DISSERTATION

THE ROLE OF SPATIAL PATTERN IN CONTROLLING FOREST DYNAMICS

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY SUZANE BIRD ENTITLED THE ROLE OF SPATIAL PATTERN IN CONTROLLING FOREST DYNAMICS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

THE ROLE OF SPATIAL PATTERN IN CONTROLLING FOREST DYNAMICS

Stand structure is a key factor in the growth, function, and disturbance regimes of forests. Many conventional descriptions of stand structure focus on stand-level collective attributes such as average tree size and density. Spatially explicit mapping and modeling of trees allow forests to be seen as compositions of individuals, with unique spatial arrangements and patterns. Analysis of these patterns provides insight into the interactions between trees, at the scales of neighboring individuals to neighboring clumps, which create structural heterogeneity and drive stand development. My dissertation explores the spatial and temporal relationships between resource availability, stand structure, and tree processes, in a natural stand of ponderosa pine in Colorado and a mixed-species plantation in Hawaii.

At coarse spatial scales, we found that patterns of ponderosa pine trees strongly influenced processes of mortality and regeneration. In turn, processes of mortality and regeneration influenced spatial patterning- creating strong clumping in young trees, regular spacing in old trees, and strong segregation of different size classes. Long term patterns in climate controlled the temporal dynamics of these pattern and process relationships.

At finer spatial scales we saw that tree pattern had enormous implications for tree growth and survival. The size and spacing of neighbors explained from 69 to 85 % of the variability in individual tree performance in both the tropical plantation and the old-growth conifer forest. Soil nutrient supply significantly modified both the nature and strength of neighbor interactions in both of these systems. In Hawaii, we saw that the effect of a *Eucalyptus* or *Falcataria* neighbor could be either competitive or facilitative depending on the supply of soil nitrogen and phosphorus. In Colorado, we saw that the strength of competitive interactions, and the importance of soil nutrient supply, are highly dependent upon the scale of the neighborhood analysis.

This dissertation underscores the need to study forest dynamics at multiple spatial and temporal scales, and along environmental gradients in soil resource supplies. Neighborhood models and spatially explicit methods revealed much greater complexity of stand structure and tree interactions would have been seen with traditional tools.

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SYNTHESIS

CHAPTER 1

INTRODUCTION

Stand structure is a key factor in the growth, function, and disturbance regimes of forests. Many conventional descriptions of stand structure have focused on stand-level collective attributes such as average tree size and density. However, the horizontal and vertical heterogeneity of forest structure influences tree growth, plant species diversity, wildlife habitat, and fire behavior (Harrod et al. 1999, Ehle and Baker 2003, Waltz et al. 2003, Homyack et al. 2004, Youngblood et al. 2004). The spatial patterning of trees may reveal tremendous insight about the historical and environmental processes which have shaped current stand structure (Moeur 1993, Pretzsch 1997, Youngblood et al. 2004). In turn, the current arrangement of trees will influence future stand development and production through controlling individual tree growth, competition, regeneration, and mortality.

In recent decades the emergence of landscape ecology, and the geostatistical tools which accompany it, have changed the way we think about forest processes. Forest studies have shifted from plot-driven, single scale questions, to research that recognizes multi-scale, pattern-process relationships which require new methods and allow for new questions. Spatially explicit mapping and modeling of trees allow forests to be seen as compositions of individuals, with unique spatial arrangements and patterns. Analysis of these patterns may provide insights into the interactions between trees, at the scales of neighboring individuals to neighboring clumps, which create structural heterogeneity and drive stand development.

Tree interactions do not occur in isolation; they are strongly influenced by external environmental controls that operate on extremely different spatial and temporal scales. Climatic conditions influence decadal scale patterns of growth, mortality, and regeneration at the stand level (Swetnam 1990, Mast et al. 1998, Brown 2004). Disturbance from fire, wind, harvesting, or disease, can have profound effects on stand patterns and processes at a range of spatial and temporal scales depending upon the severity and extent of the disturbance. At much smaller scales, patterns in soil and light resource supplies directly impact individual tree performance, and may also modify the interactions between individual (Grime 1973, 1979, Tilman 1988).

My dissertation explores the spatial and temporal relationships between resource availability, stand structure, tree processes, and disturbance using stem-mapped stands in Colorado and Hawaii. One project was conducted in a 10 ha stand of old-growth ponderosa pine in the Colorado Front Range. Chapter 1 examined the historical and contemporary controls over stand structure and development by analyzing the spatial patterns and spatial associations of tree establishment, mortality and size structure over a thirty year period. Chapter 2 looks more directly at the effect of local stand structure on growth processes. We used spatially explicit neighborhood models to look at how soil nutrient supply, competition, and scale interact to affect tree growth.

The second project (Chapter 3) was conducted in a mixed species plantation near Hilo, Hawaii. This project also used spatially explicit neighborhood growth models to look at the effects of interspecific and intraspecific competition and facilitation on tree growth and survival along gradients in soil resource supplies.

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CHAPTER 2

SPATIAL AND TEMPORAL PATTERNS IN STRUCTURE, REGENERATION, AND MORTALITY OF AN OLD-GROWTH PONDEROSA PINE FOREST IN THE COLORADO FRONT RANGE.

Abstract

Effective management and restoration of ponderosa pine forests requires an understanding of the heterogeneity of contemporary and historical stand structures. We assessed spatial and temporal patterns of tree establishment, mortality and size structure over a thirty year period in an old-growth ponderosa pine stand in the mid-montane zone of the Colorado Front Range. We analyzed spatial patterns and spatial associations using Ripley's $K(d)$ and $K_{12}(t)$ and then modeled the patterns using point process models. Forest age structure was estimated by aging a sub-sample of trees in the stand. Climate, and to a lesser extent fire, played a significant role in the timing of regeneration events. Stand structure (distribution of patches, light availability, and seed trees) influenced the location and timing of more recent regeneration events. Patchy regeneration resulted in spatial independence and some segregation of size classes. The oldest trees in the stand (40-55 cm dbh) exhibited some regularity in their spatial distribution at short distances indicating that patterns of mortality had been historically patchy. Contemporary patterns of mortality were mostly patchy, and mountain pine beetles caused a significant amount of mortality in the 1970s and 1980s. Both establishment and mortality retained spatial

patterns that were somewhat consistent with pre-settlement forests, despite changes in driving processes.

Introduction

Stand structure is a key factor in the growth, function, and disturbance regimes of forests. Forest restoration, and management based on natural disturbance ecology, has highlighted the value of a clearer understanding of the role of structure in mediating key ecosystem processes. Traditional descriptions of stand structure have focused on stand-level collective attributes such as average tree size, density, and basal area. However, the horizontal and vertical heterogeneity of forest structure influences tree growth, plant species diversity, wildlife habitat, and fire behavior (Harrod et al., 1999; Ehle and Baker, 2003; Waltz et al., 2003; Homyack et al., 2004; Youngblood et al., 2004). Spatially explicit geostatistical tools characterize forests as compositions of individual trees, with unique spatial arrangements and patterns. Spatial pattern is one component of forest structure that may reveal insights about the historical and environmental processes, such as regeneration, climate, mortality and competition, which have shaped current stand structure (Moeur, 1993; Pretzsch, 1997; Youngblood et al., 2004). This knowledge can help facilitate the development of silvicultural systems and management strategies to meet changing objectives and goals for forested lands.

Many ponderosa pine (*Pinus ponderosa* Laws.) forests have undergone major changes in stand structure since Euro-American settlement, including increases in tree densities and near-elimination of the natural fire disturbance regime (Cooper, 1960; White, 1985; Savage and Swetnam, 1990; Savage, 1991; Fule et al., 1997). A number of studies have inferred historical patterns of regeneration and stand development for southwestern ponderosa pine systems for restoration and fire management purposes (Cooper, 1960; White, 1985; Covington and Moore, 1994; Savage et al., 1996). Much less is known about the historical structure of ponderosa pine forests along the Front Range of Colorado. Differences in climate, soils, and topography result in different disturbance regimes and patterns of stand development in Colorado than in the Southwest (Peet, 1981; Goldblum and Veblen, 1992; Shinneman and Baker, 1997; Mast and Veblen, 1999). While southwest ponderosa pine forests are thought to have burned with frequent, low-severity surface fires (Cooper, 1960; Swetnam, 1990; Covington and Moore, 1994; Fule et al., 1997; Moore et al., 1999), Front Range ponderosa pine forests in the lower to mid-montane zone appear to have had less frequent mixed-severity fires displaying a greater range in fire behavior (Brown et al., 1999; Kaufmann et al., 2000). This regime may have resulted in more spatially variable patterns of stand structure across the landscape (Turner and Romme, 1994; Brown et al., 1999). Despite differences in fire return intervals and fire behavior, regeneration of ponderosa pine in both the Southwest and the Colorado Front Range is a patchy, episodic event that is largely driven by climatic conditions and disturbance events (Pearson, 1923; Peet, 1981; Savage et al., 1996; Mast et al., 1998; Mast and Veblen, 1999). Competition and self-thinning results in decreased clustering and increased size differentiation within these even-aged groups over time (Kenkel, 1988; Moeur, 1993; Mast and Veblen, 1999). The limited number of studies of ponderosa pattern and stand development along the Front Range means we have little understanding of how elevation, disturbance history, and other site differences are likely to change these expectations.

Our objective in this study was to use spatially explicit, individual tree data to describe and interpret spatial patterns and interactions of tree establishment, mortality and size structure over a thirty year period in an old-growth ponderosa pine stand in the mid-montane zone of the Colorado Front Range. We addressed four questions: 1) what role has fire and climate played in structuring the current forest? 2) what are the contemporary patterns of recruitment and tree mortality and how do they compare to our understanding of historical ponderosa pine patterns? 3) do size classes of trees differ in spatial patterning as a result of recruitment and mortality processes?

Methods

Study Area

The study was conducted in the Manitou Experimental Forest, 40 km northwest of Colorado Springs, Colorado. The elevation is 2,500 m, and the study area has a very mild slope to the southeast. Average precipitation is 40 cm/yr, 25% of which falls as snow, and the mean monthly temperature is 5 °C, with an average growing season high of 16 °C. Soils of this region are primarily developed from alluvial deposits of Pikes Peak granite. Soils in our study plot are a complex of Boyett series (coarse-loamy, mixed, superactive, frigid Typic Haplustalfs) and Frenchcreek series (Loamy-skeletal, mixed, superactive, frigid Aridic Haplustolls) formed in arkosic sandstone alluvium (Moore and Deiter, 1992).

Commercial logging of this region of the Colorado Front Range began in the late 1800s, and most of the current Experimental Forest area was heavily thinned of large diameter trees between 1880 and 1886 (Parker, 1930). Our mapping of the residual stumps in 2002 showed that about 30 trees/ha were removed, which represents about 15 % of the estimated stand density at that time. It is unlikely that many more trees were cut than what we observed because the generally dry climate and the large size of many of the stumps suggest that decomposition has been relatively slow. Many of the current trees date back 250 to 450 years, and no cutting has occurred in the plot for 120 years. There had been no recorded wildfires in the Manitou Experimental Forest since 1851, until the recent Hayman fires of 2002 which burned a portion of the Northwest part of the forest, outside of our study plot. The study plot has a pure overstory of ponderosa pine, with 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.

Sampling and analysis

In 1974 a 9.3 hectare square plot was established by the USDA Forest Service, and all stems taller than 1.37 m were tagged and mapped using an XY coordinate system. The diameters of tagged trees were measured in 1974, 1983, 1991, and 2001. New trees reaching 1.37 m height were mapped, and diameters recorded in 1991 and 2001. The mortality of tagged stems was recorded in 1983, 1991 and 2001.

The distribution of tree ages in the plot was determined from 18 random points, with cores taken to the pith on all trees counted by a prism (4.59 m^2/ha basal area factor). One-hundred trees were cored at 30 cm above ground level. Cores were surfaced, crossdated and aged according to standard procedures (Stokes and Smiley, 1968). We grouped the estimated pith dates into 10 year age classes for assessing temporal patterns in tree establishment. Actual germination dates were probably about 10 years earlier based on a study done in a ponderosa pine stand about 30 km away (Kaufmann et al., 2000).

Describing spatial patterns

Tree patterns were analyzed using Ripley's K functions (Moeur, 1993). The K(d) function estimates spatial dependence between points by considering the distances between all pairs of points in a mapped dataset. The K(d) function also provides information on the scales and magnitude of spatial patterns (Fortin, 1994; Chen and Bradshaw, 1999) by looking at the variance in the distance between all possible pairs of points (trees), instead of just the mean of the nearest neighbors as in a first order neighbor analysis. The K(d) function produces a cumulative distribution function that represents the expected number of trees within a given distance of an individual tree, and is weighted to correct for edge effects. We report results as L(d), which is a square root transformation that linearizes K(d) and stabilizes its variance. The model can be used to test point data for departure from a spatially random pattern, as described by a Poisson process. Observed patterns differ from random at $P = 0.05$ where the plot of L(d) falls outside the 95% confidence envelopes on a Monte Carlo simulated Poisson process. Clustered arrangements are indicated by an L(d) above the envelope, and regular tree spacing occurs where L(d) falls below the envelope.

Spatial associations of trees of different size classes were analyzed using a bivariate K-function, Ripley's $K_{12}(t)$ (Diggle, 1983; Rowlingson and Diggle, 1993). This function calculates the expected mean number of individuals of type two within a given distance of an arbitrary individual of type one. The null hypothesis of spatial independence between the two groups is refuted where values of $K_{12}(t)$ fall above or below a 95% confidence envelope, indicating a positive (attraction) or negative (repulsion) spatial association between the two groups. The confidence interval is calculated from a random torroidal shift of one pattern relative to the other. We estimated the bivariate K-function using the SPLANCS spatial library (Rowlingson and Diggle, 1993).

Point-process models

Point patterns that were identified by the K(d) function as differing from a Poisson distribution were modeled using homogeneous point process models. The Neyman distribution is routinely used to describe clumped spatial patterns and includes two parameters that provide measures of the average cluster size and number of individuals per cluster. The assumptions of the Neyman's distribution are that the clusters are randomly distributed, and that the number of individuals per cluster follows a Poisson distribution.

Regular patterns were modeled using a Strauss process, a type of Markov point process describing a range of spatial patterns from spatial randomness to complete regularity. A point process is Markov if the conditional density of a point depends only on the points within radius δ. The Strauss process includes two parameters that describe the distance between interacting neighbors (δ) and the probability of having two points closer together than δ (c). The Strauss process is generated using a point deletion-replacement algorithm. From the original L(d) functions we estimated input parameters for simulating either the Neyman or Strauss processes. We then generated new L(d) functions and confidence envelopes based on those simulated point patterns and plotted both figures simultaneously to see whether the observed point process (L(d)) fell within the 95% confidence envelope of the simulated process. We also tested how well a point pattern fit a given model using the Cramer-von Mises goodness-of-fit test, which compares the simulated and observed point patterns and tests the null hypothesis that the two patterns are significantly different.

Trees were grouped into 6 diameter classes (0-6, 6-15, 15-25, 25-40, 40-55, and >55 cm dbh) to identify patterns and mechanisms that may operate on cohort age or canopy position. L(d) functions and point process models were generated for all size classes in 1974 and 2001, as well as for establishment data from 1991 and 2001, and mortality data from 1983, 1991, and 2001. Bivariate K-functions were done for all pairwise combinations of size class, establishment and mortality, although not all results are reported. All spatial analyses were done in S-Plus 2000 (Mathsoft, 1999).

Results

Density, size and age structure

The study plot contained 3,657 live trees in 2001, with an average density of 420 stems/ha, and 21 m^2/ha of basal area. The diameter distribution (Fig. 1) was multimodal; discounting the large number of trees less than 5 cm dbh, the older size classes were approximately normally distributed, rather than classically J-shaped, as would be expected in an uneven-aged forest. Figure 2B shows the current age distribution in the stand, estimated from our tree cores, and therefore represents the cumulative effects of successful germination and survival. Some tree establishment occurred every decade until the early 1900s, with some larger pulses of establishment beginning around 1780, 1880, and 1960 (including the germination correction factor). There are few or no remaining trees dating to the early to mid 1900s, suggesting low regeneration and/or survival during this time. Stand density in 1870 was estimated to be about 200 stems/ha, determined by adding the number of living stems that predate 1870 with the number of stems harvested in the late 1800s, and assuming a low level of non-sapling mortality of 10 stems/decade. A fire history reconstruction based on fire scar data from this plot showed 6 fires since 1600 (Brown and Kaufmann, unpublished; Fig. 2B). A few old-growth trees remained from the early 1600s and many trees established in the 80 years prior to the last documented fire in the stand in 1851.

Contemporary patterns of recruitment

The low density of small trees in 1974 implies that recruitment was slow in the early-to- mid 1900s (absolute regeneration numbers could differ widely due to seedling mortality). The density of small trees observed doubled from 1974 to 1991 and then dramatically tripled from 1991 to 2001 (Fig. 3A). Given that it takes 20-25 years for pine seedlings to reach 1.37m (Shepperd, unpublished), these small trees would have germinated in the 1960s through 1980s. This new cohort of small trees increased stand density by 30%, though basal area increased only by 10% in 30 years (Fig. 3B). The new cohort of trees were highly clumped (Table 2). Figure 3 gives an example of a clumped L(d) function (using the 1991 establishment data) that was best modeled with a Neyman point process model. In 1991 there were half as many patches of recruitment as there were in 2001, and the patches were 30% larger in diameter than in 2001, but had nearly half as many trees per patch (Table 1).

Bivariate K-functions demonstrated that trees which established from 1983 to 1991 were spatially associated with trees in the 6-15 cm size class in 1991 (Fig. 5) at all scales up to 40 m, and with the largest canopy trees >55 cm dbh at scales of 20-35 m

(Table 2). There was repulsion between the establishing trees and all other size classes in 1991. The pulse of 1991-2001 establishment showed almost identical spatial patterns (Table 2), associated with 6-15 cm trees at scales from 3-25 m, and with trees >55 cm at 15-20 m distances. The association between 1991-2001 establishment and all other tree size classes was also negative at a similar range of scales as observed for the 1983-1991 data.

Patterns of Mortality

Rates of mortality were low but variable in magnitude and pattern over 30 years (Fig. 6). Mortality was near 9% from 1974 to 1983, or less than 1% per year, dropping to less than 0.01% mortality/yr in the last two decades. Trees that died between 1974 and 1983 occurred in large, aggregated patches across the stand, with an average patch radius of 20 m. and approximately 16 trees per patch (Table 1). Mortality patterns viewed individually for each size class (data not shown) showed that it was primarily the 25-40 cm trees that died in large patches (~30 m radius) consisting of 12 trees on average. Smaller and larger trees died in small patches of only a few individuals each. A Poisson model best described 1983-1991 mortality patterns, indicating spatial independence in the location of tree deaths (Table 1). Mortality from 1991 to 2001 was slightly clumped, primarily in the 25-40 cm size class. Other size classes had an overall random pattern of mortality.

Surprisingly, tree establishment was not spatially associated with areas of high tree mortality (Table 2). Areas of tree establishment were either segregated or spatially independent from areas of tree mortality, depending upon the pairwise combination.

Structural Patterns

Spatial patterns varied across tree size classes in 2001. Trees less than 6 cm dbh occurred in dense clusters across the stand. With increasing size class, the patchiness diminished (Fig. 7), with the average number of trees in a patch decreasing from 21 to 3 in the 15-25 cm size class (Table 1). There was only slight clustering in the 25-40 cm size class, which disappeared entirely from the 40-55 cm trees that were regularly spaced at minimum distances of 9 m (Fig. 7 and Table 1). A Poisson model best described trees larger than 55 cm dbh, but we still found that these large trees had a minimum spacing distance of 3 m.

The overall patterns of stand structure did not change considerably over the 30 years of observation, though some details of patch structure varied for the smaller size classes (Table 1). Patches of trees 0-15 cm in diameter were more numerous, smaller, and denser in 2001 than 1974. Trees 15-25 cm dbh were more strongly clumped in 2001 than in 1974. The Strauss models describing trees 40-55 cm dbh were identical for 1974 and 2001.

Discussion

Density, size and age structure

Climate appears to have played a significant role in driving pine regeneration in this stand. A large number of trees established in the late 1700s to early 1800s and survived. The Palmer Drought Severity Index indicates that this was also a period of wet climatic conditions (Fig. 2A). Cooler temperatures and adequate summer moisture create opportunities for successful germination and higher survival rates in pine. These were wet years throughout the Great Plains and Front Range, and abundant establishment during this time period has been documented in the Southwest and in the Black Hills, SD (Swetnam and Betancourt, 1998; Mast and Veblen, 1999; Brown, 2004). The long fire-free interval from 1774 to 1851 probably also contributed to higher seedling and sapling survival, while the fire in 1774 may have helped to stimulate the pulse of regeneration in the following decades (Fig. 2B). Front Range ponderosa pine stands often exhibit increased regeneration 2-12 years after a fire by decreasing competition from understory grasses and preparing a mineral seedbed (Cooper, 1960; Larson and Schubert, 1969; Goldblum and Veblen, 1992). Drought conditions from the 1830s - 1870s probably contributed to the 1846 fire, and to the lower rates of establishment and/or survival following the fire (Figs. 2A and 2B).

The next clear peak in tree recruitment and survival occurred in the 1880s and 1890s (based on the germination correction factor) (Fig. 2B). This pulse has been clearly observed in other Front Range ponderosa pine stands (Veblen and Lorenz, 1986; Mast et al., 1998; Brown et al., 1999; Mast and Veblen, 1999), and has been attributed to the favorable climate during that time, as well as the grazing, logging, and fire suppression that accompanied Euro-American settlement of these areas during the late 19th century (Peet, 1981; Mast et al., 1998). We know that some selective logging was done in our stand in the 1880s, and this may have contributed to the successful recruitment of a cohort of trees. The explosion of new trees to the stand in the late 20th Century (Fig. 3) coincided with a very wet climate, following drought years in the 1950s and 1960s when there appears to have been little successful establishment of trees (Figs. 2A and 2B). The lack of fire or other major disturbance in the stand to trigger this release of trees supports the idea that climate plays a major role in pine establishment (Mast et al., 1998). These sorts of highly episodic recruitment events driven by a combination of climate, fire and anthropogenic disturbance are consistent with Southwest (Savage et al., 1996; Swetnam and Betancourt, 1998) and Front Range (Mast et al., 1998; Brown et al., 1999; Kaufmann et al., 2000; Brown, 2004) reconstructions.

Contemporary patterns of recruitment

From the 1980s to the1990s recruitment in the stand tripled, and occurred in denser and more numerous patches (Fig. 3A & Table 1). Regeneration tended to occur near small established trees (6-15cm dbh), and roughly 15-35 m from the largest canopy trees (>55 cm). Our descriptive study cannot address the causes of patterns of tree recruitment within the stand, but we can offer some speculations. Successful ponderosa pine seedling germination and establishment generally requires a large supply of seed, a mineral seedbed, sufficient moisture, reduced understory cover, and light (Larson and Schubert, 1969; Schubert, 1974; White and Pickett, 1985; Kolb and Robberecht, 1996; Stein and Kimberling, 2003). Areas15-30 m from the largest trees may be optimal for regeneration because these trees are likely to be the best seed producers, and this distance is still within the dispersal distance for ponderosa pine (Oliver and Ryker, 1990), yet is beyond the influence of the canopy where shading and heavy litterfall may prevent successful germination or seedling survival (Covington and Sackett, 1986; Stein and Kimberling, 2003). A regression of tree regeneration as a function of litter depth (data not shown) showed a weak, negative relationship between litter depth and regeneration ($r^2=0.16$, $p<0.001$). We speculate that patches of 6-15 cm trees may be conducive to establishment since they provide some degree of shading, which is important for reducing grass cover as well as protecting seedlings from moisture stress (Larson and Schubert, 1969; White and Pickett, 1985; Stein and Kimberling, 2003), yet are too small to contribute significant amounts of litter to the forest floor. The segregation of tree establishment from all other size classes similarly suggests that new cohorts are forming in patches that are spatially distinct from pre-existing clumps or areas of high density, possibly where competition for light and water is reduced. This pattern of establishment supports Cooper's (1960) description of even-aged patches of ponderosa pine in Arizona.

Contrary to expectations for gap dynamics, tree establishment was never associated with areas of high tree mortality (Table 2). Canopy gaps created by individual tree mortality may be important for tree recruitment in shade intolerant species, yet we saw that areas of higher tree mortality were sometimes less likely to promote new establishment into the stand. It is possible that areas of higher tree mortality are also less conducive to seedling establishment and growth due to micro-environmental conditions. The fact that historical recruitment was largely driven by climate rather than disturbance also suggests that the processes of mortality and regeneration in this ponderosa pine stand may be uncoupled processes (Brown, 2004), but both of these theories need further exploration.

Cattle grazing may also have played a role in pine recruitment in our stand. Intensive grazing began in the late 19th Century in the South Platte basin (Jack, 1900), and cattle may have had opposing effects of increasing seedling mortality (by trampling or occasional browsing) and fostering seedling success by reducing competing grasses and fine fuels that would have carried surface fires. (Rummell, 1951; Johnson, 1956; Madany and West, 1983; Belsky and Blumenthal, 1997).

Size Patterns and Mortality

Recruitment was highly clumped across the stand, but that pattern slowly disappeared from successively larger size classes as the patches contained fewer trees, eventually becoming random and then regular in the 40-55 cm trees. We can assume that historical regeneration patterns were clumped (White and Pickett, 1985; Mast and Veblen, 1999), which means that the regularity in the old trees appeared over the past several centuries. Regular spatial patterns are often taken as an indicator of competitive self-thinning (Kenkel, 1988; Moeur, 1993; Mast and Wolf, 2004). In truth, any patchy mortality that leads to thinning of dense, aggregated stands can result in more regular spacing of the survivors (Kent and Dress, 1980). Although there are a number of ways for patchy mortality to occur, fire probably played a significant role in structuring the current spatial pattern of the large tree trees since most of them predate the 1851 fire. When a low intensity surface fire burns through a stand (such as the 1851 fire) clumps of smaller trees are killed because they are not yet fire-resistant, leaving larger trees alive and possibly more regularly spaced as a result.

It is possible that the regularity in the large trees was partly caused by the selective thinning in the 1880s. We mapped the locations of all visible stumps in the stand and determined that they were randomly spaced. This means that their removal had little to no impact on the regularity we observed in the current large canopy trees since random mortality will not drive a clumped or random pattern towards greater regularity (Kent and Dress, 1979; Kent and Dress, 1980).

In the absence of fire in this stand, the question remains how current mortality patterns compare to historical ones? Contemporary mortality patterns were still predominantly patchy (Fig. 6), although the scale and extent of mortality is likely lower than it was historically, with fire. There were particularly large patches of mortality from 1974-1983, indicating a fairly large scale disturbance. Records indicate that an outbreak of mountain pine beetles caused considerable mortality in the experimental forest and across the Front Range in the early 1980s (Shepperd, pers. comm., McCambridge et al., 1982). Mountain pine beetles infest high density patches of pine and, depending upon the severity of the outbreak, will kill some of the trees in the patch, creating more regularity in the survivors (McCambridge et al., 1982; Logan et al., 1998). Smaller patches of mortality, like we documented from 1991-2001 and in smaller size classes from 1974-1983, could be a sign of density-dependent mortality. A binomial logistic regression of trees that died versus trees that survived from 1983 to 2001 showed no relationship between the probability of mortality and local tree density (data not shown). Although this is not a conclusive test, we should clearly be cautious about inferring ecological processes, such as competitive self-thinning, from pattern alone.

Spatial analysis of regeneration, mortality and size structure can help us to reconstruct a story of stand development for this mature ponderosa pine forest. Climate appears to have had a major influence, historically and more currently, on the timing of recruitment events, with stand structure (distribution of patches, light availability, and seed trees) playing a significant role in the pattern of regeneration. The patchy process of regeneration results in spatial independence and some segregation of size classes (data not shown). White (1985) found that ponderosa pine grew in small groups that ranged from 0.02-0.3 ha (8-30 m radius) in size with 3-44 trees per group. Overall, our data reflect very similar patterns with patch sizes ranging from 9-35 m radius, and anywhere from 1-21 trees per patch. The relatively even ages of trees within a patch, however, is more consistent with the even-aged mosaic patterns that Cooper (1960) described for ponderosa pine in Arizona.

Both the scale and nature of disturbances have changed in contemporary forests. In the absence of recent natural wildfires in this stand, historically patchy mortality resulting from tree scorch and crown fires (Brown et al., 1999; Ehle and Baker, 2003) has been replaced with mostly random individual tree mortality, and the potential for smaller patches of mortality resulting from self-thinning or disturbance events such as mountain pine beetle outbreaks or drought. These events probably have a lesser impact on spatial pattern than historical surface fire, but may still create and maintain some regular spacing of the older trees as the stand matures. Despite the loss of fire to this system, the highly episodic and clumped patterns of regeneration events, and the spatially and temporally patchy pattern of mortality, are somewhat consistent with our idea of pre-European stand structure patterns for the Colorado Front Range (Peet, 1981; Brown et al., 1999; Mast and Veblen, 1999; Kaufmann et al., 2000).

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Table 1. Spatial pattern and model parameters for regeneration, mortality, and size class data over time. Spatial patterns are clustered (C), random (R), or regular (dispersed, D); point process models used to describe the spatial patterns are Neyman-Scott (N), Poisson (P), or Strauss (S); minimum distance is the average minimum distance between individuals; and c is the probability of finding two individuals closer than the minimum distance.

		Pattern	Model	Clusters / ha	Trees/ cluster	Cluster radius	Min. distance	c
regeneration	**2001**	C	N	6.9	18.0	9		
	1991	C	N	3.5	10.2	12		
mortality	**1983**	C	N	1.4	16.1	20		
	1991	R	P					
	2001	C	N	2.9	1.4	12		
1974 size classes								
	0 - 6 cm dbh	C	N	2.9	5.4	35		
	6 - 15 cm dbh	C	N	6.9	6.2	17		
	15 - 25 cm dbh	C						
	25 - 40 cm dbh	C						
	40 - 55 cm dbh	D	S				6	0
	> 55 cm dbh	R	P					
2001 size classes								
	0 - 6 cm dbh	C	N	6.9	21.0	12		
	6 - 15 cm dbh	C	N	11.5	4.4	10		
	15 - 25 cm dbh	C	N	18.5	3.3	15		
	25 - 40 cm dbh	C						
	40 - 55 cm dbh	D	S				6	0
	> 55 cm dbh	R	P					

Table 2. Spatial association of tree establishment with mortality and size classes. Association between groups as identified by a bivariate K-function is either negative (segregation, S), positive (association, A), or neutral (independence, I). Spatial scales (in meters) of the significant positive or negative associations are described for each pairing. All other scales have a neutral association. Size class data and establishment data for corresponding years were used in the analysis.

	Mortality			**Tree Size Class (cm dbh)**				
	1983	1991	2001	6-15	15-25	25-40	40-55	> 55
1991 establishment	S 0-40m	I		A 0-30m	S 0-35m	S 0-50m	S 0-20m	A 25-35m
2001 establishment	I	I	S 5-40m	A 3-25m	S 0-40m	S 0-35m	S 0-20m	S 0-5m, A 15-20

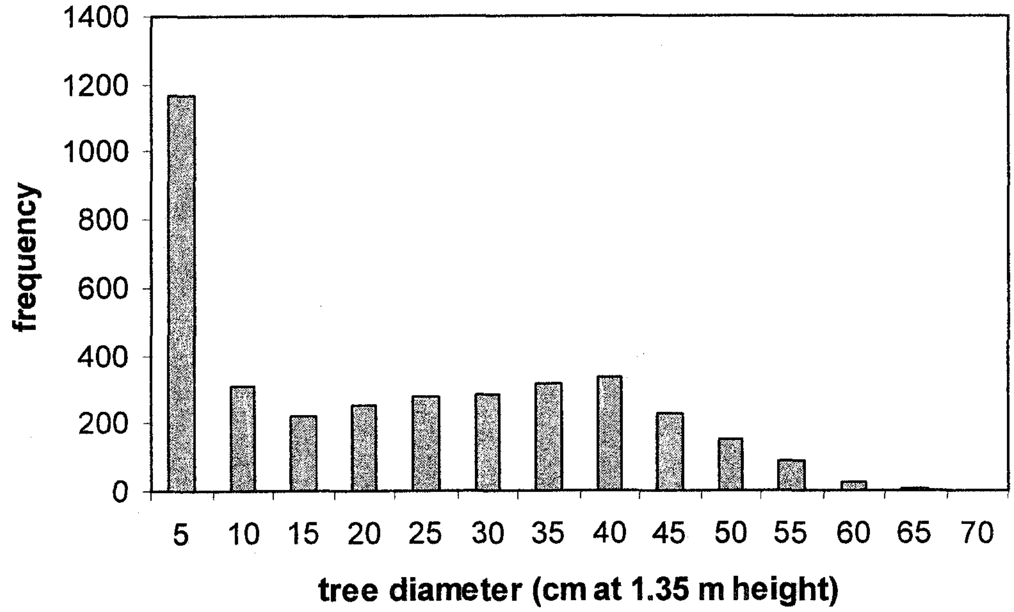

Figure 1. The size frequency of trees was dominated by the smallest diameter class, with relatively even numbers of trees in larger classes (top).

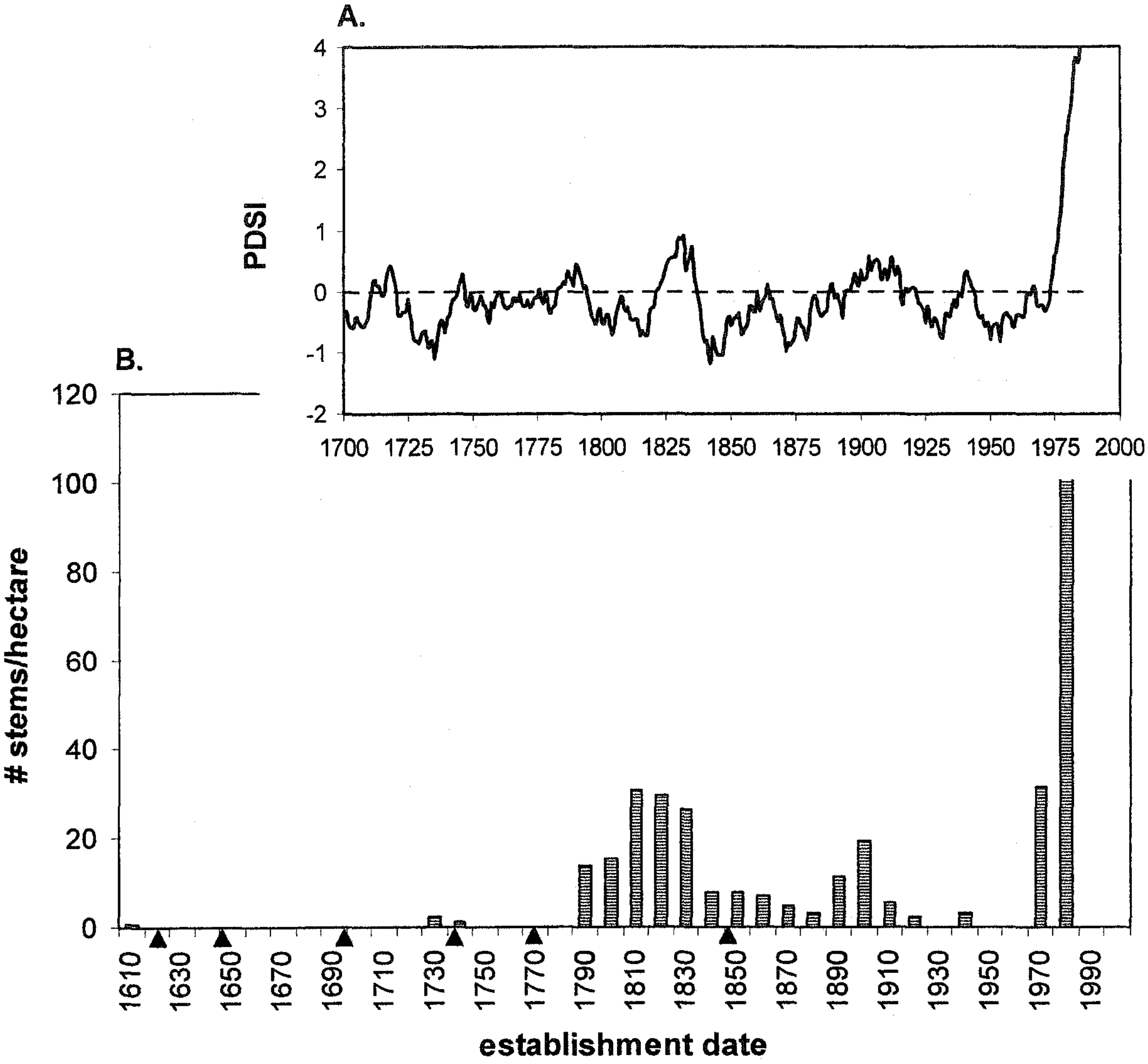

Figure 2. The age structure showed a large spike of recent recruitment, preceded by substantial recruitment and survival in most decades between 1800 and 1930 (fire years indicated by ▲). The three clearest peaks in recruitment and survival are associated with periods of wet climate (indicated by a large Palmer Drought Severity Index (PDSI for the Colorado Front Range; (Cook et al., 1999; Cook, 2000)).

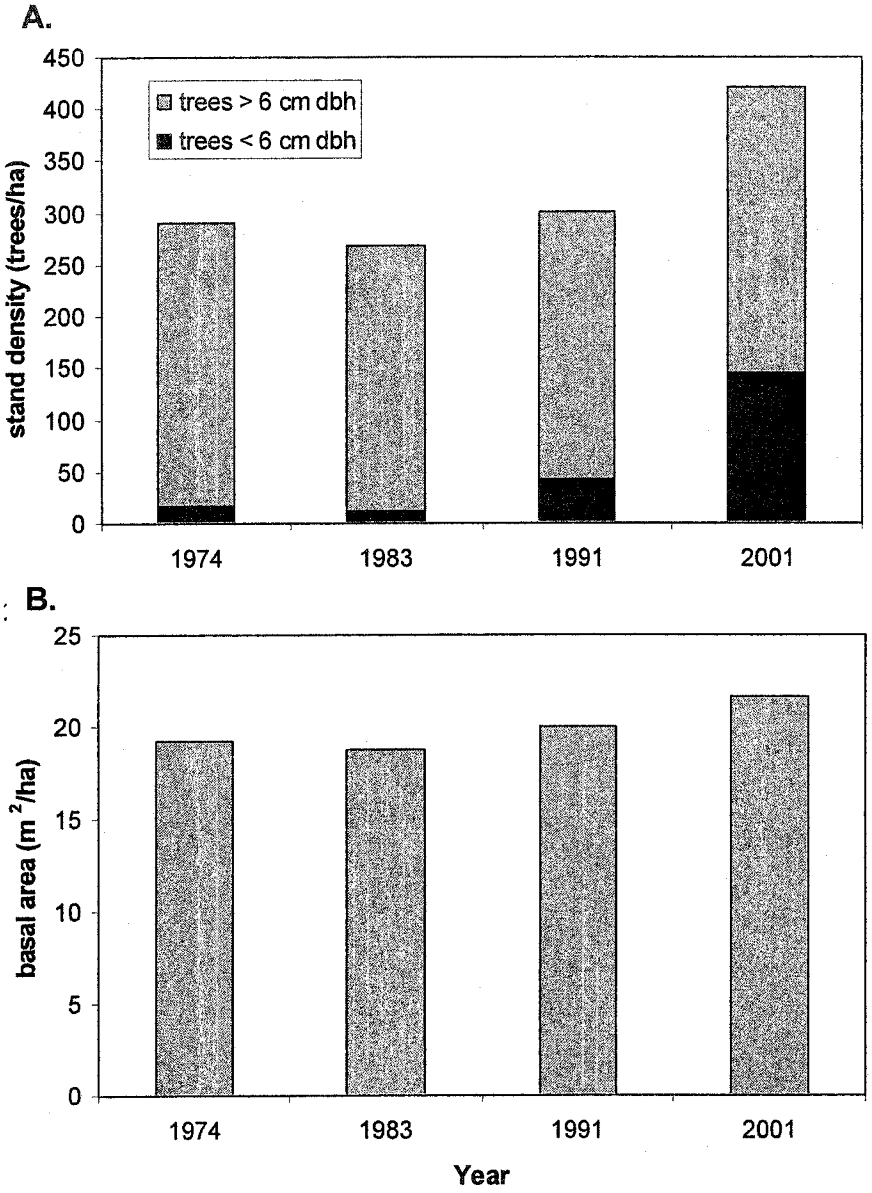

Fig. 3. Stand density increased substantially during the 30 years of intensive monitoring of this stand (A), but the change in basal area was slight (B).

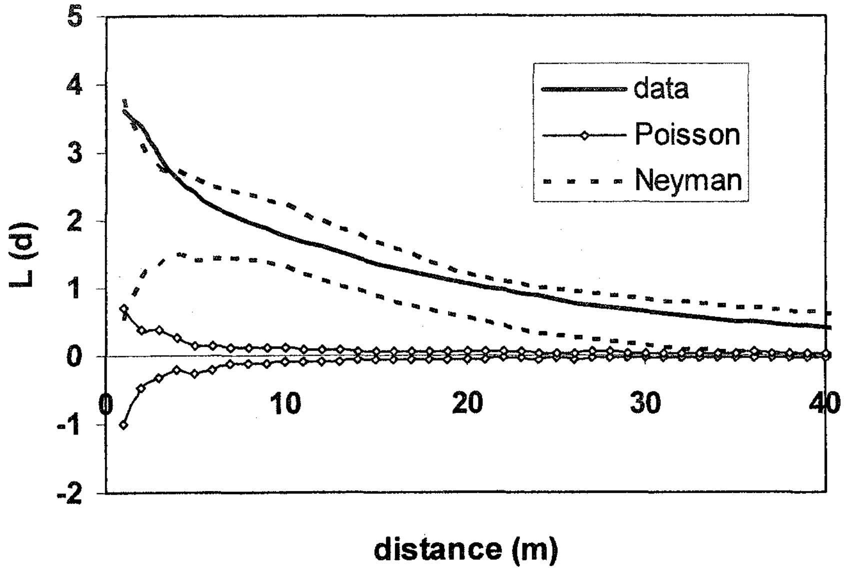

Fig. 4. Spatial pattern of 1991 establishment in relation to random and clumped point process models. 95% upper and lower confidence envelopes for each model are plotted as a function of lag distance (m) from an arbitrary individual. The plot of the actual data falls above the upper limit for a Poisson model, but within the bounds of the Neyman model, confirming that the data are spatially clumped at all distances.

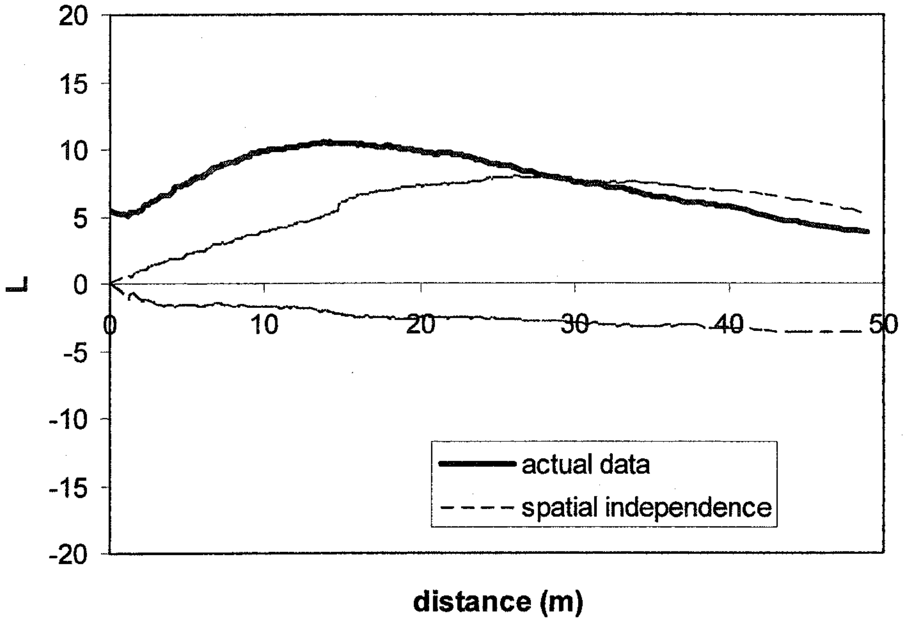

Fig. 5. Bivariate K-function for establishment and trees 6-15 cm dbh in 1991. The plot of the actual data (L vector) falls above the upper 95% confidence envelope for a spatially independent process, confirming that the 2 groups are spatially associated at scales from 0-30 m, and independent at larger lag distances.

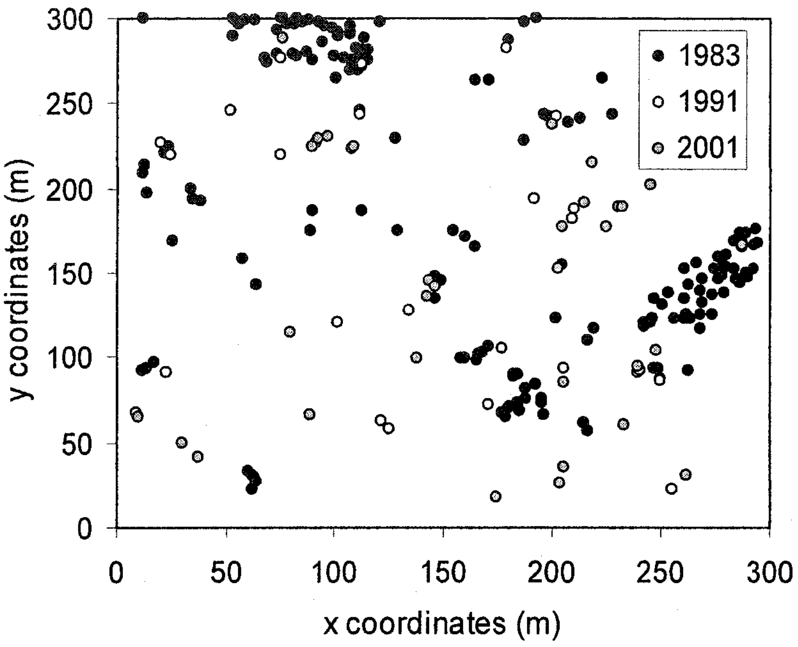

Fig. 6. Pattern of tree mortality across three decades. Map of the locations of all trees that died from 1974-1983, from 1983 to 1991, and from 1991 to 2001.

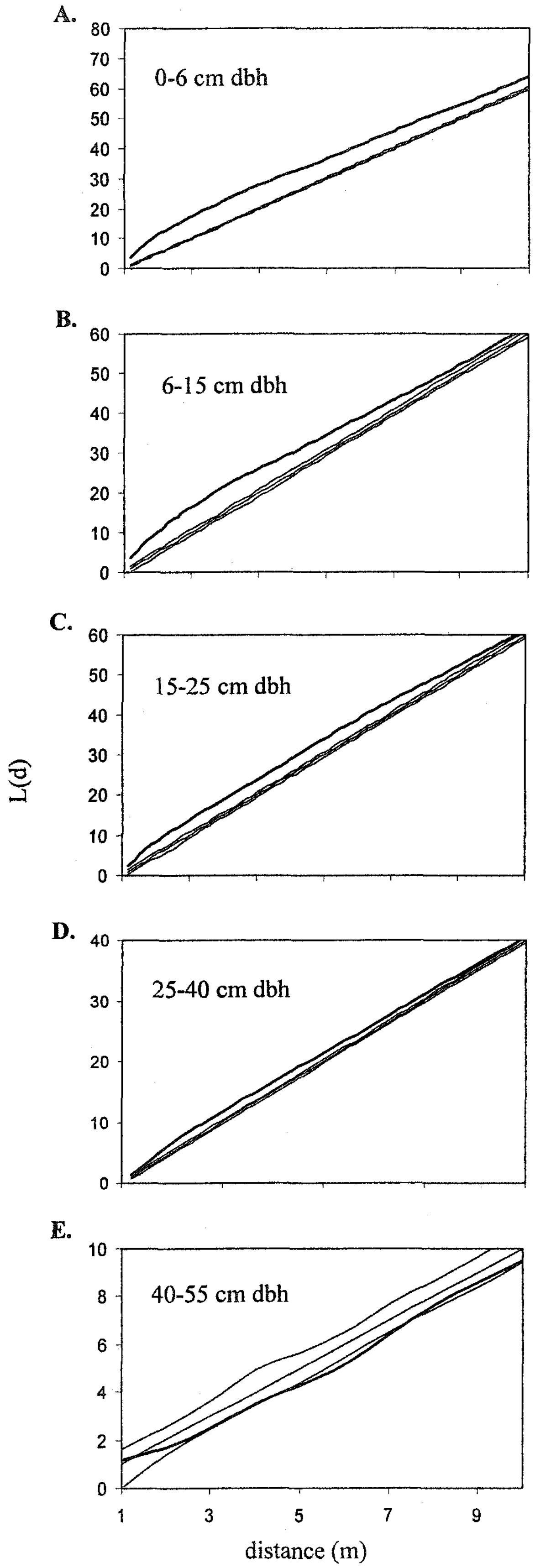
A.
80
70
60
50
40
30
20
10
0
0-6 cm dbh
B.
60
50
40
30
20
10
0
6-15 cm dbh
C.
60
50
40
30
20
10
0
15-25 cm dbh
L(d)
D.
40
30
20
10
0
25-40 cm dbh
E.
10
8
6
4
2
0
40-55 cm dbh
1
3
5
7
9
distance (m)

Fig. 7. Spatial pattern of ponderosa pine by size class in 2001. 95% upper and lower confidence envelopes for a Poisson model are plotted as a function of lag distance from an arbitrary individual with a dotted line. Actual data are plotted with a solid line. In Figs. 6a-6d the plot of the actual data falls above the upper limit for a Poisson model at some range of distances, indicating that the data are spatially clumped. In Fig. 6e the plot of the actual data falls below the lower limit for a Poisson model, indicating that 40-55 cm trees are regularly dispersed at 5-7 m neighbor distances.

CHAPTER 3

THE EFFECTS OF SOIL FERTILITY AND SCALE ON COMPETITION IN PONDEROSA PINE

Abstract

The intensity of competition between neighboring trees may be affected by gradients in soil resource supplies as well as local stand structure. We tested for variation in the nature and intensity of interactions between trees along a gradient of soil nitrogen supply in an old-growth stand of ponderosa pine in the Front Range of Colorado. We used spatially explicit competition indexes to describe the interactions between trees, and developed individual tree growth models to look at the effects of neighborhood scale and soil nitrogen supply on competition. 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. Soil nitrogen supply had a significant impact on individual tree growth if the neighborhood was small (< 6 m radius); with larger neighborhoods, the effect of soil nitrogen was swamped by other competition effects. The intensity of competition was also modified by soil resource supply; neighbors had a larger competitive effect on tree growth when nitrogen availability was higher. Spatial heterogeneity in stand structure and soil resource supplies jointly influenced the growth of individual trees.

Introduction

Forest stand structure directly influences individual tree growth and survival. Tree density is one component of forest structure that has strong and predictable relationships with tree growth, as modeled by the inverse density-yield relationships common to the forest literature (Yoda et al. 1957, White and Harper 1970). The mean effect of density on tree growth or survival does not provide information on the interactions of individual trees. Nearest neighbor analyses can be used to explore the dynamics of tree competition more closely. A number of spatially explicit competition indexes have been developed using combinations of neighbor size, distance, and angle as ways to understand local variability in tree performance (Weiner 1982, 1984, Wagner and Radosevich 1998). The effects of neighbors may differ across microsites within a stand as a result of patterns in soil nutrient supply or other factors (Boyden et al., 2005).

Research on grasses and herbaceous plants has examined two theories about the relationship 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). One theory holds that fertile habitats may have stronger competitive interactions owing to higher productivity and higher resource demands(Grime, 1973; Grime, 1979). Another theory expects the intensity of competition would not vary with resource availability or productivity, although competition may shift from belowground to aboveground resources as fertility increases (Newman, 1973; Tilman, 1988). 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 pondorosa* Laws.). Competition indexes were first developed to assess the importance of neighbor distance and the degree of asymmetry in the competitive relationships. 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 between plants is usually asymmetric, but symmetric competition can occur if plants are competing for below-ground versus aboveground 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) does neighbor distance matter to the growth of the focal tree? 2) is competition between neighboring trees symmetric or asymmetric? 3) does soil N supply significantly affect the relationship between competition and growth? 4) does neighborhood radius impact the performance of the competition indexes and growth models?

Methods

Study Area

The study was conducted in Manitou Experimental Forest, 40 km northwest of Colorado Springs, Colorado. The elevation is 2,500 m and topographic change is mild across the study area. Average precipitation is 39 cm/yr, 25% of which falls as snow, and the mean monthly temperature is 5 °C, with an average growing season high of 16 °C. 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 1800's, and most of the current Experimental Forest area was heavily thinned of large diameter trees between 1880 and 1886. The study plot was thinned lightly in the 1880s and has been undisturbed since that time.

Sampling and analysis

A 9.3 hectare square plot was established in 1974 by the USDA Forest Service and all trees 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 quadratic mean diameter of 21.4 cm, basal area of 21 m^2/ha, and average tree height of 11.5 m (Boyden et al., 2005).

Aboveground biomass (stems plus large branches, twigs and foliage) 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), the bark biomass equation from (Gholz et al., 1979).

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

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

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

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

Dbh is diameter in cm at 1.35 m, *ht* is tree height in meters, and *wd* is wood density (we used 537 kg/m^3; Hall et al., unpublished data). The annual growth of individual trees was calculated as the change in aboveground woody biomass of all live trees from 1991 to 2001, divided by 10.

The supply of available soil N (NO_3^- and NH_4^+) was indexed with ion exchange resin bags (Binkley and Hart, 1989). In May of 2000 two resin bags were buried at 2.5 cm depth every 15 m along a systematic grid, for a total of 380 sampling points throughout the stand. One resin bag from each pair was removed in October and the second was removed in May. Resins were extracted using 2M KCl and analyzed on an AlpChem automated colorimeter. Nitrogen limitation was assessed 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 of 2001. 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 was compared for fertilized and unfertilized trees with a t-test.

Statistical Analysis

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. Growth models were developed *a priori* using the available predictor variables: competition (*W*), soil N supply (*N*), and tree biomass in 1991 (*B*). Testing a limited set of models helps 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 used information theoretics (Akaike's Information Criterion, AIC) to select the best competition index and growth model by calculating the expected value of the information lost when using a model to approximate the truth. A low AIC value indicates strong performance of a model (Burnham and Anderson, 1998).

Growth Models

We modeled tree growth (aboveground woody biomass increment, kg/yr) from 1991 to 2001 as a function of competition. The relationship between all of our measures of competition and tree growth was clearly concave (Figure 1B). This is a common shape for competitive effects on plant performance (Weiner, 1982; Silander and Pacala, 1985) and has been attributed to the fact that the mean area per tree decreases hyperbolically with increased local density (Silander and Pacala, 1985). We modeled this relationship using a non-linear equation based on yield density models (Holliday, 1960;

Harper, 1977) similar to competition models used by Weiner (1982, 1984) and Silander and Pacala (1985). We adapted the basic equation with the addition of parameters that could describe different effects of tree size and soil N supply on growth (Table 2). Model 1 represents the basic concave relationship between growth and competition. Model 2 includes tree size (*B*) as a predictor variable which controls the maximum growth of the focal tree since the relationship between tree mass and growth is well established (Fig. 1A). Model 3 replaces *B* with soil N supply (*N*) as the predictor variable which directly controls the maximum growth of the focal tree. Model 4 also includes *N* with an interactive rather than an additive effect, influencing the slope of the relationship between competition (*W*) and focal tree growth. Model 5 is a combination of models 3 and 4, and includes both the interaction and tree size.

Measures of tree competition

We examined neighborhood effects around each individual focal tree (n = 692 trees). The soil N supply was assessed at 15 m intervals across the plot, and all trees less than 5 m (and more than 20 m from the boundary of the 9.3 ha stand) from a soil N sampling point were used as focal trees. For each focal tree we calculated neighborhood indexes (W_r) in three ways. Our simplest equation (Index 1) summed the biomass (*B*) of all neighbors within a circle of radius (*r*):

Biomass (Index 1):

$$C_r = \sum_{i=1}^{n} B_i$$

where *i* is the *i*th neighbor and *n* is the total number of neighbors within the given neighborhood distance. The second equation (Index 2) was similar except that a neighbor's impact decreases with the square of the distance from the focal tree (Weiner, 1984). In this model a tree's impact on a neighbor is still size-symmetric (Begon, 1984; Weiner et al., 1990):

Distance-dependant (Index 2):

$$C_r = \sum_{i=1}^{n} \frac{B_i}{d^2}$$

Index 3 was similar to Index 2, but included an additional scalar, or size-ratio term to account for size-asymmetric competition. The size-ratio is similar to one developed by Bella (1971), and divides 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. We tested three forms of this equation (eq.3 a, b, c) by changing the exponent on the size-ratio to 1, 2, or 3.

Asymmetric (Index 3):

$$C_r = \sum_{i=1}^{n} \frac{B_i}{d^2}\left(\frac{B_i}{B_j}\right)^{EXP}$$

Index 3a: EXP=1

Index 3b: EXP=2

Index 3c: EXP=3

The relative size of the neighbor versus the focal tree is given the greatest weight in Index 3c and the least weight in Index 3a. The effect of neighborhood size was evaluated for the 5 competition indexes at 9 neighborhood sizes (radii of 2m, 4m, 6m, 8m, 10m, 12m, 14m, 16m, and 20m). We tested our 4 growth models with each of our 5 competition indexes (*W*) at all 9 radii (*r*) using PROC NLIN (SAS Institute 1999). Models were compared using AIC, and then evaluated based on how well they minimized the residual sum of squares (providing highest correlation, r^2).

Results

Scale strongly influenced the importance of neighbor distance and the nature of the competitive relationship, as defined by our competition indexes. The distance-dependent competition index (Index 2) explained more of the variability in focal tree growth (13% versus ~2%) than the biomass index (Index 1) when only close neighbors were considered (radii ≤ 6 m; Table 1). For larger neighborhood areas, the distance-dependent index (Index 2) resulted in similar or worse model fits than simply summing the biomass of competitors (Index 1). The best asymmetric competition index (3b or 3c) outperformed the symmetric, distance-dependent competition index (Index 2) at all neighborhood sizes. The asymmetric index tripled the model r^2 for small neighborhoods, while explaining twice as much of the variability in growth for larger neighborhoods (Table 2). The choice of exponents in the asymmetric index affected model performance; at radii ≤ 6 m the best index was 3c, while at radii over 6 m index 3b was best. A 14 m radius optimized the performance of 4 out of 5 of the competition indexes, and explained 69% of the variation in individual tree growth when using index 3a (Table 2).

The fertilizer study showed that trees receiving N additions had 21% higher basal area growth than unfertilized trees over a 3 year period ($P < 0.001$), indicating a strong potential for competition among trees to relate in part to soil N supply. The most parsimonious of the 5 growth models was Model 4, which included an interaction between competition and soil N supply (Table3). When using the optimal competition index and radius, (Index 3b, $r = 14$ m), this model explained 69% of the variability in growth of focal trees. Although there is a strong relationship between tree size and growth (Fig. 1A), including focal tree biomass as a predictor variable in addition to competition decreased the performance of the basic model, as did including both biomass and soil N supply (Models 2 and 5; $r^2 = 0.64$ and 0.20). Although growth Model 4 was consistently the best model, its performance was strongly affected by the number of neighbors included in the competition index (Fig. 2). The r^2 increased from 0.345 to 0.694 as the neighborhood radius increased from 2 m to 14 m, after which it gradually decreased.

Increasing the logarithm of the competition index from 0 to 4 decreased the predicted growth of focal trees by nearly 90%, regardless of N supply (Fig. 3), A given level of competition could be achieved through a number of combinations of neighbor numbers, size and distance. For example, an increase from 0 to 4 (log competition) would result from increasing the number of neighbors for a 300 kg focal tree from 0 within 14 m, to 2 equally large neighbors at 4 m distance.

Soil N supply modified the effect of neighbors on focal tree growth (Fig. 3). Although growth was greater overall on high N versus low N soils, increasing competition decreased the growth of focal trees more on soils with high N than on soils with low N.

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. 4). The importance of soil N supply for tree growth decreased as the size of the modeled neighborhood increased. Using a 2 m radius, predicted tree growth increased 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 69% 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; Weiner, 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 appeared to be at least partly asymmetric at all neighborhood sizes, suggesting that trees are not competing exclusively for soil resources, and light must be important. The size scaling exponent on the best competition index was different for neighborhoods with a radius less than 6 m and over 6 m. This suggests that at small neighborhood sizes with fewer competitors the sizes of the neighbors has a larger impact on growth. As the neighborhood radius increased over 6 m the individual differences between neighbor and focal tree biomass became less important to growth. Effects of size were swamped by the sheer numbers of trees, and the magnitude of the competitive impact, which accounts for the better performance of the basic biomass model (Index 1) performed some much better for large versus small neighborhoods (Table 1)

Competition was strongest within a 14 m radius (~ 600 m^2) of the focal tree, which was a larger area of influence than we expected. The number of neighbors within a 14 m radius was as high as 36 trees. A few other studies have found competitive tree interactions to be occurring over similarly large areas (Canham et al., 2004). We did not test specifically for the mechanisms of competition in this study. The large spatial scale and asymmetric nature of the neighbor interactions suggests that above-ground competition for light was probably important (Weiner and Thomas, 1986; Wilson, 1988; Schwinning and Weiner, 1998), and competition for belowground resources has occurred (Weiner and Thomas, 1986). Asymmetric competition can be the dominant cause of size and growth variation in plants (Weiner, 1988). This has important consequences for population dynamics (Pacala and Weiner, 1991) and is likely to be a key factor in promoting and maintaining a diversified, old-growth structure in this ponderosa pine forest.

Our growth models demonstrated that increases in soil N supply also resulted in more intense competitive interactions between trees. This supports Grime's theory (1973, 1979) that competition should be more intense in more fertile habitats. We found a similar relationship in mixed species plantations in Hawaii (Bird et al 2005), but more work is needed to see whether this is a prevalent pattern for trees, as opposed to perennial or herbaceous plants. According to Goldberg and Novoplansky's two-phase resource dynamics hypothesis (1997) this sort of a relationship is more likely in systems where resource availability is pulsed, and largely controlled by abiotic factors. Our study seems to lend support to this theory, since water is both highly variable and limiting to growth in these dry ponderosa pine forests, and is likely to have a large influence on the temporal heterogeneity of available soil N.

We expected focal tree size to help explain some of the variability in individual tree growth, but our models that included biomass of the focal tree (models 2 and 5) performed very poorly. One explanation for this is that the asymmetric competition index we used (Index 3b) already includes the biomass of the focal tree in its calculation, which means that size is indirectly included in our growth model and adding it as a predictor variable would be redundant. 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 small neighborhoods were used (Fig 4). This can be explained by the physiology of nutrient adsorption by the tree root system. In dense stands a ponderosa pine trees root system tends to be limited to the width of the crown (Oliver and Ryker, 1990). 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, while increasing the explanatory power of the competition index; the effects of N are being swamped out by the large numbers of competitors. As the distance between neighboring trees increases there is also a shift from belowground competition for soil N to aboveground competition for light. Further work is needed to understand how the scale of heterogeneity and competition for water supply might also play a role in modifying competitive interactions.

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. It is likely that temporal variability in these interactions is important in addition to the spatial variability we found because soil resource supply is often pulsed rather than constant over time. We need to do more experimental studies of neighborhood interactions along spatial and temporal gradients in resource availability.

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Table 1. Performance of competition indexes for different ranges of neighborhood sizes. Correlation coefficients (r^2) were calculated using the interaction model (Model 4). Mean r^2 value is shown for neighborhood radii ≤ 6 m and > 6 m; the highest r^2 was found at a radius = 14 m.

Competition index	**Mean r^2 2-6 m radii**	**Mean r^2 8-16 m radii**	**r^2 14 m radius**
1 (biomass)	.018	.418	.451
2 (distance-dependent)	.134	.329	.437
3a (Asymmetric, exp=1)	.323	.561	.306
3b (Asymmetric, exp=2)	.444	.671	.694
3c (Asymmetric, exp=3)	.454	.522	.680

Table 2. r^2 and AIC values for 5 competing tree growth models. Models were run using competition index 3b and a neighborhood radius of 14 m.

Growth model	r^2	AIC
Model 1: $y=a/1+bW$	0.684	10968
Model 2: $y=aB/1+bW$	0.647	11033
Model 3: $y=aN/1+bW$	0.340	11464
Model 4: $y=a/(1+bW)^{cN}$	0.694	10938
Model 5: $y=aB/(1+bW)^{cN}$	0.202	11594

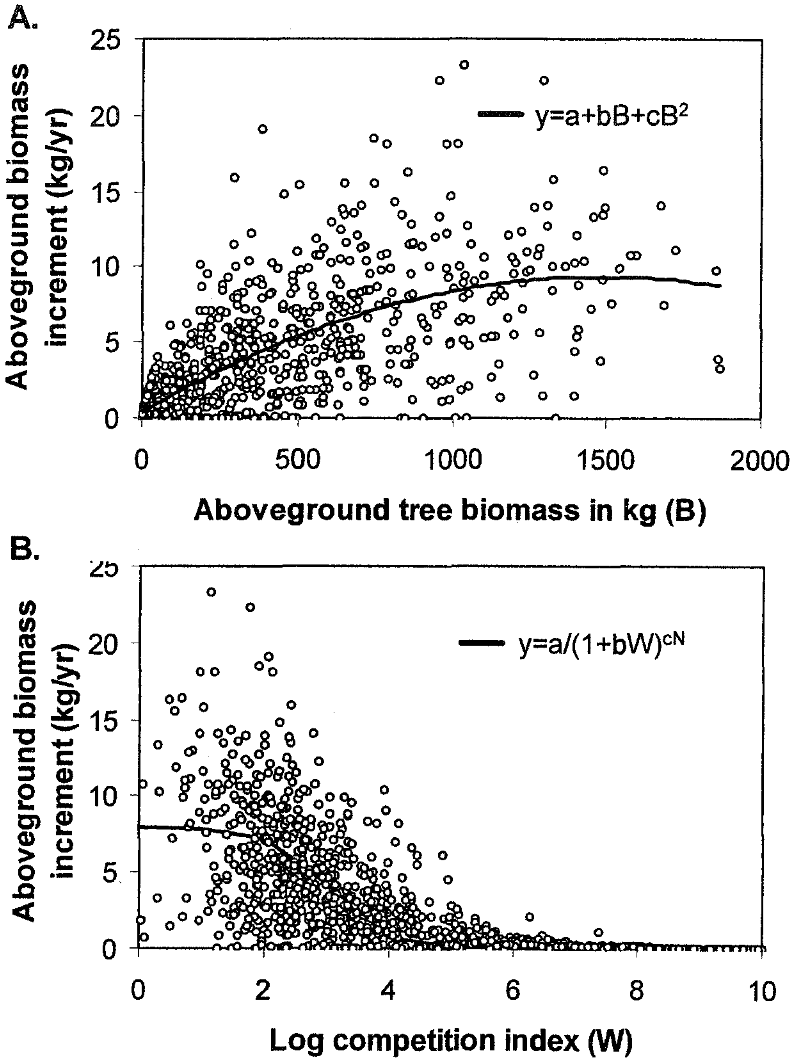

Figure 1. Competition explains more of the variability in tree growth than tree biomass. (A) We used a quadratic model to describe the relationship between tree biomass and growth: ($y = a + bx + cx^2$; r^2=0.523, $P < 0.001$). (B) Competition (*W*) was calculated using index 3b and a 14 m neighborhood radius. Growth model 4 is shown to describe the relationship between competition and tree growth: ($y=a/(1+bW)^{cN}$; r^2=.694, $P < 0.001$).

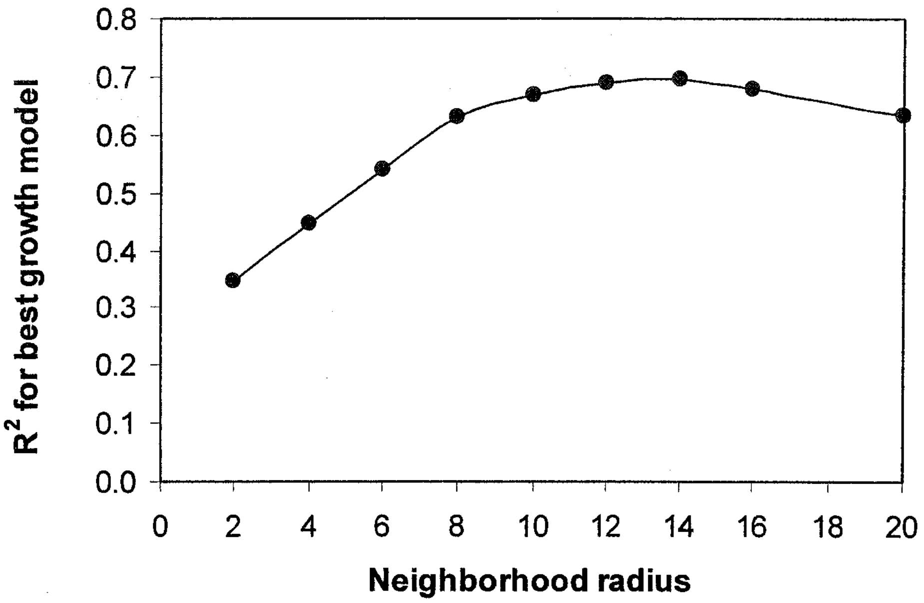

Figure 2. The competitive influence of neighbors extends 10-16 m from the focal tree. The maximum predictive ability of the best growth model (Model 4 using index 3b) was found using a 14 m radius neighborhood (r^2=0.694).

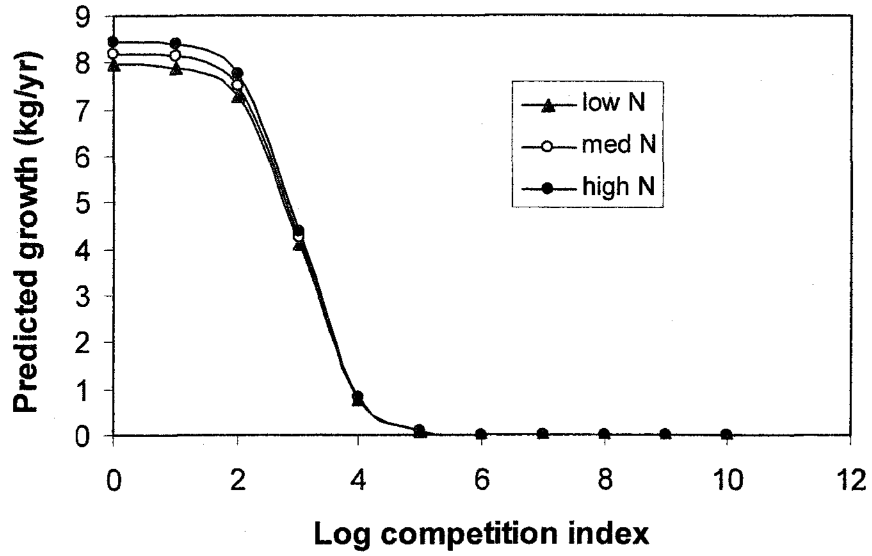

Figure 3. Growth of focal trees was influenced more strongly by competition where soil N supply was high. At very high levels of competition, the influence of soil N supply was minimal. Values for low N = 0.05 mg/resin bag, medium N = 1.0 mg/resin bag, high N = 2.0 mg/resin bag.

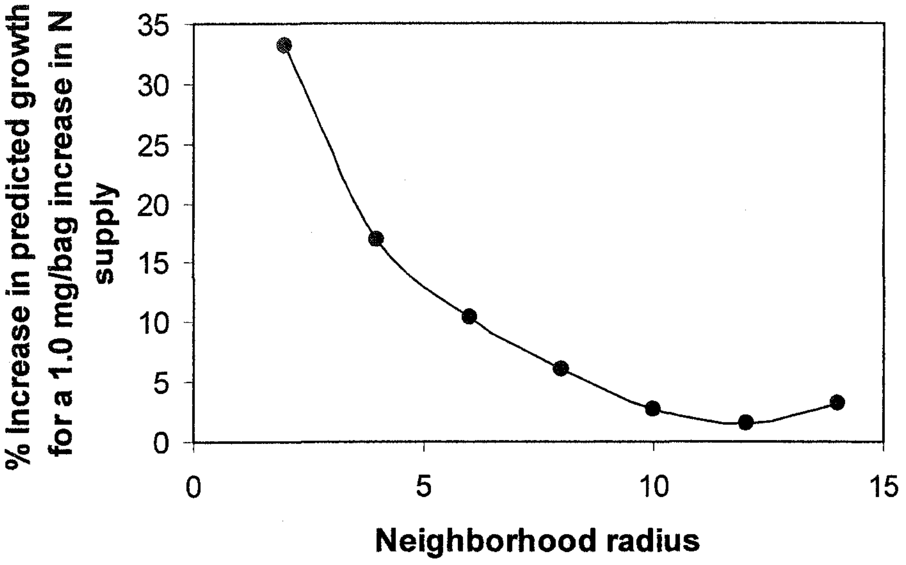

Figure 4. An increase in soil N supply had a larger impact on focal tree growth at small versus large neighborhood sizes. The level of competition in the model (Model 4, Index 3b) was held constant at its mean value.

CHAPTER 4

GROWTH AND SURVIVAL IN MIXED STANDS OF *EUCALYPTUS* AND NITROGEN-FIXING *FALCATARIA* IN RELATION TO NEIGHBORS AND SOIL FERTILITY.

Abstract

The balance between inter-tree competition and facilitation may shift in relation to gradients in soil resource supplies, determining patterns in overall stand-level production and community structure. We tested for variation in the nature and intensity of interactions between *Eucalyptus saligna* and nitrogen-fixing *Falcataria mollucana* along a gradient of soil nitrogen and phosphorus supply in Hawaii. Neighborhood indexes were used to describe competitive and facilitative interactions between trees, and spatially explicit models of individual tree growth and survival were developed to look at the effects of soil nutrient supply on those interactions. The dynamics between neighboring trees depended strongly on soil nutrient supply. Large trees generally grew faster than smaller trees, but this pattern was moderated by interactions between nutrient availability and the intensity of competition and facilitation. *Falcataria* survival decreased by up to 30% with increasing *Eucalyptus* on low nitrogen soils, but increased by nearly 70% on soils with higher nitrogen. Intraspecific interactions reduced *Falcataria* growth by up to 100% on high-phosphorus soils, yet facilitated the growth of focal trees growing on low-phosphorus soils by up to 60%. The effect of *Falcataria* neighbors on *Eucalyptus* growth also depended on P supply: increased *Falcataria* reduced predicted growth of the focal tree by 20% on low P soils, but increased growth by 8% on high P soils. Relationships between species were more dynamic at the scale of individual trees than previously indicated by stand-level assessments. The important role of soil nutrient supply in moderating both the intensity and nature of tree interactions implies that competition and facilitation studies need to consider a wide range of soil conditions to be generalizable.

Introduction

The structure and function of plant communities are strongly influenced by resource competition. The search for general patterns in the relationship between resource availability and the intensity of competition has been controversial in population and community ecology. One theory holds that fertile habitats may have stronger competitive interactions owing to higher productivity and higher resource demands (Grime 1973, 1979). Another theory expects the intensity of competition would not vary with resource availability or productivity, although competition may shift from belowground to aboveground resources as fertility increases (Newman 1973, Tilman 1988). Facilitation could confound these expectations about plant competition (Bertness and Callaway 1994). Facilitation and competition may co-occur in time and space (Walker and Chapin 1987, Choler et al. 2001, Callaway et al. 2002), producing dynamic relationships between individuals and species.

Most spatial field studies of soil nutrient supply and competition have used grasses and herbaceous plants (Silander and Pacala 1985, Goldberg 1987, Reader and Best 1989, Wilson and Tilman 1993, Reader et al. 1994, Goldberg and Novoplansky 1997). Many forest studies have provided insights on stand-level relationships between tree density, growth, and soil fertility (Assman 1970, Nambiar and Brown 1997), and there are a number of individual-based tree models that include indexes of neighborhood density and structure as determinants of size and growth variation (Opie 1968, Bella 1971, Weiner 1984, Stoll et al. 1994). This work has improved our understanding of the mechanisms of tree-tree competition, but considerably less is known about facilitation and the role of soil nutrient supply in moderating neighborhood interactions (Bertness and Callaway 1994). The balance between individual tree competition and facilitation across gradients in soil resource supplies remains under explored, yet may provide important insights into the processes that determine overall stand-level and community patterns of growth, structure, and mortality.

A 20-year-old replacement series of *Eucalyptus saligna* and nitrogen-fixing *Falcataria mollucana* in Hawaii provided a model system to study competition and facilitation along a topographic gradient in soil fertility. The range of species ratios in a replacement series provided neighborhood arrangements to isolate effects of interspecific and intraspecific competition and facilitation, while the uniform spacing and age of these plantations controls for initial size differences between trees that could otherwise obscure the effects of neighbors. Prior work in these stands demonstrated that *Eucalyptus* had greater plot-level biomass and higher growth rates when intercropped with *Falcataria* than in pure stands, suggesting that the increased nitrogen (N) availability from N-fixation by *Falcataria* is facilitating *Eucalyptus* growth (DeBell et al. 1989, DeBell et al. 1997, Kaye et al. 2000, Binkley et al. 2003a). *Falcataria* mass and growth was proportional to its ratio in the plots, indicating that there was no competitive or facilitative impact of having certain types of neighbors. The potential for simultaneous positive and negative interactions between individuals of the same and different species provides a powerful opportunity to study complex neighborhood dynamics in a model system along natural gradients of soil resource availability.

We used neighborhood competition models to assess the relative importance of interspecific and intraspecific competition versus facilitation for tree survival and aboveground growth along a soil fertility gradient. We first tested competing mechanistic neighborhood models from the literature to determine which model best described the tree interactions within a given neighbor distance (5 m) in our system. We then constructed a number of logistic and mixed regression models incorporating the effects of tree size, neighbors (using our best neighborhood model), and soil N and P supply. We examined how well these competing models predicted individual tree survival and aboveground woody growth over a 2 year period. Based on the relative yields of each species at the plot-level we expected that *Falcataria* should suffer competition from neighbors, regardless of species, while *Eucalyptus* should be facilitated by *Falcataria* neighbors and compete with conspecifics. Based on the finer resolution of the individual tree analysis, we additionally hypothesized that the balance between competition and facilitation would be modified by soil N and P supply. We predicted that:

1) *Falcataria* growth and survival would be lower with increases in the number, size, and proximity of neighbors, and the intensity of competition would not depend on the species of neighbors.

2) *Eucalyptus* growth and survival would be lower with increases in the number, size, and proximity of neighbors, but the magnitude of the effect would be smaller where the neighbors are *Falcataria* due to facilitative interactions.

3) The competitive and facilitative effects of *Falcataria* neighbors on *Falcataria* and *Eucalyptus* respectively, would be more intense with increased soil P supply.

4) The competitive effect of *Eucalyptus* neighbors on both species would be more intense with increased soil N supply.

Site description and methods

The study was conducted at 450-510 m elevation on the northeast coast of the island of Hawaii (19°30'N, 155°15'W) in a replacement series of *Eucalyptus saligna* and *Falcataria mollucana*. Average rainfall is about 4 m/yr, and the mean annual temperature is 21 °C with monthly means +/- 2 °C. The slopes are moderate (<15%) with deep soils classified as the Kaiwiki series of thixotropic isomesic Typic Hydrudands. The plots were established on abandoned sugar cane fields in 1982 to study productivity in mixed species plantations (for details on site history and management see Binkley et al 2000 and DeBell et al. 1989). Trees were planted at 2 x 2 m in a completely randomized block design with 4 blocks each containing seven plots planted with variable proportions of *Falcataria* (0, 10, 25, 34, 50, 75, and 100 %). Plot size was 30 x 30 m, except the 75% and 100% *Falcataria* plots which were 15 x 30 m. During a 36 month period after planting all plots received 108 kg P/ha and 220 kg K/ha. Over the same period the mixed plots and pure *Falcataria* plots received 120 kg N/ha, while the *Eucalyptus* plots received 240 kg N/ha (plus another 130 kg N/ha at 55 months; (DeBell et al. 1989, Binkley et al. 2003a).

Trees were mapped and diameters measured (at 1.35 m height, in cm) at ages 18 and 20 years (Binkley et al. 2003a). Aboveground woody biomass (stems plus large branches) was estimated using allometric equations developed from trees harvested from this site plus one other stand (Binkley et al. 2003a):

Eucalyptus biomass= $0.093 * \text{dbh}^{2.542} / (e^{(.91-\ln(\text{dbh}))}$

$(r^2 = 0.99$, range = 3 to 82 cm, $n = 93)$

Falcataria biomass = $0.0688 * \text{dbh}^{2.4711}$

$(r^2 = 0.98$, range = 3 to 29 cm, $n = 36)$

The growth of individual trees was calculated as the annual increment of aboveground woody biomass, calculated as the change in biomass of each surviving tree from age 18 to 20, divided by two. We also recorded tree mortality during the two year period, and mapped locations of all live and dead trees.

Eucalyptus wood biomass in the plots ranged between 230 and 300 Mg/ha at age 20, with net annual increments of 4 to 15 Mg ha^{-1} yr^{-1} (Binkley et al. 2003a). The wood biomass of *Falcataria* ranged from 45 to 180 Mg/ha, with net annual increments of 0 to 9 Mg ha^{-1} yr^{-1}.

The four blocks of the study spanned a range in soil N and P supply rates, and this topographic effect was partially modified by the influence of the species on soil N (higher under *Falcataria*) and P (higher under *Eucalyptus*; Kaye et al. 2000). The supply of available soil N (NO_3^- and NH_4^+) and P (PO_4^{3-}) was indexed with ion exchange resin bags, with five resin bags in each plot at age 17 years (data from Kaye et al. 2000). Soil sampling was not done on the 10% *Falcataria* plots, so we excluded them from our study. One of the 100% *Falcataria* plots was also omitted because it was thinned heavily at age 10 for preparing regression equations. This left 23 plots to include in our study.

Statistical Analysis

Our objective was to develop and test competing models of individual tree survival and growth to determine the nature and strength of the relationships between neighbor interactions, soil nutrient availability, and tree performance. The predictor variables that we measured and used to construct our models were tree biomass in kg at age 18 (B), soil N and P supply (N, P), and a neighbor index (C_E, C_F), which will be described in the next section. Because we were specifically interested in how neighbor interactions might be affected by soil fertility, we also considered two interaction terms: the interaction of $C_F * P$ and $C_E * N$. We expected the effect of species to be influenced most strongly by the nutrient limiting to that species (Binkley et al. 2003b), and included only these interactions.

Model selection

Survival and growth models were developed *a priori* using the set of available predictor variables, as described in the next sections. Testing a limited set of models helps avoid problems of over-fitting and spurious correlations that have been associated with stepwise or other model selection techniques (Burnham and Anderson 1998). This is particularly important when using a correlative approach. We used information theoretics (Akaike's Information Criterion, AIC) to select our best growth and survival models, which entails calculating the expected value of the information lost when using a model to approximate the truth. A low AIC value indicates strong performance of a model (Burnham and Anderson 1998).

Survival models

We modeled the probability of individual *Eucalyptus* and *Falcataria* survival with binomial logistic regression (n=175 dead *Falcataria*, n=99 dead *Eucalyptus*). We developed a set of 52 *a priori* candidate models (out of a possible set of 127); the models were all linear, nested combinations of the predictor variables (B, C_E, C_F, N, P, $C_E * N$, and $C_F * P$), and included two to seven parameters. Maximum-likelihood estimates of model parameters, their confidence intervals, and AIC values were obtained using PROC LOGISIC in SAS V8 (SAS Institute 2000). We chose the *Eucalyptus* and *Falcataria* models with the lowest AIC value as our best models.

Growth Models

We modeled tree growth (aboveground woody biomass increment, kg/yr) from age 18-20 years. The correlation between tree size and growth is typically strong (Koyama and Kira 1956, Yoda et al. 1957, Bella 1971, Stoll et al. 1994), and including initial tree biomass as a predictor variable, rather than simply modeling relative growth rate, minimized spatial dependency in the analysis (Stoll et al. 1994, Wagner and Radosevich 1998). We log transformed tree growth and the neighbor indexes to account for heteroscedasticity and non-normality in the residuals, and also removed from our set of focal trees any trees that survived but had no measurable radial increment in order to achieve a normal error distribution. This reduced our sample size from 1395 to 855 trees (n=200 *Falcataria*, n=655 *Eucalyptus*). For model simplicity we modeled growth as a quadratic function of biomass (B^2), which increased the number of possible predictor variables to 8 (B, B^2, C_E, C_F, N, P, $C_E * N$, and $C_F * P$). We developed a set of 64 candidate models (of 255 possible models) that were all linear, nested combinations of the predictor variables, and included two to six parameters. All 64 models included both focal tree biomass *(B)* and the square of focal tree biomass *(B^2)*, in addition to other predictor variables. We used PROC MIXED in SAS V8 (SAS Institute 2000) to obtain maximum-likelihood estimates of model parameters, confidence intervals, and AIC values. The mixed model design accounted for potential spatial dependency in our response variable, at the scale of individual trees, plots, or blocks, using the addition of random effects to the model (Fox et al. 2001). Failure to adjust for these types of stochastic spatial correlations in the residuals would violate the assumption of independence in our regressions and could bias estimates and confidence intervals (Legendre 1993, Fortin 1994). We tested our models with and without plot, tree, and block level random effects, and compared the models using AIC and likelihood ratio tests. The tree and block effects did not improve the model fits and were dropped from the analysis. Plot variability was a significant factor in tree growth, and was retained as a random effect in all models. To ensure that we had removed all dependency from the data we also tested the residuals for spatial autocorrelation using a Moran's I test in S-Plus 2000 (MathSoft Inc. 2000).

In order to look more closely at the specific relationships between our response and predictor variables, we expressed our model results as the percent change in focal tree growth or probability of survival, as predicted by the best model, for a range of input values for the predictor variable of interest. To simplify the interpretation of the numbers generated from the neighbor indexes, we plotted the effect of low, medium, and high index values. A low neighbor index represents a value of zero, or no neighbors within 5 m of the focal tree. For the survival plots a medium neighbor index represents about six neighbors with an average biomass of 1,000 kg in relation to focal trees about half that size. High index values are similar except there are 12 neighbors instead of six. Because the neighbor index was log transformed for the growth models, the interpretation of low and high index values are the same as in the survival models, but medium values represent only three neighbors that are approximately the same size as the focal tree.

Measures of tree interactions

We examined neighborhood effects around each individual focal tree. Edge effects were avoided by allowing the outermost two rows of trees in each plot to act as neighbors but not as focal trees. All living trees at age 18 within a 5 m radius of the focal tree were considered neighbors. We chose this distance because previous work on this site demonstrated that plot-level effects on soil carbon (C), N, and P were evident only 5 m into neighboring stands (Ewers et al. 1996). This distance is also consistent with values used in other tree competition studies (Stoll et al. 1994, He and Duncan 2000). Because we did not test for the effects of neighborhood radii, it is possible that shorter or longer distances could influence the strength of the interactions we detected (Silander and Pacala 1985). For each focal tree we calculated neighborhood indexes (C_r) in three ways. Our simplest equation (index 1) summed the biomass (B) of all neighbors within a circle ≤ 5 m radius (r):

Biomass model (Index 1): $$C_r = \sum_{i=1}^{n} B_i$$

where i is the ith neighbor and n is the total number of neighbors within the given neighborhood distance. The second equation (index 2) was similar except that a neighbor's impact decreases with the square of the distance from the focal tree (Weiner 1984). Testing separately for distance-dependent versus simple biomass interactions is important because in some cases a simpler model can adequately explain the neighborhood dynamics of a system (Martin and Ek 1984, Silander and Pacala 1985, Kikuzawa 1988). In this model a tree's impact on a neighbor is still proportionate to its size, or size-symmetric (Begon 1984, Weiner et al. 1990):

Distance model (Index 2): $$C_r = \sum_{i=1}^{n} \frac{B_i}{d^2}$$

Index 3 was similar to Index 2, but included an additional scalar, or size-ratio term to account for disproportionately large impacts of large neighbors (size-asymmetric competition; (Diggle 1978, Weiner and Thomas 1986). The size-ratio is similar to one developed by Bella (1971), and divides 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. We tested three forms of this equation (eq.3 a, b, c) by changing the exponent on the size-ratio to either 1, 1.5, or 2.

Asymmetric model (Index 3): $$C_r = \sum_{i=1}^{n} \frac{B_i}{d^2} \left(\frac{B_i}{B_j} \right)^{EXP}$$

Index 3a: EXP=1

Index 3b: EXP=1.5

Index 3c: EXP=2

Varying the exponents changes the relative importance of the neighbor versus the focal tree. The size of the neighbor has the greatest weight in index 3a (neighbor biomass has twice the impact on survival or growth of the focal tree than the focal tree biomass), and the least weight in index 3c (the neighbor has 50% more impact than the focal tree). We calculated each *C* separately for *Eucalyptus* (C_E) and *Falcataria* (C_F) neighbors to isolate each species effects. We tested the performance of the indexes by regressing them independently against individual tree survival, using PROC LOGISTIC (SAS Institute 2000), and tree growth, using PROC MIXED (SAS Institute 2000). The index with the lowest AIC value was used for all further modeling of survival and growth, described above.

Results

Neighbor Indexes

Focal trees were strongly influenced by both the distance to neighbors and their relative size. Neighbor indexes that lacked both of these parameters (the biomass and distance models, Indexes 1 and 2) were poor predictors of both survival and growth, indicating that interactions were asymmetric (Table 1). Within the asymmetric model, Index 3c performed better than Index 3b as a predictor of individual tree survival, explaining 37% and 67% of the variation in survival probabilities of *Eucalyptus* and *Falcataria*, respectively. Index 3b predicted growth better than any other model, explaining 54% of the variability in *Eucalyptus* growth, and 31% of the variability in *Falcataria* growth (Table 1). The high amount of variation in tree growth and survival explained by our neighbor indexes alone (30% to 70%) underscores the major role of neighbor interactions in structuring this community.

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Falcataria and *Eucalyptus* competition respectively (Fig. 1D). Soil nutrient availability had a large impact on *Eucalyptus* survival; nutrient availability and competition effects showed no interaction. The probability of *Eucalyptus* survival was 100% greater with each 10% increase in available N (equivalent to 0.09 mg/bag), and declined by 41% with each 10% increase in available P (equivalent to 0.03 mg/bag; Fig. 1E).

Growth

Individual tree growth was highly variable for both species, ranging from no measurable growth (39% of the stems), to 300 kg yr^{-1}. Average growth was higher for *Eucalyptus* (14.8 kg yr^{-1}) than for *Falcataria* (8.9 kg yr^{-1}), although the observed range of growth rates was the same for both species. Spatially explicit growth models have had varying success at capturing variability in tree growth, with correlation coefficients generally ranging from 20% to 80% (Bella 1971, Weiner 1984, Stoll et al. 1994, (Mailly et al. 2003). Our models performed well, explaining 69% and 85% of the variability in *Falcataria* and *Eucalyptus* growth (Table 2).

The best *Falcataria* model included all of the predictor variables with the exception of soil N supply, and accounted for 69% of the total variation in individual tree growth (Table 2). *Falcataria* growth depended strongly on the size of the focal tree; the growth of 800 kg trees averaged nine times greater than the growth of 200 kg trees, (Fig. 2A). Nutrient supply in the soil modified the effects of both interspecific and intraspecific interactions. Increasing the *Eucalyptus* neighbor index increased *Falcataria* growth by 20-100% on low N soils, but decreased growth by 20%-50% on high N soils (Fig. 2B). The model predicts a 50% decrease in the growth of a *Falcataria* focal tree at the highest levels of the *Falcataria* index when P availability is high, yet a

45% increase in growth under the same neighborhood conditions when P availability is low (Fig. 2C). The *Falcataria* growth model also included P alone as a significant predictor variable (Table 2); at low values of the *Falcataria* neighbor index, growth averaged 35% higher on high P versus low P soils.

Biomass, neighbors, and the interaction of the *Falcataria* neighbor index and P supply explained 85% of the variability in individual *Eucalyptus* growth (Table 2). The predicted relationship between *Eucalyptus* biomass and growth was very similar to the *Falcataria* model. Focal tree growth increased by more than 30 kg/yr as biomass increased from 200 to 1000 kg (Fig. 2D). Eucalyptus neighbors decreased the growth of *Eucalyptus* focal trees by up to 18% (Fig. 2E). The effect of *Falcataria* neighbors depended on P supply: increasing the *Falcataria* index reduced predicted growth of the focal tree by 20% on low P soils, but increased growth by 8% on high P soils (Fig. 2F).

Discussion

Competition

Competitive effects strongly influenced survival and growth of *Eucalyptus* and *Falcataria* in every relationship we observed (Table 3). Based on plot-level patterns (Binkley et al. 2003a), we expected that the survival and growth response of *Falcataria* trees to neighboring trees would be consistent for both species of neighbors, but this was not the case. *Eucalyptus* neighbors suppressed *Falcataria* survival more strongly than *Falcataria* neighbors, whereas *Falcataria* growth was suppressed more by *Falcataria* neighbors (Table 3). Although species interactions may have appeared consistent when summed for an entire stand, they were much more variable when observed at the individual tree scale.

Soil nutrient supply strongly modified the effects of both *Eucalyptus* and *Falcataria* neighbors on *Falcataria* growth. The competitive effect of *Eucalyptus* neighbors was stronger in plots with high soil N (Fig 2B), supporting our hypothesis (H_0 4) and Grime's theory (Grime 1973, 1979). *Falcataria* growth increased with increasing P supply where competition was absent (Fig. 2E), consistent with a P-limitation. As the intensity of interaction with *Falcataria* neighbors increased, though, the focal *Falcataria* tree grew more when on low versus high P soils. The benefit of higher P soil for the focal tree was largely outweighed by the increasing vigor and competitive ability of neighbors with increasing P supply (consistent with H_0 3). These examples illustrate that the concept of nutrient limitation may not be simple at the scale of individual trees, as increases in the supply of a limiting nutrient may lower the growth of the focal tree if competition from neighbors also increases (as proposed by (Grime 1973, 1979).

Eucalyptus trees also experienced competition, but interactions with nutrient availability were not as common as for *Falcataria* focal trees. Contrary to our hypotheses (H_0 3 & 4), soil nutrient supply did not modify the competitive impact of *Eucalyptus* or *Falcataria* neighbors on Eucalyptus survival, or *Eucalyptus* neighbors on *Eucalyptus* growth. *Falcataria* neighbors suppressed the growth of *Eucalyptus* more on low P versus high P soils (Table 3). We infer that the level of interspecific interactions determined the importance of P availability for *Eucalyptus* growth; as the number and size of *Falcataria* neighbors increased, *Eucalyptus* on low P soils were stressed increasingly by competition for P.

We expected *Eucalyptus* to be stronger competitors than *Falcataria* (H_0 2), based on plot-level patterns (Binkley et al. 2003a). However, *Eucalyptus* growth and survival responded similarly to both species of neighbors (at certain nutrient levels; Table 3), again reinforcing the importance of scale in inferences of competition.

Facilitation

Facilitation mechanisms can be grouped into two major categories: enhancement of resource supply, and modification of the environment ((Choler et al. 2001, Callaway et al. 2002). *Falcataria* survivorship increased with more *Eucalyptus* neighbors on high N soils (Table 3). Goldberg et al. (1999) suggested that facilitation of survival was more common at high standing crop or resource levels, and that facilitative interactions were more pronounced for survival than for growth. This is consistent to the pattern we observed. Because there are no obvious physical stresses acting on these trees, the best explanation is that *Eucalyptus* enhanced the supply of a limiting resource for *Falcataria.* One speculation worth testing is that arbuscular mycorrhizael (AM) connections between the two species may facilitate *Falcataria* survival by providing additional phosphorus or carbon to focal trees when N availability is high. There is a growing recognition of the importance of AM fungi in mediating plant interactions and coexistence in mixed species systems through the interspecies transfer of both carbon, phosphorus, and nitrogen (Hart et al. 2003), and *Eucalyptus* are highly associated with AM fungi even when fully mature (Adjoud-Sadadou and Halli-Hargas 2000).

Falcataria growth was facilitated by *Eucalyptus* on low N soils, but not on high N soils, which is the reverse of the effect on *Falcataria* survival (Table 3). Goldberg et al. (1997) suggested that this type of reversal in resource availability/competition relationships may be common when looking at survival versus growth responses. Previous work in these plots suggests that *Eucalyptus* may enhance the local P supply indirectly by degrading recalcitrant soil C pools better than *Falcataria* (Kaye et al. 2000, Resh et al. 2002). Although this mechanism could be occurring at all times, the positive benefit of the P additions may only be noticeable on low N soils where the competitive impact of *Eucalyptus* neighbors is reduced. Further experimentation would be necessary to determine if this is the cause of the facilitation we observed.

Falcataria neighbors also facilitated the growth of *Falcataria* focal trees at low P supply (Table 3). We speculate that this facilitation could have resulted from the effect of *Falcataria* on soil communities; the density of earthworms increased dramatically in these plots with increasing proportions of *Falcataria* (Zou 1993). Perhaps increasing influence of *Falcataria* neighbors increased earthworm densities, which could play a role in the localized supply of P in the soil; the positive benefit of the P additions only becoming noticeable on the most P-limited soils. The potential importance of soil communities as moderators of facilitation between plants warrants direct experimentation.

The last example of facilitation was the slightly positive effect of *Falcataria* neighbors on *Eucalyptus* growth on high P soils (Fig.2f), which was consistent with our hypothesis (H_0 3). Rates of nitrogen fixation often correlate positively with soil P supply (Sprent 1987), and in a bioassay with soils from this site, N fixation by *Falcataria* related strongly to soil resin P supply ($r^2 = 0.76$, $P < 0.01$; (Binkley 1997). *Falcataria* probably fixed more N on higher P soils, which diminished their otherwise competitive effect on *Eucalyptus* and shifted the balance toward a slightly facilitative relationship.

Could the apparent facilitation that we observed result from reduced competition from understory vegetation when neighbor indexes were high? We did not measure variability between plots in understory cover, but any plot level effects of the understory on tree growth were removed through our mixed model design. Any biotic or abiotic driver of the observed growth patterns would therefore have to consistently vary at the scale of individual trees, which is unlikely. There were no noticeable patterns in understory vegetation within plots, and the fact that tree biomass is 1.5 to 2 orders of magnitude greater than understory biomass led us to ignore the understory in our measures of competition.

Conclusions

Interactions between trees spanned the range from highly competitive to highly facilitative. The mechanisms driving these relationships co-occur in space and time, and the net effect on tree growth or survival depends upon resource availability. Soil nutrient availability not only affected the intensity of neighbor interactions, but also modulated the balance between competition and facilitation, which highlights the need for studies of plant competition and facilitation to encompass a wide range of soil conditions to be generalizable. The range of relationships we observed does not completely support any of the existing simple theories about plant competition and resource availability. Although the study examined patterns in only one location, we expect that replication for mixed species forests at other locations would probably find a broad range of interactions rather than narrow, generalizable patterns. Facilitation was more apparent than we expected for both survival and growth models. We agree with Bertness and Callaway (1994) that the importance of positive interactions has been underestimated, and exploration is needed to understand how facilitation should be incorporated into existing theories of community dynamics in forest ecology.

The neighborhood analysis provided insights into the stand-level patterns of growth and mortality detected from prior work in these plots. The competitive relationships between the two species were largely consistent with the plot-scale patterns, whereas the balance between facilitation, competition, and soil nutrient availability were apparent only at the scale of the individual tree's neighborhood. The enormous plasticity of species interactions suggests that the production ability of mixed species forests will be highly variable depending on soils and silviculture. Understanding what controls the balance between a competitive or facilitative relationship for a given set of species is integral to successful management of mixed species plantations.

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Table 1. Correlation coefficients and Akaike's Information Criteria (AIC) values from regression models of the neighbor indexes against individual tree survival and growth.

	Growth				Survival			
	Eucalyptus		*Falcataria*		*Eucalyptus*		*Falcataria*	
	AIC	r^2	AIC	r^2	AIC	r^2	AIC	r^2
index 1	1195.8	0.07	321.40	0.14	666.6	0.01	669.40	0.01
index 2	1201.6	0.06	322.90	0.14	662	0.02	671.20	0.01
index 3a	839.5	0.49	284.10	0.28	197.9	0.34	121.10	0.65
index 3b	**764.8**	**0.54**	**275.20**	**0.31**	166.8	0.36	94.60	0.66
index 3c	816.8	0.45	296.60	0.24	**150.6**	**0.37**	**92.60**	**0.67**

Table 2. Description of best-fit models of individual tree survival and growth from age 18-20 years.

response variable	**predictor variables**	r^2
Falcataria survival	*Euc* index, *Fac* index, N**Euc* index $(C_E, C_F, N*C_E)$	0.67
Eucalyptus survival	Biomass, *Euc* index, *Fac* index, N, P (B, B^2, C_E, C_F, N, P)	0.38
log(*Falcataria* growth)	Biomass, Biomass^2, log(*Euc* index), log(*Fac* index), N*log(*Euc* index), P*log(*Fac* index), P $(B, B^2, ln(C_E), ln(C_F), N*ln(C_E), P*ln(C_F), P)$	0.69
log(*Eucalyptus* growth)	Biomass, Biomass^2, log(*Euc* index), log(*Fac* index), P*log(*Fac* index) $(B, B^2, ln(C_E), ln(C_F), P*ln(C_F))$	0.85

Table 3. Summary of competitive and facilitative relationships, and interactions with soil N and P supply. Symbols denote the strength of the relationship, ranging from no effect of neighbors (0) to a strong effect (√√√). Overall relationship between species may include both facilitation and competition when there is a significant interaction with soil nutrient supply.

Response	Focal tree	Neighbor	Competition	Facilitation	Soil Nutrients
Survival					
	Eucalyptus	*Eucalyptus*	√	0	No interaction
	Eucalyptus	*Falcataria*	√	0	No interaction
	Falcataria	*Eucalyptus*	√√	√√√	N interaction
	Falcataria	*Falcataria*	√	0	No interaction
Growth					
	Eucalyptus	*Eucalyptus*	√√	0	No interaction
	Eucalyptus	*Falcataria*	√√	√	P interaction
	Falcataria	*Eucalyptus*	√√√	√√√	N interaction
	Falcataria	*Falcataria*	√√√	√√√	P interaction

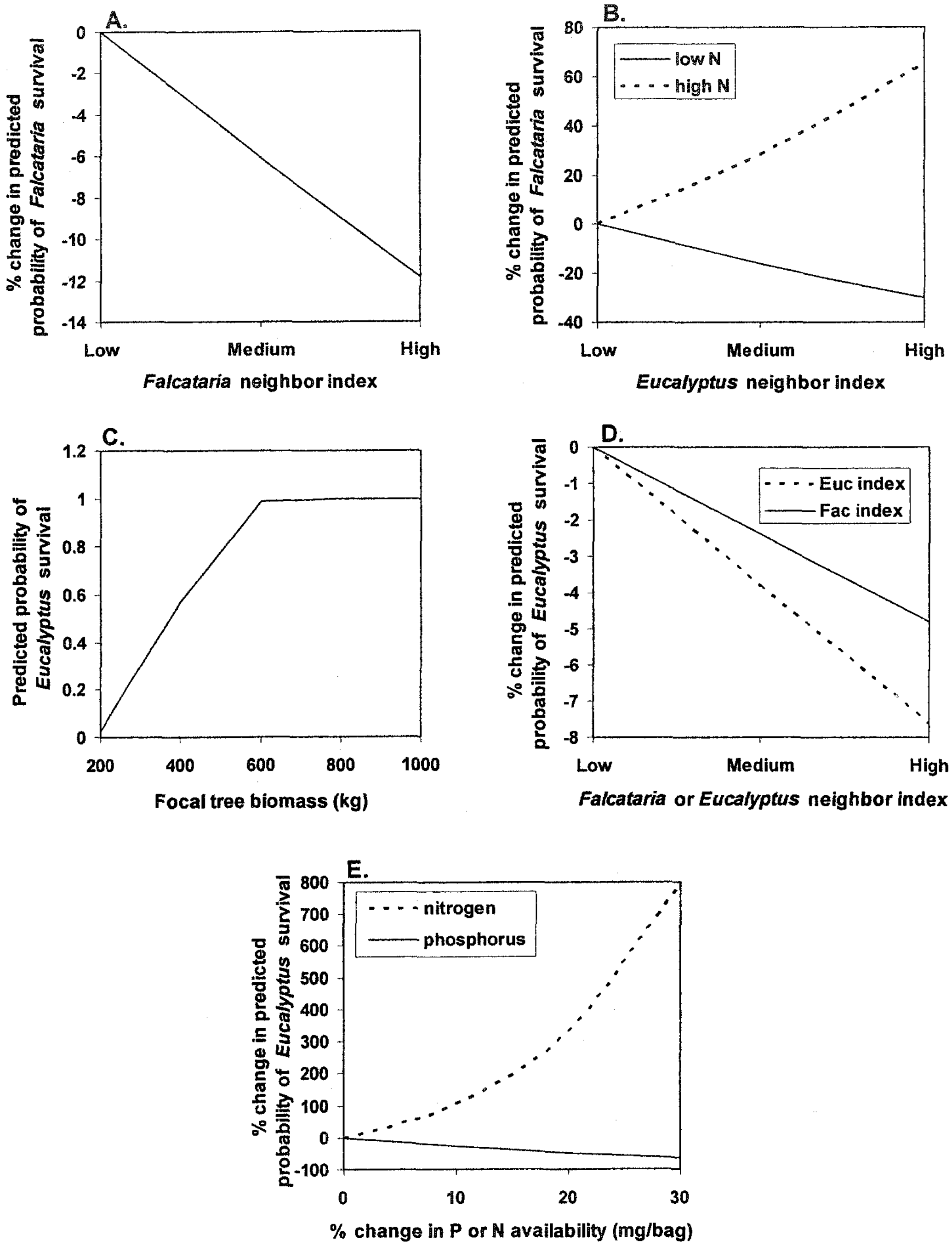

Figure 1. Logistic regression models of tree survival in response to changes in tree size, neighbor index, and soil nutrient availability.. All other predictor variables in the model are held constant at their mean value. (A, B, D, E) Plot the % change in the predicted probability of survival of the focal tree. (C) Plots the predicted probability of survival. (B) The % change in the predicted probability of survival due to changes in the Eucalyptus neighbor index in high versus low N soils. Values for high versus low N soils calculated as the mean of the upper and lower halves of the data set (low N = 0.07 mg/resin bag, high N = 0.88 mg/resin bag).

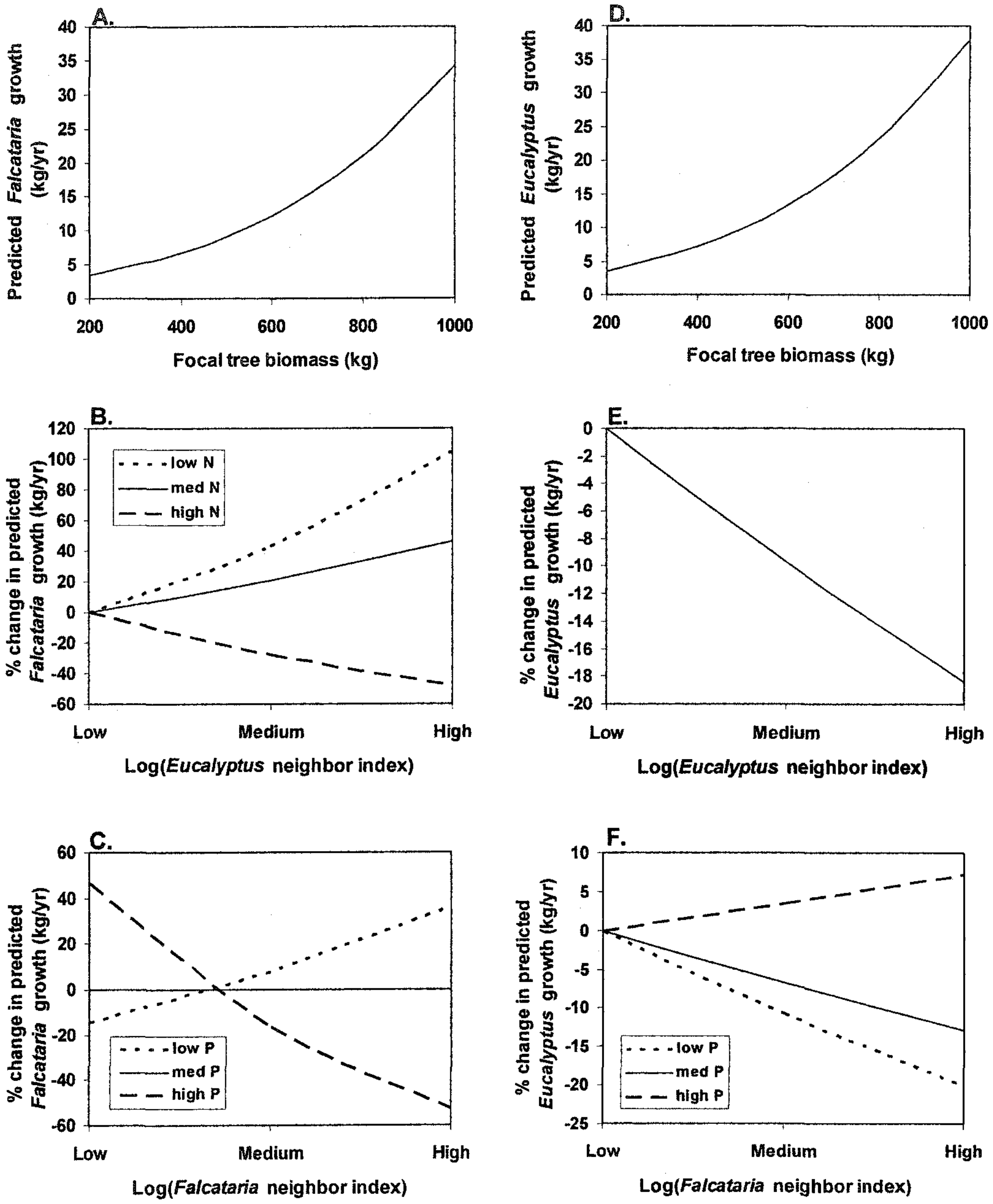

Figure 2. Predicted patterns of tree growth in response to changes in tree size, neighbor index, and soil nutrient availability. All other predictor variables in the model are held constant at their mean value. (A, D) Relationship between tree size and predicted growth for *Falcataria* and *Eucalyptus* focal trees. (B, C, E, F) Percent change in predicted growth of focal tree in response to changes in neighbor index. Values for low, medium, and high nutrient levels calculated as the mean value of the lower, middle, and upper thirds of the data set (low N = 0.07 mg/resin bag, medium N = 0.27 mg/resin bag, high N = 0.88 mg/resin bag; low P = 0.01 mg/resin bag, medium P = 0.06 mg/resin bag, high P = 0.18 mg/resin bag).

CHAPTER 5

SYNTHESIS

This dissertation clearly illustrated the basic, yet fundamental tenet of landscape ecology that pattern matters. At coarser spatial scales, patterns of trees influenced processes of mortality and regeneration, resulting in unique spatial associations and distinct groupings of different sizes. These patterns clearly result from historical and contemporary drivers such as climate, fire, disease and competition. Traditional stand level assessment tools would not have revealed the degree of structural complexity, nor given us as much insight into the ecological processes, of this stand. Analyzing spatial patterns across multiple ponderosa pine forests will help us to understand what aspects of size and age structure are integral components of the landscape, and should be retained or created as we manage and restore these forests in the future.

At fine spatial scales we saw that structural patterns of trees had enormous implications for individual tree growth and survival. The size and spacing of neighbors explained a tremendous amount of the variability in tree performance in two distinctly different forest types, a tropical plantation and an old-growth temperate forest. In both Hawaii and Colorado we observed situations where competition was actually more important than tree size alone for predicting variation in growth and survival across the stand. The use of neighborhood models to analyze interactions between trees revealed patterns and processes not evident from stand-level assessments alone.

This dissertation also clearly demonstrated the importance of resource availability to forest dynamics. Once again, these complex relationships between trees and their environment are operating at multiple spatial and temporal scales. Long term climatic variability drives water availability on a decadal scale. Water availability impacts seedling and tree survival as well as growth, and therefore drives stand level temporal patterns of recruitment in ponderosa pine. Drought conditions are also linked to the occurrence of fires and the outbreak of disease, which have clear impacts on tree mortality and future patterns of stand development.

At fine spatial and temporal scales, we saw that soil nutrient supply affects trees directly, by controlling growth and therefore survival, and indirectly by modifying the competitive and facilitative interactions between neighboring trees. The effect of soil nutrient supply on the intensity of competition or facilitation varied depending upon the species and response variable we looked at. Discounting the case of *Falcataria* facilitating *Eucalyptus* growth, we did find that competitors had a larger impact on tree growth on high versus low nutrient soils in both the mixed species plantation and the ponderosa pine stand.

Stand structure is not a simple attribute which can be summed across a stand; it is a spatially and temporally dynamic property of forests. Structure is created over time by processes that range from the patchy and pulsed availability of soil resources, to global climactic patterns. In turn, structure drives individual and stand level processes of growth, regeneration, and mortality. We need to extend our studies across space and through time to better understand the dynamics of structural development in forests. Long-term monitoring of stands like Manitou needs to be done in multiple locations in order to develop generalities about Front Range ponderosa pine systems. Similarly, we need to do many more competition studies along gradients in soil resource supplies, and over longer periods of time, to understand how spatial and temporal heterogeneity in soil resources drive tree interactions and stand structure.