

The effects of soil fertility and scale on competition in ponderosa pine

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Abstract The intensity of competition between neighboring trees depends on local stand structure, and the influence of stand structure may vary across gradients in soil resource supplies. We used model selection techniques to look for variation in the nature and intensity of interactions between trees along a gradient of soil nitrogen supply in a 9-ha stand of old-growth ponderosa pine (*Pinus ponderosa*) in Colorado, USA. We used spatially explicit competition indexes to describe the interactions between trees and developed individual tree growth models to look at how soil nitrogen (N) supply affects competition. The growth of focal trees showed an asymmetric influence of neighbors up to 14-m distance. The predictive ability of our growth models more than doubled (to an $r^2 = 0.69$) as the size of the neighborhood used to calculate the competition indexes increased from a 2-m to a 14-m radius. The supply of soil nitrogen modified competition, with increasing N enhancing competition from neighbors. Neighborhood structure and soil resource supplies jointly influenced the growth of individual trees, but at different scales. Tree interactions are both spatially and temporally complex and may be studied most usefully with explicit evaluation of gradients in resource availability.

Keywords Asymmetric competition · Competition index · Likelihood modeling · Tree neighborhood models · Production ecology

Introduction

The survival and growth of trees within forests are influenced by a variety of interacting factors. Competition is often characterized by stand structure, with the growth of each tree being influenced by the number, distance, and sizes of neighboring trees (Pretzsch 2010; Burkhardt and Tomé 2012). Tree density strongly influences growth of individual trees, often showing an inverse density–yield relationship (Yoda et al. 1957; White and Harper 1970; Harper 1977). The statistical relationship between stand density and individual tree growth or survival does not provide insight into mechanisms producing the patterns, however. Alternatively, a functional approach describes the growth of trees (and stands) in terms of the supply of resources (light, water, and nutrients) in the environment, the capture of resources by trees, and the efficiency of using resources to produce biomass (Montieth 1977; Waring 1983; Landsberg 2003; Binkley et al. 2013a). A hybrid approach can be used, where the influence of stand structure is combined with indexes of resource supply (such as soil nutrient availability) to examine competition across landscapes (Boyden et al. 2005a). Nearest-neighbor analyses can be used to explore the dynamics of tree competition (Weiner 1982, 1984; Wagner and Radosevich 1998), and variation in these patterns can be examined across gradients in resource supply to provide at least partial insight into mechanisms (Boyden et al. 2005a).

Research done primarily on grasses and herbaceous plants has examined two theories about the relationship

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between resource availability and the intensity of competition (Silander and Pacala 1985; Goldberg 1987; Reader and Best 1989; Wilson and Tilman 1993; Goldberg and Novoplansky 1997). Fertile microsites may have stronger competitive interactions owing to higher productivity and higher resource demands (Grime 1973, 1979). Alternatively, the intensity of competition may not vary with resource availability although the nature of interactions may shift from belowground nutrient competition to aboveground light competition as soil fertility increases (Newman 1973; Tilman 1988; Coomes and Grubb 2000). The intensity of competitive interactions is also likely to change as a function of scale, with the effects of neighbors decreasing with distance from the focal plant (Silander and Pacala 1985). The importance of distance relates directly to the scale of resource use by individual plants, raising the question of how these complex relationships between tree growth, competition, and soil nutrient supply vary across spatial scales.

Our objective was to use model selection techniques based on likelihood theory to test a number of neighborhood models at different scales in a monospecific stand of ponderosa pine (*Pinus ponderosa* Laws.; Fig. 1). Competition indexes were first developed to assess the relevant scales and the degree of asymmetry in the competitive interactions in this stand. Competition is two-sided, or symmetric, if a neighbor's impact on the focal tree is proportionate to the neighbor's size (Begon 1984; Weiner et al. 1990). If large neighbors are using a disproportionately large amount of the available resources, competition would be one-sided, or asymmetric (Diggle 1978; Weiner and Thomas 1986). Competition for light is usually considered asymmetric because of the dynamics of shading, while symmetric competition can occur if plants are



Fig. 1 Mortality caused by bark beetles created this small grassy meadow, with some pine regeneration occurring. A number of such gaps contribute to the heterogeneity of the stand

competing for below-ground resources (Weiner and Thomas 1986; Wilson 1988; Schwinning and Weiner 1998).

Competition indexes were incorporated into growth models for individual ponderosa pine trees, and the models were used to test the role of soil nutrient supply in modifying tree competition. We compared the performance of our competition indexes and growth models to answer the following questions: (1) Over what distance do neighbors have an impact on focal tree growth? (2) Is competition between neighboring trees symmetric or asymmetric? (3) Does soil N supply significantly affect the relationship between competition and growth?

Materials and methods

Study area

The study was conducted in Manitou Experimental Forest, 40 km northwest of Colorado Springs, Colorado, USA. The elevation is 2500 m, and topographic change is mild across the study area. Average precipitation is 39 cm/year, 25 % of which falls as snow, and the mean monthly temperatures range from -4 °C in January to 17 °C in July (based on meteorological data collected at Manitou Experimental Forest). Soils of this region are primarily developed from alluvial deposits of Pikes Peak Granite, and in the study plot they have been classified as a Boyett–Frenchcreek complex, a gravelly, coarse, sandy loam containing red sandstone (Moore 1992). The study plot has a pure ponderosa pine overstory, and an understory dominated by perennial grasses such as Arizona fescue (*Festuca arizonica*) and mountain muhly (*Muhlenbergia montana*), as well as forbs, and a small number of common juniper (*Juniperus communis*) shrubs. Commercial logging of this region of the Colorado Front Range began in the late 1800s, and most of the current Experimental Forest area had some large tree selectively logged between 1880 and 1886 (Parker 1930). Our mapping of the residual stumps in 2002 showed that about 30 trees/ha were removed from the study plot, which represents only 15 % of the estimated stand density at that time. No other logging operations have occurred since that time, resulting in an uneven-aged forest with trees dating to every decade from 1790 to 1920. The forest has been classified as an old-growth forest, and further details about the age and size structure can be found in Boyden et al. (2005b).

Sampling and analysis

A 9.3 ha square plot was established in 1974 by the USDA Forest Service, and all trees reaching 1.35 m height were mapped and tagged. New trees were tagged, and all

diameters measured (at 1.35 m height, in cm) in 1991 and 2001. The stand contained 420 trees/ha in 2001, with a mean diameter of 21.4 cm, basal area of 21 m²/ha, and average canopy height of 14 m (median 17 m). Average light interception by the canopy was 53 % (based on a sampling grid of 15 × 15 m across the site), with about 30 % of the area intercepting less than 20 % light and 30 % intercepting more than 75 %.

Aboveground biomass (stems plus large branches, twigs and foliage) of individual trees was calculated using existing allometric equations developed from destructively harvested ponderosa pine trees. The equation for stem biomass was developed from trees along the Colorado Front Range (Edminster et al. 1980). The branch and foliage equations came from Ter-Mikaelian and Korzukhin (1997), and the bark biomass equation from Gholz et al. (1979).

$$\text{Stem biomass (kg dry mass)} = (0.0000325 \times dbh^2 \times ht) \times wd \quad (1)$$

$$\text{Branch biomass (kg dry mass)} = (0.0469 \times dbh^{2.1315}) \times 1.172 \quad (2)$$

$$\text{Foliage biomass (kg dry mass)} = (0.1167 \times dbh^{1.5774}) \times 1.112 \quad (3)$$

$$\text{Bark biomass (kg dry mass)} = e^{(-4.2063 + 2.2312 \times \ln(dbh))} \quad (4)$$

In all four equations, *dbh* is tree diameter in cm at 1.35 m height, *ht* is tree height in meters, and *wd* is wood density (we used 537 kg/m³; Hall et al., unpublished data). The annual growth of individual trees (kg/year) was calculated as the change in aboveground biomass (kg) from 1991 to 2001, divided by 10.

The supply of available soil N (NO₃⁻ and NH₄⁺) was indexed with ion exchange resin bags (Binkley and Hart 1989). Two resin bags were buried at 2.5 cm below the bottom of the O horizon, every 15 m along a systematic grid in May of 2000, for a total of 380 sampling points throughout the stand. One resin bag from each pair was removed in at the end of the growing season (October), and the second was removed at the end of a full year. Resins were extracted using 2 M KCl and analyzed on an Alp-Chem automated colorimeter. We verified that N limits tree growth at this site by fertilizing 20 trees on the periphery of the plot with 250 g of N (as urea) spread in a 2 m radius around individual trees in May 2001 (equivalent to 200 kg N ha⁻¹). We measured the *dbh* of the fertilized trees and 20 paired neighboring trees of comparable sizes in 2001 and again in 2005. Increment cores from 2005 were used to look at the cumulative basal area growth of the trees 3 years prior to and following fertilization. The ratio

of basal area growth before and after fertilization showed a 20 % increase for fertilized trees.

Statistical analysis

Growth models

We developed and tested models of individual tree growth to determine the nature and strength of the relationships between neighbor interactions, soil N availability, and growth. A limited set of growth models and competition indexes were developed a priori to avoid problems of over-fitting and spurious correlations associated with stepwise or other model selection techniques (Burnham and Anderson 1998). This is particularly important when using a correlative approach.

We modeled the relationship between competition and tree growth using a nonlinear equation form which is based on yield density functions (Holliday 1960; Harper 1977) and similar to growth models used by Weiner (1982, 1984) and Silander and Pacala (1985).

Basic model : $y = a/(1 + bCI_r)$

The basic model represents the concave relationship between growth (*y*) and the competition index (CI) within a given neighborhood radius (*r*). Maximum tree growth in the absence of competition is represented by the parameter *a*, and *b* is a scaling parameter that creates flexibility in the function at low levels of competition. Low values of *b* create a plateau prior to the growth decline, and high values of *b* allow a more immediate decline in growth with increased competition, similar to a negative exponential model. We added complexity to the basic equation with parameters that could describe different effects of tree size and soil N supply on growth:

Biomass model: $y = aB_j/(1 + bCI_r)$

Biomass model: $y = aB_j/(1 + bCI_r)$

Interaction model: $y = a/(1 + bCI_rN)$

Full model: $y = aB_j/(1 + bCI_rN)$

The biomass model includes focal tree biomass (*B_j*) as a predictor variable which controls maximum potential tree growth since the relationship between tree size and growth is well established. The nitrogen model replaces *B_j* with soil N supply (*N*) as the predictor variable which directly controls the maximum tree growth. The interaction model includes *N* as an interactive effect on competition to test the hypothesis that effects of neighbors are modified by nitrogen supply. The full model is the interaction model with the addition of focal tree biomass a control over potential growth.

Measures of tree competition

Focal trees were defined as those occurring at least 20 m from the boundaries of the 9.3 ha plot, and within 5 m of one of the 15 × 15 m grid points where soil N supply was assessed. These criteria provided 692 focal trees, with other trees (within 20 m of the plot borders, or beyond 5 m from a grid point) being eligible as neighbor trees.

We calculated the competition index (*CI*) in two ways for each focal tree. The symmetric index estimates the impact of each neighbor to scale proportionately with biomass, and to decrease disproportionately with distance from the focal tree (Weiner 1984). The impact of all neighbors within a given radius (*r*) of the focal tree was summed:

$$\text{Symmetric index: } CI_r = \sum_{i=1}^n \frac{B_i}{d^2}$$

B_i is the biomass of the *i*th neighbor at a distance of *d* meters, and *n* is the total number of neighbors within the given neighborhood distance (*r*). In this model a tree's impact on a neighbor is size-symmetric (Begon 1984, Weiner et al. 1990).

The second competition index included a size ratio to account for size-asymmetric competition. The size ratio was similar to one developed by Bella (1971), and divided the biomass of the neighbor (*B_i*) by that of the focal tree (*B_j*) to create a scalar that disproportionately increases or decreases the effect of that neighbor depending on its relative size.

$$\text{Asymmetric index: } CI_r = \sum_{i=1}^n \frac{B_i}{d^2} \left(\frac{B_i}{B_j} \right)$$

Parameter estimation and model selection

We compared performance of the five alternate models using the symmetric neighbor index and the asymmetric neighbor index, for each of nine neighborhood sizes (radii of 2, 4, 6, 8, 10, 12, 14, 16, and 20 m). Models were fit using PROC NLIN (SAS Institute 2002) with a subroutine written to calculate maximum likelihood. Alternate models were compared using Akaike's information criterion adjusted for small sample sizes (*AIC_c*). *AIC_c* entails calculating the expected value of the information lost when using a model to approximate the truth, with models penalized for having more parameters. Lower *AIC_c* values indicate stronger model performance (Burnham and Anderson 1998). The strength of evidence for the best model relative to the full set of candidate models was calculated using Akaike weights. The weight of each model is the ratio of the likelihood of the model to the sum of the

likelihoods for the full set of models that were compared. A weight can be thought of as the probability of selecting a model, from the available set of candidate models, given the data. We also estimated *r*² values based on the residual sum of squares. Although tree growth across the stand is likely to be spatially autocorrelated, the estimates themselves and the model comparison are largely unaffected by spatial autocorrelation when using likelihood methods rather than parametric approaches (Uriarte et al. 2004b; Hubbell et al. 2001).

Results

Intraspecific competition is having a significant effect on ponderosa pine growth in this forest. Both neighbor indexes performed significantly better at neighborhood ranges greater than 10 m in radius and were best when a radius of 14 m was used (Table 1; Fig. 2). The *r*² for the best model increased from 0.32 to 0.70 as the neighborhood radius increased from 2 to 14 m, after which it gradually declined. The asymmetric competition index that accounted for the size differences of neighbors relative to the focal tree consistently outperformed the symmetric competition index, across all neighborhood sizes (Table 1).

Tree growth related strongly to both focal tree biomass and competition (Fig. 3), although there is a strong asymptote present in the competitive response of trees, with no impact of neighbors on growth at low levels of competition. Our data selected the interaction model as the best model of those we tested, which allowed soil N supply to modify the effect of neighbors on growth (Table 2). This model incorporated asymmetric effects of neighboring trees up to 14 m away and explained 70 % of the variation in individual tree growth across this stand. There was less support for the full model, which explicitly included the effects of focal tree size, because biomass of the focal tree was accounted for in the asymmetric neighbor index. The other four tested models did not have even moderate support in the data ($\Delta AIC_c < 10$; Burnham and Anderson 1998). With an Akaike weight of 0.996, there was a 99.6 %

Table 1 Performance of the symmetric versus asymmetric competition indexes for different ranges of neighborhood sizes

| Neighbor index | Mean <i>r</i> ² 2 to 8 m radii | Mean <i>r</i> ² 10 to 20 m radii | <i>r</i> ² 14 m radius |
|----------------|--|--|--------------------------------------|
| Symmetric | 0.324 | 0.436 | 0.461 |
| Asymmetric | 0.428 | 0.658 | 0.670 |

Correlation coefficients (*r*²) were calculated using the interaction model. Mean *r*² value is shown for small neighborhoods (radii ≤ 8 m) versus large neighborhoods (radii > 8 m); and for the optimal neighborhood radius of 14 m

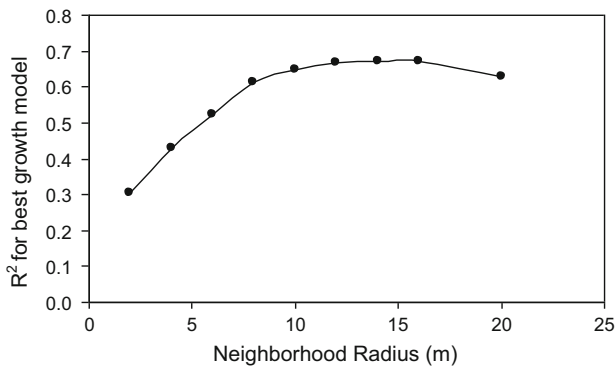


Fig. 2 Competitive influence of neighbors increases up to 14 m from the focal tree. The maximum predictive ability of the best growth model (interaction model) was found using a 14 m radius neighborhood ($r^2 = 0.701$)

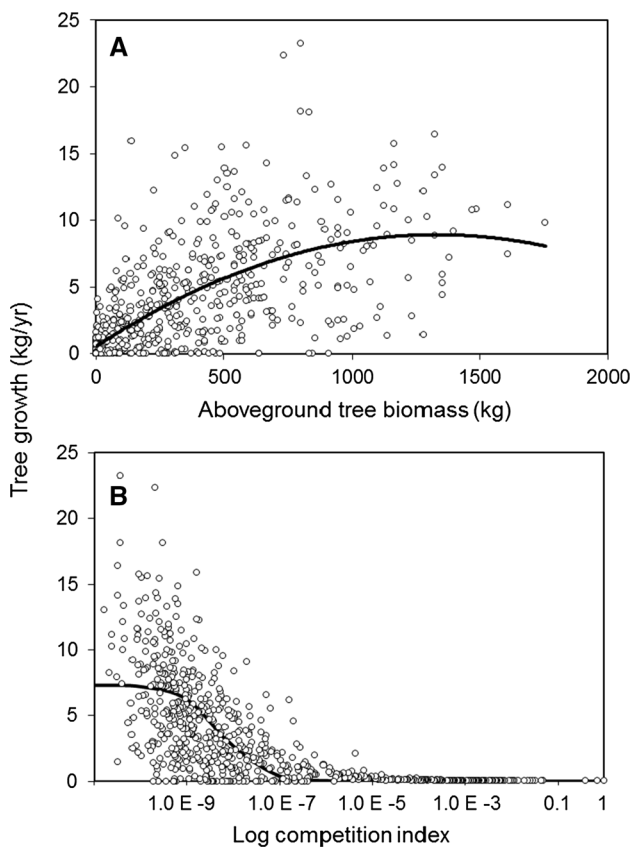


Fig. 3 Competition explains more of the variability in tree growth than tree biomass. We used a quadratic model to describe the relationship between tree biomass (B) and growth: ($y = 0.5496 + 0.0126B + -5E-06B^2$; $r^2 = 0.458$, $P < 0.001$). The competition index was calculated using an asymmetric index and a 14-m radius neighborhood. The relationship between competition (CI) and tree growth is modeled using the interaction model: ($y = 7.32/(1 + 0.00089 \times CI \times N)$; $r^2 = 0.694$, $P < 0.001$). The regression represents a scenario of 2 mg N/resin bag. Values for the neighbor index were plotted on a log scale and scaled from 0 to 1 for ease of interpretation and viewing

Table 2 Comparison of alternate models based on goodness of fit and AIC

| Growth model | r^2 | ΔAIC | w_r |
|--|-------|--------------|-------|
| Basic: $y = a/(1 + bCI_r)$ | 0.690 | 11 | 0.004 |
| Biomass: $y = aB/(1 + bCI_r)$ | 0.362 | 218 | 0 |
| Nitrogen: $y = aN/(1 + bCI_r)$ | 0.354 | 229 | 0 |
| Interaction: $y = \alpha/(1 + bCI_rN)$ | 0.701 | 0 | 0.996 |
| Full: $y = \alpha B/(1 + bCI_rN)$ | 0.647 | 21 | 0 |

Models are fit using an asymmetric competition index and a neighborhood radius of 14 m

The dependent variable is aboveground biomass increment (kg/year), CI_r is the competition index calculated for a given radius (r), B is aboveground tree biomass (kg), N is soil nitrogen supply ($\mu\text{g NO}_3^-$ and NH_4^+ /bag), a represents the maximum tree growth in the absence of competition, and b is a scaling parameter. ΔAIC is the difference in AIC between the given model and the best model (interaction model), and w_r is the probability of the given model being the best model. See “Material and methods” for more details

probability of the interaction model being the best of the five candidate models given the observed data. The next best model, with a ΔAIC_c of 11, was the Basic model. The ratio of the Akaike weights for the two best models (0.996/0.004) is 249, which tells us that there is an evidence ratio of 249:1 for a model which includes an interactive effect of nitrogen supply in addition to an understanding of neighborhood structure (the relative sizes and distances of neighbors). Our model residuals also had some heteroscedasticity, which reflects a significant pattern of greater tree to tree variation in growth in favorable than unfavorable environments, as seen in Fig. 3b, and therefore should not be removed through transformation.

Parameterizing the interaction model revealed that higher soil nitrogen supplies enhanced the competitive effect of neighbors on focal tree growth (Fig. 4). Increasing the logarithm of the competition index from $1.0E-11$ to $1.0E-8$ had almost no effect on the average growth of trees with low soil N supplies, but resulted in a greater than 50 % reduction in the growth of trees on high N soils. A given level of competition could be achieved through a number of combinations of neighbor numbers, size, and distance. For example, the change in the competition index from $1.0E-11$ to $1.0E-10$ could result from increasing the competition for a 200 kg focal tree from 0 neighbors within 6 m distance, to 9 neighbors that are about three times larger than the focal tree in that same distance.

We used the best growth model to plot the change in the predicted focal tree growth for a given increase in soil N supply at variable neighborhood radii (Fig. 5). The relative importance of soil N supply in the model decreased as the size of the modeled neighborhood increased and the

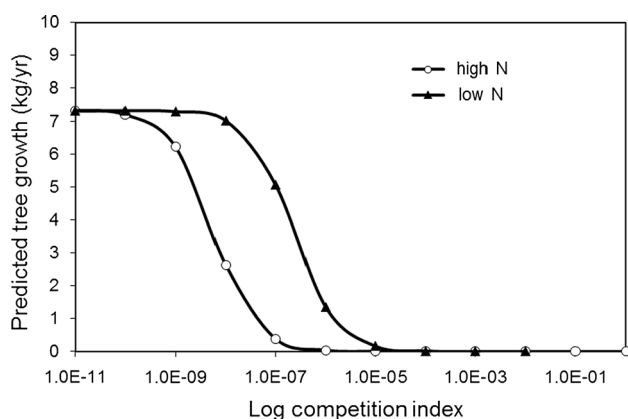


Fig. 4 Growth of focal trees was influenced more strongly by competition where soil N supply was high. Values for low N = 0.05 mg/resin bag, high N = 2.0 mg/resin bag. Growth was predicted for varying levels of competition and nitrogen using the interaction model. Values for the neighbor index were plotted on a log scale and scaled from 0 to 1 for ease of interpretation and viewing

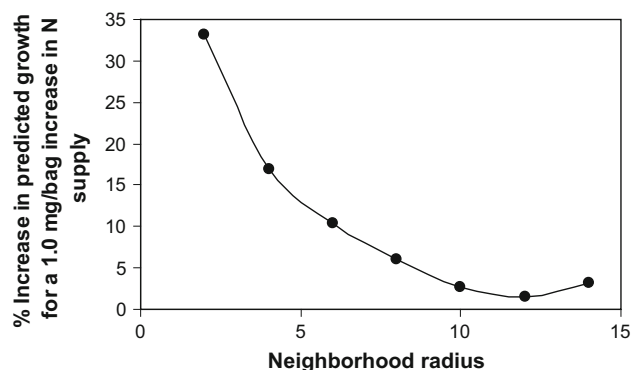


Fig. 5 Changes in the importance of soil nitrogen as a function of the scale of the neighborhood analysis. Growth models are sensitive to soil nitrogen supplies when only close neighbors are used to calculate the competition index

importance of competition was accurately accounted for, once again highlighting the importance of using the best neighborhood radius in tree-based competition models. Using a 2 m radius, tree growth was predicted to increase by more than 30 % with a 0.1 mg/bag increase in soil N supply, yet at a 12 m neighborhood radius, the same change in soil N only resulted in a 2 % increase in focal tree growth.

Discussion

The spatial distribution of trees had a large impact on the growth of individuals in this ponderosa pine stand. Neighbor interactions explained as much as 70 % of the variability in focal tree growth, when both the competition

index and the neighborhood radius were optimized. An arbitrary choice of neighborhood size (Weiner 1982, 1984; Stoll et al. 1994) would have reduced the variance explained to about 50 % (5 m) to 60 % (20 m), but would not change any of the overall conclusions about the influence of competition on focal trees. Competition was strongest within 14 m of the focal tree, and this neighborhood size could include as many as 36 trees. Other studies have found that competitive tree interactions occur over large areas with a radius approaching the height of trees (Canham et al. 2004; Uriarte et al. 2004a, b).

We did not test specifically for the mechanisms of competition in this study. The large spatial scale and asymmetric nature of the neighbor interactions may indicate that competition for light is important (Weiner and Thomas 1986; Wilson 1988; Schwinning and Weiner 1998), but direct measurement of individual tree light use would be needed to assess the importance of shading by neighbors (cf. Binkley et al. 2013b).

Evidence of asymmetric competition does not preclude the importance of belowground interactions, given that root competition can be asymmetric (Beyer et al. 2013), and nitrogen is clearly an important resource at this site. The fertilization study indicated that soil N supply limited tree growth, and our growth models demonstrated that a focal tree's relationship with neighbors depended on the supply of soil nitrogen. Specifically, nitrogen supply affected the plateau, or competition threshold, above which trees were unaffected by neighbors. In more fertile soils, that threshold shifted left, resulting in negative effects of competition at fairly low CI values. This result supports both Grime's original CSR theory (1973, 1979) and the stress-gradient hypothesis developed by Bertness and Callaway (1994). We found a similar relationship in mixed species plantations in Hawaii (Boyden et al. 2005a), as did Baribault and Kobe (2011) in northern hardwood forests. Recent experimental work has, however, demonstrated the opposite pattern (Trinder et al. 2012), and a multi-species study by Coates et al. (2013) demonstrated both positive and negative relationships between competition intensity and fertility depending upon the tree species. They further demonstrated that in subalpine fir competitive effects increased with soil fertility if the competition index was a measure of shading (light competition) versus crowding (belowground competition). Our data may be consistent with these results if we assume that light competition dominates this pine stand, as indicated by the asymmetry of the competition index. Clearly, more work is needed across a greater range of tree species to test the prevalence of these patterns. However, we would like to echo an important question raised by Coates et al. (2013) about the extent to which these long-standing debates need to focus on the importance of the fertility–competition relationship

to measures of population success, rather than on the existence of a universal organizing principle. The relatively small increase in r^2 from the basic model to the interaction model, however significant, suggests that competition and the relative sizes of competitors are the most important drivers of growth in this system.

We expected focal tree size to help explain some of the variability in individual tree growth, but our analysis showed that focal tree biomass did not add information beyond what was represented in the asymmetric competition index. In this highly competitive environment, size of a focal tree was less important for determining growth than was its size relative to neighbors.

Not only do the nature and strength of the competitive interactions change as a function of neighborhood size, as seen by our test of different competition indexes, but the limiting resource also changes. Soil N supply had the largest impact on our model predicted tree growth when only close neighbors were used (Fig. 5). We note that the spatial interactions among trees should not be expected to fit a single neighborhood size; in our case, the overall effect of competition between trees had a radial scale of 14 m, but the influence of soil N was captured most effectively at a neighborhood scale of 5 m (Fig. 5). In dense stands, the spatial reach of ponderosa pine trees roots tends to be limited to the radius of the crown (Oliver and Ryker 1990), and the average crown radius for this stand was about 2 m (data not shown). This combined with the fact that N will only diffuse about 1 cm in soil solution (Tisdale et al. 1985), means that direct competition for soil N is primarily limited to immediate neighbors. Increasing the neighborhood radius beyond 2 m decreased the explanatory power of soil N and increased the relative importance of the neighborhood index. As the distance between neighboring trees increases, there is also likely to be a shift from belowground competition for soil N to competition for other resources such as light or water. Further work is needed to fully understand how supply and competition for different resources vary across spatial scales, and the role of water and light resources in modifying competitive interactions between trees.

The choice of neighborhood size had large ramifications for fitting models and inferring the competitive effect of neighbors. Distance between neighbors modified the strength of competitive interactions, the relative importance of focal tree versus neighbor size, and the importance of aboveground versus belowground resources in the model. Temporal variability in these interactions is undoubtedly important in addition to the spatial variability we examined, as soil resource supplies are often pulsed rather than constant over time. We need to do more studies of neighborhood interactions along spatial and temporal gradients in resource availability.

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