Multiple resource limitation and ontogeny combined: a growth rate comparison of three co-occurring conifers

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Abstract: The combined effects of light, soil fertility, and ontogenetic changes on plant growth rates are poorly understood, yet these three factors play fundamental roles in structuring plant communities. We sought to determine how lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia*), interior spruce (*Picea glauca* × *engelmanii* (Moench) Voss), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) sapling growth responds to the combination of light, soil fertility, and ontogeny and how these three dominant conifer species in sub-boreal forests of British Columbia differ in their responses. Using maximum likelihood methods, we found that 0.20–4 m tall sapling growth rates changed during ontogeny and were limited by both light and soil resources. The strongest differences among species' growth rates were due to tree size, with smaller differences due to soil fertility, and there were no differences among species in the shape of their growth responses to light. Rank order in growth rates for small saplings (pine > spruce > fir) inversely corresponded to classic shade-tolerance ratings, thus supporting the carbon balance theory. Interior spruce height growth rates increased relative to lodgepole pine with increasing soil fertility, clearly matching the landscape-scale increase in canopy dominance of interior spruce over lodgepole pine with increasing soil fertility.

Résumé : On comprend mal les effets combinés de la lumière, de la fertilité du sol et des changements ontogénétiques sur le taux de croissance des plantes bien que ces trois facteurs jouent un rôle fondamental dans l'établissement de la structure des communautés végétales. Nous avons cherché à déterminer comment la croissance des gaules de pin tordu (*Pinus contorta* Dougl. ex Loud. var. *latifolia*), d'épinette de l'intérieur (*Picea glauca* × *engelmanii* (Moench) Voss et de sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.) réagit à la combinaison de lumière, de fertilité du sol et d'ontogénie et de quelle façon la réaction de ces trois espèces dominantes de conifères diffère dans les forêts subboréales de la Colombie-Britannique. À l'aide des méthodes du maximum de vraisemblance, nous avons trouvé que le taux de croissance des gaules de 0,20 à 4 m de haut a changé durant l'ontogénie et était limité par la disponibilité de la lumière et des ressources du sol. Les plus grandes différences entre le taux de croissance des espèces étaient dues à la dimension des arbres et dans une moindre mesure à la fertilité du sol; il n'y avait pas de différence entre les espèces quant à la forme de leur réaction de croissance à la lumière. L'ordre du classement du taux de croissance des petites gaules (pin > épinette > sapin) correspond à l'inverse du classement classique pour la tolérance à l'ombre, ce qui supporte la théorie de l'équilibre du carbone. Le taux de croissance de l'épinette de l'intérieur a augmenté par rapport à celui du pin tordu avec l'augmentation de la fertilité du sol, ce qui correspondait clairement, à l'échelle du paysage, à l'augmentation de la dominance de l'épinette de l'intérieur dans le couvert au détriment du pin tordu en lien avec l'augmentation de la fertilité du sol.

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Introduction

A major goal of plant ecology is to understand how plant species' responses to multiple environmental factors affect plant community distributions across landscapes (Chapin et al. 1987), competitive and successional dynamics within a community, and species coexistence (Tilman 1990). According to the results of economic cost–benefit analyses (Chapin et al. 1987), a plant's growth and fitness are maximized when resource allocation is regulated within a plant to create limitation by multiple resources. However, a resource allocation strategy that optimizes growth in one environment will be suboptimal in a different environment (Tilman 1990). Because species vary in their resource allocation patterns and physiological requirements, different combinations of environmental resources alter community dynamics, thereby affecting plant growth directly through limitation and indirectly through competitive interactions among species (Chapin et al. 1987).

In forest communities, the environmental resources best known to limit tree growth and affect competition are light and soil fertility (Latham 1992; Kobe 1996), and compari-

sons of growth rates among species along light or soil fertility gradients have generally corresponded with changes in forest canopy composition across landscapes (Read 1995; Montague and Givnish 1996; Lusk and Matus 2000). Species are typically not equally fast growing or competitive along an entire resource gradient, which often is explained using the carbon balance theory — the trade-off between allocating carbon to plant attributes that promote fast growth at high resource availability or to attributes that support survival at low resource availability (Givnish 1988). Evidence from many studies suggesting that carbon allocation patterns may change over different life stages (McConnaughay and Coleman 1999; Lusk 2004; Niinemets 2006) complicates our understanding of plant carbon balance and distinct species niches along light and soil fertility gradients (Gilbert et al. 2006; Niinemets 2006). Further investigation is required into how ontogeny (i.e., the history of structural and developmental change in an organism) affects growth rate comparisons and our interpretations of forest dynamics. Some studies have provided supporting evidence for ontogenetic differences among species (e.g., Clark and Clark 1999; Boyden et al. 2009), while others have found that most species change similarly through their life stages (e.g., Gilbert et al. 2006; Kneeshaw et al. 2006). Furthermore, large methodological differences exist among studies (Gilbert et al. 2006). McConnaughay and Coleman (1999) found that light, soil fertility, and ontogeny had important effects on annual plant growth in a greenhouse experiment, but the combined effects of these factors on woody plant growth along natural resource gradients are poorly understood. In the case of the major boreal and sub-boreal tree species of North America, the effect of light availability on growth has been explored as well as the combined effect of light availability and ontogeny, but the combined effect of light, soil fertility, and ontogeny has not been explored through a field experiment to date. In our study area, the sub-boreal forest of northern interior British Columbia, lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia*) decreases in canopy dominance over interior spruce (*Picea glauca* × *engelmanii* [Moench] Voss) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) along strong landscape gradients of increasing soil fertility (Kranabetter and Simard 2008). Soil fertility in this article refers to correlated soil moisture and nutrient availability gradients (>200% change in gravimetric soil moisture content, available N, and exchangeable cations) corresponding to changes in forest productivity (Kranabetter et al. 2007; Kranabetter and Simard 2008). The conifers we studied are also known to differ in mortality rates in low light (pine > spruce > fir; Kobe and Coates 1997) and in growth rates in high light (pine > spruce > fir; Wright et al. 1998) and to have growth rates influenced by ontogeny (Claveau et al. 2002). Our goal for this research is to further our understanding of the combined effects of resource availability on three major conifers species to improve our overall understanding of stand and forest dynamics by exploring two research questions. (1) How is sapling growth affected by light, soil fertility, and ontogeny? and (2) How do three co-occurring conifer species differ in response to limited resources and ontogeny?

To address our research questions, we develop multiple working hypotheses in a model comparison framework. These hypotheses are a series of nested equations that include combinations of light availability, soil nutrient and moisture availability, and tree size to predict tree growth rates. We use parameters estimated during the model comparison to quantitatively assess how light, soil fertility, and ontogeny affect growth rates, and we rigorously test which of these parameter estimates represent important differences among species.

Materials and methods

Study area and field sampling

The study sites were located near Smithers (54°35′N, 126°55′W), northwestern British Columbia, in the Sub-Boreal Spruce (Moist Cold subzone Babine Variant) part of the Canadian Boreal Forest Region. The continental climate of the sub-boreal spruce forest has cold, snowy winters with temperatures below 0 °C for 4–5 months and short, warm summers; 25%–50% of the 440–900 mm mean annual precipitation falls as snow (Meidinger et al. 1991). Three conifer species dominate the landscape but vary in abundance across soil fertility gradients. Lodgepole pine stands dominate on the poorer and drier soils in the region, where coarse soil texture, steep slopes, and shallow soils limit water availability and lead to an understory dominated by *Ericaceae* and lichen, where N is available primarily as dissolved organic nitrogen. Interior spruce and subalpine fir tend to dominate mature forests on moisture-receiving sites (toe slopes, riparian areas, etc.) where finer textured soils and higher water availability have led to a herbaceous understory community and higher N availability as dissolved organic nitrogen, NH_4^+, and NO_3^-. Sites characterized by intermediate soil moisture and nutrient availability often support mixed forests of all three conifer species, with *Ericaceous* and herbaceous understory vegetation (Kranabetter et al. 2007; Kranabetter and Simard 2008). Landscape drainage patterns create soil fertility gradients over very short distances, and stands of different canopy composition can be of similar age (Kranabetter et al. 2007) and even originate from a single extensive fire event. Historically, most stands in this region were initiated by wildfires and experienced semi-synchronous recruitment by lodgepole pine, interior spruce, and subalpine fir soon afterwards. For stands on mesic soils, two main succession trajectories have been identified for the first 200 years after fire: (*i*) lodgepole pine establishes in high numbers and quickly dominates the stand due to its rapid early growth, and (*ii*) lodgepole pine establishment is limited and interior spruce and subalpine fir dominate the stand (Kneeshaw and Burton 1997; Clark et al. 2003).

We sampled saplings of different sizes from across a wide range of light levels and soil fertility levels (Fig. 1). We obtained an evenly distributed sample by purposeful sampling from 100 categories consisting of five height classes, namely 20–80 cm, 80–160 cm, 160–240 cm, 240–320 cm, and 320–500 cm, combined with five estimated light classes, namely 0%–20%, 20%–40%, 40%–60%, 60%–80%, and 80%–100%, and four site types, ranging from dry and nutrient poor to nutrient rich and moist, with distinct and well-described vegetation associations: *Cladonia* spp., Huckleberry (*Vaccinium membranaceum* Dougl. ex Torr.), Oakfern (*Gymnocarpium dryopteris* (L.) Newman), and Devil's club (*Oplopanax horridus* (Sm.) Miq.) (Banner et al. 1993). The relatively low

Fig. 1. Distribution of sampled lodgepole pine ($n = 265$), interior spruce ($n = 372$), and subalpine fir ($n = 468$) saplings across light and soil nutrient availability gradients.
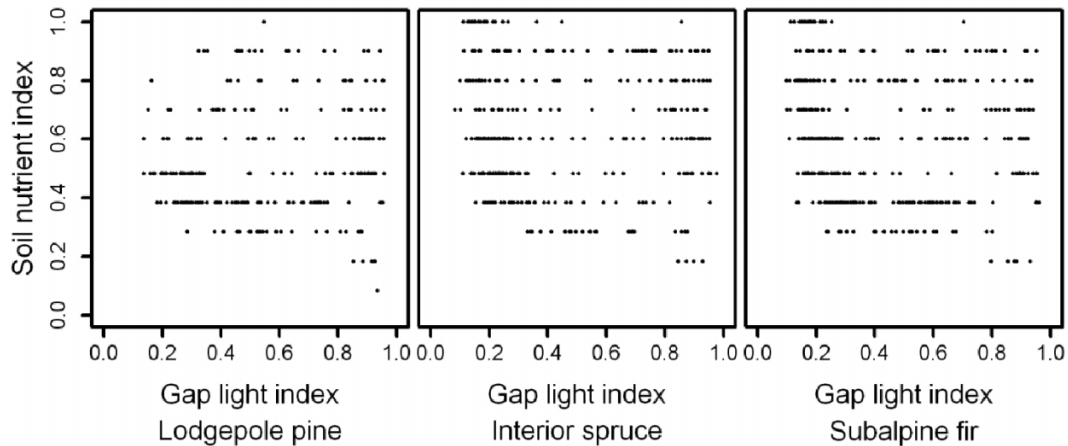
frequency of certain combinations of resource availability (e.g., low light, low soil fertility, and large saplings) rendered purposeful sampling the only feasible sampling scheme to yield a full representation of the resource gradient in an efficient manner. We identified 132 plots with these environmental conditions located in 51 different forest stands within a 50 km radius of Smithers, B.C. The canopy cover of the plots included full forest cover, natural forest gaps, partial cuts, and full clear-cuts. Soil moisture and nutrients were correlated on this fertility and productivity gradient, and we avoided sampling from sites with organic or saturated soils or with cold air drainage that could have confounded the limitations to tree growth through low O_2 availability or low temperatures. To avoid other possible confounding factors, we did not sample trees with obvious biotic or abiotic damage or trees from logged areas where site preparation had occurred, and a further requirement was that all sites had a minimum of 6 years of release since disturbance.

During late summer and fall 2007, we sampled 468 subalpine fir saplings, 372 interior spruce saplings, and 265 lodgepole pine saplings and measured their total height and height growth increment for the last three growing seasons (2005–2007). Stem cross sections from all saplings were collected at a height of 10 cm above the forest floor, air dried, and measured for 2005–2007 radial growth increments on two average radii using a Velmex Inc. (Bloomfield, New York, USA) measuring unit. Initial height and diameter at 10 cm (diameter$_{10}$) were calculated by subtracting the 2005–2007 growth increments from the 2007 height and diameter$_{10}$. A hemispherical photograph was taken at 1.3 m above the stump of each sapling using a Nikon (Mississauga, Ontario, Canada) Coolpix 5000 digital camera with a fisheye lens. Hemispherical canopy photos were analyzed with Gap Light Analyzer software (GLA 2.0) (Frazer et al. 2000) to obtain the gap light index (GLI), a measurement from 0 to 1 of the proportion of photosynthetically active radiation above the canopy transmitted to a point in the understory over the growing season (Canham 1988). Soil moisture and nutrient availability indices were each assessed on a scale from 0 to 1 (0 = xeric or very poor and 1 = hygric or very rich) from soil pits within a few metres of each sapling. Assessments were based on field-identifiable soil characteristics (slope po-

sition, soil texture, coarse fragment content, depth to bedrock, water table fluctuations and depth, pH, presence and depth of eluviation in the A horizon, and humus form) according to the B.C. Biogeoclimatic Classification System soil moisture regime key and soil nutrient regime table (Banner et al. 1993). This classification has been shown to define a strong soil moisture and nutrient availability gradient that is linearly related to dissolved inorganic and organic nitrogen, gravimetric soil moisture, and asymptotic stand height (Kranabetter et al. 2007; Kranabetter and Simard 2008). As a direct measure of soil nutrient availability, foliar N concentration was measured from needles collected from the 2007 growth of each sapling. After oven-drying at 70 °C for 24 h, the needles were separated from the twigs by hand, milled using a cyclonic mill (FOSS Tecator Cyclotec, Höganäs, Sweden), and analyzed on a Fisons Carlo-Erba NA-1500 (CE Elantech, Lakewood, New Jersey, USA) combustion-type NCS analyzer at the B.C. Ministry of Forests and Range Analytical Laboratory in Victoria, B.C.

Modeling approach

To determine how multiple resources and ontogeny influence sapling growth, we developed models to predict sapling height and radial growth as a function of light availability, soil resource availability, and sapling size. Based on the theory of multiple resource limitation, each species in our models has a maximum potential growth rate (MaxPG), which is the growth rate achieved by a hypothetical tree with full resource availability. MaxPG is reduced by light limitation and also by soil resource limitation, which are applied as multipliers ranging between 0 and 1, depending on the resource availability. Ontogenetic changes in resource acquisition from the environment and in within-plant carbon allocation are represented by size function (also a multiplier ranging between 0 and 1):

$$[1] \quad \text{Realized growth} = \text{MaxPG} \times L \times R \times S$$

where MaxPG is the parameter estimated from the data, L is the light limitation function, R is the soil resource limitation function, and S is the size function. In this model, at a resource limitation of 0, growth is 0, and at a resource limitation of 1, growth is no longer limited by that resource.

Table 1. Tested model functional forms, parameters, and biological interpretations using the variables gap light index (GLI), soil resource availability (measured by soil nutrient index SN), and tree size (measured as height or diameter$_{10}$) to predict annual height growth or annual radial growth at 10 cm.

Model	Functional form	Parameters	Biological interpretation
1	MaxPG	MaxPG: maximum potential annual growth	Growth is not affected by factors measured in the study
2	$\text{MaxPG} \times (\text{GLI} - \iota)^a$	a: shape of the light limitation curve	Growth is limited by light availability
		ι: x intercept of the light limitation curve (light compensation point)	
3	$\text{MaxPG} \times \text{SN}^b$	b: shape of the soil resource limitation curve	Growth is limited by soil nutrient availability
4	$\text{MaxPG} \times (1 - \text{e}^{(-c \times \text{Size})})$	c: shape of the size limitation curve	Growth is limited by tree size
5	$\text{MaxPG} \times (\text{GLI} - \iota)^a \times \text{SN}^b$		Growth is limited by light and soil nutrient availability
6	$\text{MaxPG} \times (\text{GLI} - \iota)^a \times (1 - \text{e}^{(-c \times \text{Size})})$		Growth is limited by light availability and tree size
7	$\text{MaxPG} \times (\text{GLI} - \iota)^a \times \text{SN}^b \times (1 - \text{e}^{(-c \times \text{Size})})$		Growth is limited by light availability, soil nutrient availability, and tree size

Multiplicative relationships among the limitation functions allow for synergistic plant responses to multiple resources (Chapin et al. 1987).

The severity of a resource limitation at a given resource level is determined by the resource limitation function. We used a power function to represent soil resource limitation:

$$[2] \qquad R = (\text{soil resource availability})^b$$

A power function has the flexibility to represent an asymptotic, exponential, or linear relationship when the estimated parameter b is less than 1, greater than 1, or 1, respectively. We tested three different measurements of soil resource availability in the model: soil nutrient index, soil moisture index, and foliar N concentration. Light limitation was represented by a power function with an intercept parameter because total growth limitation by light was expected at a GLI level greater than 0:

$$[3] \qquad L = (\text{GLI} - t)^a$$

where the estimated parameter t represents the light compensation point and where, like b in eq. 2, the estimated parameter a determines the shape of the curve. The size-effect curve was represented by a Weibull function:

$$[4] \qquad S = 1 - \text{e}^{(-c \times \text{size})}$$

where c is an estimated parameter that determines at what size (initial height or diameter$_{10}$) the asymptote of 1 is approached. We expected an asymptotic shape for the size curve because size effects on growth rate have been shown to diminish as size increases (Claveau et al. 2002).

Model comparison and parameter estimation

To investigate the strength of light, soil resource, and size effects on sapling growth, we compared seven nested models for each species (Table 1). The full model included light, soil resource, and size effects (a, b, and $c \neq 0$), and the suite of reduced models was considered by setting R, L, and (or) S to

1 (Table 1). The difference in AIC$_c$ between the best model and each other model (ΔAIC$_c$) was compared. According to Burnham and Anderson (2002), models with ΔAIC$_c$ of 0–2 have substantial support from the data, models with ΔAIC$_c$ of 4–7 have considerably less support, and models with ΔAIC$_c > 10$ have essentially no support. We used a simulated annealing algorithm (Goffe et al. 1994) implemented in R (R Development Core Team 2007) in the likelihood package (Murphy 2006) to parameterize the models and calculate support intervals (Edwards 1992) for parameter estimates.

Model residuals were distributed normally but exhibited heteroscedasticity. Consequently, the models were fit with a normal probability density function (error distribution) where the variance increased proportionally to the predicted value. The error (ε_i) for the ith observation was modeled as

$$[5] \qquad \varepsilon_i = \varepsilon_1 \times X_i$$

where X_i is the predicted value and ε_1 is a parameter estimated with maximum likelihood simultaneously with all the parameters from the functional form.

To assess the degree of differential resource limitation among species, we tested for species-specific differences among parameters a, b, c, t, and MaxPG in the full model (model 7, Table 1). The test was performed in two steps: (1) five tests, one for each of parameters a, b, c, t, and MaxPG, to identify whether the parameters exhibited species-specific differences, and (2) a post-hoc pairwise comparison to identify for which of the three species combinations the differences were valid (analogous to tests such as Tukey's HSD). Both steps were implemented by utilizing (0–1) indicator variables for the tested species-specific parameters while fitting all other parameters as non-species-specific. Step 2 was only implemented for parameters that were found to differ in step 1. In both steps, a ΔAIC$_c$ value of greater than 2 for models with identical parameters among or between species was taken as substantial support from the data that model 7 with a species-specific parameter was the better model.

Table 2. ΔAIC_c and R^2 comparison of models 1–7 for (a) height and (b) radial growth for all species.

		Lodgepole pine		Interior spruce		Subalpine fir	
Model	Variables	ΔAIC_c	R^2	ΔAIC_c	R^2	ΔAIC_c	R^2
(a) Comparison for height growth							
1	Null	377	0.00	645	0.00	715	0.00
2	Light	191	0.40	296	0.41	346	0.39
3	Soil nutrients	357	0.08	620	0.03	698	0.01
4	Size (height)	329	0.10	582	0.05	628	0.07
5	Light and size	70	0.64	132	0.64	120	0.55
6	Light and soil nutrients	162	0.45	241	0.44	274	0.46
7	Light, soil nutrients, and size	0	0.68	0	0.70	0	0.65
(b) Comparison for radial growth							
1	Null	618	0.00	838	0.00	855	0.00
2	Light	318	0.50	382	0.46	319	0.47
3	Soil nutrients	584	0.10	822	0.02	850	0.00
4	Size (diameter$_{10}$)	378	0.40	612	0.18	647	0.16
5	Light and size	113	0.75	132	0.73	73	0.66
6	Light and soil nutrients	252	0.56	331	0.47	263	0.49
7	Light, soil nutrients, and size	0	0.82	0	0.80	0	0.71

Results

Model comparison

ΔAIC_c comparisons revealed that across all species, model 7 ($\Delta AIC_c = 0$) had the most support in predicting both height and radial increment (Table 2). This indicates that sapling growth was limited by light and soil resource availability and that growth rates were affected by ontogeny. The amount of variation explained by model 7 was high, with respective height and radial increment models associated with R^2 values of 0.68 and 0.82 for lodgepole pine, 0.70 and 0.80 for interior spruce, and 0.65 and 0.71 for subalpine fir (Table 2; Fig. 2). Considering the three explanatory variables independently, light availability explained the most variation in growth rates, whereas soil resource availability explained the least (Table 2).

When model 7 was tested with different soil resource availability measurements as predictors of sapling growth rates, foliar N concentration models had the most support for subalpine fir, soil nutrient index models had the most support for lodgepole pine, and the soil nutrient index and foliar N models were similar for interior spruce. Soil moisture index models had the least support (Appendix A, Table A1). Overall, the soil nutrient index models had the lowest ΔAIC_c scores across species and are used hereafter in the presentation of the results and discussion, although the same conclusions would have been drawn using soil moisture or foliar N as the soil resource availability measurement.

Parameter estimates and growth predictions

We found ΔAIC_c support for differences among species in soil nutrient limitation on height growth (b_{height}) and for differences among species in patterns of height (c_{height}) and radial (MaxPG$_{radius}$) growth across ontogeny, with stronger support for ontogenetic differences than soil nutrient limitation differences (Table 3, column 2). The post-hoc pairwise species comparison indicated that the b_{height} estimate for pine growth differed from that of spruce, the c_{height} estimate for pine growth differed from those of both spruce and fir, and

the MaxPG$_{radius}$ estimate for fir growth differed from those of both pine and spruce (Table 3, columns 3–5). There was no support for differences among species for seven out of 10 of the height and radial growth parameters, including those for growth responses to light (Table 3, column 2).

The parameter estimates for a (shape of the light limitation curve) were close to 1, and estimates for t (the light compensation point) ranged from 3.8% to 7.8%, indicating that all species had a linear growth response to light availability and that growth was completely limited somewhere below a <10% light availability threshold (Table 4). According to model 7 growth predictions, at 25% light, all species were growing at similarly slow rates across sapling sizes and soil nutrient availabilities (Fig. 3). As light availability increased, all species' growth rates increased and their different height growth responses to size and soil nutrient availability became apparent, as did their different maximum radial growth rates (Fig. 3).

The difference between the b (shape of the soil nutrient limitation curve) parameter estimate between lodgepole pine (0.58) and interior spruce (0.83) height growth indicates that pine height growth had a more asymptotic response to increasing soil nutrient availability, whereas spruce had a more linear response (Table 4). Pine height growth was less limited by low soil nutrient availability than spruce, but the height growth rates of spruce increased more than those of pine at high soil nutrient availability (Fig. 3a). On very rich soils, spruce height growth rates of saplings over 3 m tall matched those of pine (Fig. 3a). In contrast, radial growth rates had very similar b estimates among species, and spruce radial growth rates never approached the growth rates of pine across the soil nutrient gradient (Table 4; Fig. 3b). The b estimate for subalpine fir height growth was between the estimates for the other two species, and ΔAIC_c results indicated that firs' response to soil nutrient availability did not differ substantially from the responses of either pine or spruce.

The height growth parameter estimates for c (the shape of the size effect curve) parameter were the inverse of classic

Fig. 2. Model 7: predicted versus observed (*a*) height and (*b*) radial growth rates of sampled lodgepole pine (*n* = 265), interior spruce (*n* = 372), and subalpine fir (*n* = 468) saplings compared with a 1:1 line including goodness of fit.
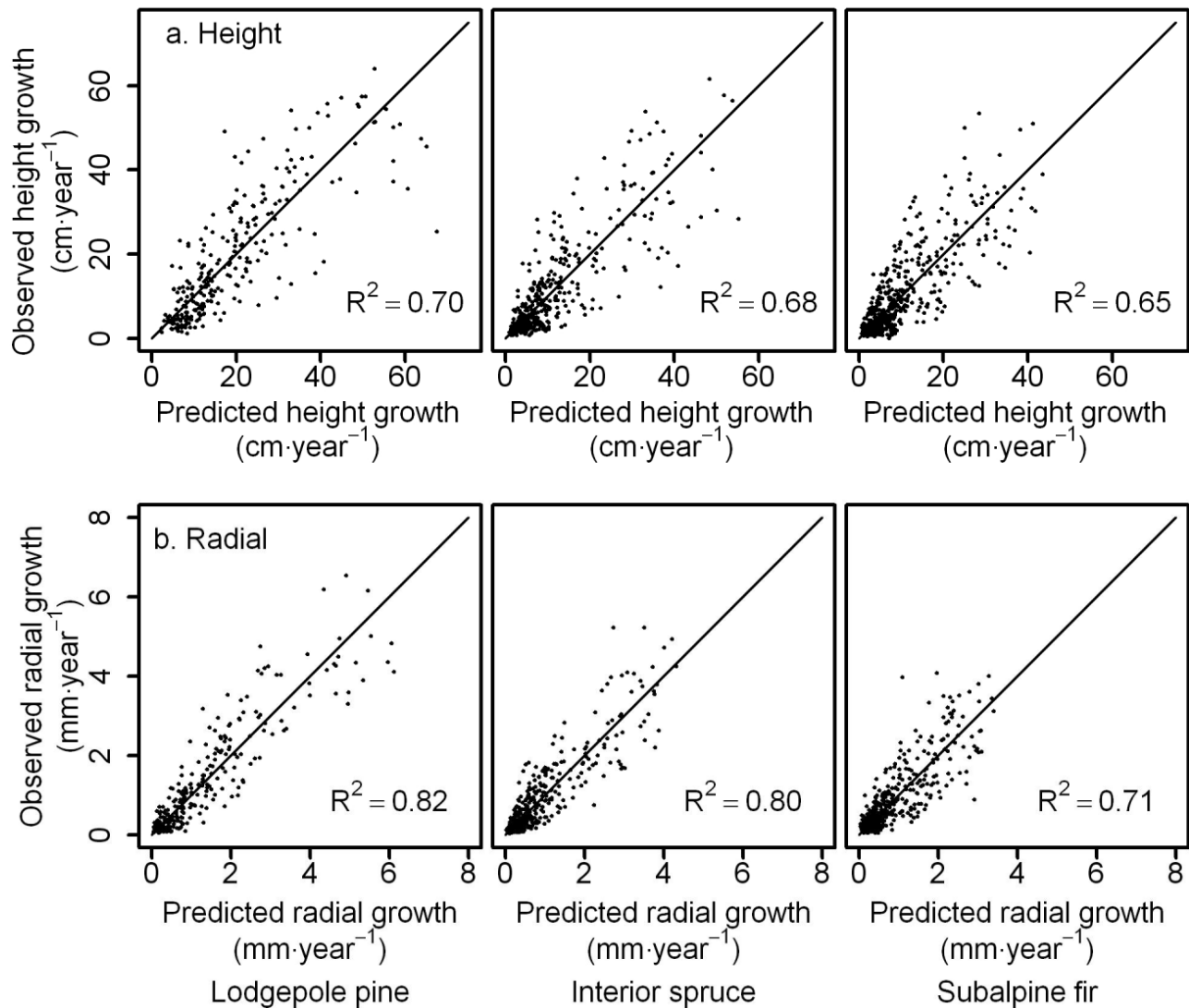
shade-tolerance rankings (subalpine fir > interior spruce > lodgepole pine): $c = 0.0146$ for pine, $c = 0.0068$ for spruce, and $c = 0.0051$ for fir (although the c estimates for spruce and fir were not differentiated from each other by ΔAIC_c evidence). For saplings under 3 m tall, lodgepole pine height growth rates always exceeded spruce and fir height growth rates, but pine approached its height growth asymptote at smaller sapling sizes than spruce and fir, which were able to "catch up" in growth rate in the case of saplings over 3 m tall on rich sites (Fig. 3*a*). Although pine had a different ontogenetic path for reaching its maximum height growth, its MaxPG estimate for height was similar to that of spruce and fir, indicating that all species are capable of attaining the same maximum growth rate at some point during their lives.

For radial growth, the species followed similar patterns of increasing growth rates with increasing size, but subalpine fir had a lower MaxPG estimate than pine and spruce (Tables 3 and 4) and consequently slower radial growth rates for all tree sizes. In general, model 7 predicted the fastest radial and height growth rates for pine, followed by spruce and

then fir, over most of the size range, except for the tallest saplings (>3 m) on very rich soils, where pine no longer outgrew spruce and only slightly outgrew fir (Figs. 3*a* and 3*b*).

Discussion

Forest dynamics studies have previously found interactions between the effects of light and soil nutrients and between the effects of light and tree size on sapling growth, but the present study is one of the first to examine all three effects simultaneously (for comparisons of light and size effects in three contrasting sites, see also Kobe 1996). Our results are in line with earlier research on light and tree size interactions showing that the growth rate response of conifer saplings to higher light environments increases with sapling size (Claveau et al. 2005) and that saplings show very little growth response to tree size below a threshold light level (Claveau et al. 2002). In studies of light and soil nutrient interactions on hardwood saplings (Kobe 2006), soil nutrients generally influenced growth in high light levels, but not in low light lev-

Table 3. ΔAIC_c values for (*a*) height and (*b*) radial growth between model 7, with all species-specific parameters ($\Delta AIC_c = 0$), and model 7 formulated with a general (identical among species) parameter for pine, spruce, and fir (PSF) for each parameter at a time.

Parameter	PSF	P, SF	PS, F	PF, S
(*a*) ΔAIC_c values for height growth				
a	−2			
b	4	1	5	2
c	33	0	18	33
t	−2			
MaxPG	−3			
(*b*) ΔAIC_c values for radial growth				
a	2			
b	0			
c	0			
t	−3			
MaxPG	12	7	−2	13

Note: When $\Delta AIC_c > +2$, which indicates support for species differences in a parameter, post-hoc pairwise species comparisons were made by formulating model 7 such that only spruce and fir had identical parameters (P, SF), only pine and spruce had identical parameters (PS, F), and only pine and fir had identical parameters (PF, S); $\Delta AIC_c > +2$ for the post-hoc pairwise comparisons indicates support for differences in the parameter estimate between species in the pair. *a*, the shape of the light limitation curve; *b*, the shape of the soil nutrient limitation curve; *c*, the shape of the size effect curve; *t*, the light compensation point.

els. Across many forest types, greater effects of soil resources (experimentally altered by trenching) on seedling and sapling growth have been reported in forests with high light levels or in forest gaps compared with closed forests with low light levels (Coomes and Grubb 2000). Our model of how the combination of three factors — light, soil nutrients, and size — affects sapling growth supports and integrates the results from these above-mentioned forest dynamics studies. Additionally, we found evidence that the often overlooked interaction between soil resource and size effects can be critical for understanding shifts in competitive ranking among species.

Why do saplings show little soil fertility or tree size response in low light levels?

One explanation for why saplings show little soil fertility or tree size response in low light levels is that their growth is so strongly limited by light that their requirements for water and nutrients are reduced, and consequently, the effects of soil fertility, when detectable, are small (Machado et al. 2003) and may often be statistically undetectable. Similarly, very slow growth rates across all sizes of saplings in conditions of low light may render any ontogenetic effects on growth undetectable. Alternatively, although larger trees are assumed to be capable of intercepting more light and are growing faster than smaller trees due to their larger leaf area, they also have a larger proportion of nonphotosynthetic biomass, which creates a larger respiration cost and a potential disadvantage in low light (Messier et al. 1999). Although size and soil fertility have minimal effects on species' growth rates in low light levels, they may have an important influence on species' survivorship in understories. For many for-

ests, shade tolerance and succession are most strongly affected by differences among species in surviving low light conditions until a disturbance opens the canopy and reduces growth limitation by light (Kobe 1996; Kobe and Coates 1997; Wright et al. 1998).

Growth rate responses to tree size

Although we did not measure survivorship, inferences about growth–survival trade-offs (i.e., the carbon balance) can be drawn from species differences in the shapes of the size (height) – growth relationships and in maximum radial growth rates (the c_{height} and $MaxPG_{radius}$ parameters). Lodgepole pine saplings under 3 m tall grew the most quickly in height and radius, which is probably the result of allocating more carbon to leaf area, having shorter-lived needles than spruce and fir, and allocating less carbon to root development. Eis (1970) documented this trend in decreasing investment in roots compared with shoots with decreasing shade tolerance for 2-year-old lodgepole pine, interior spruce, and subalpine fir (shoot to root ratios of 3.4:1, 2.0:1, and 1.3:1, respectively). Claveau et al. (2002) found lodgepole pine to have younger needles (5 years) than interior spruce (6.8 years) and subalpine fir (6.6 years). These high growth rates in pine were achieved at the cost of survival levels in the shade (Kobe and Coates 1997). Subalpine fir had the most conservative grown pattern of the three species, with a maximum radial growth rate substantially lower than spruce or pine. For subalpine fir, investment in roots and storage may also trump investment in radial growth, a strategy that would help this species to survive extended periods in low resource conditions (Chapin et al. 1987). Subalpine firs over 100 years old are common in the forest understory, and subalpine fir is the dominant species in the subalpine forests in our study region (Banner et al. 1993; Antos et al. 2000).

Unexpectedly, the strongest difference among species in our study was in the effect of sapling size on height growth rates. Lusk (2004) found that light-demanding species lost their growth rate advantage over shade-tolerating species as their relative biomass distribution to leaf area declined with ontogeny. Lusk (2004) concluded that this was partially due to their shorter leaf life span and because the shade-tolerant species exhibited an initial heavy investment in root biomass that decreased with ontogeny. Eis's (1970) data on biomass distribution in our study species supports Lusk's reasoning in part because subalpine fir and interior spruce start out with the lowest shoot to root ratios and increase the ratio over time. However, lodgepole pine also invests less in roots compared with shoots over time and maintained a shoot to root ratio twice as high as that of fir and spruce after 12 years (Eis 1970). Ryan (1989) attributes declining growth efficiency with size in lodgepole pine to higher sapwood maintenance costs in large trees compared with those for spruce and fir. In combination, Lusk and Ryan's conclusions explain why lodgepole pine did not retain the fastest growth rates indefinitely and had the same $MaxPG_{height}$ as interior spruce and subalpine fir. The combination of longer-lived needles in spruce and fir (allowing them to maintain their leaf area ratio with little further carbon investment), a higher initial investment in roots, and lower sapwood respiration requirements could have resulted in more carbon available for height growth in the larger size classes. We found no effect of on-

Table 4. Maximum likelihood estimates (MLE) and support intervals (SI) for parameters of (*a*) height and (*b*) radial growth from model 7.

Parameter	Lodgepole pine MLE	Lodgepole pine SI	Interior spruce MLE	Interior spruce SI	Subalpine fir MLE	Subalpine fir SI
(*a*) **MLE and SI for parameters of height growth**						
a	1.07	1.01–1.13	1.04	1.00–1.08	0.91	0.89–0.94
b	0.58	0.52–0.64	0.83	0.75–0.91	0.76	0.70–0.84
c	0.0146	0.0131–0.0163	0.0068	0.0063–0.0073	0.0051	0.0048–0.0055
t (%)	3.8	1.9–5.6	4.9	3.8–5.9	7.7	6.9–8.5
MaxPG	83	79–86	93	89–97	94	91–98
(*b*) **MLE and SI for parameters of radial growth**						
a	1.22	1.16–1.28	0.95	0.91–0.98	0.91	0.87–0.94
b	0.68	0.62–0.74	0.73	0.66–0.80	0.56	0.49–0.62
c	0.24	0.23–0.26	0.18	0.17–0.19	0.27	0.26–0.29
t (%)	5.1	3.3–6.7	7.3	6.2–8.0	7.8	6.9–8.6
MaxPG	10.5	10.1–10.9	9.3	8.9–9.7	5.8	5.6–6.1

Note: *a*, the shape of the light limitation curve; *b*, the shape of the soil nutrient limitation curve; *c*, the shape of the size effect curve; *t*, the light compensation point.

togeny on radial growth, although ontogeny is known to affect radial growth rates for larger trees of these species (Coates et al. 2009).

The effect of ontogeny on height growth rates was to reduce interspecific differences rather than create rank reversals in growth of the type that Clark and Clark (1999) and Lusk (2004) have detected between initially fast-growing light-demanding species and shade-tolerant species. Kneeshaw et al. (2006) found that species converge in shade tolerance with ontogeny, and in our study, too, lodgepole pine, interior spruce, and subalpine fir growth rates similarly converged as trees grew taller, implying that their relative shade tolerances also converged. We take these results as evidence that growth rate comparisons for small saplings do not necessarily remain consistent for larger saplings, thus indicating that traits contributing to initially fast growth rates may be different from traits contributing to fast growth rates later in a sapling's life.

Growth rate responses to light availability

Light availability was the most important driver of sapling growth in the study, and growth rates increased linearly with light for three species of contrasting shade tolerance. The standard shape for sapling growth–light relationships in temperate conifer (Moores et al. 2007) and hardwood (Pacala et al. 1994) forests and tropical rainforests (Poorter 1999) has been asymptotic, with growth rates of 50% achieved below 50% light. On the other hand, several studies from boreal and sub-boreal conifer-dominated forests have shown quasi-linear light growth responses for radial growth (Wright et al. 1998; Coates and Burton 1999). One explanation for the discrepancies between this study and studies that show strongly asymptotic light–growth responses is that our study species do not grow in light levels as low as those of temperate and tropical forest understories. The parameter estimate for *t* (the extrapolated whole plant or field light compensation point (Givnish 1988)) in our sub-boreal forests is a light level of 3%–8%, whereas saplings have positive growth rates in 1.3% light in temperate hardwood forests and 0.5% light in tropical rain forests (Canham et al. 1990). The ability of extremely

shade-tolerant species to adapt in low light conditions may be disadvantageous in conditions of high light (e.g., Poorter (1999) observed bleaching of leaves at full irradiance in *Tachigali* spp., tropical species ranked intermediate in shade tolerance). A second explanation for more linear light–growth relationships in northern forests is that lower resource availability in colder climates with shorter growing seasons could prevent sapling survival and growth at the lowest light levels (Messier et al. 1998), whereas lower temperatures and lower water stress reduce sapling exposure in high light levels (Wright et al. 1998). Thirdly, although asymptotic growth–light relationships for spruce have been measured in boreal mixedwood forests (Lieffers and Stadt 1994), this may be explained by differences in the timing and quality of light experienced by conifers under broadleaf deciduous canopies compared with evergreen coniferous canopies. Broadleaf deciduous understories receive higher light levels during spring and autumn leaf-off periods and more diffuse light with fewer sunflecks during leaf-on periods (Messier et al. 1998).

Growth rate responses to soil nutrient availability

All three species in the study performed best with full resource availability. However, compared with pine, the height growth rates of tall spruce saplings (and to a lesser extent fir) increased as soil nutrient availability increased, a finding that supports the model of shifting competitive hierarchy (Latham 1992). The combined pattern of ontogeny and performance along the soil resource gradient is probably a driver of patterns in species composition in mature forests across the landscape, where the dominance of lodgepole pine in relation to interior spruce and subalpine fir decreases as soil fertility increases (Kranabetter and Simard 2008). Pine had the overall fastest growth rates but the smallest response to nutrient availability, which is the reverse of the patterns in canopy composition documented by Read (1995), Montague and Givnish (1996), and Lusk and Matus (2000), in which dominance by the fastest growing tree species increased at the richer end of a soil fertility gradient. On the natural fertility gradients in our study area, where the form of N co-varies along with total N availability, soil moisture, and mycorrhizal

Fig. 3. Model 7: (*a*) height and (*b*) radial growth rate predictions as a function of initial tree size across light and soil nutrient availability gradients. (Figure 3 is concluded on the next page.)
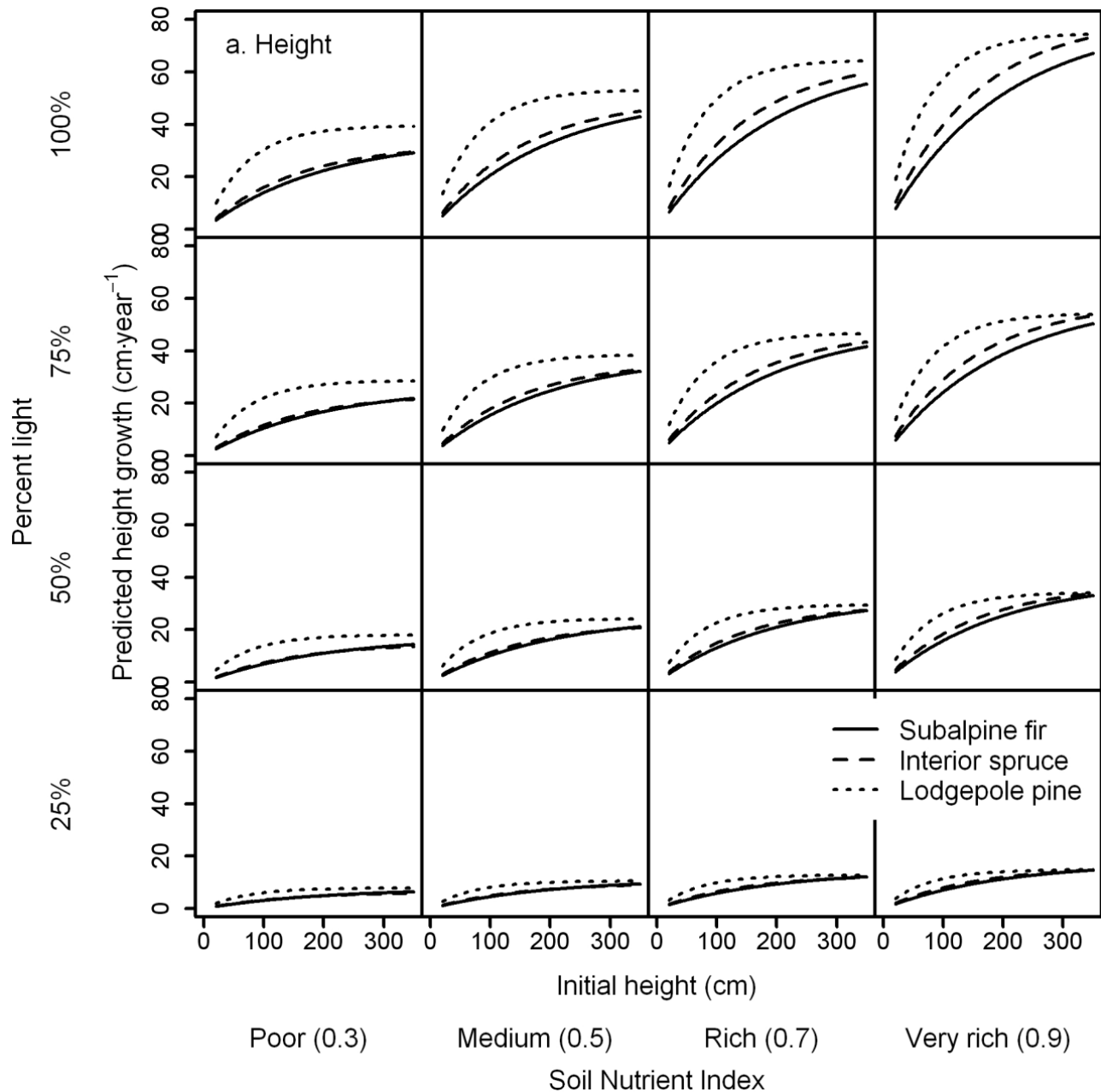
fungi community composition (Kranabetter et al. 2007, 2009), root adaptations in *Pinus* spp. that increase resource uptake at low N availability may not be advantageous at medium or high N availability. Characteristics conferring the superior performance of *Pinus* spp. on poor soils (Coomes and Grubb 2000), but not necessarily on richer soils, could include high N-use efficiency (resulting from a combination of high N productivity due to high foliar efficiency and low N losses due to efficient N translocation from senescing needles (Bothwell et al. 2001)), associations with the high N containing mycorrhizal fungi *Suillus* spp. (Bothwell et al. 2001; Kranabetter et al. 2006), and deep rooting patterns in coarse soils (Eis 1970).

The role of growth rate comparisons in predicting stand development

The ontogeny-influenced shifting hierarchy in height growth rates among the studied three species is only one of the drivers of stand development in sub-boreal spruce forests. Position along soil moisture and nutrient gradients potentially interacts with fire severity, substrate composition, and seed availability to affect the amount, timing, and configuration of sapling establishment and growth, thus determining future canopy composition (Kneeshaw and Burton 1997; Clark et al. 2003). For example, Boyden et al. (2009) found that in densely planted stands, differences in growth rates among species with ontogeny had little effect on stand development

Fig. 3 (concluded).
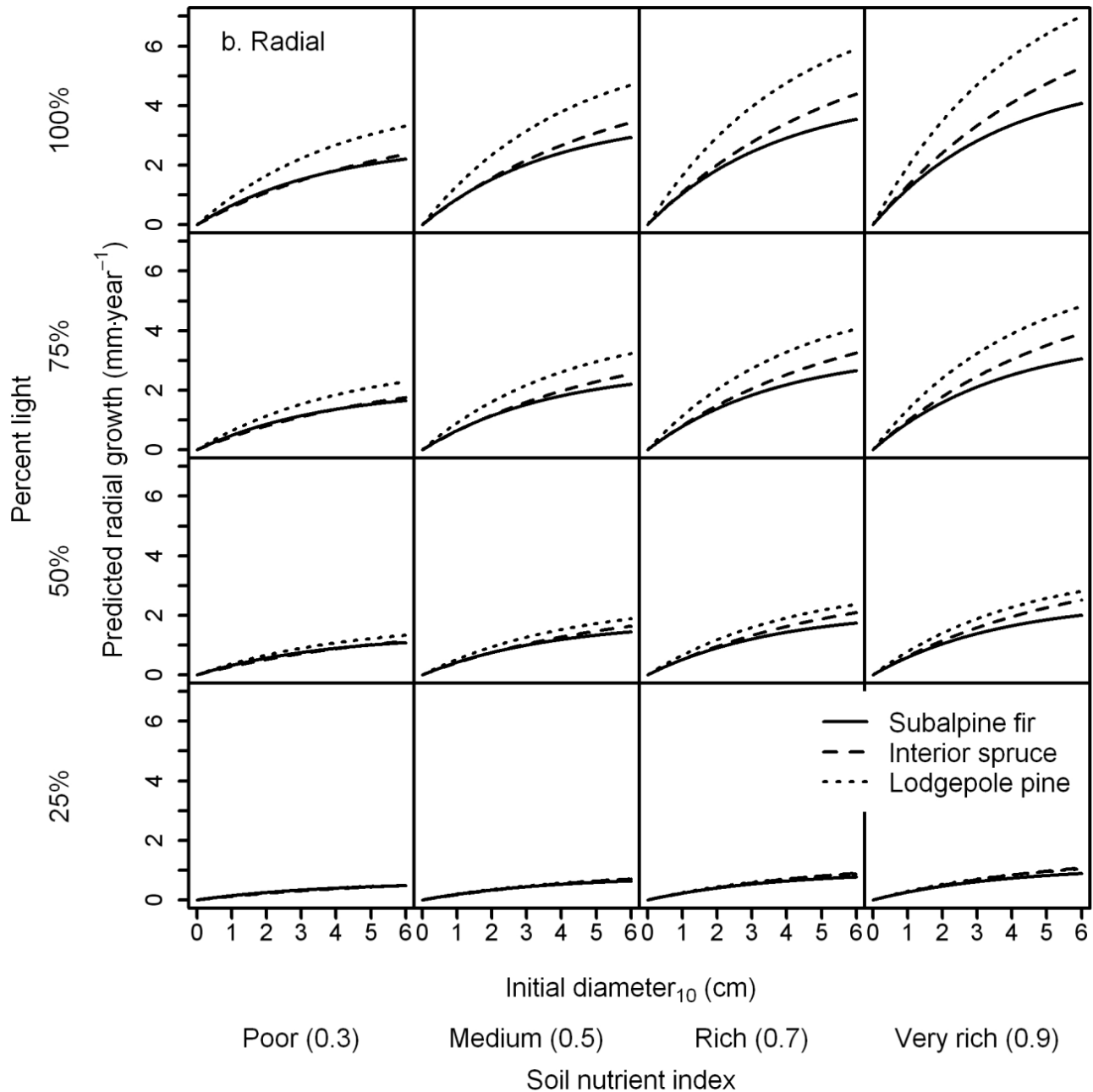
because size-asymmetric competition suppressed the initially slower growing species. The same dynamics undoubtedly occur in sub-boreal forests in which the initial recruitment density of lodgepole pine has long-lasting effects on succession (Clark et al. 2003). Limited pine recruitment could occur via several postdisturbance mechanisms that would have stronger effects with increasing soil fertility: the absence of a seed source (Clark et al. 2003), light competition by mixed shrubs (Kneeshaw and Burton 1997), and reduced secondary regeneration in lower understory light levels (Kranabetter and Simard 2008). Those factors could operate either with or independently of the shifting hierarchy in height growth rates to decrease the likelihood of pine dominating very fertile sites. Today, industrial forestry and an unprecedented mountain pine beetle epidemic (Astrup et al. 2008) are the main

disturbance agents in Canadian sub-boreal forests. In this context, understanding differences in height growth rates between species over time and across different soil types will be central to predicting stand development. Our results suggest that the effects of ontogeny on growth rate comparisons can be more important than the effects of light or soil fertility, and in the future, more emphasis should be placed on research that integrates and quantifies interactions among these three important variables.

Acknowledgements

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Appendix A

Table A1. ΔAIC_c and R^2 comparison of soil resource availability measurements: soil nutrient index (SN), soil moisture index (SM), and foliar N concentration (FN) as predictors of (*a*) height and (*b*) radial growth.

Model	Variables	Lodgepole pine		Interior spruce		Subalpine fir	
		ΔAIC_c	R^2	ΔAIC_c	R^2	ΔAIC_c	R^2
(*a*) As predictors of height growth							
$MaxPG \times (GLI - \iota)^a \times SN^b \times (1 - e^{(-c \times Size)})$	Light, soil nutrients, and size	0	0.68	1	0.70	53	0.65
$MaxPG \times (GLI - \iota)^a \times SM^b \times (1 - e^{(-c \times Size)})$	Light, soil moisture, and size	2	0.70	35	0.70	56	0.65
$MaxPG \times (GLI - \iota)^a \times FN^b \times (1 - e^{(-c \times Size)})$	Light, foliar N, and size	54	0.62	0	0.66	0	0.67
(*b*) As predictors of radial growth							
$MaxPG \times (GLI - \iota)^a \times SN^b \times (1 - e^{(-c \times Size)})$	Light, soil nutrients, and size	0	0.82	0	0.80	73	0.71
$MaxPG \times (GLI - \iota)^a \times SM^b \times (1 - e^{(-c \times Size)})$	Light, soil moisture, and size	10	0.84	38	0.79	66	0.72
$MaxPG \times (GLI - \iota)^a \times FN^b \times (1 - e^{(-c \times Size)})$	Light, foliar N, and size	81	0.74	3	0.75	0	0.75