

Sapling size influences shade tolerance ranking among southern boreal tree species

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Summary

1 Traditional rankings of shade tolerance of trees make little reference to individual size. However, greater respiratory loads with increasing sapling size imply that larger individuals will be less able to tolerate shade than smaller individuals of the same species and that there may be shifts among species in shade tolerance with size.

2 We tested this hypothesis using maximum likelihood estimation to develop individual-tree-based models of the probability of mortality as a function of recent growth rate for seven species: trembling aspen, paper birch, yellow birch, mountain maple, white spruce, balsam fir and eastern white cedar.

3 Shade tolerance of small individuals, as quantified by risk of mortality at low growth, was mostly consistent with traditional shade tolerance rankings such that cedar > balsam fir > white spruce > yellow birch > mountain maple = paper birch > aspen.

4 Differences in growth-dependent mortality were greatest between species in the smallest size classes. With increasing size, a reduced tolerance to shade was observed for all species except trembling aspen and thus species tended to converge in shade tolerance with size. At a given level of radial growth larger trees, apart from aspen, had a higher probability of mortality than smaller trees.

5 Successional processes associated with shade tolerance may thus be most important in the seedling stage and decrease with ontogeny.

Key-words: boreal forest, carbon balance, ontogeny, Québec (Canada), radial growth, sapling mortality, shade tolerance, succession

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Introduction

Shade tolerance is an important ecological concept that is viewed as a driving mechanism behind succession, where shade-intolerant species are replaced by species that are able to reproduce and grow in their own and other species' shade. This sequence is an essential component behind many of the classic theories of succession in which, in the absence of large-scale disturbance, forests become increasingly dominated by shade-tolerant individuals (Whitmore 1989; Kobe *et al.* 1995; Catovsky & Bazzaz 2000).

Shade tolerance in tree species, however, is a difficult concept to quantify. Early classifications of species shade tolerance were based on a relative ranking of one species to another (Baker 1949; Ellenberg 1979; Burns & Honkala 1990). Thus the class 'intolerant' conveys the requirement of open, high-growth conditions, 'mid-tolerant' describes the ability to tolerate shade during some phases of the tree's life cycle, and 'tolerant' describes species that are able to reproduce and survive in low growth conditions found under heavy shade (e.g. balsam fir). Recent applications of maximum likelihood (Kobe *et al.* 1995; Kobe 1996; Kobe & Coates 1997), Bayesian methods (Wyckoff & Clark 2000, 2002) and survival analysis (Lin *et al.* 2001) have attempted to quantify shade tolerance in seedlings and saplings by examining

the functional relationship between recent growth and the probability of mortality. Growth is used as a predictor because it integrates the effects of different stresses, particularly light availability, on tree vigour and carbon balance and thus on the risk of mortality (Buchman *et al.* 1983; Pedersen 1998). These studies have successfully reproduced generally accepted ranks of species shade tolerance, with the added benefit of yielding quantitative metrics that can be compared. In this paper, we also use growth-dependent mortality to gain insight into shade tolerance, recognizing that growth-dependent mortality differs from shade tolerance (mortality under low light) because of species differences in low-light growth.

Studies of shade tolerance have tended to focus on differences among species for young and/or small individuals (Walters & Reich 1996) without explicit consideration of size (but see Buchman *et al.* 1983). It is not clear, however, whether shade-tolerance rankings should remain constant across all stages of development. Trees experience ontogenetic shifts in several important traits as they increase in size (Clark & Clark 1992; McConnaughay & Coleman 1999; Messier & Nikinmaa 2000; Enquist & Niklas 2002; Lusk 2004). For example, the decrease in the ratio of photosynthetic to non-photosynthetic biomass with increasing size (Waring 1987; Givnish 1988) suggests that size should be explicitly considered. The few studies that have evaluated the effect of size on the risk of mortality, compared overstorey and understorey trees (Wyckoff & Clark 2002) in which differences in both size-dependent growth and environmental conditions would be expected to be extreme. In terms of population mortality rates, large individuals often have lower mortality rates than smaller individuals (Goff & West 1975; Harcombe 1987), but population-level rates potentially confound the effects of tree size, access to resource availability and carbon balance.

We examined size-class and species differences in the functional relationship between mortality and recent growth for seedlings and saplings across a light gradient. In particular, we tested two hypotheses: (i) species differences in growth-dependent mortality (as a proxy for mortality in low light) are related to conventional shade tolerance ranking; and (ii) larger individuals within the same species will have a higher mortality at a given growth rate than smaller individuals.

STUDY SITES

All tree species except yellow birch were sampled in the Lake Duparquet area (latitude 48°30' N, longitude 79°27' W) of the northern clay belt, a large physiographic region in Quebec and Ontario created by lacustrine deposits of the maximum post-Wisconsin extension of the proglacial lakes Barlow and Ojibway (Vincent & Hardy 1977). This region is located at the southern limit of the boreal forest and the forests are dominated by balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) (BSP)), paper birch (*Betula*

papyrifera Marsh.), white spruce (*Picea glauca* (Moench) Voss), and trembling aspen (*Populus tremuloides* Michx.). Jack pine (*Pinus banksiana* Lamb.) is also present on some sites and eastern white cedar (*Thuja occidentalis* L.) may dominate where fire has not occurred for long periods. The mean annual temperature is 0.6 °C, mean annual precipitation is 820 mm and the annual frost-free period is 64 days. However, freezing temperatures may occur throughout the year.

Yellow birch (*Betula alleghenensis* Britton) was sampled in the Portneuf region of central Québec, Canada (47°N latitude and 72°W longitude), within the balsam fir–yellow birch forest zone where there is a mix of the species found in boreal forests to the north and hardwood forests to the south. Dominant tree species include red spruce (*Picea rubens* Sarg.) as well as balsam fir and yellow birch and, in some stands, there may also be important concentrations of red maple (*Acer rubrum* L.), paper birch and pin cherry (*Prunus pennsylvannica* L.f.). A number of shrub species are also important elements of the understorey community, including mountain maple (*Acer spicatum* Lam.), striped maple (*Acer pennsylvanicum* L.) and hobblebush (*Viburnum angustifolium*). Topography in the region is hilly and soils are primarily till-derived.

Mean annual temperature in the Portneuf region varies between 1.0 and 2.5 °C and total annual precipitation from 900 to 1100 mm. As the Portneuf region is in close proximity to urban centres, much of the region's forests have experienced some form of harvesting in the past. We selected study sites that showed no signs of recent cutting or other human disturbances.

Methods

FIELD SAMPLING AND GROWTH MEASUREMENTS

We developed and evaluated field-parameterized models of probability of mortality as a function of recent radial growth for seven species important in boreal and near boreal forests. The species evaluated were trembling aspen, paper birch, yellow birch, white spruce, mountain maple, balsam fir and eastern white cedar. For each species, we attempted to sample an equal number of individuals across different size classes. Size classes varied depending on species growth rate, with fast growing species sampled in larger size classes (Table 1). For example, aspen, a clonal species reproducing primarily from root suckers, exhibits rapid early growth, often attaining a height of up to 1 m in the first year. Aspen clonal connections, although maintained in smaller saplings, may disappear in larger individuals (DesRochers & Lieffers 2001). When species were not abundant, we sampled two size classes, whereas for abundant species we used three size classes (Table 1).

Two criteria were employed in choosing appropriate field sites for our statistical methods: adequate sample sizes to estimate parameters for the mortality model

Table 1 Characteristics of live and dead trees by size class and composition. Species are ordered by shade tolerance ranking as suggested in the literature (Burns & Honkala 1990 for the tree species and Rook 2002 for mountain maple)

Species	Class (m)	Dead				Live			
		d.b.h. (mm)		Total height (cm)		d.b.h. (mm)		Total height (cm)	
		Average	SD	Average	SD	Average	SD	Average	SD
Balsam fir	0–1	8.0	4.6	54.4	16.6	9.97	3.6	61.7	20.32
	1–2	21.9	8.6	146.7	59.2	22	7.1	143.6	38.7
	2–4	33.1	9.9	281.1	81.6	34.68	9.5	271.4	98.8
White cedar	0–1.5	11.2	5.7	81.8	29.6	12.66	7.6	86.7	49.1
	1.5+	23.2	8.1	186.9	61.0	31.5	9.4	178.2	43.2
Mountain maple	0–2	13.1	6.8	136.1	46.6	31.75	13.4	134.3	109.7
	2–4	31.8	13.4	334.8	109.7	25.07	10.3	350.3	107.3
White spruce	0–1	7.6	6.0	62.8	22.1	8.95	2.5	64.7	23.7
	1–3	14.1	4.8	138.5	35.1	16.67	4.5	143.3	37.2
Yellow birch	0–1	6.1	4.6	64.1	3.6	6.1	4.6	94.0	36.1
	1–2	10.2	6.4	108.1	6.0	10.2	6.4	178.1	78.0
	2–4	25.9	11.6	242.2	11.9	25.9	11.6	342.2	99.3
Paper birch	0–2	13.6	14.7	118.4	45.2	11.0	4.3	107.3	45.5
	2–4	20.1	6.3	281.0	78.6	23.6	7.8	401.6	389.0
Aspen	0–2	13.2	10.3	145.6	44.7	17.2	32.4	184.6	89.7
	2–4	24.7	8.7	272.8	81.0	27.7	13.6	369.3	160.8
	4+	49.1	11.8	644.0	159.6	46.1	10.5	618.6	140.9

and sufficient variation in the predictor variable (see below). Our sampling protocol requires finding sufficient numbers of live and recently dead individuals of a focal species at the same sampling site. Finding adequate sample sizes for live individuals was rarely a problem, but finding adequate numbers of recently dead individuals was often difficult. Hence, the minimum size of a sample site had to be large enough to include a target of 30 recently dead individuals of the focal species. This resulted in variably sized sample sites ranging from approximately 40 to 8000 m². The smaller sample areas were for the more common species (e.g. balsam fir and trembling aspen), for which high densities of individuals occurred in the smaller size classes. Larger individuals, as well as species with lower densities (e.g. cedar and the largest size class of aspen) required the largest sample areas. We sampled three replicate sites of each species size-class combination for a total of 45 sites. Sampling occurred in 1998 for balsam fir, white spruce and trembling aspen, in 1999 for mountain maple, cedar and paper birch and in 2000 for yellow birch. Sample sites were located where we expected variation in the recent growth of individuals (the predictor variable), i.e. across light gradients found between gap and non-gap environments. To span variation in growth rates, we randomly sampled live individuals, stratified across the heterogeneous growth environments at each site.

Three sets of field data were collected at each sample site: (i) the numbers of live and dead individuals of the focal species at the site were used to estimate mortality rate; (ii) a random sample of live individuals was selected for growth measurements; and (iii) a random sample of dead individuals allowed growth leading up to death to be measured. The total numbers of live and

dead individuals of a focal species were estimated by either sampling the entire population or subsampling with randomly placed rectangular quadrats. Depending on the sample site, a different number (between three and eight) and different size (5 m², 10 m², 20 m², 50 m² and 100 m²) of quadrats was used.

Stem cross-sections at 10 cm above the root collar were obtained for a random sample of live individuals ($25 \leq N \leq 55$) and a random sample or the entire population of recently dead individuals ($21 \leq N \leq 57$). For our approach to work, it is important that our sample of recently dead trees contains only individuals whose likely cause of death was growth-related suppression. We carefully excluded any recently dead trees that showed signs of disease, herbivory, insect-infestation or mechanical damage. Annual growth rings 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 VELMEX digital ring analyser (0.025 mm resolution) connected to a 40X stereo microscope. In young individuals (< 10 years) all rings were measured, whereas in older individuals only the 10 most recent rings were measured.

Dead saplings used for growth measurements were estimated to have died within the last 3 years (i.e. 'recently dead' individuals were defined using methods developed by Kobe *et al.* (1995) and Kobe & Coates (1997) and validated for our study sites). By selecting only individuals that show no external causes of death we focus on growth-related mortality and by focusing on the three most recent years of growth we are able to evaluate whether the risk of mortality for an individual sapling increases as growth rate decreases.

Time since death was estimated using the best discriminating features of buds (presence, intactness, colour), bark (coverage, intactness), stem suppleness and leaves (estimate of leaves/needles remaining, how easily the leaves are removed, colour, brittleness, intactness), as determined from characteristics sampled from trees that were known to have been dead (killed in spacing and weeding operations) for 1, 2, 3, 4 and 5 years. Two additional sources of information were used to establish time since death criteria. Spruce and fir saplings ($n = 10$ for each species) were transplanted into buckets and killed through lack of water and characteristics were observed over 4 years (1999–2003). In addition, criteria were validated, similarly to Newberry *et al.* (2004), against known death times from a long-term seedling monitoring project (L. Mathias *et al.*, unpublished data). For all species, we found the highest discriminating power of time of death at 3 years, as manifested by bud, bark and leaf features (Kobe & Coates 1997). Careful application of these criteria minimizes potential error in estimating time since death.

Recently dead saplings at all sites showed variation in estimated time of death, supporting the theory that mortality events occurred continuously over the 3-year window and did not occur as a response to a single anomalous event (e.g. pest outbreak, extreme drought).

PARAMETER ESTIMATION USING MAXIMUM LIKELIHOOD

We used maximum likelihood methods to estimate parameters and 95% support for species- and site-specific models characterizing the probability of mortality as a function of recent growth (g).

The statistical method that we used incorporates information from three sources in a likelihood function in order to estimate the most likely functional relationship between probability of mortality and recent growth, i.e. site-specific mortality rate based on a sampling of the population of live and dead individuals at a site, growth rates of 'recently dead' individuals (representing the last 3 years growth and thus the growth rates prior to death) and growth rates of live individuals.

We did not use the methods proposed by Wyckoff & Clark (2000) because assuming an overall mortality rate for a species and ignoring among-site variation can lead to biased estimates (R. K. Kobe, unpublished). The likelihood function that we used was

$$L = \binom{N}{D} (\bar{U}^D)(1 - \bar{U})^{N-D} \cdot \prod_{i=1}^{\#dead} \frac{h(g_i)m(g_i)}{\int_{-\infty}^{\infty} m(g)h(g)dg} \cdot \prod_{i=1}^{\#live} \frac{[1 - m(g_i)]h(g_i)}{1 - \int_{-\infty}^{\infty} m(g)h(g)dg} \quad \text{eqn 1}$$

where the first term, based on the counts of live and recently dead individuals within each study site, is the

probability that D dead saplings are encountered in a total population of N individuals (D and N estimated from the sampled quadrats) where represents the mean probability or expectation of mortality (and is estimated as the denominator in the second term), $m(g)$ is the mortality function (probability of mortality as a function of growth for an individual sapling) and $h(g)$ is the probability density function of growth rates of all saplings at a given site.

The second term in equation 1 is the conditional probability density function of growth given that a sapling will die, based on measured growth rates leading up to the mortality of the 'recently dead' saplings. The third term of the likelihood function is the probability density function of growth, conditioned on the status of being live. A search algorithm is used to test different sets of parameter values in the likelihood function to obtain those that result in the highest likelihood of replicating the data set. The conditional density function of growth given that a sapling will die is detailed in Kobe *et al.* (1995), Kobe & Coates (1997) and Caspersen & Kobe (2001).

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 & Barton 1986) to search for parameter values and functional forms of $m(g)$ and parameter values of $h(g)$ that yielded the highest likelihoods. Ninety-five per cent support intervals for all estimated parameters were estimated by inverting the likelihood ratio test (LRT) (Edwards 1992; Pacala *et al.* 1996).

We used the arithmetic average of the four most recent years of growth (excluding the last ring) based on LRT comparisons of 2, 3, 4 and 5-year averages of recent growth. Previous work (Kobe *et al.* 1995) has also shown this to provide the highest likelihoods. We excluded the most recent growth ring to ensure that growth measurements from both live and recently dead individuals were from complete growing seasons.

We specified $m(g)$ as the cumulative distribution function of an exponential random variable

$$m(g) = P(\text{death} | \text{growth}) = 1 - e^{-(t* Ae^{-B*g})} \quad \text{eqn 2}$$

where A and B are parameters to be estimated from the data. Equation 2 assumes that mortality increases with lower growth rates. Although $m(g)$ in the likelihood function could be derived analytically from density functions of growth for the live and dead individuals and mortality rate based on stem counts (Wyckoff & Clark 2000), we chose to use equation 2 instead because it is much simpler and has a more straightforward biological interpretation than the complex form of $m(g)$ derived from growth densities. In addition, the flexibility of equation 2 makes it ideal for approximating complex relationships that are analytically derived (Wyckoff & Clark 2000), as equation 2 accommodates a wide range of functional relationships between mortality and growth.

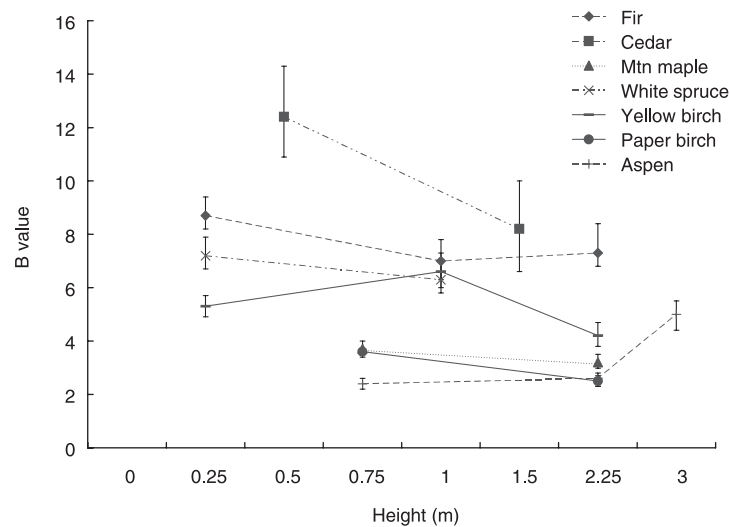


Fig. 1 The probability of mortality at low growth or B -parameter estimate for different species by size class. The B -parameter estimate is an estimate of shade tolerance.

We also tested a negative exponential model

$$m(g) = a * e^{-b*(g)} \quad \text{eqn 3}$$

and simplified forms of the negative exponential and equation 2 where A or a is set equal to one. Equation 2 with $A = 1$ resulted in the best fits weighted by the number of parameters (LRT, $P < 0.05$) and thus we report results only for this model.

VARIATION IN MORTALITY FUNCTIONS WITHIN AND AMONG SIZE CLASSES

The above methods were used to estimate parameters for species, site and size class specific mortality models. To parameterize generalized models for a species in a given size class, all three data sets for a particular species-size class combination were evaluated simultaneously. The generalized likelihood function was the product of site-specific variants of equation 2, 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 (Kobe 1996). We assessed empirical support for specifying one generalized mortality model per species-size class combination vs. site-specific mortality models with Akaike's information criteria corrected for small sample sizes (AICc). In general, the model with the lowest AICc has the greatest empirical support, with a difference of > 2 AICc units representing stronger empirical support for the model with the lower AICc (Burnham & Anderson 2002).

Similarly, we estimated a single mortality function for a given species across all sites and size classes (i.e. $m(g)$ common to all sites and size classes for a given species). The generalized species models were used as a basis for comparison with size class specific models to assess empirical support for effects of size class on the functional relationship between probability of mortality

and recent growth. We compared size class specific vs. generalized species models using AICc. All results are expressed in terms of ΔAICc , which is defined as the AICc of a given model minus the minimum AICc (Burnham & Anderson 2002); thus, the best supported model will have $\Delta\text{AICc} = 0$.

Results

INTERSPECIFIC PATTERNS IN SMALL SIZE CLASSES

As stated above, a simple one-parameter model (equation 2 with $A = 1$) was found to best describe the relationship between probability of mortality and recent growth. The B parameter, which determines how rapidly mortality decreases with increases in growth, thus serves as a simple quantitative index of species- and size-dependent effects on growth-dependent mortality: higher estimates of B characterize sharper declines in mortality with small increases in growth and thus greater tolerance of low-growth.

In smaller size classes, relationships between the probability of mortality and recent growth (as encapsulated by B estimates) tended to sort by species' recognized shade tolerance rankings (Table 2 and Fig. 1). Amongst all studied species, small cedar seedlings were most likely to survive at low growth rates ($B = 12.4$). Balsam fir ($B = 9.5$), although sometimes recognized as the most shade-tolerant species, ranked second in our study (Fig. 1). White spruce had the next lowest probability of mortality at a given growth rate ($B = 7.2$) and then yellow birch ($B = 5.3$).

Mountain maple ($B = 3.7$ with C.I. of 3.5–4.0) and paper birch ($B = 3.6$ but with similar C.I. of 3.4–4.0) in the smallest size class had relatively high growth-dependent mortality. The mortality probability of these two species at a given growth rate was thus indistinguishable and is only exceeded by that of trembling aspen ($B = 2.4$ with

Table 2 Estimates of *B* from equation 2 across species and size classes. Species are ordered by shade tolerance ranking as suggested in the literature (Burns & Honkala 1990 for the tree species and Rook 2002 for mountain maple). Details on the height class sizes and how they are determined for the small, intermediate and large size classes are given in the methods

Species	Site	<i>B</i> estimate (95% confidence interval) by size classes			Traditional shade tolerance ranking
		Small	Intermediate	Large	
Balsam fir	1	8.3 (7.2–9.9)	6.4 (5.1–8.2)	6.1 (5.2–10.4)	Very tolerant
	2	12.5 (11.49–15.2)	8.8 (7.0–10.8)	6.3 (5.6–7.1)	
	3	8.4 (7.2–9.9)	6.6 (5.6–7.5)	9.9 (8.4–16.0)	
	All	9.5 (8.4–10.05)	7.0 (6.3–7.8)	7.3 (6.7–8.0)	
White cedar	1	8.7 (6.2–11.2)	7.4 (5.3–10.0)	–	Tolerant
	2	14.1 (10.9–18.2)	8.0 (5.3–12.0)	–	
	3	18.4 (15.0–22.9)	10.0 (6.7–13.2)	–	
	All	12.4 (10.9–14.3)	8.2 (6.7–10.0)	–	
Mountain maple	1	4.5 (4.2–4.9)	2.9 (2.6–3.4)	–	Tolerant
	2	2.7 (2.3–3.2)	2.5 (2.0–3.0)	–	
	3	3.6 (3.2–4.0)	4.3 (3.7–4.9)	–	
	All	3.7 (3.6–4.0)	3.3 (2.9–3.5)	–	
White spruce	1	6.0 (5.3–6.7)	8.8 (6.3–11.7)	–	Intermediate tolerant
	2	9.2 (7.1–11.7)	6.7 (5.5–8.1)	–	
	3	8.3 (6.9–9.9)	5.7 (4.9–6.4)	–	
	All	7.2 (6.7–7.9)	6.3 (5.8–6.9)	–	
Yellow birch	1	4.9 (4.4–5.6)	6.9 (6.1–7.9)	5.8 (4.4–7.8)	Intermediate tolerant
	2	4.1 (3.2–5.3)	5.0 (3.8–6.5)	3.3 (2.7–4.0)	
	3	6.1 (5.4–6.9)	6.9 (5.6–7.6)	4.8 (4.0–5.7)	
	All	5.3 (4.9–5.7)	6.5 (5.9–7.3)	4.2 (3.7–4.7)	
Paper birch	1	2.9 (2.4–3.4)	1.5 (1.2–1.8)	–	Intolerant
	2	4.9 (4.4–5.4)	5.3 (4.9–5.7)	–	
	3	3.0 (2.5–3.6)	2.5 (2.2–2.8)	–	
	All	3.6 (3.4–4.0)	2.5 (2.3–2.7)	–	
Aspen	1	2.2 (1.8–2.6)	2.6 (2.3–3.0)	3.3 (2.7–4.3)	Very intolerant
	2	3.7 (3.1–4.1)	2.9 (2.5–3.3)	5.5 (4.4–6.6)	
	3	1.6 (1.3–1.9)	2.3 (2.0–2.7)	6.2 (5.2–7.4)	
	All	2.4 (2.2–3.7)	2.6 (2.4–2.8)	5.0 (4.4–5.5)	

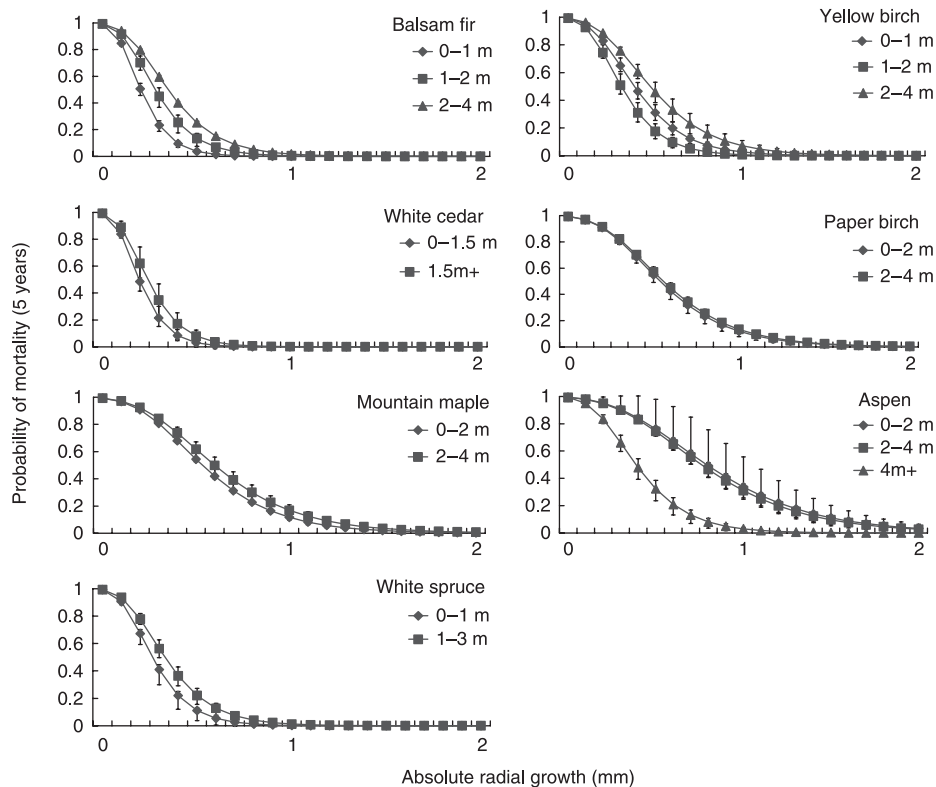


Fig. 2 Changing probability of mortality (over 4 years) as a function of recent radial growth (the arithmetic average of the five most recent complete years of radial growth) by size class using equation 2 and the calculated *B*-values for all species size class combinations.

Table 3 (a) ΔAICc values for a general model vs. separate site-specific models. Smaller values between the two columns convey stronger empirical support. It is generally accepted that empirical support for models is equivocal when $\Delta\text{AICc} < 2$; some support is indicated for the model with lower AIC when $2 < \Delta\text{AICc} < 10$; very strong empirical support is indicated for a model when $\Delta\text{AICc} > 10$ (Burnham & Anderson 2002). (b) Delta AICc values for a single general model for a species vs. models that are size class dependent

(a)		ΔAICc	ΔAICc
Species	Size class (m)	General model	Separate sites model
Balsam fir	0–1	32.7	0
Balsam fir	1–2	1.2	0
Balsam fir	2–4	10.8	0
Cedar	0–1.5	12.7	0
Cedar	1.5–3	0	3.5
Mountain maple	0–2	21.2	0
Mountain maple	2–4	19.0	0
White spruce	0–1	6.9	0
White spruce	1–2	3.2	0
Yellow birch	0–1	6.2	0
Yellow birch	1–2	0.6	0
Yellow birch	2–4	7.2	0
Paper birch	0–2	24.1	0
Paper birch	2–4	14.4	0
Trembling aspen	0–2	51.5	0
Trembling aspen	2–4	0	0.2
Trembling aspen	4 m+	16.6	0
(b)	ΔAICc	ΔAICc	
Species	General model all classes combined	Models including size classes	
Balsam fir	21.8	0	
Cedar	7.5	0	
Mountain maple	1.5	0	
White spruce	0	1.8	
Yellow birch	25.6	0	
Paper birch	23.0	0	
Trembling aspen	25.6	0	

C.I. = 2.2–2.6). Trembling aspen, consistent with expectations, had the highest growth-dependent mortality (as indicated by non-overlapping C.I.'s) (Fig. 1, Table 2).

VARIATION IN GROWTH-DEPENDENT MORTALITY AMONG SITES

Variation in growth-dependent mortality was observed among sites for most species size class combinations (Tables 2 and 3). Eastern white cedar, in the large size class, was the only species for which the data (as interpreted from the ΔAICc values) do not support site-specific mortality models (Table 3). There was relatively weak empirical support for site-specific models vs. general models ($\Delta\text{AICc} < 2$) for mid-sized balsam fir, yellow birch and trembling aspen (Table 3).

INTRASPECIFIC VARIATION WITH SIZE CLASS

Most species followed the hypothesized trend of having a greater risk of growth-dependent mortality as they increased in size (Figs 1 and 2 and Table 3). Results for cedar, balsam fir and paper birch clearly supported our first hypothesis by showing across-size class variation in the functional relationship between mortality and recent growth (Fig. 2, Table 3). Cedar's probability of

mortality at a growth of 0.5 mm varied from 1% in the smallest size class to 8% in the largest. Balsam fir's probability of mortality was clearly different between the smallest and the next two larger size classes (as indicated by non-overlapping 95% support limits and ΔAICc in Table 3). For example, at a growth rate of 0.5 mm, balsam fir's probability of mortality more than doubled from 6% in its smallest 0–1 m height size class to 14% for individuals between 2 and 4 m in height (Fig. 2). Likewise, at 0.5 mm growth the probability of mortality for the smallest paper birch stems was 51–63%, but increased to 73–79% in the largest size class.

Although yellow birch had different mortality between all size classes (as assessed by non-overlapping 95% confidence intervals in the B -value and ΔAICc in Table 3), growth-dependent mortality was slightly hump-shaped. The lowest growth-dependent mortality occurred in the middle size class (probability of mortality = 18% at 0.5 mm growth). However, consistent with most species, the highest probability of growth-dependent mortality occurred in the largest size class (46% at 0.5 mm growth) (Figs 1 and 2).

Mountain maple and white spruce, evaluated in only two size classes, exhibited similar trends in B parameter estimates across size classes as cedar, balsam fir and the two birches. However, the empirical support for differ-

ences in probability of mortality between size classes in these species was weak, with ΔAICc values < 2 for both species (Table 3). Thus, the data do not support size class specific mortality models over a general model for these two species.

The only species that responded in the opposite direction to our hypothesis was trembling aspen, which had a decreased growth-dependent mortality with increasing size class. Aspen's probability of mortality at 0.5 mm growth was 78% (C.I. 75–81%) in the smallest size class vs. 33% (C.I. = 24–39%) in the largest size class.

Interestingly, species tended to converge towards a common probability of mortality as they increased in size (Figs 1 and 2). Aspen, which has high growth-dependent mortality in smaller size classes, approached a growth-dependent mortality in larger size classes that is similar to more shade-tolerant coniferous species. For example, aspen's probability of mortality in the largest size class (24–39% at a growth rate of 0.5 mm) overlaps with that of the largest white spruce (C.I. = 14% to 25% at 0.5 mm) (Fig. 2). B -values of the largest aspen are also similar to small yellow birch, paper birch and mountain maple. The species with the lowest growth-dependent mortality in its smallest size class (cedar with $B = 12.4$, C.I. of 10.9–14.3) had a growth-dependent mortality indistinguishable from fir as it increased in size (cedar had a $B = 8.2$, C.I. 6.6 to 10.0 for individuals 1.5–3.0 m, whereas fir in the smallest size class had a $B = 8.7$ and C.I. 8.0–9.2). Similarly, white spruce in the smallest size class had B -values similar to larger firs.

Discussion

POPULATION VS. INDIVIDUAL RISK

On a per-capita basis, the risk of mortality is greater in small trees than in large trees, which results in a skewed survival curve such that probability of survival increases for members of the population as they get older and bigger (Goff & West 1975; Harcombe 1987). Demographic data have in fact shown that many more trees die when small than when large (Franklin *et al.* 1987), which superficially conflicts with our finding that growth-dependent mortality increases with size for juveniles of shade-tolerant species. However, smaller trees occur under lower light conditions and on average are growing more slowly than larger trees and thus would be expected to have a higher probability of mortality at the population level. What our study thus shows is that, for a given level of radial growth, larger trees in fact have a higher probability of mortality than smaller trees.

SPECIES COMPARISONS

In the smallest size classes, species ranks in growth-dependent mortality were generally consistent with shade-tolerance rankings noted in the literature (Baker

1949; Burns & Honkala 1990; Bergeron 2000), with cedar > balsam fir > white spruce > yellow birch > mountain maple = paper birch > aspen. In the literature balsam fir is often suggested to be the most tolerant species although this is equivocal and cedar has been reported to have varying degrees of tolerance depending on the study region (Burns & Honkala 1990). These results support our first hypothesis and are consistent with our understanding that less shade-tolerant tree species have characteristics that favour high-light growth, while limiting survival in low light or when growth is suppressed (Kobe *et al.* 1995). These characteristics may include reduced plasticity in crown architecture (i.e. they conserve metabolic structure), higher relative growth rates and higher respiration under all environmental conditions, and lower allocation to roots than more shade-tolerant species (Lei & Lechowicz 1990; Messier *et al.* 1999; Coomes & Grubb 2000; Bloor & Grubb 2003; Lusk 2004).

Our finding that mountain maple has relatively high mortality at low growth may appear to conflict with the observation that mountain maple often occurs in mixed boreal understories (DeGrandpré & Bergeron 1997). However, mountain maple density and size have been shown to increase strongly with increases in understorey light availability (Batzer & Popp 1985; Kneeshaw & Bergeron 1999). Furthermore, this species is usually abundant only under aspen canopies that transmit more than 10% full sun, and not under darker coniferous canopies (Messier *et al.* 1998). In fact, Lei & Lechowicz (1990) described mountain maple as having lower survival and plasticity in shade compared with other maple species.

Although sampling a species across a wide range of site conditions was not an explicit goal, our results suggest that there can be substantial variation among sites in growth-dependent mortality. Site variation probably reflects differences in soil resources (Kobe 1996; Caspersen & Kobe 2001; Machado *et al.* 2003; Schreeg *et al.* 2005).

SIZE EFFECTS ON SHADE TOLERANCE

Most species exhibited higher growth-dependent mortality with increasing size (Tables 2 and 3). That is, for a given growth rate, the probability of mortality for these species increased as their size increased (in some cases size may also be correlated with age). This result is consistent with the idea that more energy is allocated to support non-photosynthetic tissue (i.e. maintenance and construction costs) as tree size increases (Waring 1987; Givnish 1988), with responses including greater allocation to fine roots (Cheng *et al.* 2005), increased mechanical support (Givnish 1988; Enquist & Niklas 2001) and more complex branch architecture (Cao 2001; Farque *et al.* 2001; Claveau *et al.* 2002).

The overall recruitment strategy in shade of various tree species may therefore change not only in relation to environmental conditions and variability (Kubota

et al. 1994; Clark *et al.* 1996; Caspersen & Kobe 2001), but also due to ontogenetically related constraints. The decrease in the ability of most of the studied species to survive at low growth rates as size increases supports our second hypothesis. As further support for this ontogenic shift, examples have been reported where small tree seedlings of shade-tolerant species were able to survive in low light, but required an increase in light levels to grow to larger sizes (Messier *et al.* 1999). In fact, shade-tolerant species may lose their crown plasticity (an ability that allows them to be more tolerant) as they grow taller (Messier & Nikinmaa 2000). This decreasing ability to modify their architecture (i.e. investments in mechanical structure cannot be removed) to capture limited light could explain the increase in mortality at low growth as they increase in size.

Surprisingly, the tree species considered the most intolerant of shade (aspen) actually had decreased mortality with increases in size, contrary to our second hypothesis and not explicable by most ecophysiological comparisons between shade tolerant and intolerant tree species. However, as most ecophysiological comparisons have been conducted on smaller seedlings, it is possible that differences between shade tolerant and intolerant tree species disappear with increasing size. Although we do not have any ecophysiological explanation, it is possible that aspen becomes more tolerant to shade with increasing size, as its clonal connections become weaker. Our data indeed suggest that, as differences in growth-dependant mortality become minimal with increasing size, species may converge in shade tolerance with increasing size (Fig. 1). Messier & Nikinmaa (2000) showed that the differences in crown morphology and allocation between shade-tolerant (sugar maple and American beech) and mid-shade-tolerant (yellow birch) species disappear with increasing size. Therefore, in contrast with shade-tolerant conifers, shade-intolerant trees that survive through smaller size classes and attain larger stature may develop traits that confer shade tolerance, such as larger root mass with higher storage capabilities (Kobe 1996; Canham *et al.* 1999) and, possibly, deeper rooting depths to enable greater access to soil water that would also promote survivorship (Nicotra *et al.* 2002). Lusk (2004) also noted that intolerant species do not decrease root mass as size increases. Further studies are needed to elucidate the mechanisms underlying these ontogenetic shifts.

Conclusions

Traditional shade-tolerance rankings (Baker 1949; Burns & Honkala 1990) hold most strongly for smaller individuals. The differences among species decrease with size as most species become less shade tolerant as they increase in size. The overall regeneration strategy (i.e. growth and mortality) of understorey trees may therefore change not only in relation to environmental conditions and variability (Clark *et al.* 1996), but also due to ontogenetic constraints that vary among species groups.

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