368 (based on an arbitrarily established 1% survival rate in 10 yr) when growth rate falls below an arbitrary 1 mm per year or <10% of maximum possible growth. This same reduction is common to all species.

JABOWA-FORET may coarsely represent the relative survivorships of shade-tolerant and -intolerant species, but its fundamental assumption about the influence of light availability on their relative growth rates is unfounded. In JABOWA-FORET, shade-intolerant individuals are assigned lower growth under low light availability; thus intolerant species experience higher mortality under low light.

We find that shade tolerance involves a trade-off between high-light *growth* and low-light *survivorship*, rather than a trade-off between high-light and low-light growth as JABOWA-FORET assumes (Shugart 1984). If the JABOWA-FORET assumption were accurate, in a graph of asymptotic vs. low-light growth, species would line up in order of tolerance. Based upon saplings we sampled (Fig. 8, bottom panel), species are not positioned according to tolerance rankings in any pattern that makes ecological sense. Rather, the important trade-off occurs between low-light survivorship and high-light growth (Fig. 8, top panel): more shade-tolerant species grow slowly in high light and are less likely to die in low-light conditions than less shade-tolerant species. We hypothesize that species allocating a large fraction of photosynthate to internal stores or herbivore defenses would have higher survivorship but would preclude carbohydrate allocation to rapid growth (R. K. Kobe et al., *unpublished manuscript*). In contrast, species allocating most of their photosynthate to growth would grow relatively rapidly, but at the price of low survivorship when

resource deprived (R. K. Kobe et al., *unpublished manuscript*). This concurs with Bazzaz' (1979) observation that physiological traits maximizing a growth response to increased light differ markedly from traits associated with low-light survival. A trade-off between high-light growth and low-light survivorship has been suggested (e.g., Denslow 1980, Hartshorn 1980, Bazzaz 1984, Poulson and Platt 1989), but rarely demonstrated explicitly (Hubbell and Foster 1992).

SORTIE simulations

SORTIE simulations demonstrate the importance of species' differences in juvenile mortality for community dynamics and structure. Incorporation of species-specific mortality functions in 1000-year simulations resulted in a stand closely resembling old-growth transition northern hardwood forests (Nichols 1913, Hough and Forbes 1943, Potzger 1946, Pacala et al. 1993). SORTIE simulations without interspecific differences in juvenile mortality resulted in spurious predictions.

These simulation outcomes do not simply result from SORTIE's inclusions of mortality in its design. Hypothetically, it is possible that the same simulation outcomes could be obtained without including species-specific differences in mortality, but this would necessitate altering another component of the simulator. In fact, as discussed earlier, JABOWA–FORET models do not incorporate species differences in mortality and are "predictive."

However, in any application where the mechanism matters (and it is difficult to determine a priori when mechanism does matter), it is critical to include species differences in juvenile mortality. JABOWA-FORET models produce the right phenomena, but for substantially wrong reasons.

Juvenile mortality and forest succession

The approach that we have developed does not rely on a priori categorizations of species into shade tolerance classes. Quantifying shade tolerance in terms of juvenile mortality and growth allows the concept to be examined more rigorously. Our results show that mortality responses within species can vary across environments of different soil types. There is little difference in mortality in geographically distant sites (Connecticut and Michigan) with comparable soil pH. Most importantly, interspecific differences in mortality are a critical—but often overlooked—link of forest dynamics that have dramatic effects on predicted community structure and dynamics. Focussing more attention on juvenile mortality will enable a better understanding of forest succession and dynamics.

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APPENDIX

In this paper, mortality is predicted from growth, and growth is predicted from light availability (GLI). We also express probability of mortality as a function of GLI, using growth as an intermediary. However, error in the relationship between GLI and growth could lead to biased estimates of mortality (cf. Walters and Ludwig 1981 on estimating stock–recruitment curves). In this appendix, we analyze our methods for potential bias in predicting mortality as functions of growth and GLI.

Consider the following qualitative model:

GLI $-$ (ϵ_1)

$\rightarrow$ Total carbon gain(T) $-$ (ϵ_2) $\rightarrow$ Radial growth(g)

$\vert\text{_____}\rightarrow$ Mortality

In this model, GLI determines total carbon gain (T) with error (ϵ_1) (e.g., the effects of nutrient availability or herbivory). Whole plant carbon balance (T) (i.e., carbon compensation point) ultimately determines sapling survivorship (Givnish 1988). T also determines radial growth with error ϵ_2; ϵ_2 is due to variation in internal carbon allocation (e.g., growth in roots vs stem radius vs carbohydrate reserves). The expectation is that $\epsilon_1 > \epsilon_2$; the variation caused by external factors such as herbivory will likely be greater than variation in endogenous carbon allocation decisions. In our methods, we assume that recent growth rates (g) are an integrated measure of carbon status (T) and thus g is used as a surrogate for predicting mortality. We tested for bias in the mortality predictor by generating simulated data with the following model.

THE MODEL

The total carbon gained (T) by a sapling is a function of its light availability (GLI):

$$T = z\cdot f(\text{GLI}) + \epsilon_1 \qquad (A.1)$$

where ϵ_1 is a normally distributed error term. If $1/z$ is the proportion of T allocated to g ($z > 1.0$), then radial growth (g) is:

$$g = f(\text{GLI}) + \frac{\epsilon_1}{z} + \epsilon_2 = \frac{1}{z}\cdot T + \epsilon_2 \qquad (A.2)$$

with normally distributed error ϵ_2. The two error terms (ϵ_1 and ϵ_2) are assumed to be independent. The variance (the sum $\frac{\epsilon_1}{z} + \epsilon_2$) can be estimated simply as σ_g^2, the variance in growth among plants of constant size and GLI. This variance is estimated by regressing growth on plant size and GLI level in the field. However, we have not estimated variances of ϵ_1 and ϵ_2 separately. We thus assume that the observed growth variance (σ_g^2) is partitioned among ϵ_1 and ϵ_2 as follows:

$$\epsilon_1 \sim N(0, z^2(1 - r)\sigma_g^2), \quad \text{and} \qquad (A.3)$$

$$\epsilon_2 \sim N(0, r\cdot \sigma_g^2), \qquad (A.4)$$

where $0 \le r \le 1$, r equalling the level of coupling between error in growth and error in net carbon gain.

When $r = 0$, T and g are perfectly correlated and growth is an excellent measure of whole plant carbon status. When $r = 1.0$, T is an errorless function of GLI, but g is still subject to the observed level of error. Under this scenario, GLI is a better predictor of mortality than g (because GLI is perfectly linked to T, which in turn determines survivorship). When $0 < r < 1$, then both ϵ_1 and ϵ_2 can deviate from zero (i.e., both T and g have a component of independent error in their predictions).

We developed simulated data sets for g and T using A.1–A.4, with r varying from 0 to 1.0, and then used these data sets to estimate parameters for the mortality functions. We

TABLE A.1. Parameter estimates for mortality as a function of growth under different levels of coupling (r) between error in growth and error in total net carbon gain.

	Tolerant		Mid-tolerant		Intolerant	
	A	B	A	B	A	B
$r = 0$	0.03	3.02	0.55	3.38	0.99	5.23
$r = 0.5$	0.01	0.01	0.52	3.04	0.72	2.65
$r = 1.0$	0.01	0.324	0.37	2.42	0.66	0.84

completed this using the growth parameters of red oak, yellow birch, and American beech to span the observed range of growth functions. The initial radius of the simulated saplings was set at 1 cm.

We randomly selected 10^3 values of light availability from a negative exponential distribution to predict 10^3 values of g and T for 5 yr. In each of the five years, g and T were subject to variation randomly drawn from a normal distribution (A.3 and A.4).

Mortality as a function of T was used to determine the status of each of the 10^3 stems:

$$P(\text{mortality}/T) = a'e^{-b'T} \qquad (A.5)$$

For each of the three representative species, we chose values of a' and b' to mimic the mortality functions of a shade tolerant, mid-tolerant, and intolerant species (similar to American beech, yellow birch, and red oak). We completed simulations with z values ranging from 1.5 to 3.0, all of which yielded similar results. For the simulation results reported here, $z = 2.0$ (i.e., one-half of net carbon gain is allocated to radial growth) (see Emmanuel et al. 1984, Bolin 1986, Rastetter et al. 1991).

In summary, for 10^3 individuals of three representative species, we simulated total net carbon gain (T) and radial growth (g) as functions of GLI, under r values ranging from 0 to 1.0. Depending on the value of r, the errors of T and g vary independently or correlate perfectly. The status of each stem (live or dead) was determined as a function of T. These steps gave us data sets similar to those we obtained from the field, but allowed us to partition the error between T and g. We used the maximum likelihood estimator reported in the methods with these data sets to estimate parameters for Eq. 6 (probability of mortality as a function of growth) under different values of r. Then we compared the mortality predictions of Eq. 6 (parameterized under various assumptions of r) with the mortality rates calculated with equation A.5.

RESULTS AND DISCUSSION

Increasing r can influence the parameter estimates of mortality as a function of growth (Table A.1). As expected, the relationship between g and probability of mortality flattens as r increases (Fig. A.1). Flattening is slight for $r = 0.5$ but may be substantial at $r = 1.0$. However, our analysis shows that regardless of the value of r, our method still is able to estimate the relationship between growth and mortality without apparent bias (Fig. A.1).

We are also interested in predicting the average mortality of saplings in the field from light availability. Thus the bias of primary interest is the bias that affects these predictions. To explore this bias, we compared light-dependent mortality rates calculated as a function of growth (Table A.1) with true mortality rates (as calculated with equation A.5). For each given light level and value of r, we calculated 10^3 values of g and T; we used these g and T values to calculate two sets of 10^3 mortality probabilities. Monte Carlo trials were performed to determine the number of deads predicted from g
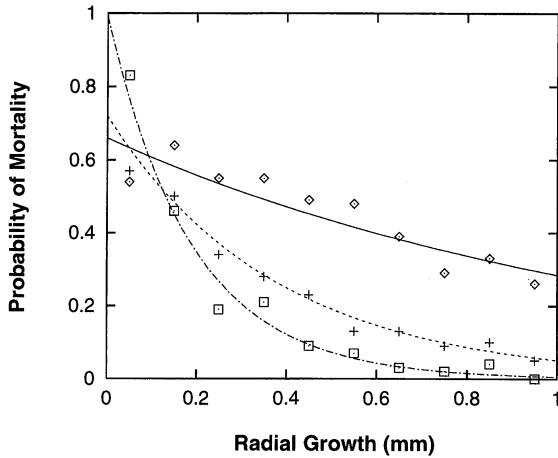
FIG. A.1. Mortality as a function of growth (lines) vs. Monte Carlo simulations of actual mortality (symbols) under $r = 0$ (——), $r = 0.5$ (– – –), and $r = 1.0$ (–·–·–). The functions are not biased in predicting mortality under any value of r.

FIG. A.2. Probability of mortality (lines labelled "M") and bias (lines labelled "B") as functions of r under a range of light availability conditions (specified in box). Under 1% of full sunlight availability, the bias is small relative to the probability of mortality.

and from T; the difference between these predictions is a measure of bias.

For the mid-tolerant and shade-tolerant species, the differences between the true and predicted mortalities are minimal. Under the worst case scenario for using our method, $r = 1$, the true mortality of the shade tolerant species at 1% GLI is 1.2%; the magnitude of the bias is 0.5%. While the bias is substantial as a proportion of the mean (5/12), the effect of the bias is negligible (true mortality of 1.2% vs. a predicted 0.7%). For the mid-tolerant species at 1% GLI and $r = 1$, bias is negligible; the true mortality is 4.2% and the estimated mortality 4.3%. The interspecific differences in mortality overwhelm the magnitude of bias under the most extreme scenarios.

The mortality predictions for the shade intolerant species showed the greatest sensitivity to increases in r. At 1% GLI and $r = 1$, bias is 13% of the magnitude of the mortality prediction (Fig. A.2). Only under high GLI (20 or 100) and $r > 0.5$, is the magnitude of bias greater than the mortality prediction (Fig. A.2). But even under these conditions, the absolute difference between mortality predicted from g and the true mortality is rather small. For example, in the most extreme case of bias ($r = 1.0$ and GLI = 20), the true mortality is 0% while using growth as an intermediate step predicts
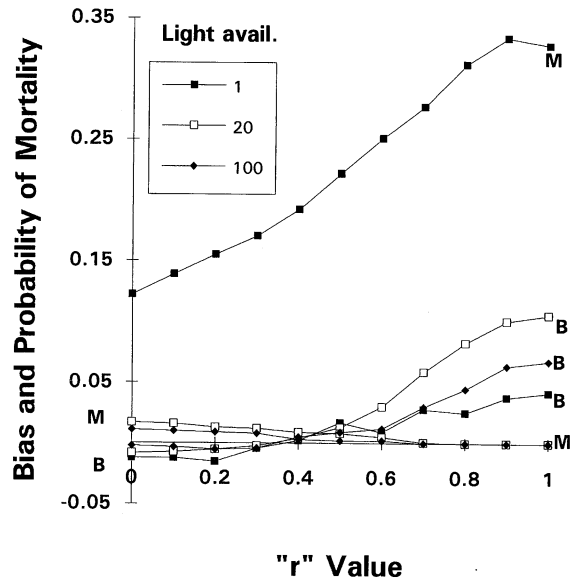
10% mortality. Moreover, note that the biased estimates (r near 1 and high light) are considerably higher than field estimates of high light mortality for any species. This point is important because bias caused by high r will generally flatten the relationship between mortality and light and thus results in relatively high mortality at high light for shade intolerants.

In summary, our predictions of mortality have the potential for bias only under the highly unlikely biological conditions ($r = 1$) where light perfectly predicts total carbon gain but none of the stochastic variation in growth is caused by fluctuation in carbon gain. Under this scenario, influences such as nutrient availability and herbivory do not influence total carbon gain and saplings exhibit unpredictable variation in carbon allocation to radial growth versus other carbon sinks (e.g., growth of roots or leaf area). Even under this extreme scenario, the magnitude of bias is minimal across a wide range of shade tolerances. Moreover, interspecific differences in low-light mortality are several times greater than the magnitude of bias generated under these extreme biological scenarios.