The effect of size and competition on tree growth rate in old-growth coniferous forests

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Abstract: Tree growth and competition play central roles in forest dynamics. Yet models of competition often neglect important variation in species-specific responses. Furthermore, functions used to model changes in growth rate with size do not always allow for potential complexity. Using a large data set from old-growth forests in California, models were parameterized relating growth rate to tree size and competition for four common species. Several functions relating growth rate to size were tested. Competition models included parameters for tree size, competitor size, and competitor distance. Competitive strength was allowed to vary by species. The best ranked models (using Akaike's information criterion) explained between 18% and 40% of the variance in growth rate, with each species showing a strong response to competition. Models indicated that relationships between competition and growth varied substantially among species. The results also suggested that the relationship between growth rate and tree size can be complex and that how we model it can affect not only our ability to detect that complexity but also whether we obtain misleading results. In this case, for three of four species, the best model captured an apparent and unexpected decline in potential growth rate for the smallest trees in the data set.

Résumé : La croissance des arbres et la compétition sont des éléments centraux de la dynamique forestière. Toutefois, les modèles de compétition négligent souvent l'importante variation des réactions entre les espèces. De plus, les fonctions utilisées pour modéliser les changements de taux de croissance en fonction de la taille ne permettent pas toujours de tenir compte de la complexité potentielle. À l'aide d'une importante banque de données sur des vieilles forêts de la Californie, des modèles ont été paramétrés pour relier le taux de croissance de quatre espèces communes d'arbres à leur taille et à la compétition. Plusieurs fonctions reliant le taux de croissance à la taille des arbres ont été testées. Les modèles de compétition comportent des paramètres pour la taille des arbres, la taille des compétiteurs et la distance des compétiteurs. Le degré de compétition pouvait varier selon l'espèce. Les modèles les mieux classés selon le critère d'information d'Akaike expliquaient entre 18 % et 40 % de la variance du taux de croissance et chaque espèce montrait une forte réaction à la compétition. Les modèles indiquaient que la relation entre la compétition et la croissance variait substantiellement entre les espèces. Les résultats indiquent aussi que la relation entre le taux de croissance et la taille des arbres peut être complexe et que la façon de la modéliser peut non seulement influencer notre capacité à détecter cette complexité, mais peut aussi produire des résultats trompeurs. Dans ce cas, pour trois des quatre espèces, le meilleur modèle a détecté une baisse apparente et inattendue du taux de croissance potentielle des plus petits arbres de la banque de données.

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Introduction

Tree growth and competition play central roles in our understanding of temperate forest dynamics. Numerous studies have shown a relationship between a given tree's competitive environment and both its growth rate and risk of mortality (e.g., Biging and Dobbertin 1992; Bravo-Oviedo et al. 2006; Coomes and Allen 2007). In fact, competition serves as the primary biological engine that drives most forest dynamics models (Pacala et al. 1996; Bugmann 2001).

Traditionally, growth rate has been predicted by fitting regressions against either stand-level competition variables that do not explicitly account for a given tree's spatial environment (distance-independent) or against individual tree competition indices (distance-dependent) that do (e.g., Bella 1971; Biging and Dobbertin 1992, 1995). Model improvement using distance-dependent models compared with distance-independent models has generally been equivocal (e.g., Daniels et al. 1986; Biging and Dobbertin 1995; Contreras et al. 2011).

In calculating individual tree competition indices, a number of simplifying assumptions are typically made, including the assumptions that all species are equivalent competitors and that competitive strength changes linearly with distance and the diameter of the competitor. Furthermore, much of the work studying the relationship between growth and competition has been conducted in plantations that lack the complexity of mixed species stands (Stadt et al. 2007).

Recent work, however, has taken advantage of increasing computational power to relax these assumptions. Researchers working in mixed species forests in the eastern United States, British Columbia, and the tropics have developed models that

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allow parameters to vary nonlinearly and for competitive interactions to be species-specific (Uriarte et al. 2004; Canham et al. 2006; Coates et al. 2009). These more complex models do appear to offer modest improvement over traditional distance-independent methods (Stadt et al. 2007; Boivin et al. 2010).

More importantly, such models provide powerful tools for improving our understanding of forest community ecology and for testing hypotheses about the mechanisms driving forest dynamics. For example, these more comprehensive approaches have been used to test the importance of neighbor identity in tropical forests (Uriarte et al. 2004), to analyze competition along environmental gradients (Canham et al. 2006; Papaik and Canham 2006), to compare the importance of above versus belowground competitive effects (Coates et al. 2009), and to compare the importance of competition, size, and climate in determining tree growth (Gómez-Aparicio et al. 2011). These approaches also offer guidance for the management of forests with more complex structure and composition and for understanding the role of competition in an era of environmental change (e.g., Canham et al. 2004; Gómez-Aparicio et al. 2011).

One of the key characteristics of these more complex models is that they explicitly estimate a relationship between potential growth rate (growth without competition) and tree size. This allows one to explore assumptions about the form of the growth–size relationship and how those assumptions affect our understanding of tree growth.

As noted by Coates et al. (2009), no commonly accepted theoretical relationship between tree growth and size exists in the literature. While metabolic theory (Enquist et al. 1999) suggests that diameter growth will follow the form of a power function with an exponent of 1/3, this theory is far from commonly accepted (Muller-Landau et al. 2006; Coomes and Allen 2009). This lack of a theory is notable given the importance of the relationship for modeling carbon accumulation, understanding the potential limits of tree growth, and for accurately assessing tree health. In the latter case, having accurate estimates of potential growth for a tree of a given size might much improve our ability to assess risk of mortality.

In the absence of accepted theory, recent studies have frequently represented the relationship between tree growth and size using a lognormal function due to its relatively flexible form. While a perfectly reasonable empirical choice, it bears comparison against other formulations of the relationship if only to increase our ability to better describe the underlying pattern and perhaps improve our understanding of the biology that drives it.

For example, Duff and Nolan (1953) found a humped shape in diameter growth for the young *Pinus resinosa* Aiton (red pine) in their study. However, the lognormal function would not be flexible enough to capture such small tree growth dynamics while also capturing the broader pattern for large trees that often show declining diameter growth for the largest individuals (i.e., it could not capture two inflection points). Many studies do not include trees smaller than 5 or 10 cm in diameter, but such trees can be important for understanding forest dynamics, given their relatively high density in many stands.

In this paper, I take advantage of a large forest demography data set from old-growth conifer forests in the Sierra Nevada of California, including 18 plots and over 17 000 trees, to study growth variation in four abundant species. Much of the recent work on tree growth variation has been conducted in tropical and cool temperate forests, with relatively little attention given to Mediterranean forests (but see Gómez-Aparicio et al. 2011). I use this data set both to elucidate competitive relationships in Sierra Nevada forests and to explore the relationship between tree size and tree growth.

Specifically, I explore (*i*) how alternative formulations of the growth–size relationship compare with one another and how they affect our estimations of tree growth, (*ii*) how tree growth is affected by tree size and tree competition, (*iii*) how distance and size of competitor trees affect competitive interactions, and (*iv*) how competitive interactions between species vary.

Materials and methods

Data set

Eighteen permanent study plots ranging in size from 0.9 to 2.5 ha were established between 1982 and 2001 in old-growth stands within the coniferous forests of Sequoia and Yosemite national parks, Sierra Nevada, California (supplemental material).[1] Other plots in the network were excluded due to recent disturbances or because the plots did not contain species of interest. The plots are arranged along an elevational gradient from 1500 to nearly 2600 m, including both mixed conifer forest types and red fir forest. The sites have never been logged. Frequent fires characterized many of the forest types prior to Euro-American settlement, but the areas containing the study plots have not burned since the late 1800s (Caprio and Swetnam 1993). The climate is montane mediterranean, with hot, dry summers and cool, wet winters in which ~25%–95% of annual precipitation (which averages 1100–1400 mm) falls as snow, depending on elevation (Stephenson 1988). Mean annual temperature declines sharply with elevation, ranging from roughly 11 °C at the lowest plots to 1 °C at the highest. Soils are relatively young (mostly inceptisols), derived from granitic parent material.

Within each plot, all trees ≥1.37 m in height were tagged, mapped, measured for diameter at 1.37 m in height (DBH), and identified to species. Diameters were remeasured at intervals of ~5 years. Growth rate was calculated by taking the difference between consecutive diameter measurements and dividing by the length of the interval between measurements.

For this analysis, I used diameter growth rates estimated between 2000 and 2009, the first measurement period in which all of the plots had been established. Furthermore, I only developed growth models for conifer species for which the data set contained more than 1000 samples to avoid poor parameter estimates due to inadequate sample sizes (Coates et al. 2009; Gómez-Aparicio et al. 2011). This resulted in growth models for four species: *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr. (white fir), *Abies magnifica* A. Murray (red fir), *Calocedrus decurrens* (Torr.) Florin (incense cedar), and *Pinus lambertiana* Douglas (sugar pine).

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[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/x2012-141.

Growth models

I adopted the general theoretical approach (e.g., Canham et al. 2004; Uriarte et al. 2004) that

[1]   RG = PRG × modifiers

where RG is observed diameter growth rate (centimetres per year), PRG is the hypothetical potential diameter growth rate of a "free-growing tree", and modifiers are factors that reduce growth. Various modifiers have been parameterized in the literature, including shading, crowding, site quality, soil variables, and climate (Canham et al. 2006; Coates et al. 2009; Gómez-Aparicio et al. 2011). Size may also be considered as a modifier (e.g., Canham et al. 2004, 2006), but for this analysis, I instead incorporated size into the PRG term (i.e., PRG is considered to be a function of size).

Given the available data, I chose only to parameterize a term for competition:

[2]   RG = PRG × f(competition)

Since data were not available for a shading term, competition was defined as crowding. Previous work has shown that growth rate is frequently substantially more sensitive to crowding than to shading (Canham et al. 2004; Coates et al. 2009). To specify crowding, I adopted the form from other recent studies (e.g., Canham et al. 2004, 2006; Coates et al. 2009):

[3] $\text{NCI}_{\text{focal}} = (\text{DBH}_{\text{focal}})^{\gamma} \sum_{i=1}^{s} \sum_{j=1}^{n_i} \lambda_i \frac{(\text{DBH}_{ij})^{\alpha}}{(\text{distance}_{ij})^{\beta}}$

where $\text{NCI}_{\text{focal}}$ is the crowding index for a given focal tree, $\text{DBH}_{\text{focal}}$ is the diameter at breast height (centimetres) of the focal tree, λ_i is a species- or group-specific coefficient that ranges from 0 to 1 and allows the competitive strength to vary for each species or group, DBH_{ij} is the diameter at breast height (centimetres) of the competitor tree j of species i, distance_{ij} is the distance (metres) between the focal tree and competitor tree j of species i, and α, β, and γ are fitted parameters. In short, NCI specifies the net competitive effect of all neighbors on the focal tree — within a neighborhood radius R — based on the size, distance, and species of the given competitor. Note that NCI is essentially a modification of the Hegyi index (Hegyi 1974; Biging and Dobbertin 1992).

The maximum neighborhood radius, R, was allowed to vary as a parameter but was constrained to vary only between 0.5 and 20 m at 0.5 m increments. Larger neighborhoods were not considered in order to limit the impact of edge effects (i.e., an R of 20 m is less than half of the length of the shortest side of any given plot — the conservative rule of thumb for the maximum distance to be considered in standard point pattern analyses (e.g., Haase 1995)). The majority of plots were 100 m × 100 m. Edge effects on NCI were handled using an area-weighted edge correction based on a circle of radius R (i.e., the raw NCI value was divided by the proportion of the area of a circle of radius R that lay inside the plot for any given focal tree).

To facilitate comparisons of λ values across the four species, the highest value of λ for a given model was set to 1 and the remaining species-specific values were divided by the maximum value (i.e., all values of λ were scaled against the strongest competitor species). To keep the number of parameters manageable, I have assumed that α, β, and γ do not vary among competitor species.

For parameterizing the effect of species identity on competitor strength (λ values), the two oak species (*Quercus kelloggii* Newberry and *Quercus chrysolepis* Liebm.) were grouped as were two closely related yellow pine species (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson and *Pinus jeffreyi* Balf.). In the case of the oak species, the sample is heavily dominated by *Quercus kelloggii* and the coefficient is primarily a reflection of its competitive effect. Other species were assigned a specific λ if there were more than 100 potential competitive interactions between the subject species and the given competitor species at an R of 10 m (i.e., if individuals of a given competitor species were in the neighborhood of at least 100 individuals of the subject species). All remaining competitor species were lumped, since in the one case where this occurred, there were too few interactions for those species to be put in more precise categories. In addition, for *Pinus lambertiana* models, *Sequoiadendron giganteum* (Lindl.) J. Buchholz was given its own λ despite having less than 100 interactions because there were no other species left with which to lump it. In addition to the *Pinus ponderosa* and *Pinus jeffreyi* group and the *Quercus kelloggii* and *Quercus chrysolepis* group, the list of potential competitor species was as follows: *Abies concolor*, *Abies magnifica*, *Calocedrus decurrens*, *Pinus contorta* Douglas ex Loudon, *Pinus lambertiana*, *Pinus monticola* Rydb., *Pseudotsuga menziesii* (Mirb.) Franco, and *Sequoiadendron giganteum*.

Growth was assumed to decline as a function of NCI:

[4] $f(\text{competition}) = \mathrm{e}^{-C\left(\frac{\text{NCI}}{\text{NCI}_{\text{max}}}\right)^{D}}$

where C is a fitted parameter that determines how quickly growth declines with NCI and D determines the shape of that decline. If $D = 1$, the decline is a negative exponential function. If $D > 1$, the decline is sigmoidal. NCI_{max} is the maximum observed value of NCI. NCI was scaled to the maximum to facilitate comparisons of the C and D parameters among species. For NCI parameters, the constraints reported by Uriarte et al. (2004) were used to keep parameters in biologically reasonable ranges and to avoid problems of parameter trade-offs.

I tested several models of PRG as a function of size. The first was the lognormal model (e.g., Uriarte et al. 2004; Canham et al. 2006; Coates et al. 2009):

[5] $\text{PRG} = \text{MaxRG} \times \mathrm{e}^{-1/2\left[\frac{\ln\left(\frac{\text{DBH}}{X_0}\right)}{X_b}\right]^2}$

where MaxRG is the maximum potential growth rate, X_0 is the DBH at which MaxRG occurs, and X_b determines the breadth of the function. This functional form allows a monotonically increasing (when X_0 is large), decreasing (when X_0 is very small), or humped shape (when X_0 is in the range of DBH).

Modified versions of a power function were also used to model growth and size. The basic power function is given by

[6] $\mathrm{PRG} = a \times \mathrm{DBH}^{b}$

where a and b are fitted parameters. Since the power function only allows for monotonically increasing or decreasing growth with size, two modifications were considered that allowed the function to increase and then decline with size. The first was a modification to the exponent:

[7] $\mathrm{PRG} = a \times \mathrm{DBH}^{b \times \mathrm{e}^{-c \times \mathrm{DBH}}}$

where PRG initially increases and then decreases as the DBH grows larger, the exact inflection point determined by the value of the fitted parameter c. The equation of this form will be referred to as the "modified power function (exponent)". The second modification was to the scalar coefficient or multiplier (i.e., a Hugershoff function; e.g., Bräker and Baumann 2006):

[8] $\mathrm{PRG} = a \times \mathrm{e}^{-c \times \mathrm{DBH}} \times \mathrm{DBH}^{b}$

which also allows growth to increase with size and then decrease. Note that both eqs. 7 and 8 reduce to eq. 6 when $c = 0$. The equation of this form will be referred to as the "modified power function (multiplier)".

Finally, a more flexible function was tested that allowed more than one inflection point:

[9] $\mathrm{PRG} = a \times \mathrm{DBH}^{(b_1 \times \mathrm{e}^{-c_1 \times \mathrm{DBH}} - b_2 \times \mathrm{e}^{-c_2 \times \mathrm{DBH}})}$

where b_1, b_2, c_1, and c_2 are fitted parameters that are constrained to be positive. This function is equivalent to multiplying increasing and decreasing versions of eq. 7 together. I chose to include this more complex function in recognition of the possibility that changes in growth rate with size could potentially be more complicated than allowed for by traditional growth functions. For example, in preliminary analysis, there was some preference in the models for potential diameter growth to decline for very small size classes and then increase. Notably, eq. 9 can reduce to either eq. 6 or eq. 7 in the case that additional parameters do not improve fit.

Note that in eq. 9, if the function is declining for small trees (net negative exponent), then a DBH of 0 yields a division by 0. In addition, eq. 9 requires that the growth rate at DBH = 0 is fixed. Therefore, I modified the equation slightly to add a small value and an intercept:

[10] $\mathrm{PRG} = \mathrm{Intercept} + a$
           $\times (\mathrm{DBH} + 0.01)^{(b_1 \times \mathrm{e}^{-c_1 \times \mathrm{DBH}} - b_2 \times \mathrm{e}^{-c_2 \times \mathrm{DBH}})}$

Equations 6, 7, and 8 were modified similarly to make them consistent with eq. 10. Equation 10 will be referred to as the "double-inflection" function, although it is important to emphasize that this function does not require two inflection points but does allow for them.

Likelihood estimation and comparison of models
I used maximum likelihood methods and simulated annealing to estimate model parameters using the statistical package R 2.13.1 and the "anneal" function from the Likelihood package

age (version 1.4) written by Lora Murphy and made available by Charles Canham (http://www.sortie-nd.org/lme/lme_R_code_tutorials.html). Residuals were assumed to be normally distributed with a variance that was proportional to the mean. Models were compared using Akaike information criterion (AIC) values (Burnham and Anderson 1998). I also calculated Bayesian information criterion values, since AIC can be biased toward complex models (Astrup et al. 2008; Link and Barker 2010). Uncertainties in the parameter estimates were calculated as two unit support intervals (Edwards 1994), which are roughly equivalent to a 95% support limit defined using a likelihood ratio test. In addition, I calculated the slope of the regression, with 0 intercept, of observed growth on predicted growth as a measure of bias, with an unbiased model having a slope of 1. I also calculated the r^2 of the regression of observed on predicted as an additional measure of fit.

Results

Model comparison and evaluation
For all four species, the best model was unequivocally the double-inflection model (Table 1). Comparison of Bayesian information criterion values (not shown) also supported this same conclusion, except for the models of *Calocedrus decurrens*, where the modified exponent model is roughly equivalent to the double-inflection model. The best models were unbiased (i.e., slopes not significantly different from 1), except for *Pinus lambertiana* models, which appeared to slightly underestimate growth rate in the fastest growing trees. The best models explained between 18% and 40% of the variance depending on the species. As with similar studies (Canham et al. 2004, 2006; Papaik and Canham 2006), competition explained a decreasing proportion of the observed variance as growth rate increased (i.e., the scatter of residuals increased with growth rate; not shown).

Tree size and potential growth rate
The form of the models allowed estimation of the average potential growth rate for each species as a function of size. Note that potential growth rate in this context represents an estimate of the average diameter growth rate at these sites when a tree is free from competition (i.e., NCI = 0). It is not an estimate of the absolute maximum potential growth rate (i.e., individual open-grown trees would be expected to grow slower or faster than the estimated mean for a given tree size depending on factors such as genetics and site quality). The best ranked models (i.e., double-inflection models) indicated that the average potential growth rate for each species decreased with size for very small trees (e.g., trees with DBH < 8 cm) and then increased to a maximum, although the decrease for *Calocedrus decurrens* was very shallow (Table 2; Fig. 1). The DBH at which diameter growth rate reached a minimum occurred roughly between 3 and 8 cm depending on the species. For three of the four species, average potential growth rate reached a maximum between 35 and 55 cm DBH. For *Pinus lambertiana*, the growth rate approached an asymptote, with the growth rate leveling off at about 50 cm DBH.

The three modified power functions (including the double-inflection function) gave qualitatively the same pattern for potential diameter growth rate for trees greater than 10 cm in DBH of each species, with the rate eventually decreasing or leveling off with tree size for the largest trees.

Table 1. Model comparison.

Model	No. of parameters	ΔAIC	Akaike weight	Evidence ratio	r^2	Bias
Abies concolor (6346 trees)						
Lognormal	19	672.58	0.00	1.12×10^{146}	0.28	0.98
Power function	19	617.74	0.00	1.38×10^{134}	0.25	0.96
Modified power function (exponent)	20	57.99	0.00	3.90×10^{12}	0.33	0.98
Modified power function (multiplier)	20	58.33	0.00	4.63×10^{12}	0.33	0.99
Double-inflection function	22	0.00	1.00	1.00	0.33	1.00
Abies magnifica (3449 trees)						
Lognormal	18	427.83	0.00	7.99×10^{92}	0.36	0.99
Power function	18	302.82	0.00	5.71×10^{65}	0.32	0.95
Modified power function (exponent)	19	76.67	0.00	4.46×10^{16}	0.39	0.98
Modified power function (multiplier)	19	78.96	0.00	1.40×10^{17}	0.39	0.99
Double-inflection function	21	0.00	1.00	1.00	0.40	0.99
Calocedrus decurrens (3363 trees)						
Lognormal	18	280.94	0.00	1.01×10^{61}	0.14	1.01
Power function	18	168.91	0.00	4.78×10^{36}	0.12	0.92
Modified power function (exponent)	19	12.82	0.00	6.09×10^{2}	0.18	1.00
Modified power function (multiplier)	19	16.60	0.00	4.02×10^{3}	0.17	0.96
Double-inflection function	21	0.00	1.00	1.00	0.18	0.97
Pinus lambertiana (1134 trees)						
Lognormal	19	181.71	0.00	2.88×10^{39}	0.30	1.01
Power function	19	112.71	0.00	2.98×10^{24}	0.29	0.96
Modified power function (exponent)	20	85.44	0.00	3.58×10^{18}	0.34	0.96
Modified power function (multiplier)	20	86.20	0.00	5.22×10^{18}	0.32	0.96
Double-inflection function	22	0.00	1.00	1.00	0.31	0.95

Note: No. of parameters is the number of parameters included in the model, ΔAIC is the difference in AIC values between the given model and the best model, Akaike weight is the weight of evidence that the given model is the best model, with values across all models summing to 1.0, evidence ratio is ratio of the Akaike weight of the given model versus the best model, with larger numbers indicating weaker evidence in support of the given model, r^2 is the variance explained for the regression of observed on predicted growth, and bias is the slope of the regression of observed growth on predicted growth with a 0 intercept, an unbiased model having a slope of 1.

Pinus lambertiana models showed the most variation among the three models, with the double-inflection function leveling off rather than decreasing. The two poorest models, the lognormal and unmodified power function, suggested continuously increasing growth rate with size for all four species. This was a necessary outcome for the power function but not the lognormal function.

Comparing potential growth rate among species (Fig. 1*b*), the models suggested that _Abies concolor_ had the fastest potential rate for trees up to 70 cm DBH, with _Pinus lambertiana_ having the fastest potential rate for larger trees. _Abies concolor_, _Abies magnifica_, and _Calocedrus decurrens_ are considered shade-tolerant species, while _Pinus lambertiana_ is mid-tolerant (Burns and Honkala 1990). The growth curves do not suggest a strong relationship with shade tolerance; however, none of the species are considered truly intolerant species.

Effect of competition on growth rate

Growth rate appeared to decline steeply with increasing competition for all species (Table 3; Fig. 2), with the steepest decline in _Pinus lambertiana_ and the shallowest in _Calocedrus decurrens_. Both _Abies_ species had a very similar response to competition. All four species showed a negative exponential rather than sigmoidal decline in growth for the best model (i.e., $D = 1$), although lower ranked models for _Pinus lambertiana_ indicated a sigmoidal relationship (see supplemental material).

Effective neighborhood distance (R) varied considerably by species, with _Abies_ species having relatively large neighborhoods and _Calocedrus decurrens_ having a relatively small neighborhood. All neighborhood distances fell below the maximum of 20 m, suggesting that the data were adequate for capturing local competitive effects.

Effect of competitor size, distance, and focal tree size on the strength of competition

The α parameter indicates how the size of a competitor influences its competitive strength. For example, an α of 2 would suggest that competition scales linearly with the basal area of competitor trees, while an α of 1 would indicate that competition scales linearly with diameter. All four species had values of α substantially less than 2, with _Pinus lambertiana_ having an α less than 1 (Table 3).

The β parameter indicates how the strength of competition declines with increasing distance between a focal tree and its competitor within radius R. As with α, standard formulations of competition indices assume that the value is equal to 1. For

Table 2. Size–growth parameter estimates for the double-inflection model.

Species	Intercept	a	b_1	c_1	b_2	c_2
Abies concolor	−2.18 (−2.21 to −2.15)	2.57 (2.57 to 2.57)	0.60 (0.60 to 0.60)	0.03571 (0.03535 to 0.03571)	0.65 (0.65 to 0.65)	0.04637 (0.04637 to 0.04637)
Abies magnifica	0.08 (0.07 to 0.09)	0.31 (0.30 to 0.32)	0.29 (0.27 to 0.30)	0.01005 (0.00925 to 0.01145)	0.96 (0.92 to 1.01)	0.08199 (0.07789 to 0.08690)
Calocedrus decurrens	0.22 (0.21 to 0.22)	3.2×10^{-6} (2.9×10^{-6} to 3.5×10^{-6})	4.12 (4.12 to 4.12)	0.00623 (0.00602 to 0.00639)	7.54 (5.88 to 8.58)	0.19091 (0.17545 to 0.20816)
Pinus lambertiana	0.28 (0.26 to 0.30)	0.34 (0.30 to 0.38)	5.42 (5.21 to 5.61)	0.22354 (0.17178 to 0.33818)	7.25 (7.10 to 7.48)	0.11917 (0.10683 to 0.13251)

Note: Numbers in parentheses give the two unit support intervals for each parameter (see eq. 10). Parameter estimates for other models (e.g., lognormal model) are provided in the supplementary material.

Abies concolor models, β slightly more than 1, while for *Abies magnifica*, β was slightly less than 1. Models for *Calocedrus decurrens* and *Pinus lambertiana* indicated that competition decreased at a much slower rate with distance compared with the fir species, with the estimate of β for *Pinus lambertiana* models suggesting that competition was not affected by competitor distance (at least within a radius of 11.5 m).

The γ parameter indicates how the size of a focal tree influences the effects of competition. For three of the four species, the size of the focal tree appeared to influence competition, with *Pinus lambertiana* models showing the strongest effect. However, for all species, γ was substantially less than 1, indicating that focal tree size had a much weaker effect than assumed by standard indices (such as the Hegyi index). For *Calocedrus decurrens*, the effect was not distinguishable from 0.

Interspecific competition

For each species, I refit the double-inflection model using a formulation of NCI that did not distinguish between competitor species (i.e., $\lambda = 1$ for all competitors). In every case, the species-specific model was unequivocally better (results not shown), suggesting that interspecific differences in competition are important for modeling the effect of competition on growth.

The models did not provide a clear picture of competitive hierarchy (Fig. 3), with the relative competitive strength of various competitor species varying considerably among subject species. *Abies concolor*, for example, appeared to be a strong competitor for other *Abies concolor* and *Pinus lambertiana* but a weak competitor for *Calocedrus decurrens*. The expectation that shade tolerance might predict competitive strength was also not clearly borne out. As noted above, *Abies concolor*, *Abies magnifica*, and *Calocedrus decurrens* are considered fairly shade-tolerant species with the pines being less so (Burns and Honkala 1990). However, in some cases, pines appeared to be very strong competitors and the more shade-tolerant species relatively weak.

Intraspecific competition generally appeared to be strong, with the values for the intraspecific λ close to 1.0 for three out of four species. For *Abies magnifica*, this pattern might be masked due to two pine species (*Pinus contorta* and *Pinus monticola*), which have been estimated with relatively small samples of competitors. With these two species removed, *Abies magnifica* becomes the strongest competitor for other *Abies magnifica*.

Notably, models for both fir species (*Abies concolor* and *Abies magnifica*) showed greater variation in the strength of competitive interactions among competitor species (i.e., greater variance in λ among competitor species) than models for *Calocedrus decurrens* or *Pinus lambertiana*. For both of the latter species, all but one competitor species had a maximum likelihood estimate for λ that was greater than 0.50, with *Pinus lambertiana* in particular having all but one λ greater than or equal to 0.70.

Discussion

As in many systems, competition plays a substantial role in the dynamics of Sierra Nevada conifer forests (e.g., Das et al. 2011). The analysis here shows that relationships between competition and growth rate are both important and diverse, with different species varying in effective neighborhood size,

Fig. 1. (*a*) Estimated growth rate without competition (NCI = 0) for each species for each size-growth model. (*b*) Comparison of estimated growth rates without competition for each species for the best ranked models. In each case, the best ranked models were the double-inflection models. Note that in all figures, the range of DBH shown is the range found in the data set.
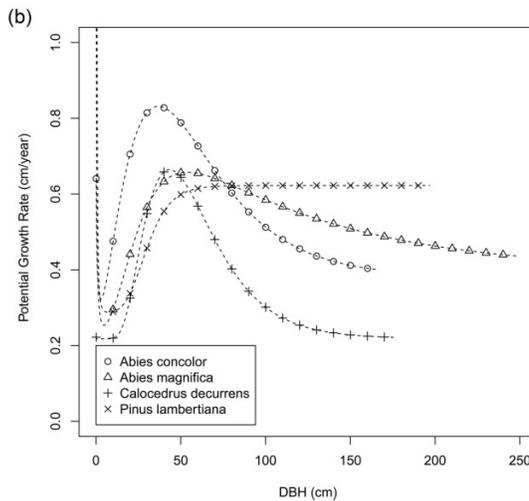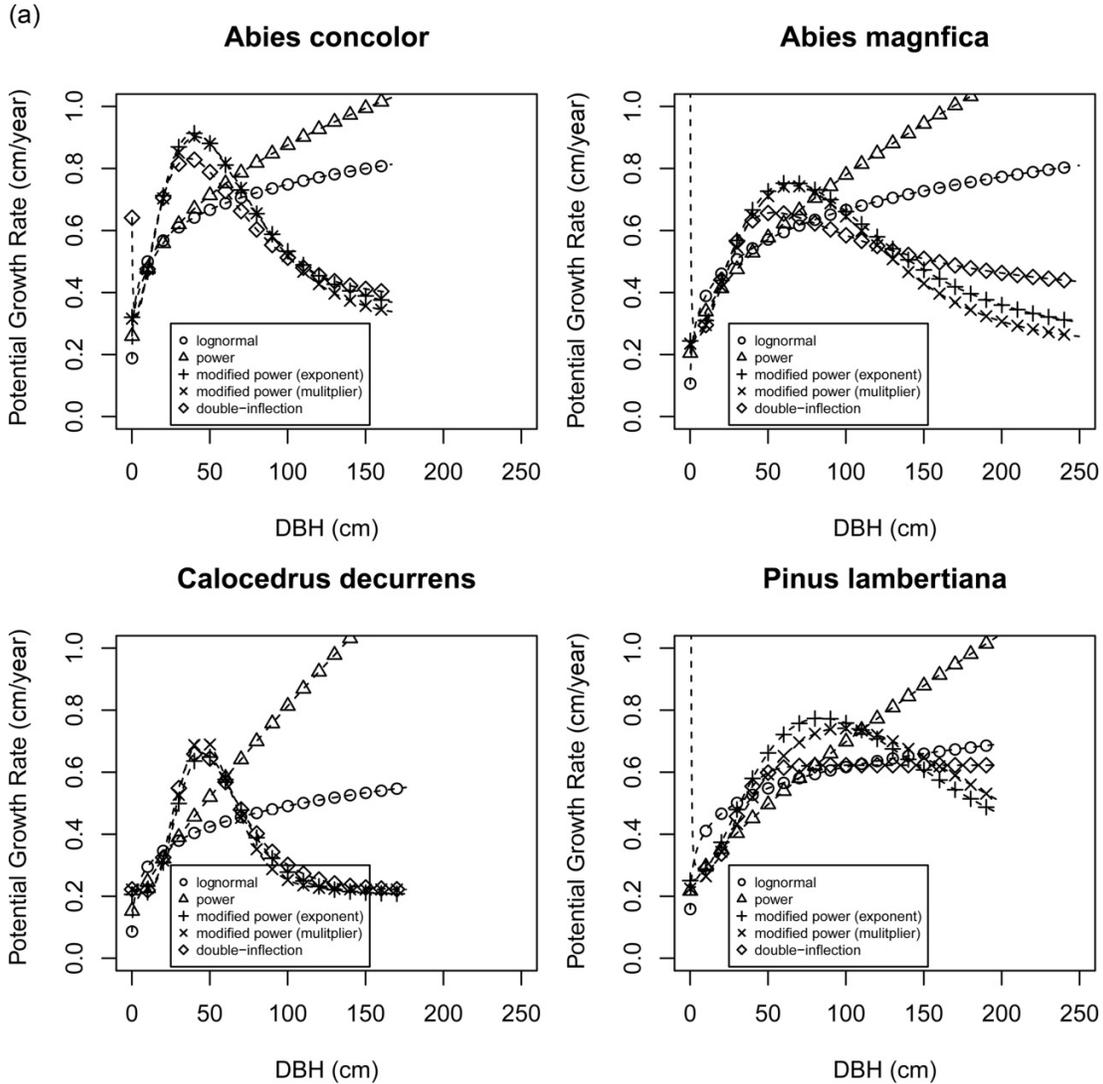
Table 3. Competition parameter estimates for the double-inflection model.

Species	C	D	α	β	γ	R
Abies concolor	3.80 (3.72 to 3.83)	1.00 (1.00 to 1.01)	1.32 (1.28 to 1.35)	1.09 (1.08 to 1.10)	−0.18 (−0.20 to −0.17)	18.5 (18.5 to 19.0)
Abies magnifica	3.85 (3.81 to 3.85)	1.00 (1.00 to 1.00)	1.31 (1.30 to 1.33)	0.85 (0.81 to 0.90)	−0.23 (−0.24 to −0.22)	19.5 (19.5 to 19.5)
Calocedrus decurrens	2.58 (2.5 to 2.65)	1.00 (1.00 to 1.02)	1.11 (1.09 to 1.12)	0.30 (0.11 to 0.42)	0.02 (0.00 to 0.03)	7.5 (7.5 to 7.5)
Pinus lambertiana	7.08 (7.08 to 7.15)	1.03 (1.02 to 1.03)	0.84 (0.79 to 0.90)	0.00 (0.00 to 0.42)	−0.48 (−0.50 to −0.45)	11.5 (11.5 to 11.5)

Note: Numbers in parentheses are the two unit support intervals for each parameter (refer to eqs. 3 and 4). Parameter estimates for other models (e.g., lognormal model) are provided in the supplemental material.

their resistance to competition with tree size, their response to neighbor distance and size, and their competitive interactions with neighboring species. The results also indicate that the relationship between tree growth rate and tree size can be complex and that how we choose to model it can affect not only our ability to detect that complexity but also, in some cases, whether we obtain misleading results (e.g., the lognormal and power functions failed to capture an apparent decline in three growth rate with size).

Competition

Not surprisingly, competition appeared to have a substantial effect on tree growth rate for all species (C parameter; Fig. 2), in keeping with an extensive literature on the subject. For example, strong sensitivity to crowding has been shown for tree species in British Columbia, eastern North America, and the tropics (Canham et al. 2004; Uriarte et al. 2004; Coates et al. 2009). And, although in this study, I have only tested the effect of competition and cannot make comparisons with other factors, Gómez-Aparicio et al. (2011) found that competition had a much larger impact on growth than climate or tree size in Iberian forests.

As with other recent studies (e.g., Canham et al. 2006; Stadt et al. 2007; Coates et al. 2009), my models indicate that, in contrast with typical formulations of competition indices, competition does not necessarily scale with an exponent of 1 with focal tree diameter, competitor tree diameter, or competitor distance. Furthermore, these characteristics vary among species, with only the two fir species showing strong similarity in parameter estimations. The effect of competitor distance ranged from a moderate rate of decline in competitive strength with distance to essentially no effect at all. The importance of focal tree size also varied considerably, although the focal tree size exponent was substantially less than 1.0 for all species, indicating a relatively weak effect. Finally, the apparent neighborhood size varied more than twofold among species, suggesting that the effective competitive neighborhood can vary dramatically within a forest.

There were also no simple criteria for determining which species were the strongest competitors, with relatively strong intraspecific competition being the most consistent pattern. In contrast with expectations, pine species appeared to be relatively strong competitors, while more shade-tolerant species varied considerably in their apparent competitive strength. In short, competition in these forests appears to be a complex process that may not be easily characterized by straightforward assumptions about the relationship between successional dynamics (i.e., shade tolerance) and competitive strength.

Potential growth rate

All four species showed the common pattern (e.g., Canham et al. 2006; Coates et al. 2009; Gómez-Aparicio et al. 2011) of diameter growth rate increasing to a maximum with tree size and then either leveling off or decreasing for the largest trees. However, for three of the four species, the best models in this analysis also indicated a sharp decline in potential diameter growth rate for the smallest trees.

For the broader pattern (i.e., trees larger than 10 cm diameter; Fig. 1*b*), the results are generally consistent with previous findings about growth for the studied species. For example, *Calocedrus decurrens* has been found to be a slower growing

Fig. 2. Change in growth rate with competition using parameter estimates for the best ranked models for each species. Growth rate with competition was calculated for trees of six different diameters (5, 10, 15, 40, and 100 cm). The competition index (NCI) is scaled against the maximum value seen in the data for each species.
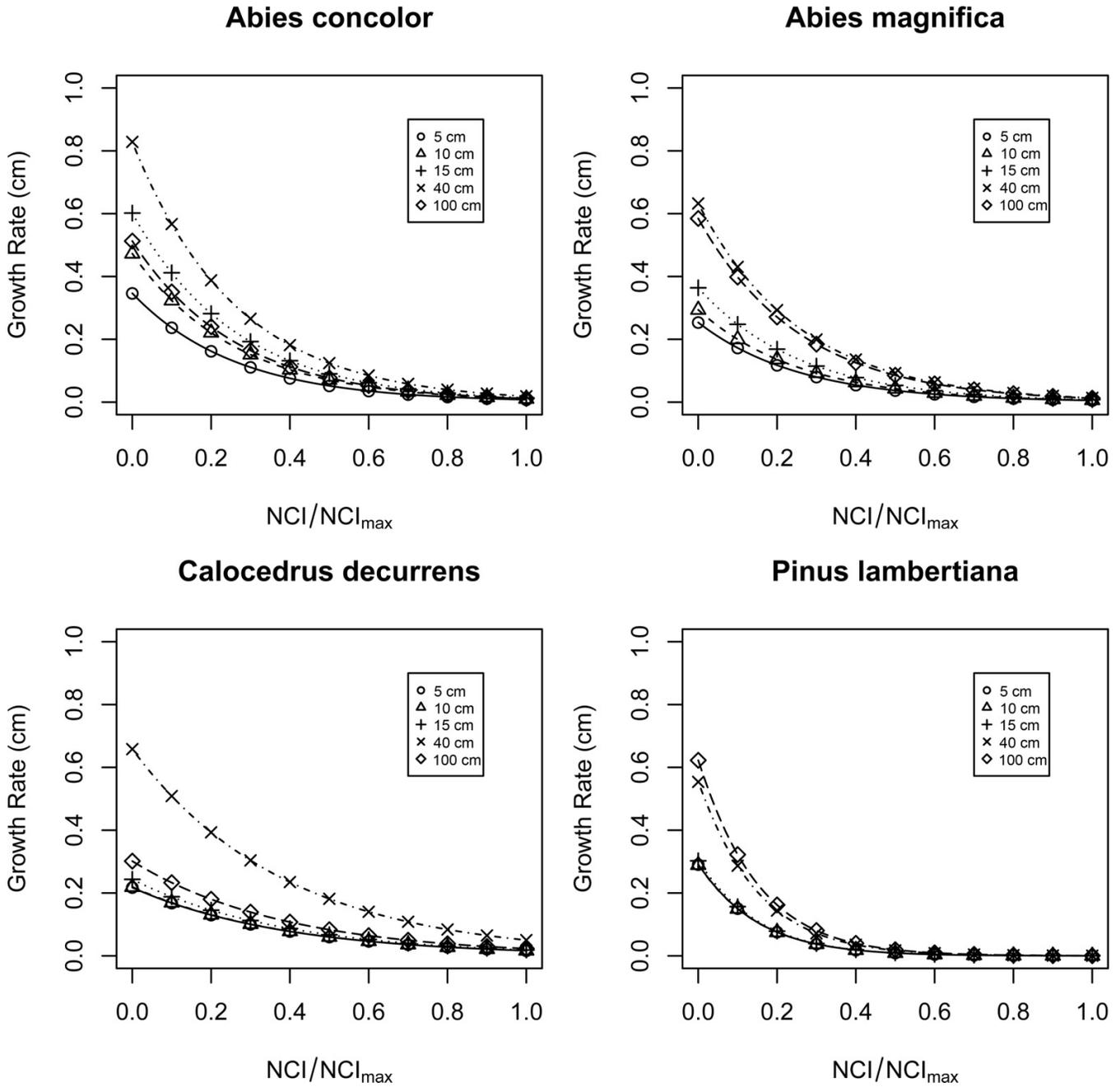

species than most of its cohorts, regardless of density, *Pinus lambertiana* has been shown to grow more slowly at small sizes but then accelerate and sustain a faster growth rate compared with its cohort species for larger diameter trees, and *Abies concolor* has been long known to have the capacity to produce large volumes of wood per unit area when not suppressed (Burns and Honkala 1990).

On the other hand, the results do not show a clear potential diameter growth rate hierarchy between the more shade-intolerant species (*Pinus lambertiana*) and the other species, as

has been found in other work (e.g., Papaik and Canham 2006). That said, the species in this study do not span a wide range of presumed shade tolerance, with none of the species being classified as very shade-intolerant.

One of the more interesting results is the apparent decline in potential growth rate for trees less than 5 or 8 cm DBH indicated by the best ranked, double-inflection models for three of the four species. Potentially, this could be the result of an artifact in the data. For example, if the smallest diameter trees occurred only in open, low-density environments or if

Fig. 3. Species-specific competition coefficients for each subject species (presented as λ in the equations). Error bars represent the two unit support intervals for each estimated parameter. Note that, for each subject species, the values are scaled against the maximum competitor (i.e., λ = 1) and therefore represent the relative competitive strength of each competitor species against the maximum. ABCO, *Abies concolor*; ABMA, *Abies magnifica*; CADE, *Calocedrus decurrens*; PILA, *Pinus lambertiana*; PIPJ, *Pinus ponderosa* and *Pinus jeffreyi*; PSME, *Pseudotsuga menziesii*; QUXX, *Quercus kelloggii* and *Quercus chrysolepis*; SEGI, *Sequoiadendron giganteum*; PICO, *Pinus contorta*; PIMO, *Pinus monticola*.
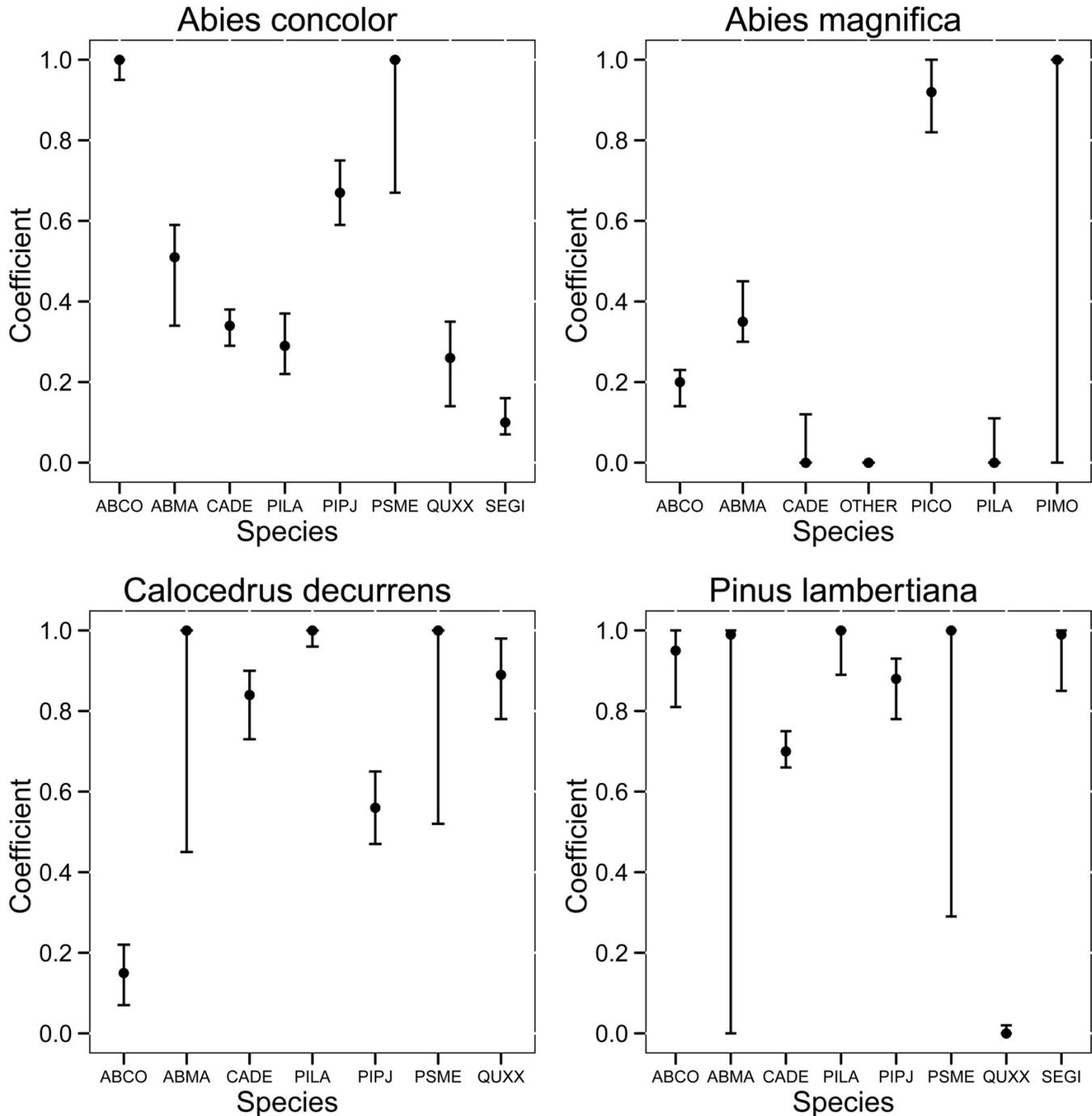
trees between 5 and 8 cm occur only in very competitive environments relative to smaller trees, then the result might simply reflect this bias. However, there was no evidence of such a bias in the data, with small trees spanning the full gamut of competitive environments.

An alternative and perhaps more plausible explanation may be found in Duff and Nolan's (1953) work with young *Pinus resinosa*. They found that, at a given height, radial growth for very young trees increased sharply over the first few years of growth but then declined over the subsequent decade. This

occurred regardless of the competitive status of the tree or the productivity of the site. They attributed the pattern to nutritional gradients along the axis of the tree. Mott et al. (1957) found a similar pattern for three other species. My analysis did not show the sharp increase in growth for the very smallest trees, but this is not surprising given that diameter measurements in this study were made only every 5 years and the increase indicated by Duff and Nolan (1953) occurred over a very short interval. On the other hand, the decline over the subsequent decade is very much in accordance with the decrease seen in the double-inflection models for the smallest trees. Testing whether this decline is truly an inherent property of ring widths at a given tree height (as argued by Duff and Nolan 1953) would require substantially more detailed growth data than we currently possess, but such intrinsic changes in apparent growth rate at a given tree height certainly deserve attention. It is important to note that Duff and Nolan (1953) did not argue that this pattern proved a decrease in overall tree growth rate with size but rather that they had identified an aspect of tree development that resulted in an artifact in the ring width record at a given tree height. They recommended that for studying extrinsic effects on tree growth (e.g., competition) that one should compare growth rings at different heights as well as different ages (a type 3 sequence in their parlance). Unfortunately, such data are rare and difficult to obtain.

Transferability

As with any empirical model, the models developed here can only be considered reliable for making predictions within the range of conditions adequately represented by the model building data. For example, the models might not perform well for sites with substantially more or substantially less productive soils (e.g., the potential growth rates probably vary among sites). Furthermore, these models might only poorly predict growth for trees in competitive conditions that are outside the range of the data, as perhaps with trees that are growing in a truly open field. However, the data set here is fairly robust with regard to tree size, competitive condition, and growth rate. These old-growth forests contain trees of all sizes growing in a wide variety of conditions. For each of the species examined, there were fast- and slow-growing trees across the range of tree sizes. In addition, for three of the four species, trees were found in a robust range of competitive environments across much of their diameter range, with the smallest trees showing the widest variation and the largest the least (i.e., large trees by virtue of their size tend to have low estimates for NCI). In contrast, for *Pinus lambertiana*, most trees greater than 20 cm DBH were not found in very competitive environments, perhaps owing to their lower shade tolerance and an inability to survive beyond small sizes in competitive circumstances.

Unexamined factors

A fundamental assumption — and one often made when studying tree growth — is that the reduction in tree growth rates with increasing tree density is solely a function of resource competition. However, there are alternative mechanisms that could also contribute to density-dependent changes in tree growth rate. In tropical forests, for example, density-dependent effects are frequently attributed to increased susceptibility to biotic attack rather than competition (i.e., Janzen-Connell hypothesis; Janzen 1970). In the forests in this study, a root rot could decrease the diameter growth rate of a tree, unrelated to competition, and risk of infection might increase with neighbor density (e.g., Das et al. 2008). Similar arguments could be made for other biotic agents in these stands. Certainly, one would expect competition to have a major, perhaps dominant, role in controlling tree growth. But biotic attackers appear to play an important part in Sierran forests (Das et al. 2011), and their potential effect on tree growth should be explored.

In addition, several other factors merit future investigation and require additional data collection. For example, I have not in this analysis accounted for differences in site (Canham et al. 2006; Stadt et al. 2007) and climate (Gómez-Aparicio et al. 2011), nor have I tested whether the fundamental nature of tree competition might vary with tree size (Woodall et al. 2003). Growth rate in *Calocedrus decurrens* in particular appears to be controlled by factors other than competition, given the low r^2 of the models. Either the approach used here neglects an important driver unrelated to competition or its representation of competition is inadequate for this species.

Implications for future research

The finding that the relationship between tree size and tree growth may be more varied than commonly assumed has potentially important implications for our ability to model and predict forest dynamics. For example, in this case, some tree species appear to have a sharp decline in potential growth rate across the smallest size class, a result that was only captured through use of a more flexible function. And, since growth rate is often tied tightly to assessments of tree health and risk of mortality, our ability to model small tree demographics and their likely trajectory is at least in part tied to our ability to accurately model their growth. Notably, while small trees store a relatively small proportion of the biomass in a forest, they frequently comprise the bulk of the density and also the pool of individuals from which future forest structure and composition will be drawn.

In general, we risk modeling tree growth rate poorly whenever we parameterize it across a wide range of tree size. For example, the lognormal function — used with apparent effectiveness in other studies — performed inadequately on this data set, failing even to capture the broad decline or leveling off in tree diameter growth rate for the largest trees. The likely cause of this failure was the abundance of small trees in this data set, as comparable studies often only include trees with a DBH greater than 5 or 10 cm. As a test, I refit all of the models for *Abies concolor* excluding trees with a DBH less than 10 cm (results not shown). While modified power functions still gave the best ranked models, the lognormal function did then capture the decline in potential diameter growth for larger trees. Not surprisingly, with small trees removed, the double-inflection function no longer offered any advantage over its less complex counterparts.

Ultimately, we would be well served to try to determine a theoretical form for expected tree growth rate with size, presuming one exists, as this would give us a baseline from which to interpret our data. In the meantime, we should not always assume that the relationship is straightforward, and we should make some effort to detect variability in that relationship, if

only to provide fodder for the development of hypotheses about the underlying mechanisms.

Acknowledgements

References

Astrup, R., Coates, K.D., and Hall, E. 2008. Finding the appropriate level of complexity for a simulation model: an example with a forest growth model. For. Ecol. Manage. **256**(10): 1659–1665. doi:10.1016/j.foreco.2008.07.016.

Bella, I. 1971. A new competition model for individual trees. For. Sci. **17**(3): 364–372.

Biging, G.S., and Dobbertin, M. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. **38**(3): 695–720.

Biging, G.S., and Dobbertin, M. 1995. Evaluation of competition indexes in individual tree gorwth models. For. Sci. **41**(2): 360–377.

Boivin, F., Paquette, A., Papaik, M.J., Thiffault, N., and Messier, C. 2010. Do position and species identity of neighbours matter in 8–15-year-old post harvest mesic stands in the boreal mixedwood? For. Ecol. Manage. **260**(7): 1124–1131. doi:10.1016/j.foreco.2010.06.037.

Bräker, O.U., and Baumann, E. 2006. Growth reactions of sub-Alpine Norway spruce (*Picea abies* (L.) Karst.) following one-sided light exposure (case study at Davos "Lusiwald"). Tree-Ring Res. **62**(2): 67–73. doi:10.3959/1536-1098-62.2.67.

Bravo-Oviedo, A., Sterba, H., del Rio, M., and Bravo, F. 2006. Competition-induced mortality for Mediterranean *Pinus pinaster* Ait. and *P. sylvestris* L. For. Ecol. Manage. **222**(1–3): 88–98. doi:10.1016/j.foreco.2005.10.016.

Bugmann, H. 2001. A review of forest gap models. Clim. Change, **51**(3–4): 259–305. doi:10.1023/A:1012525626267.

Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer, New York.

Burns, R.M., and Honkala, B.H. (*Technical Coordinators*). 1990. Silvics of North America. U.S. Dep. Agric. Agric. Handb. 654. U.S. Department of Agriculture, Forest Service, Washington, D.C.

Canham, C.D., LePage, P.T., and Coates, K.D. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Can. J. For. Res. **34**(4): 778–787. doi:10.1139/x03-232.

Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., and Twery, M.J. 2006. Neighborhood analyses of canopy tree competition along environmental gradients in new England forests. Ecol. Appl. **16**(2): 540–554. doi:10.1890/1051-0761(2006)016[0540:NAOCTC]2.0.CO;2. PMID:16711043.

Caprio, A.C., and Swetnam, T.W. 1993. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. *In* Symposium on Fire in Wilderness and Park Management. U.S. For. Serv. Gen. Tech. Rep. INT-GTR-320.

Coates, K.D., Canham, C.D., and LePage, P.T. 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. J. Ecol. **97**(1): 118–130. doi:10.1111/j.1365-2745.2008.01458.x.

Contreras, M.A., Affleck, D., and Chung, W. 2011. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. For. Ecol. Manage. **262**(11): 1939–1949. doi:10.1016/j.foreco.2011.08.031.

Coomes, D.A., and Allen, R.B. 2007. Effects of size, competition and altitude on tree growth. J. Ecol. **95**(5): 1084–1097. doi:10.1111/j.1365-2745.2007.01280.x.

Coomes, D.A., and Allen, R.B. 2009. Testing the metabolic scaling theory of tree growth. J. Ecol. **97**(6): 1369–1373. doi:10.1111/j.1365-2745.2009.01571.x.

Daniels, R.F., Burkhart, H.E., and Clason, T.R. 1986. A comparison of competition measures for predicting growth of loblolly pine trees. Can. J. For. Res. **16**(6): 1230–1237. doi:10.1139/x86-218.

Das, A., Battles, J., van Mantgem, P.J., and Stephenson, N.L. 2008. Spatial elements of mortality risk in old-growth forests. Ecology, **89**(6): 1744–1756. doi:10.1890/07-0524.1. PMID:18589538.

Das, A., Battles, J., Stephenson, N.L., and van Mantgem, P.J. 2011. The contribution of competition to tree mortality in old-growth coniferous forests. For. Ecol. Manage. **261**(7): 1203–1213. doi:10.1016/j.foreco.2010.12.035.

Duff, G.H., and Nolan, N.J. 1953. Growth and morphogenesis in the Canadian forest species: I. The controls of cambial and apical activity in *Pinus resinosa* Ait. Can. J. Bot. **31**(4): 471–513. doi:10.1139/b53-037.

Edwards, A. 1994. Likelihood: expanded edition. Johns Hopkins University Press, Baltimore, Md.

Enquist, B.J., West, G.B., Charnov, E.L., and Brown, J.H. 1999. Allometric scaling of production and life-history variation in vascular plants. Nature, **401**(6756): 907–911. doi:10.1038/44819.

Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P., and Zavala, M.A. 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. Glob. Change Biol. **17**(7): 2400–2414. doi:10.1111/j.1365-2486.2011.02421.x.

Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: introduction and methods of edge correction. J. Veg. Sci. **6**(4): 575–582. doi:10.2307/3236356.

Hegyi, F. 1974. A simulation model for managing jack-pine stands. *In* Growth models for tree and stand simulation. *Edited by* J. Fries. Royal College of Forestry, Stockholm, Sweden. pp. 74–90.

Janzen, D.H. 1970. Herbivores and number of tree species in tropical forests. Am. Nat. **104**(940): 501–528. doi:10.1086/282687.

Link, W.A., and Barker, R.J. 2010. Bayesian inference with ecological applications. Academic Press, San Diego, Calif.

Mott, D.G., Nairn, L.D., and Cook, J.A. 1957. Radial growth in forest trees and effects of insect defoliation. For. Sci. **3**(3): 286–304.

Muller-Landau, H.C., Condit, R.S., Chave, J., Thomas, S.C., Bohlman, S.A., Bunyavejchewin, S., Davies, S., Foster, R., Gunatilleke, S., Gunatilleke, N., Harms, K.E., Hart, T., Hubbell, S.P., Itoh, A., Kassim, A.R., LaFrankie, J.V., Lee, H.S., Losos, E., Makana, J.-R., Ohkubo, T., Sukumar, R., Sun, I.-F., Nur Supardi, M.N., Tan, S., Thompson, J., Valencia, R., Munoz, G.V., Wills, C.,

Yamakura, T., Chuyong, G., Dattaraja, H.S., Esufali, S., Hall, P., Hernandez, C., Kenfack, D., Kiratiprayoon, S., Suresh, H.S., Thomas, D., Vallejo, M.I., and Ashton, P. 2006. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. Ecol. Lett. **9**(5): 575–588. doi: 10.1111/j.1461-0248.2006.00904.x. PMID:16643303.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., and Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol. Monogr. **66**(1): 1–43. doi:10.2307/2963479.

Papaik, M.J., and Canham, C.D. 2006. Multi-model analysis of tree competition along environmental gradients in southern New England forests. Ecol. Appl. **16**(5): 1880–1892. doi:10.1890/1051-0761(2006)016[1880:MAOTCA]2.0.CO;2. PMID:17069379.

Stadt, K.J., Huston, C., Coates, K.D., Feng, Z., Dale, M.R.T., and Lieffers, V.J. 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. Ann. For. Sci. **64**(5): 477–490. doi:10.1051/forest:2007025.

Stephenson, N.L. 1988. Climatic control of vegetation distribution: the role of the water balance with examples from North America and Sequoia National Park, California. Cornell University, Ithaca, N.Y.

Uriarte, M., Condit, R., Canham, C.D., and Hubbell, S.P. 2004. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? J. Ecol. **92**(2): 348–360. doi:10.1111/j.0022-0477.2004.00867.x.

Woodall, C.W., Fiedler, C.E., and Milner, K.S. 2003. Intertree competition in uneven-aged ponderosa pine stands. Can. J. For. Res. **33**(9): 1719–1726. doi:10.1139/x03-096.