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Spatial and temporal patterns in structure, regeneration, and mortality of an old-growth ponderosa pine forest in the Colorado Front Range

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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 30-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 $K(t)$ 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 appeared to play a significant role in the coarse-scale temporal pattern of regeneration events. Stand structure (distribution of patches, light availability, and seed trees) influenced the spatial and temporal pattern of more recent regeneration events. Patchy regeneration resulted in spatial independence and some segregation of size classes. Older 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.

Keywords: Disturbance; Mortality; Ponderosa pine; Regeneration; Spatial pattern; Stand structure

1. 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

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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 (mainly Arizona and New Mexico) 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, which is the easternmost mountain range of the Rocky Mountains, north of the Arkansas River. 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). Ponderosa pine patch structure has been described as even-aged (Cooper, 1960, 1961) or uneven-aged (White, 1985) depending on the severity of the overstory mortality, and the intensity and spatial pattern of the fire which prepared the mineral seedbed for germination. Mast and Veblen (1999) demonstrated that in the pine-grassland ecotone of the Colorado Front Range competition and self-thinning resulted in mixed-size, but even-aged patches of mature trees. 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 30-year period in an old-growth ponderosa pine stand in the mid-montane zone of the Colorado Front Range. We addressed three 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?

2. Methods

2.1. Study area

The study was conducted in the Manitou Experimental Forest, 40 km northwest of Colorado Springs, CO. The elevation is 2500 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). There have been no other logging operations in the stand, so we assumed that all visible stumps dated to this time period. 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. There had been no recorded wildfires in the Manitou Experimental Forest since 1846, 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.

2.2. Sampling and analysis

In 1974, a 9.3 ha 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 (Fig. 1). 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.

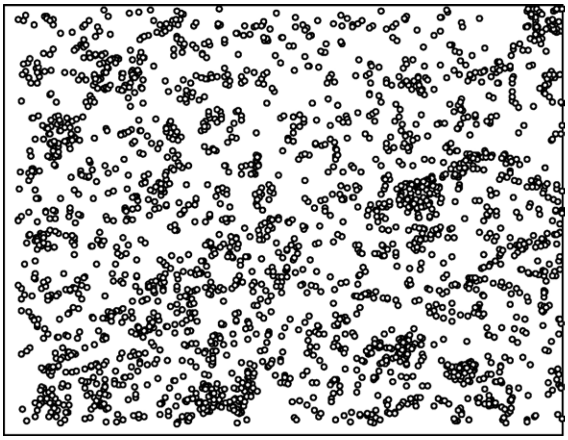

Fig. 1. Spatial distribution of trees across the 9.2 ha study area.

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. A detailed study of destructively harvested pines in a ponderosa pine stand about 30 km away (Kaufmann et al., 2000) estimated that the difference in the pith date from 30 cm to the ground (actual germination) was ~10 years. Using the prism method to reconstruct age structure assumes that there is a strong relationship between tree age and size. Age and size were correlated ($n = 100$, $r^2 = 0.54$), but the variability in the relationship means that inferences about age structure should be limited to only large scale temporal patterns.

2.3. Describing spatial patterns

Tree patterns were analyzed using Ripley's *K* functions (Moeur, 1993). The $K(t)$ function estimates spatial dependence between points of the same type (e.g., one size class) at a range of spatial scales. The $K(t)$ 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 (Ripley, 1981; Fortin, 1994; Chen and Bradshaw, 1999). We report results as $L(t)$, which is a square root transformation that linearizes $K(t)$ 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. We computed 95% confidence intervals on a Monte Carlo simulated Poisson process using 99 simulations (Besag and Diggle, 1977). Observed patterns differ from random at $P = 0.05$ where the plot of $L(t)$ falls outside the simulated confidence envelope. Clustered arrangements are indicated by an $L(t)$ above the envelope, and regular tree spacing occurs where $L(t)$ falls below the envelope.

Spatial associations of trees of different size classes were analyzed using a bivariate K-function, Ripley's $K_{12}(t)$ (Lotwick and Silverman, 1982; 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. A 95% confidence interval is calculated using random toroidal shifts of one pattern relative to the other during each of 99 Monte Carlo iterations. $L(t)$ and $K_{12}(t)$ were calculated for lag distances up to 150 m (half the distance of the shortest plot axis), but if spatial patterns were consistent at all lag distances, results were plotted at shorter distances for easier viewing.

2.4. Point-process models

Clumped trees, as identified by the $K(t)$ function, were modeled using a Neyman–Scott point-process model in order to gain more insight into the nature and intensity of the patterns, and therefore the mechanisms that drive them (Ripley, 1981; Cressie, 1993; Geyer, 1999). The Neyman–Scott distribution is routinely used to describe clumped spatial patterns, particularly for plants that are patchy as a result of their regeneration methods (Neyman, 1939; Neyman and Scott, 1957). The algorithm generates a Poisson process with a certain intensity (λ) to describe the distribution of the parents, and then replaces each parent point by a random cluster of offspring. The offspring are located in a radially symmetric way around the parents according to a bivariate Gaussian distribution, and the number of offspring per parent follows a Poisson distribution.

The process of testing whether a point pattern fits a Neyman–Scott process is identical to the method for using a K-function for testing departure from randomness. In this case the confidence envelope is generated using the Neyman–Scott rather than the Poisson distribution, after the parameters have been fit to the data. Input parameters for simulating the Neyman–Scott process can be estimated by looking at the plots of the original $L(t)$ functions. The lag distance and value of $L(t)$ at the point of maximum divergence from a random process can be used to estimate the average cluster size and cluster intensity. Providing the initial parameter estimates, the Neyman–Scott process is then fit to observed point patterns using least squares techniques (Diggle, 1983; Batista and Maguire, 1998; Reich and Davis, 1998) to optimize the model parameters. The K-function for a Neyman–Scott process is given by

$$K(h, \sigma^2, \rho) = \pi h^2 + \rho^{-1}\{1 - \exp(-h^2/4\sigma^2)\}$$

where ρ is the intensity of the parent process, and $2\sigma^2$ is the mean squared distance to an offspring.

A 95% confidence envelope for the final point process model is generated through 99 iterations of a Monte Carlo simulation. If the $L(t)$ plot for the observed data falls within the simulated envelope for the Neyman–Scott process, it suggests that the pattern has the properties of that specified model. We also tested how well an observed 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 (Cressie, 1993).

Trees were grouped into six 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. We used narrower size-ranges for the smaller diameter classes because of the large number of small trees, and in order to separate the saplings as much as possible from the pole-sized trees. $L(t)$ 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 logical pairwise combinations of size class, establishment and mortality, although not all results are reported. All spatial statistics were computed using Reich and Davis's online spatial library (Reich and Davis, 1998) in S-Plus 2000 (Mathsoft, 1999).

3. Results

3.1. Density, size and age structure

The study plot contained 3657 live trees in 2001, with an average density of 420 stems/ha, and 21 m^2/ha of basal area. The diameter distribution (Fig. 2) 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. Fig. 3B 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 larger cohorts of trees dating to periods beginning around 1780, 1880, and 1960 (these dates include the germination correction factor, but are not precise given the limitations of our reconstruction method). 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 chronology was reconstructed for the plot by cross-dating fire scars from a sub-sample of trees in the stand (methods in Brown and Shepperd (2001)). The chronology showed six fires had burned in the stand since 1600 (Fig. 3B). 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 1846.

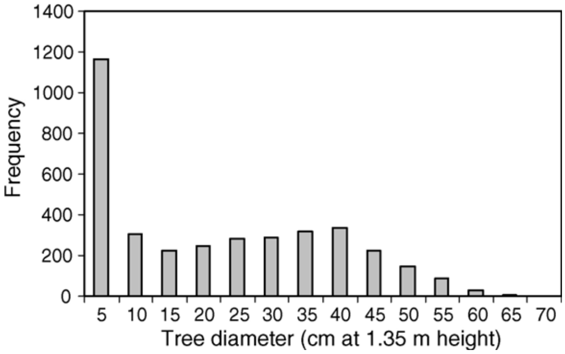

Fig. 2. The size frequency of trees was dominated by the smallest diameter class, with relatively even numbers of trees in larger classes (top).

3.2. Contemporary patterns of recruitment

The low density of small trees in 1974 (Fig. 4) suggests 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 doubled over 20 years, from 1974 to 1991, and then dramatically tripled in the subsequent decade (Fig. 4). Given that it takes 20–25 years for pine seedlings to reach 1.37 m (Shepperd, unpublished), these small trees would have germinated in the 1960s through 1980s. This new cohort of small trees increased stand density by 30% over 30 years, though basal area increased by only 10% during the same period (data not shown). The trees themselves were highly clumped (Table 2). Fig. 5 gives an example of a clumped $L(t)$ function (using the 1991 establishment data) that was best modeled with a Neyman–Scott point process model. New saplings were not only more numerous in 2001, but the patches were smaller and denser, with nearly twice as many trees per patch than in 1991 (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. 6) at all scales up to ~30 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 to 25 m, and with trees >55 cm at 15–20 m distances. The association between 1991 and 2001 establishment and all other tree size classes was also negative at a similar range of scales as observed for the 1983–1991 data.

3.3. Patterns of mortality

Rates of mortality were low but variable in magnitude and pattern over 30 years (Fig. 7). Mortality was near 9% from 1974 to 1983, or less than 1% per year, dropping to less than 0.01%

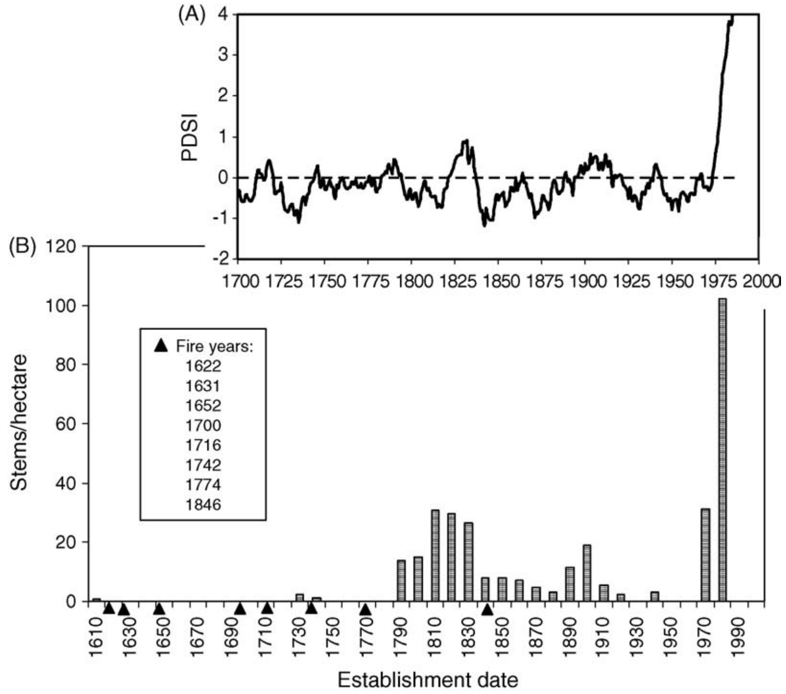

Fig. 3. The age structure (B) showed a large spike of recent recruitment, preceded by substantial recruitment and survival in most decades between 1800 and 1930. Tree ages shown are based on the age-size relationship (n = 100, r^2 = 0.56) for a sub-sample of trees selected by a prism (4.59 m^2/ha basal area factor). Ages are not adjusted for the germination correction factor (~10 years earlier). Fires recorded as scars on two or more trees are indicated by (▲). The three clearest peaks in recruitment and survival are associated with periods of wet climate (A) (indicated by a large Palmer drought severity index (PDSI for the Colorado Front Range; Cook et al., 1999; Cook, 2000)).

mortality per year 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

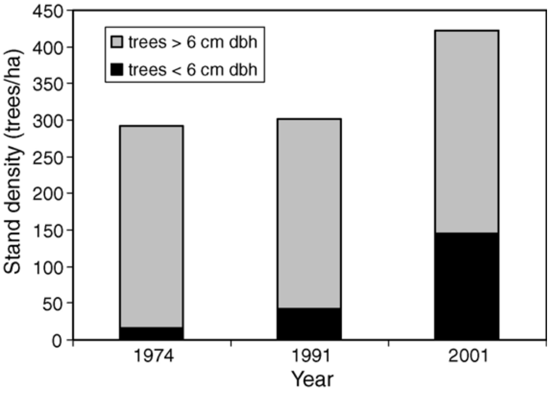

Fig. 4. Changes in regeneration rates and stand density during the 30 years of intensive monitoring of this stand.

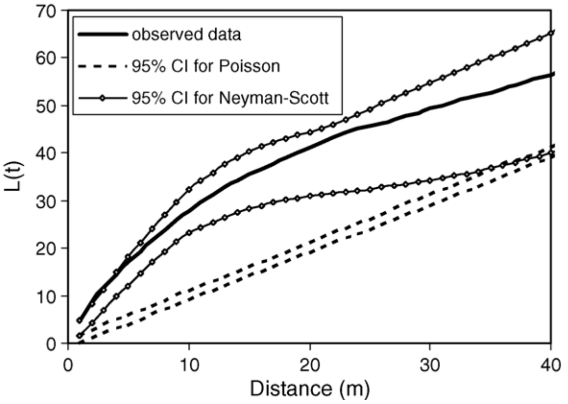

Fig. 5. Spatial pattern of 1991 establishment in relation to random and clumped point process models. A 95% upper and lower confidence envelopes for each model are plotted as a function of lag distance (m) from an arbitrary individual. The plot of the actual data falls above the upper limit for a Poisson model, but within the bounds of the Neyman–Scott model, confirming that the data are spatially clumped at all distances.

Table 1
Within class spatial patterns and model parameters for regeneration, mortality, and size class data over time

	Spatial pattern	Model type	Clumped model parameters	
			Trees per patch	Patch radius
Regeneration				
1991–2001	C	N	18.0	9
1983–1991	C	N	10.2	12
Mortality				
1974–1983	C	N	16.1	20
1983–1991	R	P		
1991–2001	C	N	1.4	12
1974 size classes (cm dbh)				
0–6	C	N	5.4	35
6–15	C	N	6.2	17
15–25	C[a]			
25–40	C[a]			
40–55	D			
>55	R	P		
2001 size classes (cm dbh)				
0–6	C	N	21.0	12
6–15	C	N	4.4	10
15–25	C	N	3.3	15
25–40	C[a]			
40–55	D			
>55	R	P		

Spatial patterns are clustered (C), random (R), or regular (dispersed, D); point process models used to describe the spatial patterns are Neyman–Scott (N) or Poisson (P). Reported point-process models all had significant fit to the data (Cramer–von Mises goodness-of-fit test; $p < 0.05$).

[a] These size classes had inhomogeneous clustered patterns which violate the assumptions of the Neyman–Scott model and therefore could not be modeled. This type of pattern is often caused by a gradient in tree density across a stand.

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.

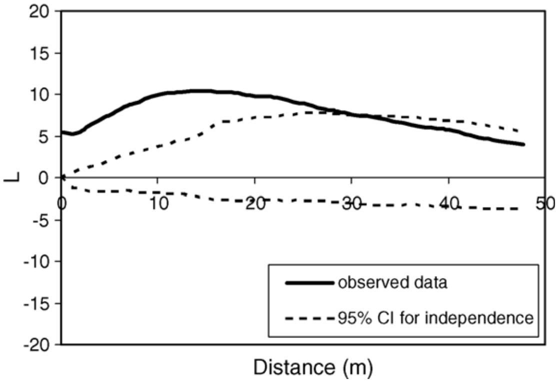

Fig. 6. Bivariate *K*-function for establishment and trees 6–15 cm dbh in 1991. The plot of the actual data (L vector) falls above the upper 95% confidence envelope for a spatially independent process, confirming that the two groups are spatially associated at scales from 0 to 30 m, and independent at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

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.

3.4. 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. 8), 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 to 55 cm trees that were regularly spaced (Fig. 8 and Table 1). A Poisson model best described trees larger than 55 cm dbh, which is probably due to the smaller sample size.

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 smaller and denser in 2001 than 1974. Trees 15–25 cm dbh were more strongly clumped in 2001 than in 1974.

Table 2
Between class spatial associations of tree establishment with mortality and size classes

Mortality			Tree size class (cm dbh)				
1983	1991	2001	6–15	15–25	25–40	40–55	>55
1991 establishment							
S (0–40 m)	I		A (0–30 m)	S (0–35 m)	S (0–50 m)	S (0–20 m)	A (25–35 m)
2001 establishment							
I	I	S (5–40 m)	A (3–25 m)	S (0–40 m)	S (0–35 m)	S (0–20 m)	A (15–20 m)

Association between groups as identified by a bivariate *K*-function is either negative (segregation, S), positive (association, A), or neutral (independence, I). Spatial scales (m) 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.

4. Discussion

4.1. Density, size and age structure

Climate appears to have played a significant role in driving pine establishment and survival in this stand. A large number of surviving trees appear to have established in the late 1700s to early 1800s. The Palmer drought severity index for the region (Cook et al., 1999; Cook, 2000) indicated that this was also a period of wet climatic conditions (Fig. 3A). 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 1846 was probably conducive to higher seedling and sapling survival during this time. Drought conditions from the 1830s to 1870s may also have contributed to the 1846 fire (Fig. 3A and B).

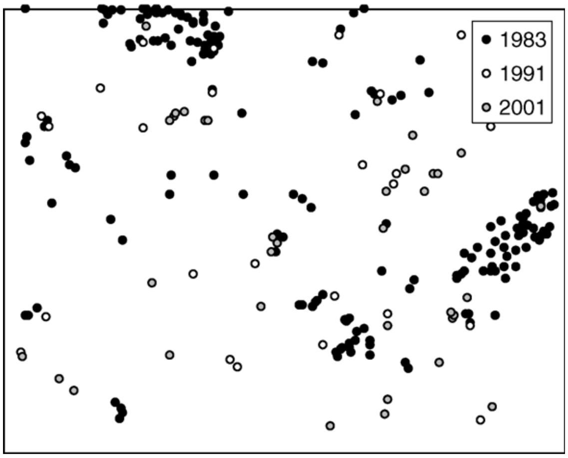

Fig. 7. Pattern of tree mortality across three decades. Map of the locations of all trees that died from 1974 to 1983, 1983 to 1991, and 1991 to 2001.

A large number of surviving trees also dated to the 1880s and 1890s (based on the germination correction factor) (Fig. 3B). A pulse in tree establishment has been clearly observed in other Front Range ponderosa pine stands during this time period (Veblen and Lorenz, 1986; Mast et al., 1998; Brown et al., 1999; Mast and Veblen, 1999), and has been attributed to the favorable climate, 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. 4) coincided with a very wet climate, following drought years in the 1950s and 1960s when there appears to have been little successful establishment, or high mortality, of trees (Fig. 3A and B). 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 (although there is little evidence for that from our limited reconstruction) 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.

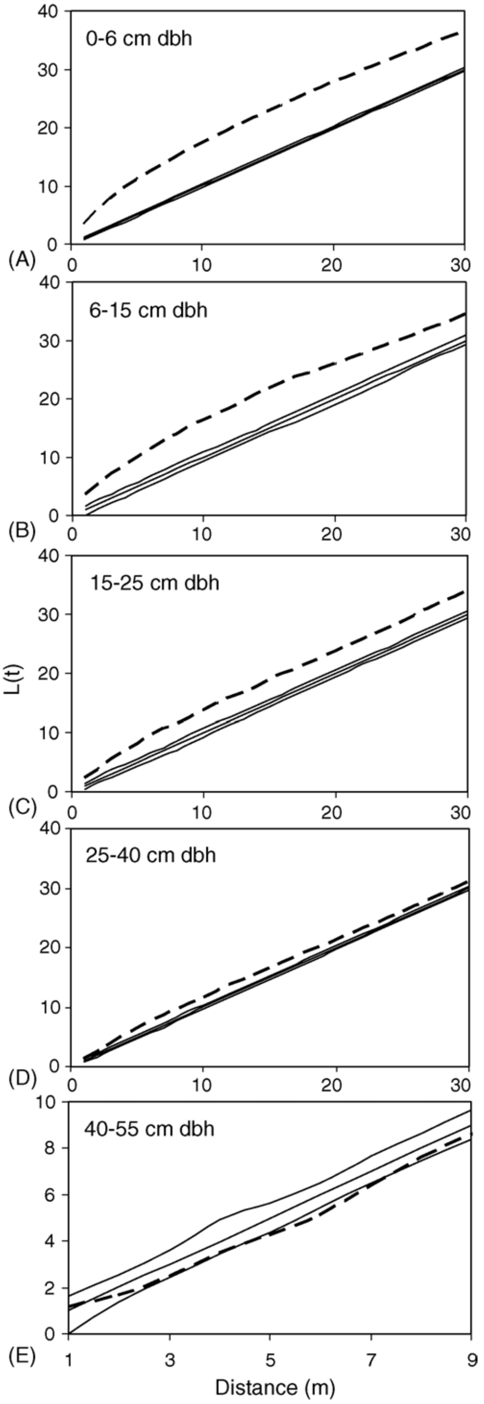

Fig. 8. Spatial pattern of ponderosa pine by size class in 2001. A 95% upper and lower confidence envelopes for a Poisson model are plotted as a function of lag distance from an arbitrary individual with a dotted line. Actual data are plotted with a solid line. Note that the scale of the axes differs in (E). In (A)–(D) 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 (E) 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.

4.2. Contemporary patterns of recruitment

From the 1980s to the1990s recruitment in the stand tripled, and occurred in denser and more numerous patches (Fig. 4 and Table 1). Regeneration tended to occur near small established trees (6–15 cm 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 seems strongly influenced by climate rather than disturbance also suggests that the processes of mortality and regeneration in this ponderosa pine stand may be temporally 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).

4.3. Size patterns and mortality

Recruitment was highly clumped across the stand, but that pattern slowly disappeared from successively larger size classes as the patches thinned, 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 trees since we can assume that most of them predate the 1846 fire. When a low intensity surface fire burns through a stand (such as the 1846 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, 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. 7), 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 to 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. communication, 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 to 2001 and in smaller size classes from 1974 to 1983, could be a sign of self-thinning. 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 to 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 to 35 m radius, and anywhere from 1 to 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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