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Characterizing shade tolerance by the relationship between mortality and growth in tree saplings in a southeastern Texas forest

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Abstract: We investigated the relationship between shade tolerance and sapling mortality using data collected over 15 years in a mesic forest in southeastern Texas. Seven species representing a range of shade-tolerance classes were included in the study. We used survival analysis to estimate species-specific sapling mortality risk (hazard) as a function of recent growth. We found that shade-intolerant species had higher mortality risk at zero growth than shade-tolerant species. The results strongly support the point that shade tolerance can be characterized by the relationship between sapling mortality and growth.

Résumé : Nous avons étudié la relation entre la tolérance à l'ombre et la mortalité des gaules à l'aide de données accumulées pendant 15 ans dans une forêt mésique du sud-est du Texas. Sept espèces représentatives d'une gamme de classes de tolérance à l'ombre ont été incluses dans l'étude. Nous avons eu recours à l'analyse de la survie pour estimer le risque (la chance) de mortalité des gaules de chaque espèce en fonction de leur croissance récente. Nous avons découvert que le risque de mortalité est plus élevé chez les espèces intolérantes que chez les espèces ombrophiles lorsque la croissance est nulle. Les résultats supportent fortement l'idée qu'il est possible de caractériser la tolérance à l'ombre par la relation entre la mortalité des gaules et leur croissance.

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Introduction

Interspecific differences in shade tolerance have been widely considered as the driving force of forest succession (Horn 1971; Bormann and Likens 1979; Shugart 1984; Glizenstein et al. 1986). Nevertheless, the mechanism of shade tolerance is still unclear and quantification of shade tolerance has been difficult. Tables that placed tree species into groups of shade-tolerance categories based on experience and observation have been used to describe relative shade tolerance among different tree species (e.g., Baker 1949; Fowells 1965; Burns and Honkala 1990).

Although this way of grouping has been proven to be useful, a better understanding of shade tolerance and its role in forest dynamics requires attention to the underlying mechanisms and associated life-history traits. In the construction of SORTIE, a forest dynamics model in which parameters were estimated from field data, Kobe et al. (1995) developed explicit functions that predict sapling mortality from growth and growth from light. They found that intolerant species have higher mortality in low light than tolerant species. They also found that, in general, shade-tolerant species survive better than intolerant species at low growth rates. They concluded that the parameters of these functions could serve as quantitative measures of shade tolerance. Later results at different study sites supported this point (e.g., Kobe 1996; Kobe and Coates 1997).

However, the function relating mortality and growth was developed using cross-sectional census data. The cross-sectional approach depends on the critical assumption that the counts of dead and live saplings along experimental transects can provide a reliable estimate of death rate. A more direct way of predicting mortality from growth is to conduct a long-term study on growth and mortality in a sapling population (Pacala et al. 1996; Kobe and Coates 1997). So far, few longitudinal studies on sapling growth and mortality in natural forests have been reported. In this study, we used survival analysis on sapling demographic data collected over more than 15 years to characterize shade tolerance by the relationship between sapling mortality and growth for seven species.

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Methods

The study site, Wier Woods, is located in Hardin County, Texas (30°16′N, 94°12′W), approximately 16 km north of Beaumont. The

Table 1. Comparison of growth and size as mortality predictors.

Species	Shade tolerance	Sample size	Full model (S + G)	Reduced model (G)	Reduced model (S)	Chi-square (H_0: no size effect)	Chi-square (H_0: no growth effect)
LIST	I	252	−245.66	−247.46	−270.33	3.60	49.34**
ACRU	T	354	−266.89	−267.34	−299.79	0.90	65.80**
NYSY	T	529	−466.70	−480.61	−481.26	27.82**	29.12**
MAGR	T	423	−169.26	−171.10	−181.80	3.68	25.08**
COFL	VT	190	−108.90	−109.03	−110.12	0.26	2.44
ILOP	VT	1917	−421.59	−421.67	−428.94	0.16	14.70**
FAGR	VT	206	−55.15	−56.17	−55.69	2.05	1.09

Note: The full model includes both size and growth (S + G). The two reduced models include only growth (G) or size (S). The null hypothesis of the likelihood ratio test (LRTs) is no effects of size or growth, respectively. Columns 4–6 give the logarithm of likelihood of the full model and the two reduced models, respectively. Species are coded as follows: LIST, *Liquidambar stryraciflua*; ACRU, *Acer rubrum*; NYSY, *Nyssa sylvatica*; MAGR, *Magnolia grandiflora*; COFL, *Cornus florida*; ILOP, *Ilex opaca*; FAGR, *Fagus grandifolia*. They are listed in ascending order of shade tolerance (after Burns and Honcala 1990; I, intolerant; T, tolerant; VT, very tolerant). **, $p < 0.01$ (LRT, df = 1).

stand dominants include loblolly pine (*Pinus taeda* L.), water oak (*Quercus nigra* L.), upland laurel oak (*Quercus hemisphaerica* Bartr.), white oak (*Quercus alba* L.), American beech (*Fagus grandifolia* Ehrh.), southern magnolia (*Magnolia grandiflora* L.), blackgum (*Nyssa sylvatica* Marsh.), and sweetgum (*Liquidambar stryaciflua* L.). Important understory trees include American holly (*Ilex opaca* Ait.), red maple (*Acer rubrum* L.), and flowering dogwood (*Cornus florida* L.). The soil is a fine, loamy, thermic Glossaqualf. The mean understory light availability is 6.1% full sun (R. Hall, unpublished data).

The seven species included in this study are shade-intolerant sweetgum; shade-tolerant red maple, blackgum, and southern magnolia; and very shade-tolerant American beech, American holly, and flowering dogwood (the shade-tolerance classes here are based on Burns and Honkala 1990).

Surveys of live trees and saplings have been performed since 1981 on a 4-ha plot. All trees with DBH (diameter at breast height, about 1.4 m from the ground) ≥2.0 cm were tagged and DBH was measured to the nearest 0.1 cm with a DBH tape every 3 years (every 2 years in early measurements). In addition to the periodic measurements, each tagged tree was checked annually to see whether it was alive or dead. All dead and live saplings with 2.0 cm ≤ DBH ≤ 10.0 cm were included in this study (see Table 1 for numbers by species). The size-class limit was chosen because most saplings with 10 cm DBH were not tall enough to have foliage reaching canopy height.

The growth value for a sapling that died during the study was the difference in radius over the last full interval prior to death divided by interval length. The growth value for a live sapling was the difference in radius between 1995 and 1998 divided by 3. (Because different time intervals were involved for live saplings, we tested the growth variation among intervals, and it was not significant; results are not shown.)

Survival time was calculated as the length of time a sapling was followed during the course of the study. If a sapling died, then its survival time would be the difference of time between the year of death and the year when it entered the study. If a sapling was still alive at the end of the study (1998), its survival time was calculated as the difference between 1998 and the year when it entered the study, and the individual was flagged as right censored (Cox and Oakes 1984; Lee 1992). The contributions of censored and noncensored individuals to the overall likelihood function differ.

We checked the underlying distribution for survival time and found that the data can be described by the exponential distribution. Thus, the probability density function is (Cox and Oakes 1984; Lee 1992):

$$[1] \qquad f(T) = \lambda\,e^{-\lambda T}$$

where T is the lifetime in years and λ is the instantaneous mortality risk (hazard) given the sapling has survived to time T.

The survival function gives the probability that the lifetime of a sapling is equal to or greater than arbitrary time length t (Cox and Oakes 1984; Lee 1992). It is defined as

$$[2] \qquad S(T) = P(T \geq t) = e^{-\lambda t}$$

where T is the lifetime, t is any time length we define, and λ is the same as in eq. 1.

If a sapling survived the final census date (censored), then its contribution to the likelihood is $S(T)$. If a sapling died during the study, then its contribution to likelihood is $f(T)$. Let r be the number of saplings that die during the time of study and $n - r$ be the number of saplings that are censored. T_i and t_i are lifetime of a noncensored and censored sapling i, respectively. The likelihood function for all saplings is then (Lee 1992):

$$[3] \qquad L = \prod_{i=1}^{r} \lambda\, e^{-\lambda T_i} \prod_{i=1}^{n-r} e^{-\lambda t_i}$$

The goal of this analysis is to predict λ (mortality risk or hazard) using potential covariates, such as recent growth (radial increment) and initial size (radius). The parameter λ can be predicted with different models depending on the relationship between mortality risk and potential predictor variables (covariates). For the negative exponential function, the relationship between λ and the covariates is then

$$[4] \qquad \lambda = e^{-\beta_0 - \sum_{i=1}^{n} \beta_i X_i} \times \theta$$

where X_i is the potential predictors. The parameters to be estimated are the βs. We used a multiplicative error term θ so that the model could be linearized to a familiar form.

We tried different combinations of predictor variables, starting with a full model including both size (radius) and growth (annual radial increment), as well as their interaction. Since the interaction term was only significant for one species out of seven (results not shown), we dropped it as a key predictor variable. We further fitted two reduced models with only growth and with only initial size. Model fitting was done by the SAS LIFEREG procedure (SAS Institute Inc. 1994). The procedure works by maximizing the likelihood function (eq. 3) and finding the maximum likelihood estimates of parameters (βs). Likelihood ratio tests were used to test for significant effects of each predictor variable.

To identify differences among species, pairwise comparisons of parameter estimates were performed by fitting a full model with dummy variables coded for different species. Then we fitted a se-

Table 2. Parameter estimates of the negative exponential model for different species.

Species	Shade tolerance	b_0	b_1	95% CI of b_0	95% CI of b_1	Mortality risk (λ)	95% CI of λ
LIST	I	2.756**	2.153**	2.538–2.973	1.755–2.551	0.0636a	0.0511–0.0790
ACRU	T	2.854**	2.276**	2.620–3.088	1.930–2.622	0.0576a	0.0456–0.0728
NYSY	T	3.167**	2.299**	3.152–3.182	1.851–2.747	0.0421ab	0.0415–0.0428
MAGR	T	3.339**	1.629**	2.985–3.693	0.942–2.315	0.0355ab	0.0249–0.0505
COFL	VT	3.623**	0.675	3.219–4.028	0.215–1.134	0.0267bc	0.0178–0.0400
ILOP	VT	4.585**	0.976**	4.310–4.860	0.710–1.243	0.0102d	0.0078–0.0134
FAGR	VT	4.824**	0.608	3.890–5.759	0.000–1.238	0.0008cd	0.0032–0.0205

Note: Species-specific mortality risk (λ) at zero growth is calculated as $\exp(-b_0)$. Values within a column not sharing a same letter are significantly different from each other based on the likelihood ratio test (LRT, df = 1) followed by Bonferroni adjustment for multiple comparisons (the familywise α level is controlled at 0.05). Species and tolerance codes are the same as in Table 1. b_0 and b_1 are estimates of βs from eq. 4. **, $p < 0.01$ (χ^2 test, df = 1).

ries of reduced models as special cases of the full model. Since the reduced models and the full model were nested, the likelihood ratio tests were used to test for significant effect of species on model fitting. The Bonferroni adjustment for multiple comparisons was used to reduce the probability of making a type I error.

Results

Growth was better than size as a predictor of mortality (Table 1). The growth effect was highly significant for five of the seven species; the effect of size was only significant for blackgum. For the sake of consistency, we dropped size as a predictor variable for mortality. Other studies have also shown that size did not have direct influence on mortality for small saplings (Kobe et al. 1995; Kobe 1996) and that initial seedling size alone could not guarantee long-term survival unless growth rates were high as well (Grubb et al. 1996; Walters and Reich 1996).

Comparing species, there were differences in the shape of the mortality–growth relationship (Fig. 1). In particular, mortality risk at zero growth decreased as shade-tolerance rank increased (Table 2, Fig. 2). It may be noted that species did not clump into distinct classes corresponding to shade-tolerance classes. This pattern is consistent with the idea that there is a continuum of shade tolerance (Carter and Klinka 1992; Pacala et al. 1993, 1994; Wang et al. 1994; Kobe and Coates 1997).

The estimated slope parameter (β_1) represents how fast mortality risk changes as growth increases. The results indicate that the more shade tolerant a species, the less sensitive it is to changing growth (Table 2, Fig. 1). None of the pairwise comparisons was significant (Table 2). This may be due to the relatively conservative nature of the statistical tests (Bonferroni adjustment for multiple comparison), or it may be that differences in sensitivity to growth among species are relatively weak, making species-specific slope parameter a less important component of shade tolerance.

Expected lifetimes at different growth rates (the inverse of λ) were calculated to facilitate interspecific comparisons. Species varied by a factor of eight in the expected lifetime at zero growth (Fig. 3), from only 15 years for sweetgum to 125 years for beech. The two most shade-tolerant species (beech and holly) retained their survival advantage over a fairly broad range of growth rates, but above about 1 mm/year the expected lifetimes of the intolerant species increased rapidly, as might be expected. Although expected lifetimes would exceed actual lifetimes because of mortality that is unrelated to growth, comparisons are helpful in identifying the range of conditions over which species in various tolerance classes might predominate.

Discussion

Our findings that parameters representing survival at low growth correspond to the traditional shade-tolerance classification are consistent with results of previous studies (Kobe et al. 1995; Kobe 1996; Kobe and Coates 1997) using cross-sectional data. Going beyond that, the comparison of the expected lifetimes indicates that the growth threshold below which shade tolerance determines future dominance may be relatively high. That is, shade-tolerant species retain their competitive advantage even at above-average growth rates when growth is not strongly suppressed (e.g., holly and beech at radial growth rates of 1 mm/year). Only if large-scale disturbance occurs and higher growth rates ensue are less tolerant species expected to gain a substantial competitive advantage.

The pattern of mortality risk among different species is in agreement with successional roles predicted by previous studies in this forest (Harcombe and Marks 1983; Glitzenstein et al. 1986). Harcombe and Marks (1983) found that beech, magnolia, and holly have low mortality rates in all size classes, and they predicted that this forest would approach to beech–magnolia–holly climax. The results obtained from the mortality–growth model in this study strongly support this prediction. The agreement of this study with that of Harcombe and Marks (1983) strongly supports the point that interspecific differences in mortality are important to forest dynamics.

Kobe et al. (1995) used cross-sectional data to find the best-fit mortality–growth function that reshapes the overall growth distribution into growth distributions for dead and live saplings. The survival analysis that we used is more direct, and it requires fewer assumptions.

Since this study was performed in a different forest with different methods, the consistent results suggest that the shade-tolerance theory as described by the mortality–growth model may apply across a fairly wide range of systems. This study strongly supports the assertion that the mortality–growth relationship is a key life-history characteristic that determines shade tolerance.

Fig. 1. Predicted probability of mortality (λ) with 95% confidence interval for each of the seven species. Broken lines are the upper and lower limits of prediction; solid lines are the mean predictions. The probability of mortality was computed using parameter estimates of eq. 4 in text. Species are arranged in descending order of λ values at zero growth from top to bottom and left to right.
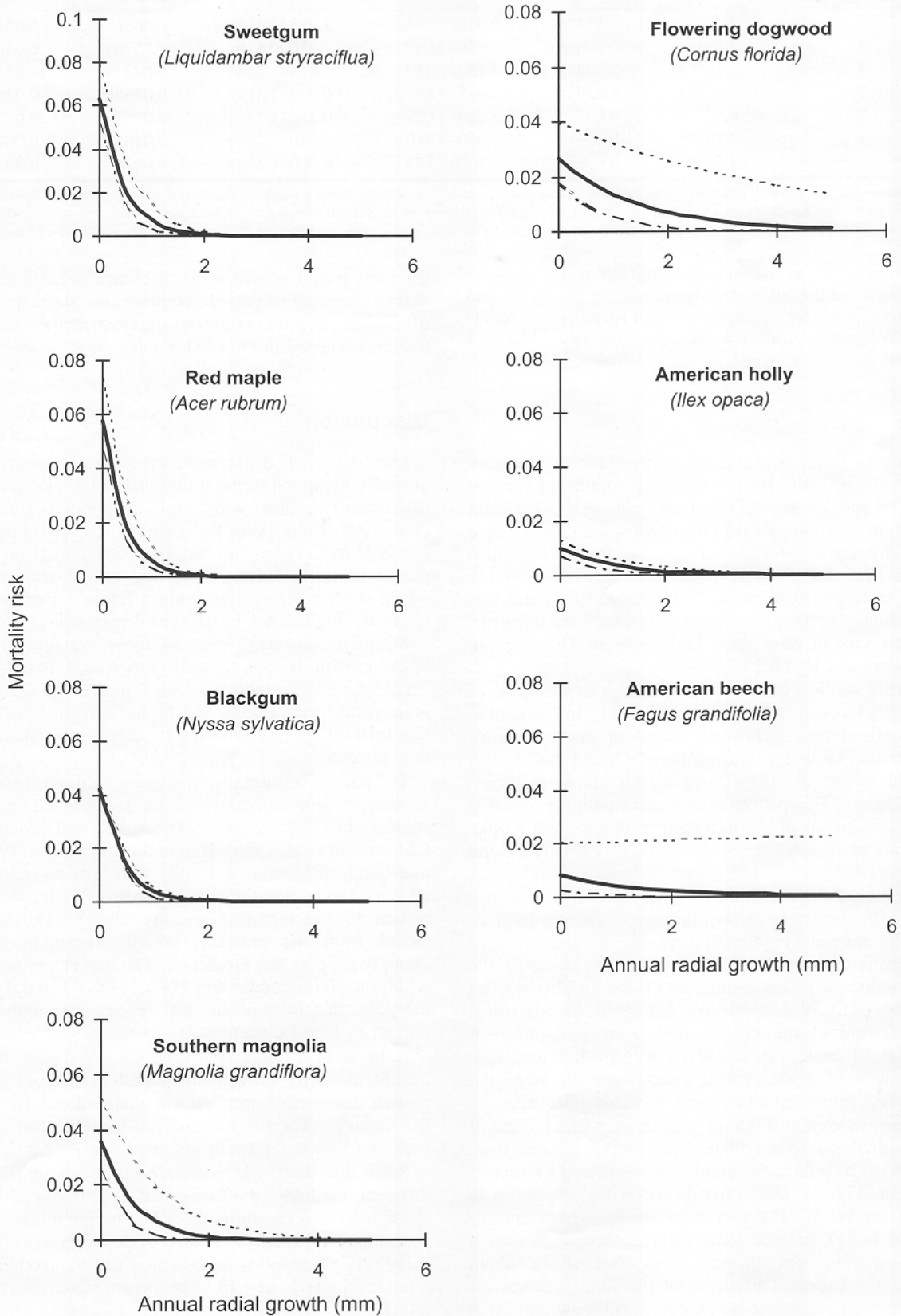
Fig. 2. Comparisons of predicted mortality risk (λ) at zero growth with 95% confidence interval for different species. Species are arranged from left to right according to their shade tolerance ranks. Species tolerance codes are given in Table 1.
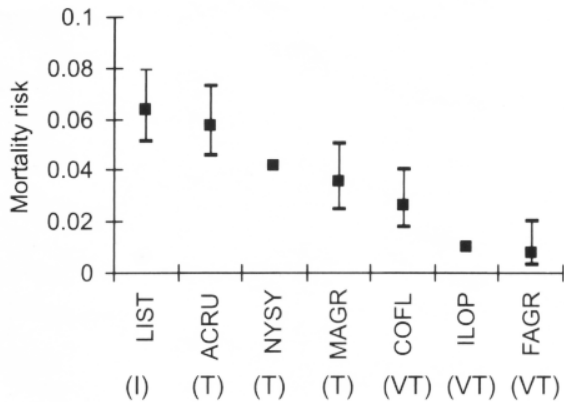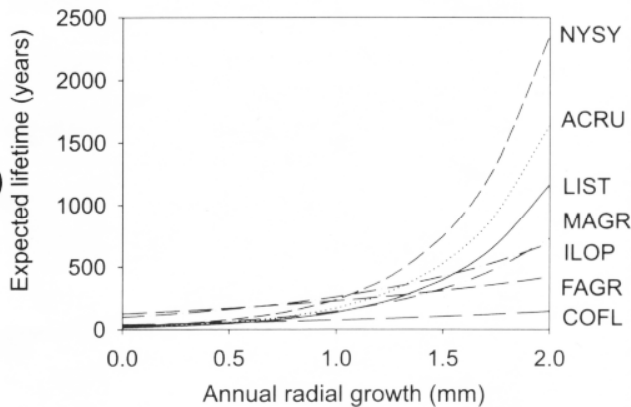

Fig. 3. Expected lifetime as a function of annual radial growth for different species. Expected lifetimes were calculated as the inverse of mortality risk. Species codes are given in Table 1.

Acknowledgments

References

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

Bormann, F.H., and Likens, G.E. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. Am. Sci. **67**: 660–669.

Burns, R.M., and Honkala, B.H. (*Technical coordinators*). 1990. Silvics of North America. Vol 2. Hardwoods. U.S. Dep. Agric. Agric. Handb. 654.

Carter, R.E., and Klinka, K. 1992. Variation in shade tolerance of Douglas fir, western hemlock, and western red cedar in coastal British Columbia. For. Ecol. Manage. **55**: 87–105.

Cox, D.R., and Oakes, D. 1984. Analysis of survival data. Chapman & Hall, New York.

Fowells, H.A. 1965. Silvics of forest trees of the United States. U.S. Dep. Agric. Agric. Handb. 271.

Glizenstein, 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.

Grubb, P.J., Lee, W.G., Kollmann, J., and Wilson, J.B. 1996. Interaction of irradiance and soil nutrient supply on growth of seedlings of ten European tall-shrub species and *Fagus sylvatica*. J. Ecol. **84**: 827–840.

Harcombe, P.A., and Marks, P.L. 1983. Five years of tree death in a *Fagus–Magnolia* forest, southeast Texas (USA). Oecologia, **57**: 49–54.

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

Kobe, R.K. 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. Ecol. Monogr. **66**: 181–201.

Kobe, R.K., and Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Can. J. For. Res. **27**: 227–236.

Kobe, R.K., Pacala, S.W., Silander, J.A., Jr., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. **5**: 517–532.

Lee, E.T. 1992. Statistical methods for survival data analysis. John Wiley & Sons Inc., New York.

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.

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.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Jr., Kobe, R.K., and Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol. Monogr. **66**: 1–43.

SAS Institute Inc. 1994. SAS/STAT user's guide, version 6. 4th ed. SAS Institute Inc., Cary, N.C.

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

Walters, M.B., and Reich, P.B. 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. Ecology, **77**: 841–853.

Wang, G.G., Qian, H., and Klinka, K. 1994. Growth of *Thuja plicata* seedlings along a light gradient. Can. J. Bot. **72**: 1749–1757.