# Competitive interactions across a soil fertility gradient in a multispecies forest

**K. David Coates[1,2]\*, Erica B. Lilles[2] and Rasmus Astrup[2,3]**

[1]*Ministry of Forests, Lands and Natural Resource Operations, Bag 6000, Smithers, BC V0J 2N0, Canada;* [2]*Bulkley Valley Centre for Natural Resources Research and Management, Box 4274, Smithers, BC V0J 2N0, Canada; and* [3]*Norwegian Forest and Landscape Institute, Høgskoleveien 8, Postboks 115, 1431 Ås, Norway*

## Summary

**1.** Whether plant competition grows stronger or weaker across a soil fertility gradient is an area of great debate in plant ecology. We examined the effects of competition and soil fertility and their interaction on growth rates of the four dominant tree species in the sub-boreal spruce forest of British Columbia.

**2.** We tested separate soil nutrient and moisture indices and found much stronger support for models that included the nutrient index as a measure of soil fertility.

**3.** Competition, soil fertility and their interaction affected radial growth rates for all species.

**4.** Each species supported a different alternate hypothesis for how competitive interactions changed with soil fertility and whether competition intensity was stronger or weaker overall as soil fertility increased depended on the context, specifically, species, neighbourhood composition and type of competition (shading vs. crowding).

**5.** The four species varied slightly in their growth response to soil fertility.

**6.** Individual species had some large variations in the shapes of their negative relationships between shading, crowding and tree growth, with one species experiencing no net negative effects of crowding at low soil fertility.

**7.** Goodness-of-fit was not substantially increased by models including competition–soil fertility interactions for any species. Tree size, soil fertility, shading and crowding predicted most of the variation in tree growth rates in the sub-boreal spruce forest.

**8.** *Synthesis*. The intensity of competition among trees across a fertility gradient was species- and context-specific and more complicated than that predicted by any one of the dominant existing theories in plant ecology.

**Key-words:** crowding, environmental gradient, Grime–Tilman debate, light, neighbourhood models, plant–plant interactions, plant competition, productivity, soil moisture and nutrients, tree growth

## Introduction

There is no single widely supported theory for how plant interactions change with soil fertility. Instead, there are two dominant viewpoints with conflicting predictions (Craine 2005). One field of thought predicts that neighbouring plants will have a less competitive effect at low soil fertility as articulated by the stress gradient hypothesis (Bertness & Callaway 1994) and the CSR strategy theory (Grime 2007). To the contrary, other scientists argue that competition for resources is the key factor structuring plant communities across the entire soil fertility gradient but that the mode of competition switches from predominantly for light at high fertility to predominantly for nutrients at low fertility (i.e. resource-ratio

theory described by Tilman 1985, 2007). By inference, the resource-ratio theory implies competition for soil resources will be stronger where soil fertility is lower (Trinder *et al.* 2012). Both opposing viewpoints have found support and criticism in the literature (Grace 1991; Craine 2005). Even in the last few years, new experiments have found that competition increased at low soil fertility in one case (Trinder *et al.* 2012) and decreased at low soil fertility in another case (Baribault & Kobe 2011). To understand these conflicting results, further hypothesis refinement and experimental testing are necessary (Craine 2005; Miller *et al.* 2005; Maestre *et al.* 2009).

For reasons of research efficiency, experimental studies to test these theories do not typically use trees. They are often implemented over short time intervals or with short-lived species. There are considerable advantages to this approach, for example, ensuring that the same species are present across the

whole soil fertility gradient and that the number of interspecific interactions remains manageable. In addition, short-term controlled experiments have the potential for measuring the mechanism of competition (e.g. nutrient or water uptake) rather than just the outcome as measured by, for example, biomass production (Trinder *et al.* 2012). These short-term experiments, however, provide little direct insight into the outcomes of competition across soil fertility gradients in long-lived multispecies forests.

In contrast, neighbourhood studies of multispecies forests incorporate another methodology for understanding plant competition. Neighbourhood studies have found a high degree of predictability in individual tree growth from information about the characteristics of their tree neighbourhood (Gratzer *et al.* 2004). To date, most neighbourhood studies have quantified the growth response of target trees to surrounding competitors on soils of medium nutrient and moisture availability and have not explicitly considered how competitive interactions might vary with site productivity (e.g. Canham, LePage & Coates 2004; Canham *et al.* 2006; Coates, Canham & LePage 2009). Presumably, the usefulness of predicting tree growth from tree neighbourhood dynamics for ecological understanding and forest management decisions should be substantially increased with the knowledge of how competitive interactions among tree species change with soil fertility (e.g. Baribault & Kobe 2011). Tree species may differ in their competitive effects on other trees across a resource gradient and/or differ in their growth responses to competition–fertility interactions overall. Such species-specific effects and responses would present opportunities for careful matching of tree species composition and site type to minimize competition and maximize productivity in managed stands.

For this article, we are fortunate in having an ecological system that allows us to draw on the strength of different research methods for studying plant competition. The sub-boreal forest ecosystem of British Columbia has several characteristics that make it a valuable resource for comparing different theories about how plant interactions change with soil fertility. First, with only four dominant tree species, the number of interspecific competitive interactions is limited and conceivably quantified by a research programme. Second, all four species are present across strong landscape-scale gradients in soil fertility, but differ in relative abundance (Meidinger, Pojar & Harper 1991; Kranabetter, Dawson & Dunn 2007). Third, the tree species' life-history strategies and trait trade-offs are reasonably well understood and differentiate the species into recognizable niches. Finally, competition among communities of long-lived tree species, across natural gradients of soil fertility, may provide insights into the current alternate theories of plant interaction not possible from manipulative studies of short-lived species in artificial settings. From these forests, we have an extensive and well-balanced sample of target and neighbour trees from a wide range of tree size, density and neighbourhood composition and from across a strong soil fertility gradient. Soil fertility is the productive capacity of the soil as determined by correlated soil moisture and nutrient availability gradients using the

well-described biogeoclimatic system of ecosystem classification in British Columbia (Pojar, Klinka & Meidinger 1987; Banner *et al.* 1993).

We use a model comparison framework to test hypotheses of competitive interactions among tree species across soil fertility gradients in sub-boreal spruce forests. These hypotheses are alternate answers to the three basic questions set forth by Rees, Childs & Freckleton (2012): '(i) How do changes in the quality of the environment in the absence of competition affect plant performance? (ii) How do changes in competition affect performance? and (iii) how do the effects of competition and the environment interact with each other?' Specifically, our study was designed to detect whether competition changed with soil fertility and to detect whether competitive effects were stronger (reduced tree growth more) or weaker (reduced tree growth less) as soil fertility increased. Our analysis differentiated between soil fertility effects on competition for light versus soil fertility effects on crowding (crowding incorporates all direct and indirect interactions among trees other than shading). Crowding, as it is formulated in our models and in many previous tree neighbourhood studies (e.g. Canham, LePage & Coates 2004; Canham *et al.* 2006; Coates, Canham & LePage 2009), incorporates the effects of neighbour tree abundance, size, distance and species (components of crowding) and the response of the target tree to the sum of all components. Soil fertility may affect the individual competitive effects of the components of crowding and/or the response to the sum of all components in the overall crowding term. Our analysis also examined these interactions.

## Materials and methods

### STUDY AREA DESCRIPTION

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 (Banner *et al.* 1993). The continental climate of this area 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, Pojar & Harper 1991). Subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), interior spruce (*Picea glauca × engelmanii* [Moench] Voss) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia*) are the dominant coniferous tree species and often occur in mixed stands with the dominant broad-leaved species, trembling aspen (*Populus tremuloides* Michx.).

Topographical and geomorphic variation over the mountainous landscape has led to a wide range of soil fertility conditions in our study area that have been described by Banner *et al.* (1993). Glacial and alluvial deposits and processes have created this diverse mixture of site types, sometimes in very close association and not necessarily predicable because of slope position. Briefly, the driest, poorest sites are typically found on shallow, rocky or coarse-textured soil with acidic Ae horizons and a thin forest floor dominated by fungi. The medium sites best reflect the climactic inputs of the region with medium-textured, well-drained soil, little soil acidification (no Ae horizon) and a thicker forest floor with fungal and soil fauna influences. The richest sites have finer-textured soils with organic matter incorporated

into the mineral soil (Ah horizon) by active soil fauna and quickly decomposing herbaceous flora.

### TREE SAMPLING AND MENSURATION

Our goal was to sample trees distributed evenly across a soil fertility gradient, across a range of stand age, density and composition and across tree size. We selected trees for sampling from 126 stem-mapped sites located in over 50 geographically separate locations to represent the full range of soil fertility and stand type present in the landscape (Table 1), including stands initiated from fire in 1784, 1854, 1863, 1907 and 1936, stands with partial cutting and under planting throughout the 1950's and stands clear-cut between 1964 and 1983. Stem maps included subalpine fir, interior spruce, lodgepole pine and/or trembling aspen target trees (cored trees with DBH > 5 cm and no disease, pests or physical deformities such as forks or large scars) and the neighbour trees (live trees with DBH > 5 cm) within 8 m around them. Target trees were selected to cover the full range of canopy positions, including overtopped trees, emergent trees and canopy trees in tree neighbourhoods with different species combinations. Our data set contains 651 fir, 825 spruce, 484 pine and 267 aspen target sample trees. We had good sample size for all species across all site types except for aspen target trees on the poorest sites (Table 1). This low sample size could cause parameter estimation difficulties (c.f. Astrup, Coates & Hall 2008)

Target and neighbourhood trees (14 357 trees total) in stem maps were identified to species, and all DBHs and tree stem coordinates were measured and recorded. Tree cores were taken at a height of 1.3 m from target trees and were mounted, dried and sanded with progressively finer grades of sandpaper as necessary until tree rings were clearly visible. A Velmex microscope-sliding stage system (Velmex Inc., Bloomfield, NY, USA) was used to measure ring widths for the last five full growing seasons on each core. The annual radial growth of each target tree was determined by taking the mean of the five ring width measurements. The diameter of each target tree prior to the measured five growing seasons was calculated by subtracting twice the radial growth over five years from the outside bark diameter.

### SOIL SAMPLING

As a measure of soil fertility, both soil moisture and nutrient availability indices were assessed from soil pits within each stem map. Small stem maps with consistent slopes and understorey plant communities

**Table 1.** Species composition of stands sampled (e.g. PlBl), number of stem maps, sample trees and cored trees by site type

| | At/AtSx | AtPl/AtPlBl | AtPlSx | AtSxBl/AtPlSxBl | Bl | Pl | PlBl | PlSxBl | PlSx | Sx | SxBl | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Poor sites** | | | | | | | | | | | | |
| Stem maps | 1 | 0 | 0 | 0 | 0 | 5 | 4 | 10 | 4 | 0 | 2 | 26 |
| Total trees | 98 | 0 | 0 | 0 | 0 | 422 | 439 | 501 | 110 | 0 | 242 | 1812 |
| **No. Cored trees** | | | | | | | | | | | | |
| Aspen | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 2 | 20 |
| Lodgepole pine | 0 | 0 | 0 | 0 | 0 | 35 | 24 | 40 | 8 | 0 | 7 | 114 |
| Interior spruce | 3 | 0 | 0 | 0 | 0 | 1 | 2 | 37 | 8 | 0 | 25 | 76 |
| Subalpine fir | 0 | 0 | 0 | 0 | 0 | 0 | 22 | 32 | 0 | 0 | 21 | 75 |
| **Medium sites** | | | | | | | | | | | | |
| No. Stem maps | 2 | 2 | 1 | 4 | 1 | 2 | 5 | 9 | 13 | 1 | 3 | 43 |
| No. Trees | 469 | 506 | 123 | 413 | 81 | 218 | 383 | 1079 | 2210 | 44 | 249 | 5775 |
| **No. Cored trees** | | | | | | | | | | | | |
| Aspen | 40 | 15 | 6 | 29 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 93 |
| Lodgepole pine | 0 | 7 | 4 | 4 | 1 | 19 | 31 | 39 | 86 | 1 | 3 | 195 |
| Interior spruce | 15 | 0 | 3 | 29 | 2 | 0 | 4 | 65 | 86 | 5 | 16 | 225 |
| Subalpine fir | 5 | 13 | 1 | 15 | 7 | 4 | 16 | 45 | 33 | 0 | 21 | 160 |
| **Rich sites** | | | | | | | | | | | | |
| No. Stem maps | 5 | 0 | 2 | 0 | 3 | 1 | 2 | 5 | 4 | 3 | 9 | 34 |
| No. Trees | 365 | 0 | 465 | 0 | 345 | 198 | 199 | 1026 | 664 | 280 | 1398 | 4940 |
| **No. Cored trees** | | | | | | | | | | | | |
| Aspen | 87 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 101 |
| Lodgepole pine | 0 | 0 | 21 | 0 | 4 | 18 | 18 | 40 | 19 | 2 | 12 | 134 |
| Interior spruce | 12 | 0 | 65 | 0 | 11 | 0 | 7 | 45 | 76 | 40 | 114 | 370 |
| Subalpine fir | 0 | 0 | 0 | 0 | 55 | 0 | 25 | 41 | 0 | 0 | 155 | 276 |
| **Very rich sites** | | | | | | | | | | | | |
| No. Stem maps | 5 | 0 | 1 | 0 | 2 | 0 | 2 | 2 | 1 | 2 | 8 | 23 |
| No. Trees | 443 | 0 | 228 | 0 | 9 | 0 | 65 | 98 | 88 | 54 | 845 | 1830 |
| **No. Cored trees** | | | | | | | | | | | | |
| Aspen | 41 | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 53 |
| Lodgepole pine | 3 | 0 | 16 | 0 | 0 | 0 | 4 | 5 | 7 | 0 | 6 | 41 |
| Interior spruce | 39 | 0 | 2 | 0 | 0 | 0 | 2 | 18 | 20 | 18 | 55 | 154 |
| Subalpine fir | 0 | 0 | 0 | 0 | 3 | 0 | 10 | 12 | 0 | 0 | 115 | 140 |

Species composition codes are as follows: At = trembling aspen; Pl = lodgepole pine; Sx = interior spruce; Bl = subalpine fir; PlBl = mixed pine and fir; AtPlBl = mixed aspen, pine and fir; At/AtSx = aspen and mixed aspen and spruce; and so on. Species representing < 10% composition of the stand were not included in species composition codes

contained at least one soil pit. Larger stem maps and any stem maps with changes in slope or plant community contained more than one soil pit as needed to accurately classify the soil fertility for each target tree. Soil moisture index was assessed on a scale from 0 to 1 (0 = xeric and 1 = hygric) based on landform, aspect, slope position, depth to bedrock, water-table fluctuations and depth, soil texture and coarse fragment content according to the B.C. Biogeoclimatic Classification System soil moisture regime key (Banner *et al.* 1993). Soil nutrient index was assessed on a scale from 0 to 1 (0 = very poor and 1 = very rich) based on slope position, depth to bedrock, soil texture, coarse fragment content and type, pH, presence and depth of eluviation in the A horizon, soil colour and humus form according to the B. C. Biogeoclimatic Classification System soil nutrient regime table (Banner *et al.* 1993). This classification has been shown to define strong correlated soil moisture and nutrient availability gradients. From poor sites to very rich sites, there is a linear increase of more than 200% in gravimetric soil moisture, available N and exchangeable cations and a 170% increase in asymptotic stand height (Kranabetter, Dawson & Dunn 2007; Kranabetter & Simard 2008).

## MODEL DEVELOPMENT

We began our analysis on competitive effects across soil fertility gradients by building on our previous work and that of our colleagues in tree neighbourhood dynamics in mesic forests (e.g. Uriarte *et al.* 2004; Canham *et al.* 2006; Coates, Canham & LePage 2009). Model 1 (full function in Table 2) contained the principal components found to be most important for predicting tree growth in previous work and for sub-boreal spruce forests (see Table S1 in Appendix S1 of Supporting Information):

$$\text{Annual radial growth} = MaxGrowth \times \text{Size effect} \times \text{Light competition effect} \times \text{Crowding effect} \qquad \text{eqn 1}$$

*MaxGrowth* was the maximum potential growth rate experienced by a hypothetical 'free-growing' tree, which was multiplied by growth modifier functions representing the growth–tree size relationship, the effect of light competition and the effect of crowding (all remaining effects of neighbouring trees after accounting for shading; Coates, Canham & LePage 2009).

A lognormal function represented the change in growth rate with tree size in model 1. In this function, $X_0$ determined the DBH (of the target tree) at which peak growth occurred, and $X_b$ determined peak width and tail slope:

$$\text{Size effect} = \exp^{-1/2\left[\frac{\ln(DBH/X_0)}{X_b}\right]^2} \qquad \text{eqn 2}$$

To simplify the interpretation of soil fertility effects on competition, $X_0$ and $X_b$ values were set *a priori* from parameter estimates of trees on mesic and rich sites using the full model (without $\gamma$) from Coates, Canham & LePage (2009). Parameter estimates were 20, 13, 10 and 5.8 (for $X_0$) and 1.5, 1.1, 0.9 and 1.5 (for $X_b$) for subalpine fir, interior spruce, lodgepole pine and aspen, respectively (data not shown)

The light competition effect in model 1 was a power function forced to go through the origin and (1, 1) that had the flexibility to represent an asymptotic curve if the estimated parameter $A < 1$, an exponential curve if $A > 1$ or a linear relationship if $A = 1$ (Sit & Poulin-Costello 1994):

$$\text{Light competition effect} = \text{Light}^A \qquad \text{eqn 3}$$

where Light was the proportion of above canopy light reaching the target tree as determined by a canopy tree shading model (described

by Canham, LePage & Coates 2004). Briefly, the canopy tree shading model represents neighbouring tree crowns as opaque two-dimensional billboards that block light (incident, seasonal total photosynthetic photon flux density) from reaching the target tree. Tested in interior cedar hemlock forests also containing all of our study species, this model predicted understorey light levels with an $R^2$ of 80% (Canham, LePage & Coates 2004).

The effect of crowding on tree growth incorporated all direct and indirect interactions among trees other than shading. These interactions may include negative effects on growth like water and nutrient pre-emption and positive or negative effects on growth that are less well understood like shared mycorrhizal networks, nutrient enhancement by litterfall or disease transmission. The crowding effect function had the same form as in Coates, Canham & LePage (2009) where the net degree of crowding overall was represented by a Neighbourhood Competition Index (NCI). In the crowding effect function, the response of a target tree to a given NCI was adjusted by the estimated parameter $C$ in a negative exponential function:

$$\text{Crowding effect} = \exp^{-C \times NCI} \qquad \text{eqn 4}$$

In the NCI, the crowding effects of neighbours were a net measurement of positive and negative interactions that had the possibility of changing according to neighbour number, size, species and distance:

$$NCI = \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_i \frac{DBH_{ij}^{\alpha}}{DISTANCE_{ij}^{\beta}} \qquad \text{eqn 5}$$

Neighbour effects were assumed to decrease with increasing distance between trees and increase with increasing diameter of the neighbour tree. The estimated parameter $\alpha$ determined the shape of the size effect, and the parameter $\beta$ determined the shape of the distance effect. A species-specific competition index parameter ($\lambda_i$) ranging between 0 and 1 adjusted the crowding effect of each neighbour tree depending on its species. The total crowding effect was the summed effect of all neighbours ($j = 1, …, n$) of all species ($i = 1, …, s$) within an 8 m radius of the target tree. Four species-specific competition indexes were included in our models: $\lambda_{fir}$ for subalpine fir neighbours, $\lambda_{spruce}$ for interior spruce neighbours, $\lambda_{pine}$ for lodgepole pine neighbours and $\lambda_{aspen}$ for trembling aspen neighbours. Neighbour trees of other species were few and were included in the above competition indexes: western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) were grouped with subalpine fir, black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenburg) were grouped with interior spruce and paper birch (*Betula papyrifera* Marsh.), and black cottonwood (*Populus balsamifera* subsp. *trichocarpa* [Torr. & A. Gray] Brayshaw) were grouped with aspen.

To determine how soil fertility interacts with competition to affect tree growth rates, we then developed a series of nested models that corresponded with our alternative hypotheses (Table 2). In the simplest alternative model (model 2), soil fertility directly affected tree radial growth rates, but did not affect any neighbourhood competitive dynamics. In model 2, the soil fertility effect was multiplied by *MaxGrowth* and the growth modifier functions in eqn 1 to account for the well-understood decline in growth rates with decreasing soil fertility (Table 2):

$$\begin{aligned}\text{Annual radial growth} = {} & MaxGrowth \times \text{Size effect} \\ & \times \text{Light competition effect} \times \text{Crowding effect} \\ & \times \text{Soil fertility effect}\end{aligned}$$

$$\text{eqn 6}$$

We also took advantage of the flexibility of a power function for the soil fertility effect to allow asymptotic, exponential or linear relationships between soil fertility (SF) and growth rates:

**Table 2.** Tested model functional forms, parameters, and corresponding hypotheses using variables target tree diameter (dbh), soil fertility (SF; tested with soil nutrients and soil moisture separately) and neighbour tree diameters (DBH), species and distances to predict annual radial growth at breast height (1.3 m)

| Model No. | Functional form | Parameters | Hypothesis tested |
|---|---|---|---|
| 1 | $MaxGrowth$ $\times (\exp^{-0.5\times(\ln(\text{dbh}/X_o)/X_b)^2})$ $(\text{Light})^A$ $(\exp^{-C\times\text{NCI}})$ | $MaxGrowth$: maximum potential radial growth (mm) $X_b$: width of growth peak and slope of the tail $A$: shape of the response to light competition $C$: shape of the response to overall crowding $Xo$: dbh at which peak growth occurs NCI: $\Sigma\Sigma\ \lambda_i \times (\text{DBH}_i{}^\alpha/\text{DISTANCE}_i{}^\beta)$ $\alpha$: shape of the neighbour size effect $\beta$: shape of the neighbour distance effect $\lambda_i$: magnitude of the competitive effect of each species ($i$) | Tree growth rates do not change in response to soil fertility either directly or through effects on competitive relationships |
| 2 | $MaxGrowth \times (\text{SF})^N$ $\times (\exp^{-0.5\times(\ln(\text{dbh}/X_o)/X_b)^2})$ $\times (\text{Light})^A$ $\times (\exp^{-C\times\text{NCI}})$ | $N$: shape of the change in $MaxGrowth$ with SF | Growth rates respond directly to soil fertility, but do not respond to soil fertility effects on competitive relationships. |
| 3 | $MaxGrowth \times (\text{SF})^N$ $\times (\exp^{-0.5\times(\ln(\text{dbh}/X_o)/X_b)^2})$ $\times (\text{Light})^{A\times(\text{SF})^\wedge m}$ $\times (\exp^{-C\times\text{NCI}})$ | $m$: modifier of the SF effect on $A$ (shape of the response to light competition) | Growth rates respond directly to soil fertility. Growth responses to light competition also change with soil fertility |
| 4 | $MaxGrowth \times (\text{SF})^N$ $\times (\exp^{-0.5\times(\ln(\text{dbh}/X_o)/X_b)^2})$ $\times (\text{Light})^A$ $\times (\exp^{-C\times(\text{SF})^o\times\text{NCI}})$ | $o$: modifier of the SF effect on $C$ (shape of the response to overall crowding) | Growth rates respond directly to soil fertility. Growth responses to overall crowding also change with soil fertility |
| 5 | $MaxGrowth \times (\text{SF})^N$ $\times (\exp^{-0.5\times(\ln(\text{dbh}/X_o)/X_b)^2})$ $\times (\text{Light})^{A\times(\text{SF})^m}$ $\times (\exp^{-C\times(\text{SF})^o\times\text{NCI}})$ | | Growth rates respond directly to soil fertility. Growth responses to light and to overall crowding also change with soil fertility |
| 6 | $MaxGrowth \times (\text{SF})^N$ $\times (\exp^{-0.5\times(\ln(\text{dbh}/X_o)/X_b)^2})$ $\times (\text{Light})^A$ $\times (\exp^{-C}$ $\times((\lambda\text{aspen}\times(\text{SF})^\wedge\mu\times\text{NCIaspen})$ $+(\lambda\text{pine}\times(\text{SF})^\wedge\omega\times\text{NCIpine})$ $+(\lambda\text{spruce}\times(\text{SF})^\wedge\theta\times\text{NCIspruce})$ $+(\lambda\text{fir}\times(\text{SF})^\wedge\upsilon\times\text{NCIfir}))$ | $\mu$: modifier of the SF effect on aspen competition $\omega$: modifier of the SF effect on spruce competition $\theta$: modifier of the SF effect on pine competition $\upsilon$: modifier of the SF effect on fir competition | Growth rates respond directly to soil fertility. Species-specific neighbour effects on growth rates also change with soil fertility |
| 7 | $MaxGrowth \times (\text{SF})^N$ $\times (\exp^{-0.5\times(\ln(\text{dbh}/X_o)/X_b)^2})$ $\times (\text{Light})^A$ $\times (\exp^{-C\times(\text{SF})^o\times}$ $((\lambda\text{aspen}\times(\text{SF})^\wedge\mu\times\text{NCIaspen})$ $+(\lambda\text{pine}\times(\text{SF})^\wedge\omega\times\text{NCIpine})$ $+(\lambda\text{spruce}\times(\text{SF})^\wedge\theta\times\text{NCIspruce})$ $+(\lambda\text{fir}\times(\text{SF})^\wedge\upsilon\times\text{NCIfir}))$ | | Growth rates respond directly to soil fertility. Species-specific neighbour effects on growth rates also change with soil fertility, as do growth responses to overall crowding |
| 8 | $MaxGrowth \times (\text{SF})^N$ $\times (\exp^{-0.5\times(\ln(\text{dbh}/X_o)/X_b)^2})$ $\times (\text{Light})^A$ $\times (\exp^{-C}$ $\times\Sigma\Sigma\lambda i\times(\text{DBH}i^\wedge(\alpha\times(\text{SF})^\wedge x))$ $/(\text{DISTANCE}i^\wedge(\beta\times(\text{SF})^\wedge v))$ | $x$: modifier of the SF effect on $\alpha$ (shape of the neighbour size effect) $v$: modifier of the SF effect on $\beta$ (shape of the neighbour distance effect) | Growth rates respond directly to soil fertility. The crowding effects of neighbouring tree size and distance on growth rates also change with soil fertility |
| 9 | $MaxGrowth \times (\text{SF})^N$ $\times (\exp^{-0.5\times(\ln(\text{dbh}/X_o)/X_b)^2})$ $\times (\text{Light})^A$ $\times (\exp^{-C\times(\text{SF})^o}$ $\times\Sigma\Sigma\lambda i\times(\text{DBH}i^\wedge(\alpha\times(\text{SF})^\wedge x))$ $/(\text{DISTANCE}i^\wedge(\beta\times(\text{SF})^\wedge v))$ | | Growth rates respond directly to soil fertility. The crowding effects of neighbouring tree size and distance on growth rates also change with soil fertility, as do growth responses to overall crowding |

Soil fertility effect $= SF^N$                                       eqn 7

The alternative models 3–9 were built from model 2. They allowed soil fertility to affect growth directly as in model 2 and also indirectly by modifying tree competition via shading, crowding, intra- and inter-specific effects and neighbour distance and size effects. To accomplish this analysis, the parameter estimates for $A$, $C$, $\alpha$, $\beta$, $\lambda_{fir}$, $\lambda_{spruce}$, $\lambda_{pine}$ and $\lambda_{aspen}$ were allowed to vary with soil fertility using the soil fertility effect function (eqn 7) as a multiplier (Table 2). In models 3 and 4, parameters $A$ (shape of the response to light competition) and $C$ (shape of the response to overall crowding), respectively, varied with soil fertility, and in model 5, both $A$ and $C$ did. In model 6, $\lambda_{fir}$, $\lambda_{spruce}$, $\lambda_{pine}$ and $\lambda_{aspen}$ (species-specific competitive effects) varied with soil fertility, and in model 7, $C$ was allowed to vary with the $\lambda$s. In Model 8, $\alpha$ (shape of the neighbour size effect) and $\beta$ (shape of the neighbour distance effect) varied with soil fertility, and in model 9, $C$ was allowed to vary with $\alpha$ and $\beta$ (Table 2). We tested separate soil nutrient and soil moisture availability indices as the soil fertility measurement in our models.

## MODEL SELECTION AND PARAMETER ESTIMATION

We used likelihood methods and Akaike Information Criterion (AIC) to compare our models (Burnham & Anderson 2002; Canham & Uriarte 2006). A simulated annealing algorithm (neighlikeli package; Murphy 2006) in the statistical software R v. 2.6.1 calculated maximum-likelihood estimates and support intervals for the parameters in each model after 50 000 iterations (Goffe, Ferrier & Rogers 1994; R Development Core Team 2007). Models were selected based on AIC corrected for a small sample size ($AIC_c$), although our sample sizes were generally appropriate for the number of parameters in the models and the sample size correction was small. We included a probability density function in all models that allowed the variance to

increase with the mean, which provided a better fit to the data than did the assumption of heterogeneous variance.

## Results

### MODEL COMPARISON

The soil nutrient availability index had consistently much greater support as the soil fertility measurement than the soil moisture availability index, whether they were compared with $\Delta AIC_c$ or $R^2$ ($\Delta AIC_c$ for nutrient models was always more than 10 points lower than that for moisture models; Table 3). This finding was consistent with results comparing moisture and nutrient indices for predicting seedling and sapling growth rates in the same forest type (Lilles & Astrup 2012). Consequently, the following results and discussion of soil fertility are based on the best soil nutrient availability model for each species.

All models that incorporated soil fertility into the growth prediction (models 2–9) had much greater support than model 1, which did not incorporate soil fertility. However, the best model varied among tree species, resulting in several of our alternative hypotheses for competitive interactions being supported by the data (Table 3). The response of subalpine fir to light competition and to overall crowding changed with soil fertility (model 5). For interior spruce, soil fertility changed the effect of inter- and intraspecific competitive relationships (model 6). For lodgepole pine (model 8), soil fertility changed the effects of neighbour sizes and distances. For trembling aspen (model 9), soil fertility changed the effects of neighbour sizes and changed the response to overall crowding.

**Table 3.** $\Delta AIC_c$ and $R^2$ comparison of model 1 with alternative models 2–9 using (a) soil nutrient availability and (b) soil moisture availability as the soil fertility measurement for each species. The best model(s) for each species are indicated with bold type

| Model | Subalpine fir | | Interior spruce | | Lodgepole pine | | Aspen | |
|---|---|---|---|---|---|---|---|---|
| | $\Delta AIC_c$ | $R^2$ | $\Delta AIC_c$ | $R^2$ | $\Delta AIC_c$ | $R^2$ | $\Delta AIC_c$ | $R^2$ |
| 1 | 168 | 0.36 | 402 | 0.37 | 191 | 0.56 | 52 | 0.31 |
| *(a) Soil nutrient models* | | | | | | | | |
| 2 | 47 | 0.50 | 10 | 0.61 | 13 | 0.75 | 30 | 0.44 |
| 3 | 30 | 0.50 | 12 | 0.62 | 15 | 0.75 | 32 | 0.44 |
| 4 | 40 | 0.51 | 12 | 0.61 | 4 | 0.75 | 28 | 0.44 |
| 5 | **0** | **0.52** | 14 | 0.62 | 3 | 0.74 | 31 | 0.44 |
| 6 | 46 | 0.50 | **0** | **0.62** | 8 | 0.75 | 24 | 0.45 |
| 7 | 48 | 0.50 | 3 | 0.62 | 10 | 0.75 | 25 | 0.45 |
| 8 | 37 | 0.51 | 13 | 0.62 | **0** | **0.75** | 6 | 0.47 |
| 9 | 39 | 0.51 | 11 | 0.62 | 2 | 0.75 | **0** | **0.49** |
| *(b) Soil moisture models* | | | | | | | | |
| 2 | 94 | 0.45 | 267 | 0.45 | 111 | 0.63 | 53 | 0.33 |
| 3 | 78 | 0.46 | 269 | 0.45 | 113 | 0.63 | 54 | 0.33 |
| 4 | 80 | 0.45 | 266 | 0.45 | 102 | 0.63 | 53 | 0.32 |
| 5 | 56 | 0.46 | 268 | 0.45 | 101 | 0.63 | 55 | 0.33 |
| 6 | 81 | 0.45 | 264 | 0.45 | 104 | 0.63 | 38 | 0.36 |
| 7 | 83 | 0.45 | 266 | 0.45 | 106 | 0.64 | 40 | 0.36 |
| 8 | 84 | 0.45 | 254 | 0.45 | 102 | 0.64 | 24 | 0.39 |
| 9 | 84 | 0.45 | 260 | 0.45 | 102 | 0.64 | 13 | 0.42 |

## MAXIMUM POTENTIAL GROWTH AND DIRECT EFFECTS OF SOIL FERTILITY

The combined effects of the size, light, crowding and soil fertility functions on growth rates were different among species across the soil fertility gradient (Fig. 1). The shape of the predicted growth curves closely followed the actual growth rates for each species (Fig. 1). The estimated maximum potential radial growth rates (*MaxGrowth* parameter) were 7.7 mm year$^{-1}$ for spruce, 5.4 mm year$^{-1}$ for pine, 4.8 mm year$^{-1}$ for aspen and 4.3 mm year$^{-1}$ for fir (Table 4), which coincided with observed maximum growth rates being highest for interior spruce (Fig. 1). *N* parameter estimates (shape of the change in *Max-Growth* with soil fertility) also varied among species (Table 4; Fig. 2).

## GROWTH RESPONSES TO SHADING AND CROWDING

Subalpine fir's radial growth rate responded differently to light competition as soil fertility increased. According to the best model for subalpine fir, light availability had little effect on fir growth (*A* = 0.06) on poor sites, a slightly asymptotic effect (*A* = 0.23) on medium sites and a near linear effect (*A* = 1.13) on very rich sites (Table 4 and Fig. 2). For interior spruce, lodgepole pine and aspen, the ΔAIC$_c$ for model 2 was 1 or 2 points higher than ΔAIC$_c$ for model 1, showing that light competition was not affected by soil fertility for three of four species. Aspen, spruce and pine radial growth rates showed linear or semi-linear responses to light availability (*A* = 0.97, 0.72 and 1.26, respectively; Table 4 and Fig. 2).

The shape of growth responses to variation in overall crowding was determined by the *C* parameter. For all species, growth rates dropped off rapidly, following a negative exponential curve, as NCI increased (Fig. 2), and the shape of the curve depended on soil fertility for subalpine fir and aspen. For example, subalpine fir growth rates decreased more quickly with NCI on poor sites than on medium, rich or very rich sites so that an equivalent tree neighbourhood (NCI = 0.4) that decreased growth by more than 50% on very rich sites would decrease growth by over 90% on poor sites (Fig. 2). Soil fertility had no effect on the *C* parameter for interior spruce or lodgepole pine in their best models.

## NEIGHBOUR SIZE AND DISTANCE EFFECTS

The *β* parameter determined the decline in the effect of a neighbour with increasing distance from a target tree. The relationship captured by the *β* parameter only changed across soil fertility for lodgepole pine. Pine's *β* was 0.54 on poor sites and decreased to 0.24 on very rich sites, indicating that close neighbours had a more negative influence on poor sites than on rich sites and the distance over which neighbour competition mattered was shorter on rich sites than on poor sites (Fig. 3). Soil fertility had no effect on the *β* parameter estimates for aspen, interior spruce or subalpine fir. For interior spruce *β* = 0.53 and for subalpine fir *β* = 0.89, indicating that a square root or inverse linear function represented the decline of neighbour effects with distance (Table 4 and Fig. 3). For the three conifer species, *β* increased with increasing shade tolerance (except on poor sites where pine and spruce had similar *β*s). The *β* estimate for aspen was essentially zero, suggesting that neighbour distance was not important for predicting aspen radial growth rates within a neighbourhood radius of 8 m (Fig. 3).

The *α* parameter determined how the effects of neighbouring trees change with their size. Lodgepole pine and aspen *α* parameter estimates varied across the soil fertility gradient. Lodgepole pine's *α* parameter changed simultaneously with *β* as soil fertility increased, but in the opposite direction (*α* = 1.4 on poor sites and 2.3 on very rich sites). The effect of *α* changes was still to create a stronger negative effect of neighbours on poorer sites (Figs 3 and 4). For example, a 30-cm DBH neighbouring tree would have about twice the negative effect on a poor site as compared to the negative effect on a very rich site (Fig. 4). The *α* estimate for aspen increased with decreasing soil fertility from 0.94 on very rich sites to 7.5 on poor sites, leading to very small NCI's (<0.05) on poor sites and very large NCI's (up to 8) on rich and very rich sites (Figs 3 and 4). Parameter *C* appropriately rescaled this large spread in NCI so that the range of NCI values for each site type corresponded with proportionate effects on *MaxGrowth* (Fig. 2). The combined effects of parameters *C* and *α* on aspen growth rates were an increasing negative effect of fir, spruce and intraspecific neighbours as soil fertility increased (Fig. 5). Aspen on poor sites expe-
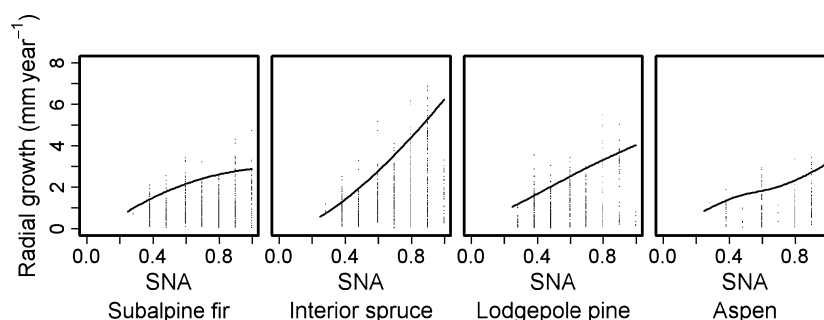


**Fig. 1.** Actual (points) and predicted radial growth rates (lines) across the soil fertility gradient (measured by soil nutrient availability; SNA). Predicted growth curves include direct effects of soil fertility on growth via *N* parameter estimates and indirect effects of soil fertility on growth via *A*, *C*, *λ*, *α* and *β* parameter estimates as determined from the best model for each species. Curves predict growth for 10-cm DBH trees growing in a neighbourhood that includes 1 subalpine fir, 6 interior spruce, 9 lodgepole pine and 8 aspen. Points are the observed growth rates from target trees of all sizes and neighbourhood compositions.

**Table 4.** Maximum-likelihood estimates (MLE) and support intervals (SI) for parameters *MaxGrowth*, *N* (shape of the change in *MaxGrowth* with soil fertility), *A* (shape of the response to light competition), *C* (shape of the response to overall crowding), $\alpha$ (shape of the neighbour size effect), $\beta$ (shape of the neighbour distance effect), $\lambda_{fir}$, $\lambda_{spruce}$, $\lambda_{pine}$, and $\lambda_{aspen}$ (inter- and intraspecific competition coefficients) from the best model for each species. Parameter estimates that were affected by soil fertility interactions (measured by soil nutrient availability; SNA) are indicated with bold type.

| Parameter | Subalpine fir | | Interior spruce | | Lodgepole pine | | Aspen | |
|---|---|---|---|---|---|---|---|---|
| | MLE | SI | MLE | SI | MLE | SI | MLE | SI |
| *MaxGrowth* | 4.3 | 4.2–4.4 | 7.7 | 7.4–7.9 | 5.4 | 5.3–5.6 | 4.8 | 4.5–5.1 |
| *N* | 0.65 | 0.57–0.73 | 1.5 | 1.4–1.5 | 0.64 | 0.57–0.70 | 1.1 | 1.0–1.3 |
| *A* | **1.5×SNA$^{2.7}$** | 1.34×SNA$^{2.3}$–1.6×SNA$^{3.1}$ | 0.72 | 0.65–0.78 | 1.3 | 1.1–1.4 | 0.97 | 0.84–1.1 |
| *C* | **1.3×SNA$^{-1.3}$** | 1.2×SNA$^{-1.4}$–1.3×SNA$^{-1.2}$ | 1.5 | 1.5–1.6 | 1.8 | 1.7–2.0 | **0.09×SNA$^{-5}$** | 0.08×SNA$^{-5}$–0.1×SNA$^{-4.6}$ |
| $\alpha$ | 1.3 | 1.3–1.3 | 1.7 | 1.5–1.7 | **2.4×SNA$^{0.42}$** | 2.4×SNA$^{0.39}$–2.4×SNA$^{0.45}$ | **0.77×SNA$^{-1.9}$** | 0.73×SNA$^{-2.0}$–0.77×SNA$^{-1.8}$ |
| $\beta$ | 0.89 | 0.87–0.92 | 0.5 | 0.51–0.56 | **0.2×SNA$^{-0.74}$** | 0.2×SNA$^{-0.87}$–0.2×SNA$^{-0.59}$ | 2.6×10$^{-75}$ | 1.46×10$^{-90}$–2.6×10$^{-3}$ |
| $\lambda_{fir}$ | 0.76 | 0.72–0.81 | **1×SNA$^{0.10}$** | 0.9×SNA$^{0.18}$–1×SNA$^{0.41}$ | 0.43 | 0.27–0.59 | 0.43 | 0–1.0 |
| $\lambda_{spruce}$ | 0.42 | 0.34–0.50 | **1×SNA$^{0.25}$** | 0.9×SNA$^{-0.01}$–1×SNA$^{0.52}$ | 0.44 | 0.28–0.61 | 0.96 | 0.79–1.0 |
| $\lambda_{pine}$ | 0.34 | 0.28–0.41 | **0.2×SNA$^{-1.6}$** | 0.2×SNA$^{-1.9}$–0.2×SNA$^{-1.3}$ | 0.94 | 0.89–1.0 | 0 | 0–0.33 |
| $\lambda_{aspen}$ | 0 | 0 | 0 | 0 | 0.27 | 0–0.54 | 0.92 | 0.87–1.0 |

rienced no net negative effects of neighbours in the best aspen model (Fig. 5). The low sample size for aspen on poor sites (Table 1) could have affected the interaction between parameters *C* and $\alpha$ and the shape of the aspen growth rate predictions. For interior spruce and subalpine fir, $\alpha$ estimates were between 1 and 2 across all sites, indicating that crowding effects of neighbours were roughly proportional to part-way between neighbour DBH and neighbour biomass.

### INTRA- AND INTERSPECIFIC COMPETITION COEFFICIENTS

Interior spruce was the only species for which the best model included changes in intra- and interspecific competition coefficients with soil fertility (Table 3). Lodgepole pine neighbours had a low net negative effect on spruce trees on very rich sites ($\lambda_{pine}$ very rich = 0.22), but the effect increased as soil fertility decreased until it was a very strong net negative effect on poor sites ($\lambda_{pine}$ poor = 1.3; Fig. 4). Compared to pine neighbour effects, fir and spruce neighbour effects on spruce were lesser in magnitude and changed in the opposite direction. Fir neighbour effects ($\lambda_{fir}$ for spruce) increased with soil fertility from 0.89 on poor sites to 0.99 on very rich sites, and spruce intraspecific neighbour effects increased from 0.74 on very poor sites to 0.97 on very rich sites (Fig. 4). Intra- and interspecific competition coefficients for lodgepole pine, subalpine fir and aspen remained constant across the soil fertility gradient (Fig. 4), and it was clear from the $\lambda$ parameter estimates that aspen consistently had the weakest neighbour effects with little or no net negative effect on conifer growth rates (Table 4 and Fig. 4). Across species, it was also clear that intraspecific neighbours had a stronger negative effect on growth rates than interspecific neighbours (Table 4 and Fig. 4).

### MODEL FIT

The alternative models provided an explanation for 33–75% of the variation in radial growth for the dominant tree species of sub-boreal spruce forests (Table 3). Model residuals (predicted–observed vs. predicted growth) were evenly distributed around zero, and models were unbiased (slopes of predicted vs. observed growth were < 1.02 and > 0.98).

We found strong evidence that competitive relationships were affected by the soil fertility gradient. Model 2, where soil fertility did not affect competitive relationships, had $\Delta AIC_c$ = 10–47 compared to the best alternative models that did include soil fertility effects on competitive relationships (Table 3). Although we had clear evidence for the effects of soil gradients on competitive relationships, our best models did not dramatically improve $R^2$ (Table 3). Competition and soil fertility effects on their own improved $R^2$ and $AIC_c$ by more than their interaction, with competition reducing $AIC_c$ by 138–572 and soil fertility reducing $AIC_c$ by 22–392 (Tables 3 and S1).

**Fig. 2.** Effect of light, neighbourhood competition index (NCI) and soil fertility (measured by soil nutrient availability; $SNA_{poor} = 0.3$, $SNA_{medium} = 0.5$, $SNA_{rich} = 0.7$, $SNA_{veryrich} = 0.9$) on estimated maximum potential radial growth rates (*MaxGrowth*; Table 4) for the four study species as predicted by the parameter estimates for *A* (shape of the response to light competition), *C* (shape of the response to overall crowding) and *N* (shape of the change in *MaxGrowth* with soil fertility) from the best model for each species. Soil fertility affected the *A* and *C* parameter estimates for subalpine fir and the *C* parameter estimate for aspen.
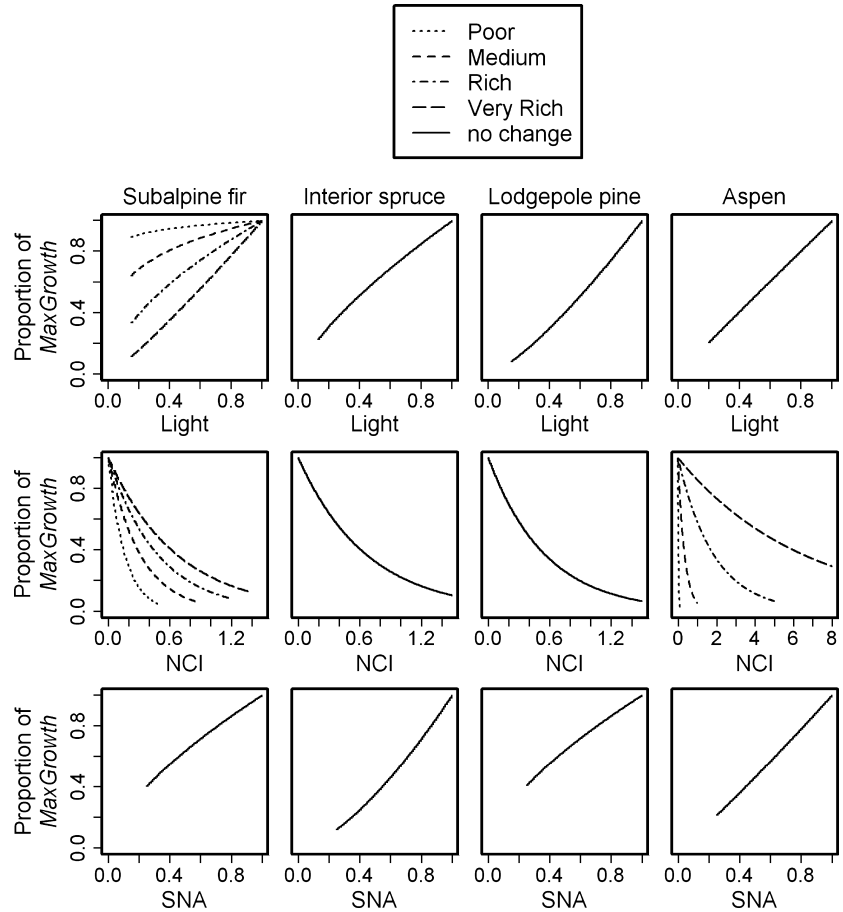


**Fig. 3.** Effect of neighbour distance (of 10 15 cm diameter neighbours) on neighbourhood competition index (NCI) for the four study species as predicted by the $\alpha$ and $\beta$ parameter estimates from the best model for each species. Estimates for $\alpha$ and $\beta$ changed with soil fertility (measured by soil nutrient availability; $SNA_{poor} = 0.3$, $SNA_{medium} = 0.5$, $SNA_{rich} = 0.7$, $SNA_{veryrich} = 0.9$) for lodgepole pine, and $\alpha$ estimates changed with soil fertility for aspen.
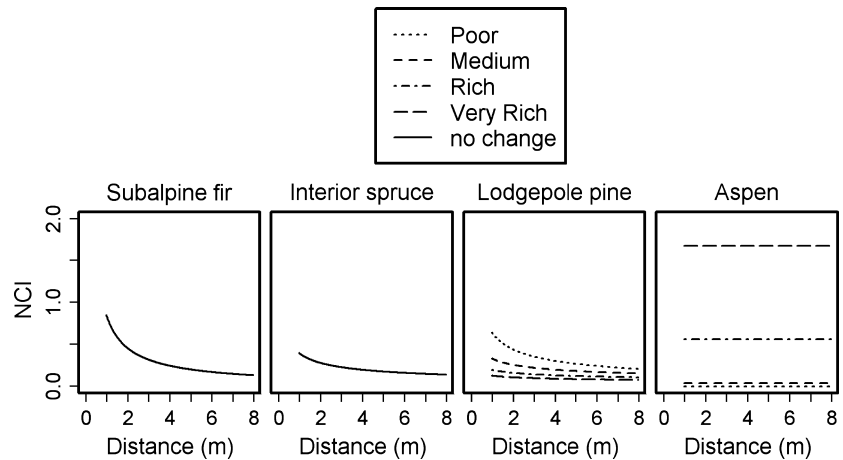
## Discussion

### COMPETITION-FERTILITY INTERACTIONS

We used a neighbourhood approach and model selection techniques to better understand how competitive interactions among long-lived tree species vary with soil fertility. Our extensive sample of 2227 target trees and 14 357 neighbouring trees covered a range of successional stages, species compositions, densities and tree sizes across a wide natural soil fertility gradient in sub-boreal forest ecosystems. We determined the amount of support for alternate models that accounted for competition, soil fertility and their interactions. Soil fertility clearly affected tree growth in these sub-boreal forests. Soil fertility also had multiple and often contradictory effects on competitive interactions among the dominant tree species. The direction and magnitude of soil fertility effects were context-dependent. Competition–soil fertility interactions were species-specific and varied with the composition of local neighbourhood tree species and varied when
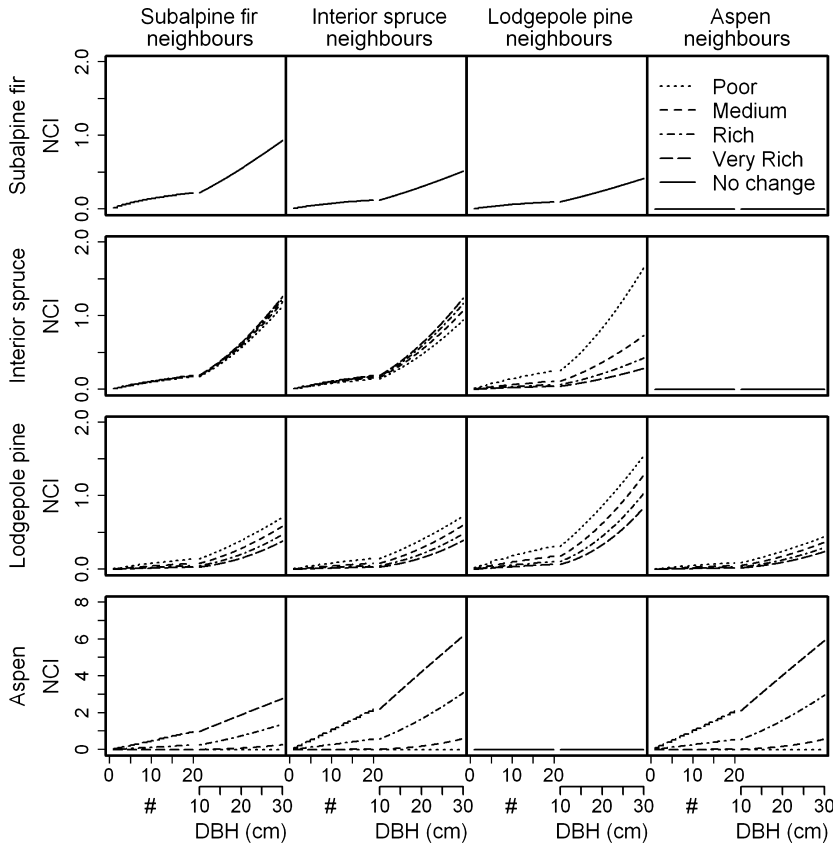
**Fig. 4.** Effect of the number (0–20), sizes (10–30 cm DBH) and species of neighbouring trees on the neighbourhood competition index (NCI) experienced by the four study species as predicted by the parameter estimates for $\alpha$, $\beta$ and $\lambda$ from the best model for each species. Soil fertility (measured by soil nutrient availability; $SNA_{poor} = 0.3$, $SNA_{medium} = 0.5$, $SNA_{rich} = 0.7$, $SNA_{veryrich} = 0.9$) affected NCI for all species except subalpine fir. Neighbour distance increased as a function of the number of trees (distance = No. trees $\times$ 0.3 + 1.5) for these curves.
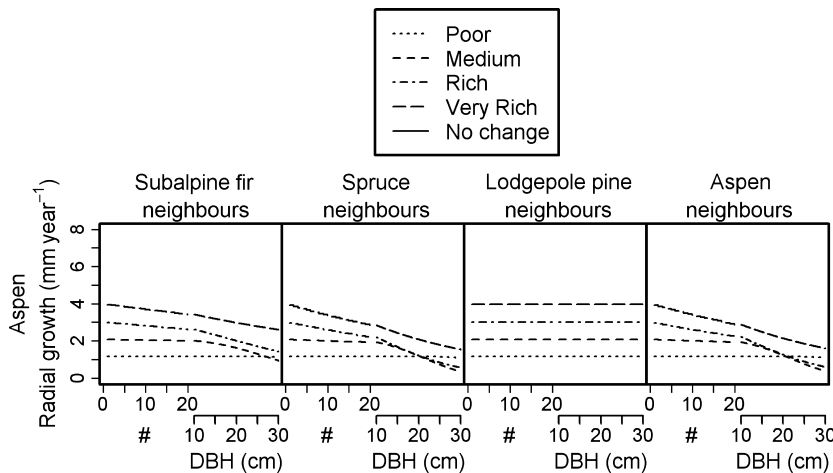


**Fig. 5.** Effect of the number (0–20), sizes (10–30 cm DBH) and species of neighbouring trees, and of the soil fertility (measured by soil nutrient availability; $SNA_{poor} = 0.3$, $SNA_{medium} = 0.5$, $SNA_{rich} = 0.7$, $SNA_{veryrich} = 0.9$) on the radial growth rate of 10-cm DBH aspen trees (assuming no shading) as predicted by the parameter estimates for *MaxGrowth*, N, C, $\alpha$, $\beta$ and $\lambda$ from the best model for aspen (model 9). Neighbour distance increased as a function of the number of trees (distance = No. trees $\times$ 0.3 + 1.5) for these curves.

competition was dominated by above- or below-ground processes.

For some species and neighbourhood compositions, our results were consistent with the stress gradient hypothesis (Bertness & Callaway 1994) and CSR strategy theory (Grime 2007), and for other species and neighbourhood compositions, our results were consistent with the resource-ratio theory (Tilman 1985). Regardless of neighbour composition, growth reductions due to crowding in lodgepole pine increased at low soil fertility, as expected from the resource-ratio theory. In contrast, growth reductions due to crowding in trembling aspen decreased at low soil fertility, as expected from the

stress gradient hypothesis. The direction of growth reductions for interior spruce depended on neighbour composition. When interior spruce was surrounded by pine neighbours, growth reductions due to crowding increased at low fertility but when interior spruce was surrounded by subalpine fir and spruce neighbours, growth reductions due to crowding decreased at low fertility.

In the case of subalpine fir, the type of competition under consideration controlled whether soil fertility decreased or increased the negative effects of competition on growth. Subalpine fir experienced less negative effects of shading at low soil fertility but higher negative effects of crowding at low

soil fertility. Subalpine fir's response was actually supportive of Tilman's (1985) prediction that competition switches from light competition at high soil fertility to soil resource competition at low soil fertility.

Inconsistent findings for competitive interactions along fertility gradients are common in plant ecology and have even occurred in relatively simple studies with only two species. Competition increased, decreased or remained the same when different competition indices were used (Carlyle, Fraser & Turkington 2010) or different forms of nitrogen were measured (Trinder *et al.* 2012) in two recent laboratory experiments. Many explanations and refinements to theories have been developed to explain contrasting results like these and others (e.g. Grace 1991; Maestre *et al.* 2009).

Another way that the level of support for one competition theory or another may depend on the context of the experiment is whether the same species are compared (i.e. the magnitude and direction of pairwise species interactions can be measured) or different species are compared (i.e. the frequency of competitive versus facilitative interactions in the community are evaluated; Maestre *et al.* 2009). Similarly to our study, Baribault & Kobe (2011) used forest neighbourhood dynamics modelling to look at tree competition across a soil fertility gradient. Unlike our study, they found consistent support for CSR strategy theory. Baribault & Kobe (2011) were constrained by the distribution of species in their study area and could not compare the same species across the soil fertility gradient, whereas we were able to sample the same four species for nearly the whole range of soil fertility in our study area (with the exception of the most xeric sites where only lodgepole pine occurs naturally). Studies with broad measurements of all species in the community have found decreases in competition at low soil fertility more consistently than studies measuring the intensity of pairwise interactions (Maestre *et al.* 2009).

Even though we measured only pairwise interactions in this study, we quantified most of the pairwise interactions in our species-poor community. Across the wide successional stages and tree sizes that we examined, on poor through very rich sites in sub-boreal spruce forests, we conclude that the intensity of competition among trees across a fertility gradient is species- and context-specific and more complicated than that predicted from any one existing ecological theory, as suggested by Grace (1991).

### INTRA- AND INTERSPECIFIC COMPETITIVE EFFECTS

Among the community of tree species in these sub-boreal spruce forests, there was no clear pattern in the direction of competitive interactions across the soil fertility gradient, but there were other consistent results relevant to tree competition. Most importantly, intraspecific competition had a stronger negative effect on growth rates than interspecific competition. Other neighbourhood dynamics studies have previously found that competition between functionally very similar neighbours is stronger than competition between functionally dissimilar neighbours (Canham *et al.* 2006; Coates,

Canham & LePage 2009). More genetically, similar trees have also been found to be stronger competitors than genetically dissimilar trees (Boyden, Binkley & Stape 2008), and these results have been explained by the resource partitioning hypothesis. Soil pathogen conspecific effects could also be an important factor affecting the strength of intra- and interspecific competition (Mangan *et al.* 2010).

Another meaningful result from our analysis was that aspen was consistently a very weak competitor. Lodgepole pine was the only conifer to experience net negative effects on growth due to aspen neighbours, with slightly stronger effects of aspen crowding on poor sites. For interior spruce and subalpine fir, the net effect of aspen was zero, but we were unable to establish whether negative effects of aspen competition were balanced by positive effects of facilitation. Facilitative effects of aspen could be attributed to the positive effects of aspen litter on nitrogen mineralization (Côté *et al.* 2000). We had expected that any facilitative effects of aspen litter would be stronger on poor sites, but the only species in our data set that supported that conclusion was aspen itself. Aspen experienced no net negative effects of crowding on poor sites and may have benefited from the soil ameliorating effects of its own litter.

### IMPLICATIONS OF COMPETITION INTENSITY AND IMPORTANCE FOR FOREST COMMUNITY DYNAMICS

A reduction in growth rates due to neighbour interactions signifies competition *intensity*, which is different than competition *importance*–the relative effect of competition compared with other factors (Welden & Slauson 1986; Grace 1991; Freckleton, Watkinson & Rees 2009). What competition *importance* is, how to measure it, at what scale it operates, on what kind of gradient and on what portion of the gradient it should be assessed are all controversial topics (Grace 1991; Brooker & Kikvidze 2008; Freckleton, Watkinson & Rees 2009; Maestre *et al.* 2009). Treading lightly through this conflict, we have considered measuring competition importance using several approaches.

One way to assess the overall importance of soil fertility effects on competition for sub-boreal forest trees is to compare the goodness-of-fit ($R^2$) and AIC$_c$ support for growth prediction models including competition, soil fertility and competition–fertility interactions. We found that changes in competition intensity with soil fertility were relatively unimportant for predicting tree growth overall. The improvements in $R^2$ and AIC$_c$ due to competition–fertility interactions were small compared with the other factors we measured, and the effects were inconsistent across species. We would exclude competition–fertility interactions from future models to maintain parsimony (Astrup, Coates & Hall 2008; Dormann *et al.* 2012). Tree size, soil fertility, light competition and crowding already predict most of the variation in tree growth rates on poor to very rich sites in sub-boreal forests and have a clearer ecological foundation for incorporation into our models of forest productivity.

Did the importance of competition for individual tree growth change with soil fertility, even if those interactions were rela-

tively unimportant overall? We were able to calculate competition importance relative to soil fertility ($C_{imp}$) according to Brooker *et al.* (2005), but like Rees, Childs & Freckleton (2012), we found that $C_{imp}$ always increased with increasing soil fertility (Fig. S1) because of the way the index is constructed and not because of the underlying ecology. If competition importance is defined as the impact of competition on growth relative to soil fertility on growth, then it will always decrease at low soil fertility for our study species. Even for the combinations of species, neighbourhood composition and type of competition that experienced increases in competition intensity at low soil fertility, the amount of growth reductions caused by increased competition did not begin to approach the amount of growth reductions caused by infertility on low fertility soils.

Competition–fertility interactions were relatively unimportant for predicting tree growth, but they still might have important effects on forest community dynamics. Freckleton, Watkinson & Rees (2009) recommended combining the effects of competition on all parts of the life cycle to measure the importance of competition at larger scales than individual plant growth. Our study could not directly address this issue, but it should be possible to test the relative importance of competition through simulation modelling using the parameter estimates from our study in a population dynamics model like SORTIE-ND that has incorporated studies of recruitment, growth and mortality to better understand the dynamics of northern forests (Kobe & Coates 1997; Wright *et al.* 1998; LePage *et al.* 2000; Coates, Canham & LePage 2009). For example, competition–fertility interaction effects on tree mortality and reproduction in sub-boreal spruce forests, over time, could influence community composition more than their direct effects on growth rates. Species differences in mortality, as a function of recent growth, are already known to have a more important effect on understorey tree community dynamics than absolute differences in growth rates in these forests (Kobe & Coates 1997). The SORTIE-ND model could incorporate competition–fertility interactions and investigate the importance of these complicated yet subtle changes in competitive relationships across a soil fertility gradient for community level consequences in forests.

## Acknowledgements

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Competitive interactions across a soil fertility gradient in a multispecies forest.

**Figure S1.** Competitive importance as a function of neighbourhood competition index (NCI) and soil fertility.

**Table S1.** $\Delta AIC_c$ and $R^2$ comparison of tree growth model FULL and models NO LIGHT, EQUIVALENT COMPETITORS, and NO CROWDING.