

Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia

Richard K. Kobe and K. Dave Coates

Abstract: We have developed models of sapling mortality for the eight dominant tree species of northwestern British Columbia in order to better understand forest community dynamics and succession in this important forest region. The species-specific models characterize an individual's probability of mortality as a function of recent growth (a surrogate for whole-plant carbon balance). Interspecific comparisons of survival under low growth rates (i.e., suppression) provide a quantitative measure of the effective shade tolerance of these tree species. In particular, the more shade tolerant species exhibited more rapid decays in mortality probability with increased radial growth. The broad and continuous range in shade tolerance ranking was as follows: *Thuja plicata* Donn ex D. Don > *Tsuga heterophylla* (Raf.) Sarg. = *Abies lasiocarpa* (Hook.) Nutt. > *Picea glauca* (Moench) Voss × *Picea sitchensis* (Bong.) Carrière > *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. > *Populus tremuloides* Michx. > *Populus balsamifera* ssp. *trichocarpa* (Torr. & A. Gray) Brayshaw = *Betula papyrifera* Marsh. At low growth rates, mortality varied between *T. plicata* and *B. papyrifera* by more than an order of magnitude. For some species, the three replicate sites exhibited significant variation, suggesting that shade tolerance may vary with site conditions (presumably soil moisture in our study sites). The mortality models are consistent with previous qualitative categorizations into shade tolerance classes and parallel the dominance of different species in postdisturbance succession. Our results suggest that species differences in noncatastrophic mortality are critical to understanding and predicting forest dynamics.

Résumé : Les auteurs ont élaboré des modèles de mortalité des semis de huit espèces arborescentes dominantes du nord-ouest de la Colombie-Britannique en vue de mieux comprendre la dynamique des communautés forestières et la succession dans cette importante région forestière. Les modèles spécifiques caractérisent la probabilité individuelle de mortalité en fonction de la croissance récente qui remplace le bilan du carbone de la plante entière. Les comparaisons interspécifiques de survie à de faibles taux de croissance (c.-à-d., suppression) fournissent une mesure quantitative de la tolérance effective à l'ombre de ces espèces. En particulier, les espèces plus tolérantes présentaient une décroissance plus rapide de la mortalité avec une augmentation de la croissance radiale. La gamme large et continue de tolérance relative à l'ombre était la suivante : *Thuja plicata* Donn ex D. Don > *Tsuga heterophylla* (Raf.) Sarg. = *Abies lasiocarpa* (Hook.) Nutt. > *Picea glauca* (Moench) Voss × *Picea sitchensis* (Bong.) Carrière > *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. > *Populus tremuloides* Michx. > *Populus balsamifera* ssp. *trichocarpa* (Torr. & A. Gray) Brayshaw = *Betula papyrifera* Marsh. À de faibles taux de croissance, la mortalité de *T. plicata* et *B. papyrifera* différait de plus d'un ordre de grandeur. Pour certaines espèces, les trois sites utilisés comme répétitions montraient des variations significatives, suggérant que la tolérance à l'ombre peut varier selon les conditions de stations; présumément à cause de l'humidité du sol sur les stations étudiées. Les modèles de mortalité sont cohérents avec les classifications qualitatives antérieures de tolérance à l'ombre et correspondent à la dominance des différentes espèces au cours de la succession après une perturbation. Les résultats font ressortir la nécessité de connaître les différences interspécifiques dans le cas de la mortalité qui ne découle pas d'une catastrophe pour comprendre et prédire la dynamique forestière.

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R.K. Kobe.¹ Institute of Ecosystem Studies, Box AB, Route 44A, Millbrook, NY 12545-0129, U.S.A.

K.D. Coates. British Columbia Forest Service, Research Section, Bag 5000, Smithers, BC V0J 2N0, Canada.

¹ Author to whom all correspondence should be addressed. Present address: Michigan State University, Department of Forestry, Natural Resources Building, East Lansing, MI 48824-1222, U.S.A.

Introduction

Early characterization of shade tolerance in trees was based largely on subjective observation (e.g., Baker 1949; Minore 1979). For example, the tables of Baker (1949) and species descriptions by Fowells (1965) and Burns and Honkala (1990) placed species into 3–5 categories of shade tolerance. Whitmore (1989) believed tree species could be grouped into two qualitative groups: pioneer species (those that do not occur under canopy shade) and climax species (those that establish

and grow under canopy shade). Several recent studies focusing on shade tolerance have examined growth rates at low light or over a range of light conditions (e.g., Carter and Klinka 1992; Klinka et al. 1992; Walters and Reich 1996). In contrast, relatively few studies have explicitly characterized sapling mortality as a component of shade tolerance (Kitijima 1994; Kobe et al. 1995; Walters and Reich 1996).

To predict forest community dynamics and succession, species differences in sapling mortality are probably equally or more important than growth (Good and Good 1972; Harcombe and Marks 1978; Lorimer 1981). For example, sensitivity analyses of demographic studies have pointed to the importance of juvenile survivorship to population dynamics (e.g., Hartshorn 1972; Pinero et al. 1984). For oak-transition northern hardwood forests of the northeastern United States, Kobe et al. (1995) and Pacala et al. (1994, 1996) demonstrated that species differences in resource-dependent mortality were critical to predict the relative dominance of different tree species during succession.

In this paper, we present sapling mortality models developed for the eight dominant species of coastal-interior transition forests of northwestern British Columbia. We used recent growth as a predictor of mortality for two reasons. From a practical perspective, field and statistical methods recently developed by Kobe et al. (1995) enabled us to efficiently calibrate models of mortality as a function of growth based upon measurements of recent annual growth rings of live and dead saplings. More conventional approaches, such as binomial regression, require a long-term study or a very large sample size, which probably have been impediments to more studies of sapling mortality.

From a theoretical perspective, the functional relationship between the probability of mortality and recent growth (a surrogate for whole-sapling carbon balance) lends insight into interspecific variation in shade tolerance (Kobe et al. 1995). By definition, shade-tolerant species survive even with the marginal carbon balance and suppressed growth rates possible under heavily shaded conditions, while less shade tolerant species simply cannot survive periods of suppression. Within a species, individuals in higher resource environments would be expected to grow faster (and (or) have a more favorable carbon balance) and therefore be less likely to die. Numerous studies have pointed out the strong relationship between light availability and seedling and sapling growth (e.g., Walters and Reich 1996; Pacala et al. 1994; Carter and Klinka 1992). Therefore, interspecific differences in mortality under low growth rates induced by shade provide a quantitative measure of shade tolerance. In this paper, our objectives are to characterize patterns of sapling mortality as a function of recent growth for the eight dominant tree species of northwestern British Columbia, use the models to provide a quantitative measure of the shade tolerance of these species, and examine the relationship between our measures of shade tolerance and successional dynamics in these forests.

Methods

Study area and species

This study is a component of the Date Creek Silvicultural Systems Experiment (Coates et al. 1997), located near Hazelton, northwestern British Columbia (55°22'N, 127°50'W). Study

sites were located in the Interior Cedar – Hemlock, Moist Cold biogeoclimatic subzone (ICHmc) and in the Sub-Boreal Spruce Moist Cold subzone Babine Variant (SBSmc2). The ICH zone is transitional between the Coastal Western Hemlock zone and the interior SBS zone. See Pojar et al. (1987) or Meidinger and Pojar (1991) for a description of this system of vegetation classification and Banner et al. (1993) for detailed descriptions of the ICH and SBS zones of northwestern British Columbia.

Forests in the ICHmc are mixtures of conifer and deciduous tree species and have among the highest richness of tree species of any subzone in British Columbia. We focused on the eight dominant tree species in these systems. In mature forests at the Date Creek Research Area, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) dominates, but is mixed with western redcedar (*Thuja plicata* Donn ex D. Don), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), hybrid spruce (the complex of white spruce (*Picea glauca* (Moench) Voss), Sitka spruce (*Picea sitchensis* (Bong.) Carrière), and occasionally Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* (Torr. & A. Gray) Brayshaw). In SBS zone forests, western hemlock and western redcedar are absent and hybrid spruce is replaced by interior spruce (mix of white and Engelmann spruce).

The species we examined span a range of shade tolerances. Western redcedar, western hemlock, and subalpine fir are considered very shade tolerant (Krajina et al. 1982; Burns and Honkala 1990). They dominate all canopy positions in older forests and are all capable of regenerating in canopy gaps. Hybrid spruce is considered intermediate in shade tolerance followed by lodgepole pine (very intolerant), with aspen, birch, and cottonwood all considered intolerant (Krajina et al. 1982; Burns and Honkala 1990). Detailed autecological characteristics of these species can be found in Krajina (1969), Minore (1979), Krajina et al. (1982), Burns and Honkala (1990), and Coates et al. (1994).

We sampled three sites (replicates) for each of the eight tree species (see Table 1) for a total 24 sampling sites. Two replicates each of lodgepole pine, subalpine fir, and trembling aspen were located in the SBSmc2 subzone. All other replicates were from the ICHmc subzone either at or near the Date Creek Research Area. We assessed the soil moisture regime at each sampling site following the methods of Banner et al. (1993).

Field sampling and growth measurements

To estimate parameters for species-specific mortality models, we used a slight modification of the field sampling, growth measurement, and maximum likelihood estimation techniques of Kobe et al. (1995). These methods provide field-calibrated models of the probability of mortality as a function of recent growth for the average sapling of a species at a particular site and across sites. The mean size of saplings averaged on a site basis ranged from 12.23 to 32.07 mm radius (see Table 1).

As in Kobe et al. (1995), two criteria were employed in choosing appropriate field sites for these statistical methods: adequate sample sizes to estimate parameters for the mortality model and sufficient variation in the predictor variable. Three types of field sites met these criteria: (1) young self-thinning

stands with no mature canopy influence, where we sampled lodgepole pine (14–19 years), trembling aspen (16–22 years), black cottonwood (17–22 years), and paper birch (10–22 years); (2) self-thinning stands growing in canopy gaps, where we sampled western redcedar (two replicates, 36–50 years), western hemlock (33–52 years), and hybrid spruce (33–36 years); and (3) broken overstories, where we sampled western redcedar (1 replicate, ages up to 123 years) and subalpine fir (ages up to 70 years).

To ensure adequate sample sizes of live and dead individuals, we defined the boundaries of the sites to include a target of 50 recently dead individuals of the focal species because dead individuals were less common than lives. This resulted in variably sized sample sites ranging from approximately 500 to 4500 m², except for one replicate each of paper birch (8000 m²), trembling aspen (25 000 m²), and western redcedar (50 000 m²), where large areas were required to locate dead individuals.

Field sites were located where we expected variation in the predictor variable (recent growth of individuals), because our goal was to regress the probability of mortality on recent growth. It is a requirement of any regression to span a sufficient range of variation in the predictor variable. To span variation in growth rates, we randomly sampled saplings, stratified across the heterogeneous light environments at each site. Individuals expected to be growing relatively slowly included those located under a dense canopy, on the southern, heavily shaded edge of a gap or those overtopped by similar-aged neighbors. Conversely, saplings expected to be growing more rapidly were those at the northern end of a gap and those that were taller than immediate neighbors.

To provide data for the Kobe et al. (1995) likelihood estimator (details below), three sets of field data were required from each study site: the numbers of live and dead individuals of the focal species at the site, a random sample of live individuals from which growth is to be measured, and a random sample of dead individuals from which growth leading up to death is to be measured. Within each study site, the total numbers of live and dead individuals of a focal species were estimated by subsampling with randomly placed circular quadrats. Depending on the site, a different number ($4 \leq N \leq 10$) and different size (5, 10, and 20 m²) of quadrats were used. Total areas sampled with quadrats ranged from 30 to 240 m². Four quadrats (the smallest number used anywhere) of 20 m² each were used for trembling aspen at Boulder Creek (site 1), and the largest number of quadrats (12) of 20 m² were used at Fulton Lake (site 3) for trembling aspen.

To obtain the two sets of growth data, from each site we harvested stem cross sections at 10 cm above the root collar for a random sample of live individuals ($48 \leq N \leq 55$) and a random sample or the entire population of recently dead individuals ($36 \leq N \leq 55$). We did not include diseased or insect-infested saplings in our samples to ensure that the most likely cause of death was suppression. The harvested stem cross sections were numbered and taken to the laboratory. The 10 most recent annual growth rings (or all rings for saplings <10 years old) for each individual were measured along a representative radius (the radius bisecting the angle formed by the longest and shortest radii of the cross section). Growth rings were measured with a digital ring analyzer (0.025 mm) using a high-resolution colour video camera connected to a 40× stereo microscope.

Following the methods of Kobe et al. (1995), dead saplings used for growth measurements must have been dead within a certain window of time (i.e., fitting the criteria of recently dead). The actual length of the time window corresponding to the recently dead criteria is determined according to when the best discriminating bud, bark, and leaf features are manifested. To determine the recently dead criteria for field sampling, samples were collected from trees that were known to have been dead for 1, 2, 3, 4, and 5 years. Areas that had been manually brushed, thinned, or aerially sprayed from 1990 to 1995 were located from local knowledge, forest cover maps, and silviculture information listings. Stand reconstruction plots (stem analysis) completed at the Date Creek study site were also sampled. Each sample consisted of foliage (if present), and branches (and (or) stems) of several dead trees per species per year. For species and for each year that a sapling had been dead, specific tree features such as bud characteristics (presence, intactness, colour), leaf or needle retention (estimate of leaves or needles remaining, how easily the leaves are removed), suppleness of the stem, bark characteristics (bark presence, intactness), leaf base characteristics, leaf or needle characteristics (colour, brittleness, intactness), and other features were described. A collection of these characteristics from 1 to 5 years dead was compiled for each species (P. Bartemucci and K.D. Coates, unpublished manuscript). For all species but redcedar, we found the highest discriminating power in recently dead characteristics at 3 years; thus we sampled dead individuals in the field that we estimated to have been dead ≤ 3 years. For western redcedar, the clearest demarcation was at 4 years; thus in the field we sampled redcedar individuals that we estimated had been dead ≤ 4 years.

Parameter estimation using maximum likelihood

We used the likelihood function of Kobe et al. (1995) to estimate parameters and 95% support for species- and site-specific models characterizing probability of mortality as a function of recent growth (g). Let $m(g)$ represent the functional relationship between mortality probability and g ; $m(g)$ depicts the probability of mortality of the average individual of a species at a particular site or sites.

The first of three components of the likelihood function is based on the counts of live and recently dead individuals within each study site. The probability that D dead saplings are encountered in a total population of N individuals (D and N estimated from quadrats) is a series of Bernoulli trials (live or dead):

$$[1] \quad \bar{U}^D (1 - \bar{U})^{N-D}$$

where \bar{U} represents the mean probability or expectation of mortality.

The second component of the Kobe et al. (1995) likelihood function is the conditional density function of growth given that a sapling will die. This component arises from the measured growth rates leading up to the death of the “recently dead” saplings. 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 their death is

$$[2] \quad Y_D(g|\text{death}) = \frac{h(g)m(g)}{\int_0^{\infty} m(g)h(g) dg}$$

In words, the density function of growth, given that a sapling will die, is equal to the product of the probabilities of

growth and mortality, normalized by the expectation of mortality (or \bar{U}). The third component of the likelihood function is the density function of growth for live individuals:

$$[3] \quad Y_L(g|\text{survivorship}) = \frac{h(g)[1 - m(g)]}{\int_0^{\infty} [1 - m(g)]h(g) dg}$$

The likelihood function is then

$$[4] \quad L = \bar{U}^D (1 - \bar{U})^{N-D} \prod_{i=1}^{\# \text{dead}} \frac{h(g_i)m(g_i)}{\bar{U}} \times \prod_{i=1}^{\# \text{live}} \frac{[1 - m(g_i)]h(g_i)}{1 - \bar{U}}$$

Note that (D) and ($N - D$) represent quadrat counts of dead and live individuals, while # dead and # live are the numbers of stem cross sections harvested for growth analysis to develop the growth density functions.

The likelihood is a function of the parameters and functional forms of the underlying models $m(g)$ (mortality as a function of growth) and $h(g)$ (the density function of growth rates of live individuals in a site) (Edwards 1992). Several different functional forms were evaluated for $m(g)$ (see below section). As in Kobe et al. (1995), we used a gamma density function to specify $h(g)$ because the two-parameter gamma is flexible in shape and by definition $g \geq 0$. We used the Metropolis algorithm (Szymura and Barton 1986) to search for parameter values and functional forms of $m(g)$ and parameter values of $h(g)$ that yielded the highest likelihoods. Support intervals of 95% for all estimated parameters were estimated by inverting the likelihood ratio test (LRT) (Edwards 1992; Pacala et al. 1996). Note that these statistical methods are not available in commercial software as we have applied them; all of the statistical analyses were performed with modifications of programs written in Turbo Pascal by Kobe et al. (1995).

Tests of different formulations for $m(g)$

We tested different numbers of years of recent growth history (g) to use as the predictor variable and several functional forms for $m(g)$. For g , we used the arithmetic average of the 4 most recent years of growth (excluding the last ring) because it resulted in higher likelihoods for more species than averages of the 2 and 3 most recent years of growth. We excluded the last (1995 for the live individuals) growth ring from the average to ensure that the growth measurements from both live and recently dead individuals were from complete growing seasons. Because some saplings were 5 years old and the last ring was excluded, we were unable to evaluate time periods >4 years for g .

We evaluated three models for $m(g)$. Following Kobe et al. (1995) and Kobe (1996), we tested a two-parameter negative exponential decay:

$$[5] \quad m(g) = P(\text{death}|\text{growth}) = A e^{-Bg}$$

where A and B are parameters to be estimated as described in the maximum likelihood methods above. A can be interpreted as the probability of mortality at zero growth (and controls where the function crosses the y -axis) and B represents the sensitivity of mortality probability to changes in growth or whole-plant carbon status (corresponding to the function's decay).

One of our underlying goals was to use a mortality model that was simple and parsimonious but that provided equally good statistical fits as more complex models. Because many of the estimates for A were close to one, we tested a simpler one-parameter variant of eq. 5 for $m(g)$:

$$[6] \quad m(g) = P(\text{death}|\text{growth}) = e^{-Bg}$$

where B is the only parameter to be estimated and has the same biological interpretation as above. Equations 5 and 6 were compared with LRTs. In 23 of 24 comparisons, the likelihood resulting from eq. 6 was not significantly lower than the likelihood based upon eq. 5 (LRT test criteria: $p < 0.05$). Therefore, the simpler one-parameter negative exponential decay is the basis of further model development here.

The disadvantage of eqs. 5 and 6 is that they must apply to the length of the time period defined by the recently dead criteria and do not allow for flexibility in time interval length. Equations 5 and 6 present a problem for comparing species because our definitions of recently dead for cedar was ≤ 4 years and for all other species was ≤ 3 years. To standardize the time interval, we evaluated an additional mortality model that offers flexibility in interval length and can be decomposed to an annual basis: the cumulative distribution function (cdf) of an exponential random variable:

$$[7] \quad P\{X \leq t\} = \int_0^t \lambda \exp[-\lambda x] dx \\ = 1 - \exp[-\lambda t] \\ = 1 - \exp[-(te^{-Cs})]$$

where $P\{x \leq t\}$ is the probability that outcome X will occur before or at time t , and λ is a parameter whose reciprocal is the statistical expectation. In this case, $P\{x \leq t\}$ is the probability of death over a defined time interval t and λ^{-1} is the expected lifetime of the average sapling of a species at a specified growth level. A negative exponential decay (similar to eq. 6) was substituted for λ .

Because time can be specified in the likelihood function, the advantage of eq. 7 is that species' estimates of C can be directly compared. Equations 6 and 7 also provided similar fits (significantly higher likelihoods for four species with eq. 6, three species with eq. 7, and no difference between the two equations for one species). For these reasons, we emphasize eq. 7.

Generalized species models and within-species variation

The above methods were used to calibrate 24 species- and site-specific mortality models. We also wanted to parameterize generalized species models (without respect to intraspecific variation among sites) and to explicitly characterize and statistically test for significant intraspecific variation in mortality models among sites. Both of these goals were accomplished as parts of the same analysis.

To calibrate generalized species models, all three data sets for a particular species were evaluated with the same likelihood function. The generalized likelihood function was the product of site-specific variants of eq. 4, with a mortality model [$m(g)$] common to all three sites. That is, each site retained its site-specific N , D , \bar{U} , and $h(g)$, but one generalized $m(g)$ was estimated for all three sites. Thus, the generalized likelihood function is

$$[8] \quad L = \prod_{j=1}^{\#sites} (\bar{U}_j^{D_j})(1 - \bar{U}_j)^{N_j - D_j} \prod_{i=1}^{\#dead} \frac{h_j(g_i)m(g_i)}{\bar{U}_j} \\
 \times \prod_{i=1}^{\#live} \frac{[1 - m(g_i)]h_j(g_i)}{1 - \bar{U}_j}$$

where the subscript j denotes site-specific values or functions. The other terms are interpreted the same as in eq. 4.

To test for significant differences in $m(g)$ among sites, we derived a “saturated” likelihood function that allowed $m(g)$ to vary among sites. This was accomplished by assigning coefficients to account for site variation. In the component of the likelihood function (eq. 8) attributable to site 1 ($j = 1$), $m(g)$ (using eq. 7) is equal to $(1 - \exp(-te^{-Cg}))$; for $j = 2$ (site 2), $m(g)$ is equal to $(1 - \exp(-te^{-(CD)g}))$; and for $j = 3$ (site 3), $m(g)$ is equal to $(1 - \exp(-te^{-(CK)g}))$. Using LRTs, we tested whether the coefficient values (D and K) were significantly different from unity and from each other.

Results

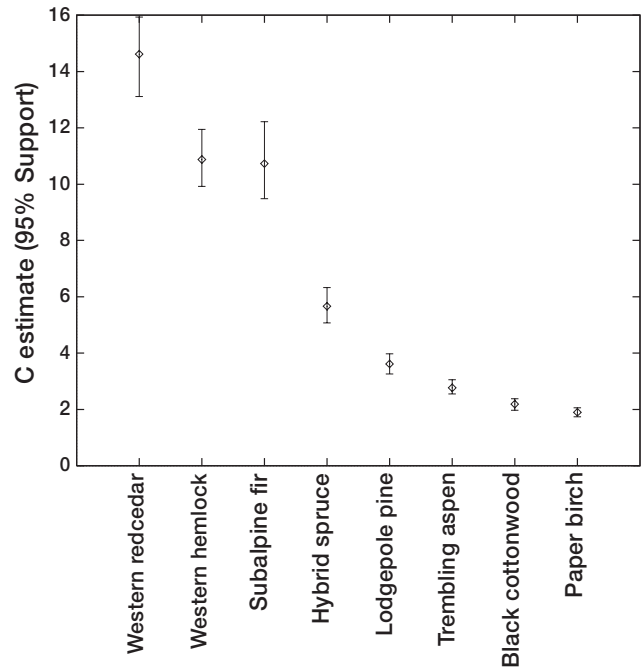
Generalized species models

The eight tree species exhibited statistically significant differences in the C estimates (eq. 7) of the generalized mortality functions (Fig. 1, Table 1). General species C estimates will be referred to as C_{gen} estimates to distinguish them from site-specific estimates. For a given level of growth, a species with a higher C_{gen} value will experience lower mortality than a species with a lower C_{gen} value. Thus, species with the highest estimates of C_{gen} can be viewed as the most shade tolerant. The rank order of shade tolerance based upon the maximum likelihood estimates of C_{gen} was western redcedar > western hemlock = subalpine fir > hybrid spruce > lodgepole pine > trembling aspen > black cottonwood = paper birch (Table 1, Fig. 1). It is highly unlikely that our range of sapling sizes influenced species’ ranking and significant differences in C_{gen} , as there is no correlation between sapling size and C_{gen} estimates (Table 1).

There was a broad continuum of mortality patterns among these eight tree species (Fig. 2). The more shade tolerant species (western redcedar, western hemlock, and subalpine fir) exhibited rapid decreases in the probability of mortality with higher growth (Fig. 2). Hybrid spruce, lodgepole pine, and aspen were intermediate in their mortality functions. The least shade tolerant species (cottonwood and paper birch) exhibited slower decreases in risk of mortality with increases in growth. For example, at 0.1 mm radial growth (averaged over 4 years), the probability of mortality for western redcedar was approximately half that of paper birch (0.50 vs. 0.92). At 0.3 mm growth, the difference in mortality between these two species was more than an order of magnitude (0.037 vs. 0.82) (Fig. 2).

Species’ differences in mortality are also shown by mapping the 95% support limits of the C_{gen} estimates onto the mortality function (eq. 7) at several levels of recent growth (Fig. 2). Because eq. 7 is nonlinear, significantly different C_{gen} estimates do not map to significantly different mortality probabilities at all growth rates. At 0.1 mm radial growth, the mortality of redcedar < (western hemlock = fir) < spruce < (lodgepole pine = aspen = cottonwood = birch). At 0.3 mm radial growth, the significantly different groups change to redcedar < (hemlock = fir) < spruce <

Fig. 1. Maximum likelihood estimates and 95% support intervals for C_{gen} of the generalized mortality model (from eq. 7). The C_{gen} parameter defines the functional relationship between probability of mortality and recent growth and is a measure of effective shade tolerance.



pine < aspen < (cottonwood = birch). At 0.5 and 0.7 mm radial growth, the same grouping holds except that redcedar = hemlock = fir. Spruce joins the low mortality group by 0.9 mm, pine by 1.5 mm, and aspen by 2 mm radial growth. All species show relatively low mortality at growth rates above 2.5 mm.

Shade tolerance has traditionally been viewed as a species’ ability to persist in the understory under conditions of suppressed growth (Fig. 3). Recall from the methods that the expected lifetime of the average sapling of a species growing at a specified g is $(e^{-Cg})^{-1}$. For example, once an average radial growth rate of 0.3 mm/year is attained, the average redcedar individual can be expected to survive for indefinite periods. Spruce, a midtolerant species, is expected to survive for <2 years at 0.3 mm average radial growth/year, 16 years at 0.5 mm average growth/year, and indefinitely at approximately 0.8 mm/year (Fig. 3). In contrast, the least shade tolerant species, paper birch, is expected to persist for <2 years at growth rates <0.8 mm and for 20 years at 1.6 mm/year average annual radial growth (Fig. 3).

Species- and site-specific models

For seven of the eight species, there were significant differences in mortality models among sites (Fig. 4). Based upon LRTs (criteria of $p \leq 0.05$), only hybrid spruce showed no significant differences among its three sites; three species (black cottonwood, subalpine fir, and western hemlock) each exhibited statistically indistinguishable mortality functions at two sites, which differ from the remaining site; and aspen, birch, redcedar, and lodgepole pine each showed statistically significant differences among all three sites (Fig. 4). However, even taking site variation into account, there was a clear trend

Table 1. Sapling sizes (mean and range in mm), maximum likelihood estimates of C , and associated 95% support interval for the mortality model $m(g) = 1 - \exp(-t e^{-Cs})$ for eight tree species examined at three replicate sites each in northwestern British Columbia.

Site No.	Name	Radius mean (mm) and range (mm)	C (95% support)
Western redcedar (<i>Thuja plicata</i>)			
All			14.6168 (13.116–15.942)
1	Date Creek, New Rd.	14.54 (1.83–55.22)	13.950 (11.827–16.268)
2	Date Creek, B-unit	21.59 (4.34–67.16)	26.9611 (23.330–30.945)
3	Muldoe, Gap	12.26 (2.0–51.92)	8.9831 (7.258–11.009)
Western hemlock (<i>Tsuga heterophylla</i>)			
All			10.8755 (9.919–11.941)
1	Mills Lake, Gap	20.4 (2.39–116.61)	6.4631 (5.292–7.834)
2	Date Creek, New Rd.	13.85 (2.01–48.97)	15.7259 (13.763–17.874)
3	Muldoe Gap	12.23 (1.91–78.87)	12.8692 (11.056–15.002)
Subalpine fir (<i>Abies lasiocarpa</i>)			
All			10.7295 (9.482–12.216)
1	Telkwa, 103a Rd.	23.5 (4.06–79.08)	6.2671 (4.436–8.438)
2	Nash-Y	16.87 (2.92–57.84)	14.2575 (11.765–17.087)
3	Pine Creek	26.00 (4.29–99.85)	11.4189 (9.272–13.802)
Hybrid spruce (<i>Picea glauca</i> × <i>P. sitchensis</i>)			
All			5.6614 (5.073–6.329)
1	Muldoe, Gap	13.72 (2.95–56.01)	6.0173 (5.018–7.103)
2	Mills Lake, Gap	15.48 (2.06–95.91)	5.7451 (4.690–6.966)
3	Muldoe, Gap	14.15 (3.02–57.68)	6.1586 (5.026–7.423)
Lodgepole pine (<i>Pinus contorta</i>)			
All			3.6173 (3.261–3.971)
1	Morice, For. Service Rd.	14.25 (1.52–65.38)	2.5055 (2.099–2.958)
2	Owen Lake	16.45 (1.32–84.20)	5.6709 (4.851–6.682)
3	Temlaham	16.80 (1.83–73.99)	3.9358 (3.322–4.655)
Trembling aspen (<i>Populus tremuloides</i>)			
All			2.7681 (2.547–3.050)
1	Boulder Creek	27.22 (5.54–69.95)	2.1213 (1.687–2.639)
2	Chapman Lake	24.22 (6.63–80.31)	4.3441 (3.718–5.033)
3	Fulton Lake	18.23 (5.84–58.93)	3.0224 (2.685–3.398)
Black cottonwood (<i>Populus balsamifera</i> ssp. <i>trichocarpa</i>)			
All			2.1809 (1.973–2.378)
1	Kitwancool	21.19 (6.86–106.35)	1.4685 (1.271–1.680)
2	Mudflat Creek	32.07 (6.5–120.24)	1.7955 (1.466–2.185)
3	Weber Creek	17.57 (4.47–78.94)	5.4406 (4.788–6.185)
Paper birch (<i>Betula papyrifera</i>)			
All			1.8946 (1.739–2.060)
1	Sunday Lakes	15.17 (4.67–43.23)	1.3808 (1.213–1.571)
2	Weber Creek	17.98 (4.85–57.45)	3.2218 (2.814–3.686)
3	Temlaham	17.69 (3.18–68.10)	2.3142 (1.952–2.700)

of increasing mortality from western redcedar to paper birch (Fig. 4). Size variation of saplings among sites does not appear to be related to variation in parameter estimates (Table 1).

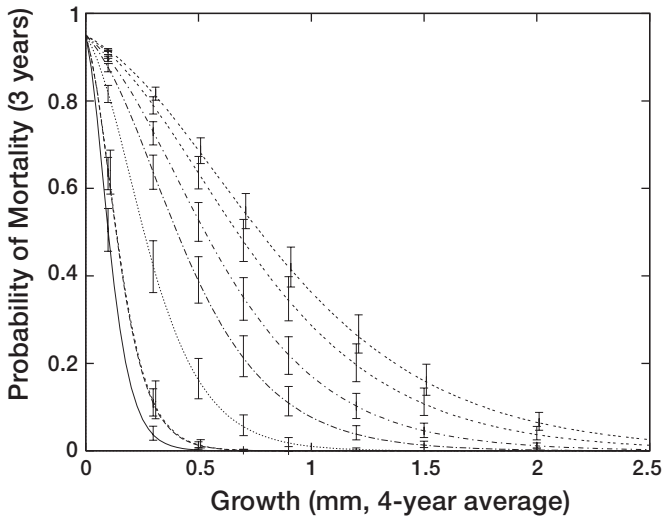
To provide good replicates, we attempted to minimize among-site variation in soil moisture (Fig. 5). Nevertheless, for six of the eight species, higher mortality was exhibited at a given growth rate at wetter sites in comparison to drier sites (Fig. 5). One of the exceptions, spruce, was sampled from very similar sites and showed no significant among-site variation in mortality models (Fig. 5). The other exception, paper birch,

exhibited the lowest growth-dependent mortality at the driest of the three sampled sites, but the highest mortality at the intermediate site (Fig. 5).

Discussion

Our study has shown significant interspecific variation in juvenile mortality among the major tree species in northwestern British Columbia. The species exhibited a broad and continuous range of variation in the functional relationship

Fig. 2. Generalized species models of mortality probability (over 3 years) as a function of recent growth (the arithmetic average of the 4 most recent complete years of radial growth) using eq. 7 and C_{gen} estimates. Note the continuous and significant variation among these species, ordered from left to right as redcedar, western hemlock, subalpine fir, hybrid spruce, lodgepole pine, aspen, cottonwood, and paper birch.



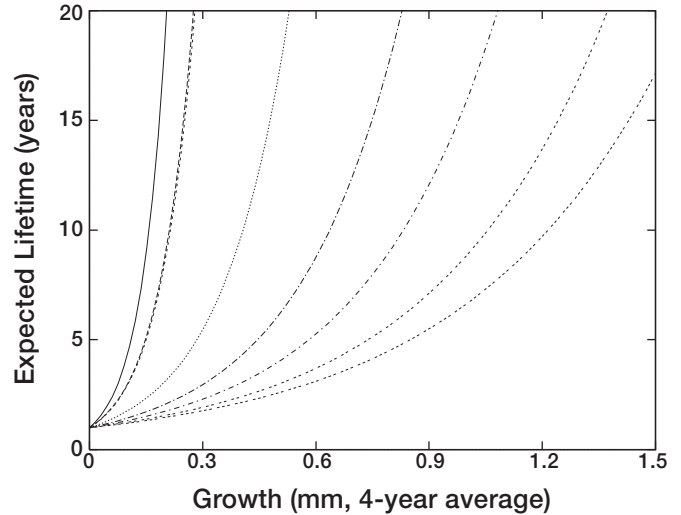
between mortality and recent growth. At certain growth rates, there was more than an order of magnitude difference in mortality between western redcedar and paper birch, the most and least shade tolerant of the species examined, respectively. Our rankings based on mortality functions were consistent with previous qualitative categorizations into shade tolerance classes (Minore 1979; Krajina et al. 1982; Burns and Honkala 1990) and with the relative dominance of these species during forest succession (Habeck 1968; Krajina 1969; Franklin and Dyrness 1973; Turner 1985).

Interspecific variation in mortality and its potential consequences

Numerous studies have grappled with finding adequate quantitative definitions of shade tolerance (Walters and Reich 1996). In a series of papers examining the same species as this study, K. Klinka and colleagues focused on relative height increment under low light, specific leaf area, and seedling vigor as components of shade tolerance. They used these measures to qualitatively rank western redcedar (Carter and Klinka 1992; Wang et al. 1994) and western hemlock (Carter and Klinka 1992) as very tolerant, subalpine fir as tolerant (Klinka et al. 1992), interior spruce as moderately tolerant (Kayahara et al. 1996), and lodgepole pine (Kayahara et al. 1996) as intolerant. In general, they found that shade-tolerant species had some combination of higher leader extension growth, specific leaf area, and vigor under low light. Our results are consistent with the shade tolerance rankings of these earlier studies; furthermore, our characterization of the relationship between mortality and recent growth has provided a direct and simple measure of shade tolerance, which we have been able to summarize with a single statistical parameter.

The mortality models, when expressed as expected lifetimes, are consistent with the idea that shade-tolerant species (redcedar, western hemlock, subalpine fir) can persist for long

Fig. 3. Expected sapling lifetime as a function of recent radial growth. The species order is the same as in Fig. 2.

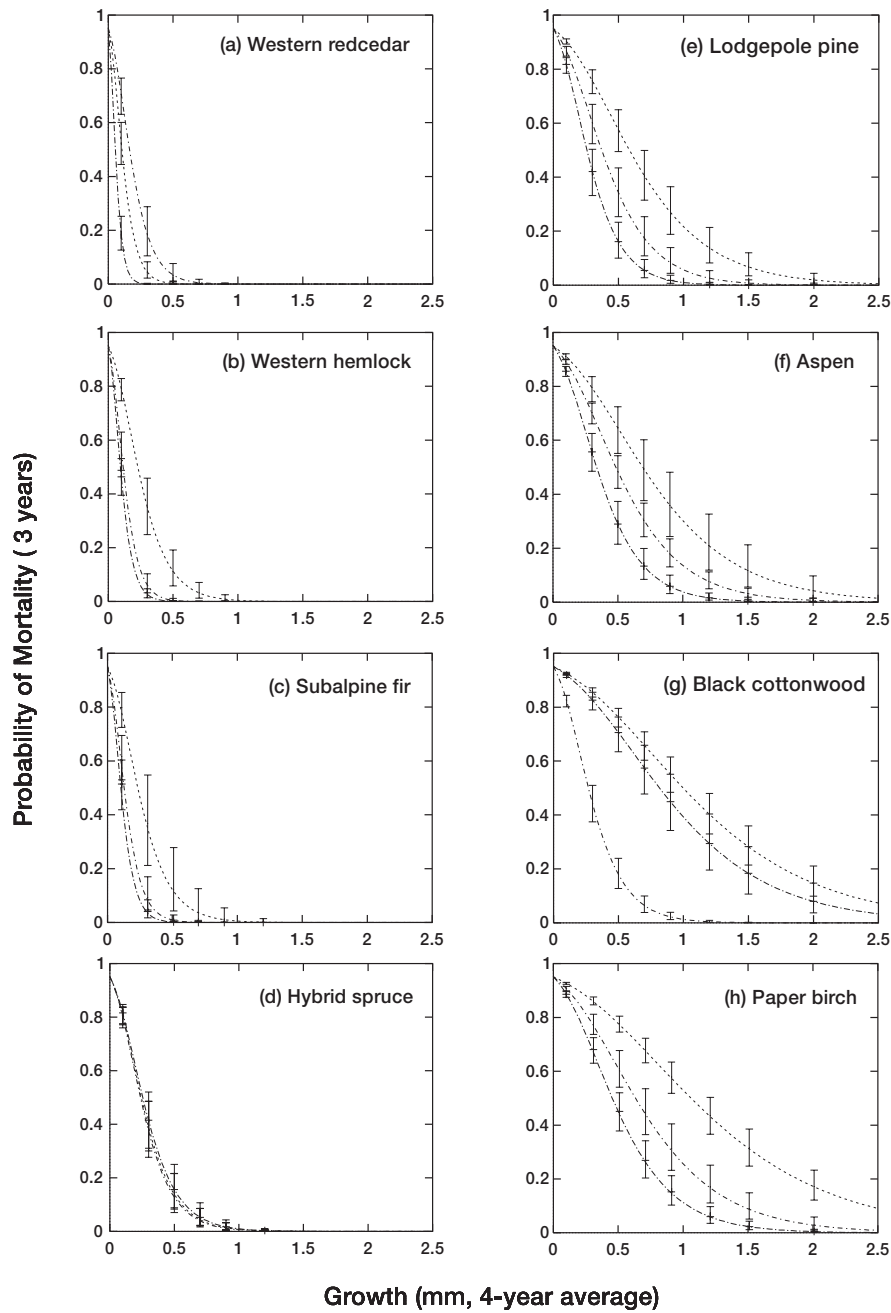


periods under suppressed growth in the understory and that shade-intolerant species (cottonwood and paper birch) cannot survive when suppressed (Canham 1985, 1989, 1990). Expressing shade tolerance in terms of persistence under suppressed growth provides a link between the species-specific mortality of individuals and the return time of enhanced light in canopy gaps. For example, consider the case where the return time of elevated levels of light for the average location in the understory is as short as 10 and 20 years (Canham et al. 1990). Even given this very short return interval, only four species (redcedar, hemlock, fir, and spruce) could persist for 10–20 years at growth rates <0.5 mm and have advance regeneration positioned to take advantage of gap openings. When gaps occur over longer intervals, even fewer species could be maintained as advance regeneration in the understory.

Our results could provide an explanation for the strong relationship between the size of gaps created in 1954–1961 and the number and kind of species that were present in 1994 at Date Creek (Coates and Burton, 1997). In gaps <75 m², only western redcedar, western hemlock, and subalpine fir were encountered, those species with the lowest mortality functions in the present study. Spruce, a midtolerant species according to our results, occurred in gaps 75–150 m². Lodgepole pine, which we found to be less shade tolerant, was only encountered in gaps >2400 m². Aspen and cottonwood, among the least shade tolerant species in the present study, were not encountered in any of the old gaps (Coates and Burton, 1997).

In a study of forest chronosequences after large disturbances, Habeck (1968) described a successional sequence of species dominance that also could be explained in part by the mortality functions presented here. Aspen and cottonwood dominance were associated with stands <50 years old, subalpine fir and lodgepole pine were associated with stands <200 years old, and redcedar and hemlock represented most of the basal area of the oldest sampled areas (400 years) (Habeck 1968). Numerous other studies have found similar successional sequences of species relative dominance after large disturbances (Franklin and Dyrness 1973). The differential ability of species to survive under conditions of suppressed growth documented

Fig. 4. Among-site variation in three species-specific mortality models. All species except hybrid spruce show significant differences in mortality models between at least two sites. There is a clear trend of less steep mortality functions moving from panels (a) through (h) corresponding to a continuum of shade tolerance.



by our mortality functions could be one of the mechanisms that lead to these successional patterns.

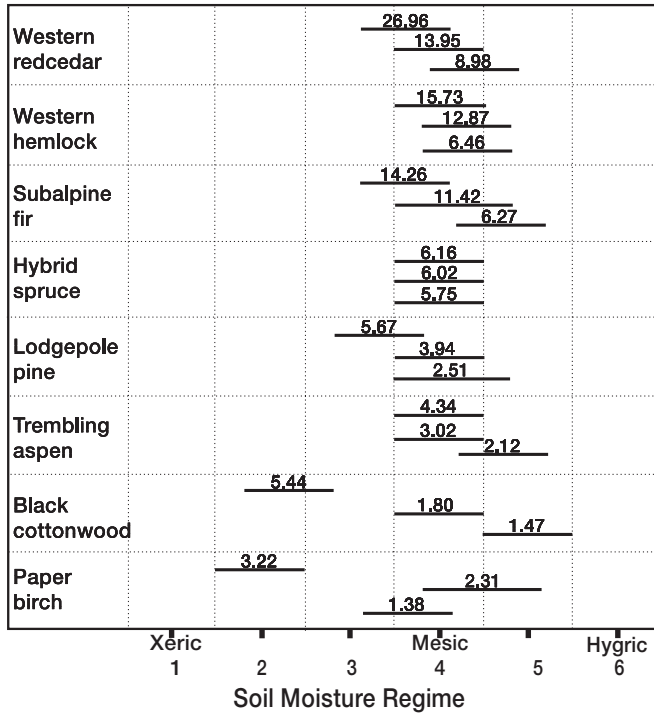
The large interspecific differences in mortality that we have characterized likely have tremendous influence on forest community dynamics and succession. Similar levels of variation in species-specific mortality in hardwood-conifer forests of southern New England are critical to understanding and predicting the dynamics of those forests (Kobe et al. 1995; Pacala et al. 1996). Once we have completed the calibration of SORTIE (Pacala et al. 1993, 1996) for the interior cedar hemlock forests of British Columbia, we will be able to undertake similar tests

of the relative importance of mortality processes in influencing forest dynamics and succession.

Intraspecific (among-site) variation in mortality

We used the three study sites for each species primarily as replicates and attempted to restrict sampling to mesic sites. Nevertheless, over even a very narrow range of site conditions, we found a negative relationship between survivorship and soil moisture. Similarly, Carter and Klinka (1992), Klinka et al. (1992), Wang et al. (1994), and Kayahara et al. (1996) found a negative relationship between soil moisture and relative height

Fig. 5. Relationship between the site-specific C parameter of the mortality model (within the box) and range of soil moisture regimes in a site. Note that we attempted to restrict sampling to mesic sites when possible in order to reduce variability. Nevertheless, variation in soil moisture is negatively correlated with mortality model parameter estimates within species.



increment under low light, but across a much wider range of soil moisture regimes (from the coast to interior) than our study.

The association between mortality and soil moisture might arise from variation in carbohydrate allocation to above- and below-ground plant components. Assume that mortality depends on total plant carbon gain (Kobe et al. 1995). In drier sites, a larger proportion of net carbon gain might be allocated to roots rather than aboveground radial increment (Madsen 1994; Creelman et al. 1990). Thus the drier site would appear to be more shade tolerant because these trees exhibit the same mortality rates at lower levels of radial growth than the wetter site. Furthermore, it is likely that a shift in carbohydrate allocation to root growth will directly enhance survivorship on drier sites. It is important to point out that the among-site variation in mortality models documented here is not likely to have significant consequences for forest dynamics. Because the relationship between soil moisture and mortality functions changes in the same direction for most species, competitive shifts among sites over this narrow range of soil moistures would not be expected to occur.

Our results demonstrate clear and significant differences in mortality among juveniles of eight canopy tree species of northwestern British Columbia. Moreover, the species ranks in mortality functions are consistent with other qualitative rankings of shade tolerance and parallel previously documented forest successional sequences after disturbance. The consistency in species order between mortality models and successional sequences suggests that species-specific differences in

noncatastrophic juvenile tree mortality are critical to understanding and predicting forest community dynamics and succession in this region.

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