

Spatial patterns of regeneration in managed uneven-aged ponderosa pine/Douglas-fir forests of Western Montana, USA

Alex Fajardo^{a,*}, John M. Goodburn^a, Jonathan Graham^b

^a College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA

^b Department of Mathematics, University of Montana, Missoula, MT 59812, USA

Received 1 September 2005; received in revised form 10 November 2005; accepted 12 November 2005

Abstract

In uneven-aged ponderosa pine (*Pinus ponderosa* Dougl.) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirbel) Franco) stands managed by individual tree selection, the recruitment of new sapling cohorts necessary to sustain structure and composition is generally assumed to occur within canopy openings created by harvest. However, few studies have examined the spatial patterns of new regeneration in relation to reserve trees in the overstory in this forest type. In this study, we analyzed the spatial distributions and associations between saplings and overstory trees using univariate and bivariate transformations of Ripley's *L*-functions. Furthermore, we introduced a ratio-based index to quantify the strength of bivariate spatial associations, which allowed us to further evaluate potential causes for the observed patterns. We found that saplings of both ponderosa pine and Douglas-fir established predominantly in clumps, and that saplings of the two species generally had a positive association with one another at short scale (up to 5 m). We found no evidence to suggest that saplings of ponderosa pine and Douglas-fir occupied separate spatial locations in these stands. We also found mixed results for bivariate associations between saplings of both species and overstory trees, where both positive and negative spatial associations occurred depending on the putative moisture level of plots indicated by habitat type group. The strength of positive spatial association between saplings and medium-sized overstory trees appeared to decrease as plot moisture-level increased, suggesting that sapling establishment and survival might be facilitated by shading on moisture-limited sites.

© 2005 Published by Elsevier B.V.

Keywords: Facilitation; Index of association; *Pinus ponderosa*; *Pseudotsuga menziesii*; Recruitment; Ripley's *L*-function; Spatial association; Uneven-aged

1. Introduction

The two-dimensional spatial pattern of individual trees in a stand can influence competition levels, growth rates, and understory development (Chen and Bradshaw, 1999; Duncan and Steward, 1991; Goreaud et al., 1999). The establishment, development, and composition of recruitment is determined in large part by the spatial pattern of larger trees, along with the variation in biophysical site factors, particularly in natural ecosystems (Duncan, 1991; Goreaud et al., 1999; Haase et al., 1996; Mast and Veblen, 1999; Szwagrzyk et al., 2001). Furthermore, studies based on local spatial association patterns have shown correlations with the direction and strength of plant interactions, giving insight into processes such as the nurse effects and niche limitations (Choler et al., 2001; Kikvidze et al., 2005). In this context, spatial patterns can be studied as a

means of inferring explanations of interspecific processes (MacArthur, 1972), given that ecological processes may be expected to give rise to spatially recognizable structures that can be examined with spatial statistical analysis (Greig-Smith, 1979; Kikvidze et al., 2005; Stoll and Bergius, 2005; Watt, 1947).

Spatial patterns of forest regeneration are the result of seed dispersal, seed germination, and seedling survival in relation to the distribution of parent trees, competing vegetation, and seedbed conditions. These interactions are in turn affected by disturbances and environmental variables across a range of scales (Nathan and Muller-Landau, 2000). In forest types where small-scale disturbances predominate, the recruitment of young trees into the overstory can occur primarily within canopy openings (Runkle, 1981). Such canopy gap disturbances often result in patches of similar-aged trees, though more variable-aged cohorts of advanced regeneration may be released in many forest types (Brokaw, 1985; McClure et al., 2000; Uhl et al., 1988; Webster and Lorimer, 2005). The size and spatial configuration of canopy openings have long been reported to

* Corresponding author. Tel.: +1 406 243 6307; fax: +1 406 243 6656.

E-mail address: alex.fajardo@umontana.edu (A. Fajardo).

potentially influence both the amount and species composition of regeneration, particularly for more light-demanding tree species in mesic forests (Brokaw, 1985; Fajardo and de Graaf, 2004; Gray and Spies, 1996; Minckler and Woerheide, 1965). In moisture-limited forests, however, the spatial pattern of regeneration might not be as clearly associated with canopy openings, particularly if establishment of new germinants is facilitated by the greater moisture availability under larger nurse plants (Callaway, 1992; Niering et al., 1963).

In recent years, there has been increased interest in the application of uneven-aged silvicultural systems (both single-tree and group selection) in Western North American forests (Fiedler et al., 1988; Guldin, 1996; O'Hara, 1996), particularly in lower elevation ponderosa pine (*Pinus ponderosa* Dougl.) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirbel) Franco) forests. Uneven-aged management can pose difficult silvicultural challenges, however, in part because selection harvests must consider both the recruitment of a new age class and the maintenance of vigorous growth on the reserve growing stock (i.e., the older cohorts). While identifying suitable allocation of growing space among different age cohorts to meet both considerations remains an active area of silvicultural research (O'Hara, 1996; Seymour and Kenefic, 2002), few studies have considered the actual spatial distribution of trees in different cohorts (Kunstler et al., 2004; Paluch, 2005; Rock et al., 2004; Woodall, 2000). Under the single-tree selection system, managers emulate natural gap phase replacement and implicitly consider the spatial structure of a stand by assuming that canopy gaps constitute potential growing space for new cohorts (Nyland, 2002; Smith et al., 1997). However, it is unclear to what extent regeneration occurs in clumps in managed ponderosa pine/Douglas-fir forests, and whether these two species tend to occur together or in separate microsites. Under low reserve basal area on moisture-limited sites within these forests, the spatial pattern of regeneration may not be as clearly associated with canopy openings. Previous studies in natural ponderosa pine stands have indicated that younger trees tend to be clumped, while larger trees tend to become more randomly dispersed over time (Cooper, 1961; Harrod et al., 1999; Mast and Veblen, 1999; Woodall, 2000).

While point pattern analyses (Dale, 1999) of a single species or bivariate spatial analyses between different groups do not directly identify causal factors involved in stand dynamic processes, they could enhance our understanding of competitive and spatial relationships among different tree species and age classes. Moreover, such analyses of spatial patterns may be used to identify possible underlying processes and to generate hypotheses (Legendre, 1993; Liebhold and Gurevitch, 2002; Szwagrzyk, 1990). For instance, a positive spatial association between two species may suggest that they share similar environmental site requirements, or that the species are somehow dependently linked to each other. Alternatively, a negative association may imply that one species is excluding the other (Dale, 1999), or that the species may differ in resource use, dispersal and germination mechanisms, or reproductive strategies

(Bazzaz, 1990). In addition, new statistical strategies that attempt to quantify the strength of spatial associations may allow us to strengthen inferences from spatial pattern analyses.

Over the last several years, methods based on Ripley's $L(t)$ -function, and particularly Ripley's $L_{1,2}(t)$ -function, have undergone rapid development and are now being widely used in plant ecology (Barot et al., 1999; Call and Nilsen, 2003; Camarero et al., 2000; Duncan, 1991; Goreaud et al., 1999; Goreaud and Pélissier, 2003; Haase et al., 1996; He and Duncan, 2000; Mast and Veblen, 1999; Szwagrzyk et al., 2001; Wiegand and Moloney, 2004). One argument in favor of Ripley's $L_{1,2}(t)$ -function is that it uses the information from all inter-point distances between observed units, and therefore provides more information on the scale of the pattern than do statistics that use nearest neighbor distances only (i.e., Diggle's nearest neighbor functions G or F ; Barot et al., 1999; Diggle, 1983). Second, the function describes the characteristics of the point pattern over a range of distance scales, and can therefore detect mixed patterns (e.g., association at smaller distances and repulsion at larger distances). This is an important property because virtually all ecological processes are scale dependent and their characteristics may change across scales (Gustafson, 1998; Levin, 1992; Wiegand and Moloney, 2004). However, this qualitative determination of association or disassociation based on significance testing makes it difficult to quantitatively compare different cases, and further to evaluate hypotheses regarding the underlying processes involved. We propose the use of an index of association based on the relative strength of positive or negative association present in a particular bivariate point pattern at a particular distance.

Under the assumption that processes generate patterns, we tested links between patterns of spatial association among saplings and overstory trees and relative moisture availability in managed uneven-aged ponderosa pine/Douglas-fir forest stands in Western Montana. We examined the spatial pattern of overstory and understory trees on stem-mapped plots in these managed stands. The $L(t)$ -function (Besag, 1977), a transformation of the original Ripley's $K(t)$ -function (Ripley, 1977), was used to evaluate the univariate spatial pattern of individual species and size-classes (i.e., clumped, uniform, or random), while the intertype function $L_{1,2}(t)$ (Diggle, 1983; Lotwick and Silverman, 1982) was used to evaluate bivariate spatial association between species and size-classes. Statistics summarizing of univariate and bivariate spatial patterns were evaluated to test the following hypotheses: (1) the spatial distributions of young cohorts of ponderosa pine and Douglas-fir in the understory are clumped; (2) saplings of ponderosa pine and Douglas-fir are negatively associated with each other (i.e., the two species are utilizing different microsites or one species might be excluding the other); (3) the saplings of these species are negatively associated with older cohorts (i.e., positively associated with canopy openings). In addition, we utilized a novel strategy to numerically measure the strength of spatial association between tree size-classes in order to evaluate potential causal factors for such associations. We used this "index of association" to examine whether some of the

variation in the degree of spatial association (or disassociation) between saplings and overstory trees could be explained by minor differences in relative moisture availability among our study sites.

2. Methods

2.1. Study area

The study area was located in Western Montana, approximately 170 km Northwest of Missoula, on the Flathead Indian Reservation (FIR) of the Salish and Kootenai Tribes (Sanders County). The mean annual precipitation in the lower elevation forests examined for this study is between 400 and 520 mm (Plan Confederation Salish and Kootenai Tribes, 1999). The soils are formed from residual and colluvial materials eroded from Precambrian metasedimentary rocks (Belt formations), as well as unconsolidated tills deposited by glaciers. Ponderosa pine and Douglas-fir are the dominant tree species in the study area, along with scattered Western larch (*Larix occidentalis* Nutt.) and lodgepole pine (*Pinus contorta* Dougl. ex. Loud). The natural disturbance regime in these forests had historically been dominated by low-severity ground fires with a return interval of 5–30 years (Arno, 1980; Arno et al., 1995; Fisher and Bradley, 1987; Habeck and Mutch, 1973).

There is a longer history of uneven-aged management using single-tree selection on the Flathead Indian Reservation than for most ownerships in Western Montana. Stands selected for this study on the FIR represented typical uneven-aged management regimes currently being recommended and implemented for ponderosa pine forests in the Northern Rockies region (Becker, 1995; Fiedler et al., 1988). Over the past 40 years, the current study stands have been managed by some form of selective harvesting on a cutting cycle of ~20–25 years. The most recent harvest entry in study stands occurred between 14 and 18 years ago (1987–1991). Guidelines for individual tree selection system targeted a relatively low post-harvest basal area of 11–13 m²/ha across stands, to be distributed among three to five age classes. However, basal area stocking levels sampled within 10 0.1 ha study plots

approximately 15 years after selection harvest ranged between 12.2 and 39.1 m²/ha (Table 1).

2.2. Field sampling

In each of the 10 study stands, we randomly established one 33 m × 33 m square plot (~0.11 ha), allowing that locations including the presence of perennial streams, rock outcrops, roads, or log yarding areas within plot boundaries were to be relocated. The azimuth and distance (to nearest mm) from the plot center to the center of each tree >0.5 m tall was estimated using a handheld laser range finder (Forest Pro, Laser Technology, CO, USA) and a compass. These field measurements were later converted to Cartesian coordinates using trigonometric functions. For each mapped tree, we recorded the species and measured diameter at breast height (DBH, 1.37 m) for classification into different size-classes used in the spatial pattern analyses. Understory trees taller than 0.5 m but <5-cm DBH were classified as saplings, while those with bole diameters between 5 and 15-cm DBH were classified as small poles. Trees in the size range of 15–30-cm DBH were referred to as medium overstory trees, and all individuals exceeding 30-cm DBH as large overstory trees. In order to avoid overlap between size-classes in the bivariate analysis of spatial pattern, we excluded the small pole size class from the analyses and instead focused on the relationship between saplings to medium and large overstory trees.

2.3. Habitat type designation

All of the stands sampled in this study are located on low to moderate productivity sites within a relatively narrow range of habitat types (Pfister et al., 1977) in the Douglas-fir series (i.e., they support Douglas-fir as the late-successional dominant in the absence of disturbance). There are slight differences in moisture availability across the sites, however, which are reflected in the floristic composition, including whether or not they will support Western larch. In order to evaluate the effect of relative moisture availability on bivariate spatial patterns among saplings and overstory trees with our index of

Table 1
Stand structural characteristics for the 10 sampled stands on the Flathead Indian Reservation, Western Montana, sampled in 2002

Plot	Basal area (m ² /ha)				Density large trees (#/ha) ^a				Density saplings (trees/ha)			
	PP ^b	DF	WL	Total	PP	DF	WL	Total	PP	DF	WL	Total
1	13.1	4.7	0.0	17.8	100	155	0	255	532	3222	0	3754
2	17.5	6.5	0.0	24.0	146	119	0	265	202	440	0	642
3	3.6	10.0	6.9	20.5	18	229	91	338	73	2387	64	2524
4	24.9	0.0	0.0	24.9	881	0	0	881	624	0	0	624
5	10.1	2.1	0.0	12.2	294	36	0	330	367	54	0	421
6	16.0	1.5	0.0	17.5	247	54	0	301	1257	367	9	1633
7	8.2	16.9	0.2	25.3	82	321	9	413	192	1055	9	1256
8	9.1	18.5	0.0	27.6	431	431	0	862	275	238	0	513
9	37.0	2.1	0.0	39.1	358	91	0	459	725	1836	0	2561
10	22.9	1.8	0.0	24.7	440	100	0	540	2488	1286	0	3774

^a Large overstory trees represent trees with a DBH larger than 30 cm; saplings represent small trees with a DBH smaller than 5 cm and a height larger than 0.5 m.

^b PP, ponderosa pine (*Pinus ponderosa*); DF, Douglas-fir (*Pseudotsuga menziesii*); WL, Western larch (*Larix occidentalis*).

association strength, we used the Pfister et al. (1977) floristic habitat type classification system as a surrogate for site moisture level and stratified the 10 sites into 3 habitat type groups. Such grouping of assemblages of habitat types with similar environmental regimes, responses to disturbance, and potential species composition and stand structure have been widely used in Western Montana as a coarse filter for ecological delineation of different vegetation response units in a management area (Chew et al., 2004). The three habitat type groups for our analyses are referred to simply as dry, moderate, and moist, though it is recognized that these are relative terms and that most all sites at this elevation in Western Montana experience some level of moisture stress during the growing season of most years.

2.4. Spatial pattern analysis

To simplify stand spatial structure, we focused on the two-dimensional location of stems in the stand. Therefore, the sampled area is represented by the horizontal plane bounded by plot borders, and each tree is represented by a point, defined by coordinates (x, y) . The stem-mapped plot is thus reduced to a finite set of points, called a point process, the properties of which describe the horizontal spatial structure of the forest stand for each species and tree size-class. Two types of null hypotheses concerning the type and intensity of the spatial distribution of tree stems were assessed using univariate and bivariate Ripley's K -functions and the related L -function (Besag, 1977; Ripley, 1981). The first null hypothesis for univariate spatial analysis is that there is no deviation from a distribution of complete spatial randomness (CSR). The second null hypothesis for bivariate spatial analysis is that the distribution of size-class of trees (or species) is independent of other size-classes (or species) in the sampled community (Goreaud and Pélissier, 2003).

The Ripley's K -function is defined so that $\lambda \times K(t)$ is the expected number of neighbors in a circle of radius t centered at an arbitrary point of the pattern (Ripley, 1977), under the assumptions of stationarity (invariance of the process under translation) and isotropy (invariance of the process under rotation) (Dale, 1999; Goreaud et al., 1999; Haase, 1995). To simplify interpretation, it has become popular to use a linearized version of $K(t)$: $L(t) = \sqrt{K(t)/\pi} - t$ proposed by Besag (1977) and estimated as: $\hat{L}(t) = \sqrt{\hat{K}(t)/\pi} - t$, where $\hat{K}(t)$ is the estimated Ripley's K -function. This transformation makes $K(t)$ approximately linear in t , and scales its variance to facilitate comparison against the null hypothesis of complete spatial randomness (CSR) (Skarpe, 1991). The linearized function has an expectation of zero for any value of t when the pattern is random. The statistical significance of the departure from zero was tested using a Monte Carlo procedure that randomly repositions all points in the plot and generates $L(t)$ functions (Upton and Fingleton, 1985). In this study, we computed 99% confidence bands for $L(t)$ by running 99 simulations at intervals of 1 m from 1 to 16 m (half the length of the shortest side of the plot). The Cramer-von-Mises test was

used to test for significance (Haase, 2002). Since edge effects become a concern at greater distances, we used the weighted edge correction factor proposed by Ripley (1981) to account for this effect (Haase, 1995). If the deviation of the sample statistic, $\hat{L}(t)$, from zero expectation (CSR) is significantly positive or negative, a clumped or over-dispersed distribution of the sampled trees can be asserted, respectively (Diggle, 1983; Haase et al., 1996).

To test the second null hypothesis, that of spatial independence between different species or size-classes of trees, we used the modified $L_{1,2}(t)$ -function (Diggle, 1983; Lotwick and Silverman, 1982). The classical estimator for this function is $\hat{L}_{1,2}(t) = \sqrt{\hat{K}_{1,2}(t)/\pi} - t$, where $\hat{K}_{1,2}(t)$ is the standard estimator of the intertype Ripley's K -function $K_{1,2}(t)$ proposed by Lotwick and Silverman (1982). Of particular interest was to examine whether the spatial distribution of saplings was independent of overstory trees. For this we assumed that the spatial patterns of the two different size-classes (or species for similar tests) were generated by two independent processes (e.g., different dispersion process periods, different species); hence, the null model of independence was adopted (Dixon, 2002; Goreaud and Pélissier, 2003; Wiegand and Moloney, 2004). The $\hat{L}_{1,2}(t)$ function quantifies the degree and type of spatial association between size-class (or species) 1 and 2. If the value of $\hat{L}_{1,2}(t)$ is not significantly different from zero, the null hypothesis that the two species have independent spatial distributions cannot be rejected (Goreaud and Pélissier, 2003; Kenkel, 1988). A value of $\hat{L}_{1,2}(t)$ significantly larger or smaller than 0 indicates spatial attraction or repulsion, respectively, between the two size-classes at range t . Monte Carlo simulations were used to evaluate the statistical evidence of a departure from zero, where each simulation consisted of randomly assigning new coordinates to only one size-class, while the coordinates of the other size-class remain unchanged (Goreaud and Pélissier, 2003; Haase, 2002). The spatial statistics program SPPA.EXE (Haase, 2002) was used for the computations of both univariate and bivariate analyses.

2.5. Strength of association

In the case of the bivariate Ripley's $L_{1,2}(t)$ -function, the null hypothesis being tested was that there was no spatial association between two size-classes of trees. If the value of $\hat{L}_{1,2}(t)$ deviates significantly from 0, up to a distance t , this indicated spatial attraction or repulsion between the two size-classes up to that distance t . From this analysis we could answer preliminary questions about the observed patterns, such as whether the saplings had a negative spatial association with overstory trees, but we could not compare different plots. Our approach to quantifying the relative strength of positive and negative associations is rather intuitive, in that it considers the ratio between the value of $\hat{L}_{1,2}(t)$ and the corresponding (upper or lower) confidence envelope (CE) at a specific distance t ($IA(t) = \hat{L}_{1,2}(t)/CE$) (Fig. 1). For a particular distance t , larger index values (in absolute value) indicate greater departures

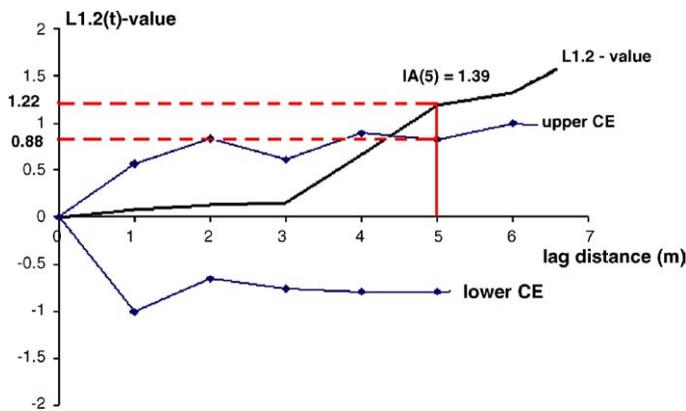


Fig. 1. Index of association (IA) as a relative measure of the strength of association between two classes of points based upon the bivariate $\hat{L}_{1,2}(t)$ function and the confidence envelopes (CE) associated with it. The IA is the ratio of the $\hat{L}_{1,2}(t)$ value to the corresponding confidence band for a specific lag distance t (i.e., upper confidence band in the case shown).

from the independence hypothesis. This index of association (IA) might logically represent the numerical strength of the point process up to a distance t (given the cumulative nature of the original function), and becomes useful when comparing groups of plots belonging to different ecological site types (e.g., habitat type groups). When comparing means, we aggregated plots to three different habitat type groups as described above to characterize minor differences in moisture availability (labeled dry, moderate, and moist) and assigned an IA value to each plot for distances $t=5$ and 10 m. These distances were selected assuming that 5 m was a fair representation of crown extension, and that 10 m extended far beyond crown influence (though perhaps not beyond the influence zone of roots). This allowed us to test the hypothesis that the strength of spatial association between saplings and overstory trees (medium and large) was not related to the habitat type group (i.e., moisture availability) of the site. Comparisons of IA for individual associations (i.e., ponderosa pine saplings versus large trees) among different habitat type groups (moisture levels) were conducted using one-way ANOVA. These analyses were carried out with SPSS (2000).

3. Results

3.1. Spatial distribution of natural regeneration

The mean density of naturally regenerated saplings (>0.5 m tall, <5-cm DBH) on the 10 study stands was 1775 trees/ha (range of 421–3774), with approximately 31% ponderosa pine and 68% Douglas-fir (Table 1). Saplings of both species exhibited clumped distributions in the understory of these managed uneven-aged stands. Ponderosa pine saplings appeared clumped in all 10 plots. For the nine plots where at least 20 saplings were present, this clumped pattern was significant across all distance classes (t) between 1 and 12 m (Table 2). Douglas-fir saplings were similarly consistent in displaying a clumped distribution across the range of distances examined (Table 2). For 8 of 10 plots with at least 20

Douglas-fir saplings present, all were significantly clumped, and 7 plots exhibited this clumped pattern for all distances up to at least 9 m.

There was no evidence in our data to support the bivariate hypothesis that saplings of ponderosa pine and Douglas-fir were negatively associated. A negative spatial association was not found in any plot at any scale. Instead, we found a positive spatial association for saplings of these two species in all but one of the plots where both were present (Table 2). In five of the seven plots where at least 20 saplings of each species were present, a significant positive spatial association was found at both small scales (up to 5 m) and at larger scales (10 m or greater).

3.2. Association of saplings with overstory trees

In these managed multi-aged stands, the pattern of bivariate spatial association between saplings of ponderosa pine and Douglas-fir and overstory trees depended upon the level of discrimination among different overstory size-classes. When the ponderosa pine saplings (<5-cm DBH) were compared against the medium-sized overstory trees (15–30-cm DBH), two plots exhibited a significant positive spatial association at scales less than 10 m (Fig. 2a), while two other plots had a significant negative spatial association at the same scales (Fig. 3a). In the other six plots there was no particular association evident. Similarly, there was no consistent trend in bivariate association between ponderosa pine saplings and large overstory trees (>30-cm DBH). While 5 of the 10 plots exhibited a significant negative association between pine saplings and large overstory trees at larger scales, two plots displayed a positive association for comparable distances between 6 and 11 m (Table 3).

Mixed results were also observed for the bivariate association between Douglas-fir saplings and medium and large overstory trees. For the nine plots in which Douglas-fir saplings were present, they were negatively associated with medium sized trees in four plots (Fig. 3b) and positively associated in three other plots (Fig. 2b). Spatial association of Douglas-fir saplings with large overstory trees was likewise mixed, though a greater proportion of plots exhibited a negative association. We found a significant negative association between Douglas-fir saplings and large trees in four plots, whereas two plots had a positive association (Table 3).

3.3. Sapling–overstory associations in relation to habitat type groups

The analysis of variation in our “index of association” (IA) among different habitat type groups indicated that some of the above variation in the spatial association between saplings and overstory trees could be related to site differences in moisture availability (Table 4). Particularly for the association between saplings and medium sized overstory trees at short scales (up to 5 m); there appeared to be a shift from positive association on drier sites to a negative association on somewhat moister sites. For Douglas-fir, this same relationship was found to be

Table 2
Patterns of spatial dispersion and association for saplings (taller than 0.5 m and less than 5-cm DBH) in 10 stands of ponderosa pine and Douglas-fir in Western Montana

Plot	Ponderosa pine saplings																p¶	Douglas-fir saplings																p
	Distance t (m) *																	Distance t (m)																
n§	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
1	58	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	351	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01
2	22	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	48	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01
3	8	c	c	c	c	c											0.10	260	c	c	c	c	c	c	c	c	c							0.01
4	68	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	0															-----	
5	40	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	6																0.76
6	137	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	40				c	c	c	c									0.01
7	21	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	118	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01
8	30	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	26	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01
9	79	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	201	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01
10	140	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	271	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01

Ponderosa pine vs. Douglas-fir saplings																	
N1/n2	Distance t (m)																p
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
1	58/351	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.01
2	22/48	+	+	+	+	+	+	+									.01
3	8/260											+	+	+	+		.03
4	68/0																---
5	40/6				+	+	+	+	+								.01
6	137/40	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.02
7	21/118		+	+	+	+	+	+	+	+	+	+	+	+	+	+	.01
8	30/26	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.01
9	79/201	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.01
10	140/271	+	+	+													.08

Data for each stand are from a 33 m × 33 m stem-mapped plot.

(§) *n* represents the number of individuals in the plot subjected to analysis; *n* stands for the number of individuals in the plot belonging to the first size-class under analysis; *n* corresponds to the second size-class; (*) the symbol *c* indicates a significantly clumped distribution; *u* indicates a regular distribution at distance *t*, based on the distribution of *L(t)*-function values. No symbol indicates a random distribution. (+) Significant positive association between both species; (–) significant negative association at distance *t*, based on *L(t)*-function. No symbol indicates independence; (¶) significance is evaluated using 99% Monte Carlo confidence intervals (99 simulations) with a 1-m step. The Cramer-von-Mises test was used to test for overall significance of patterns over the complete range of *t*, with *p*-values reported in the column titled “*p*”.

significant in the ANOVA showing clear differences between the dry and moist habitat type groups (Table 5; Fig. 4b). For ponderosa pine, the same trends were evident, but were not significant (*p*-value = 0.06) (Table 5; Fig. 4a). A similar shift in the association between saplings and medium size overstory trees from positive on drier sites to negative on more moist sites was evident at the 10 m distance as well for both species, but the ANOVA results were not statistically significant (Table 5; Fig. 5). For bivariate associations between saplings and large overstory trees, there were no significant differences among the different habitat type groups (results not shown).

4. Discussion

Spatial pattern analysis of regeneration in 10 managed uneven-aged stands selected for this study indicated that saplings of both ponderosa pine and Douglas-fir tend to be spatially clumped, though such aggregations are not necessarily associated with canopy openings. Our finding of clumped regeneration patterns is similar to results reported for ponderosa pine occurring as even-aged patches in natural stands (Cooper, 1961; Mast and Veblen, 1999; Woodall, 2000). Each harvest in

stands managed by single-tree selection may open up over 25% of the canopy area, and there is the potential for a fairly dispersed pattern of regeneration across the stand (Nyland, 2002). However, aggregated regeneration patterns in managed stands are likely driven by many of the same factors as found under natural stand dynamics. Various processes can lead to clumped patterns of recruitment, e.g., natural or mechanical soil disturbances creating patches of favorable seedbed, or increased resource availability within patches, as might be associated with canopy gaps (Franklin et al., 2002; Veblen, 1992). Clumped distributions of regeneration have likewise been reported in managed stands of *Picea abies*, *Abies alba*, and *Fagus sylvatica* (Fröhlich and Quednau, 1995) and in *Ailanthus altissima* and *Robinia pseudoacacia* (Call and Nilsen, 2003).

We found little evidence to suggest that saplings of ponderosa pine and Douglas-fir occupy separate spatial locations in these stands. The bivariate analyses for sapling distributions showed a general positive spatial association between these two species. Szwagrzyk (1992) reported a similar positive association between recruitment of two sympatric species, *Pinus sylvestris* and *Fagus sylvatica*. The existence of positive interactions between species has been

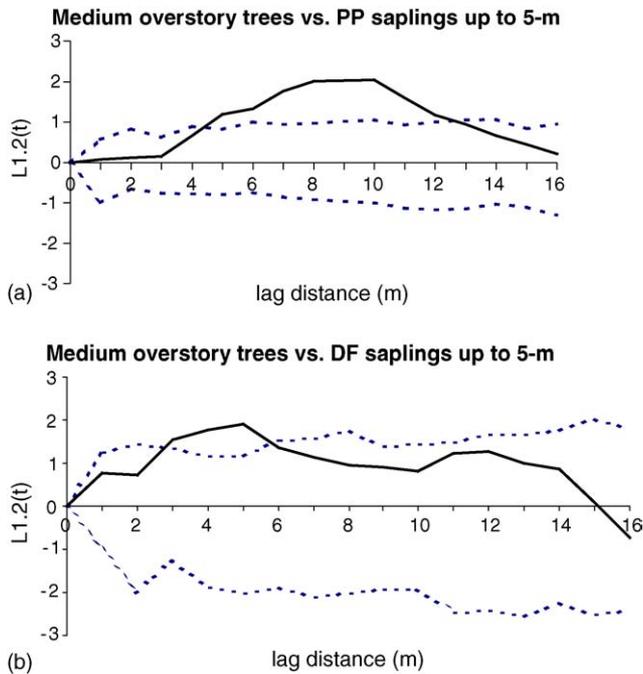


Fig. 2. $\hat{L}_{1,2}(t)$ function and the confidence envelopes (CE) associated with it for the spatial association between medium-sized overstory trees (15–30-cm DBH) and (a) ponderosa pine saplings and (b) Douglas-fir saplings in plot 6. The association between the two size-classes in this example tends to be positive (attraction).

reported to be common in many environments (Callaway, 1995; Holmgren et al., 1997). However, these positive associations have generally been reported for different layers or life forms (e.g., seedlings of one tree species and adults of another shrub species; Callaway, 1992) rather than species belonging to the same life form (e.g., trees only).

Whereas the spatial association of ponderosa pine and Douglas-fir would be easily explained if they were found to occur together in canopy gaps, we did not find that saplings were consistently clumped and separated from overstory trees (i.e., in gaps). In general, ponderosa pine and Douglas-fir saplings were either positively associated with medium-sized overstory trees (15–30-cm DBH) or independently distributed in more than half of the sample plots. In moisture-limited sites, like those examined in this study (400–520 mm/year), we might expect to see a reduced spatial association between regeneration and canopy gaps. In such sites, canopy openings are potentially less hospitable to new germinants susceptible to excessive surface temperatures and moisture stress. Germinants may recruit throughout the stand wherever available seed falls on suitable seedbeds, but survival on dry sites may be favored by the shade provided by close proximity to overstory trees. It has been argued that on more xeric habitats, reduced moisture stress under adult tree canopies may explain the increased sapling abundance beneath their canopies (Bertness and Callaway, 1994; Callaway, 1992; Niering et al., 1963). This positive spatial association may result from a facilitative relationship of larger “nurse plants” providing shelter to seedlings by buffering physical stresses, especially high temperature. Bertness and Callaway (1994)

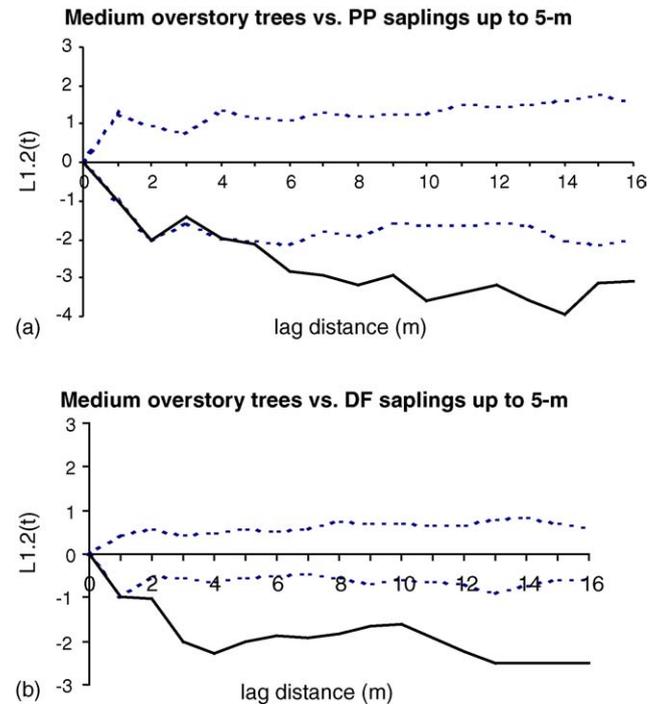


Fig. 3. $\hat{L}_{1,2}(t)$ function and the confidence envelopes (CE) associated with it for the spatial association between medium-sized overstory trees (15–30-cm DBH) and (a) ponderosa pine saplings and (b) Douglas-fir saplings in plot 7. The association between the two size-classes in this example tends to be negative (repulsion).

suggested that facilitation can potentially play a more important role than competition in stressed and resource-limited environments. Our findings support this explanation when considering medium-sized but not necessarily larger overstory trees (>30-cm DBH) (see below). However, a positive association between regeneration and adult trees might be expected to shift over time as greater resource requirements of larger regeneration leads to more direct competition with the overstory layer (Holmgren et al., 1997). While a positive association between regeneration and adult trees may be important for establishment at early development stages, once the new seedlings become established, they are likely to experience a more competitive relationship with overstory trees.

In order to further investigate bivariate associations in relation to slight differences in moisture availability between study sites, we introduced an intuitive approach to characterize the *strength* of association patterns that we termed the index of association (IA). This approach to quantifying the degree of spatial association can be used to examine the correlation between observed patterns and potential causal factors, thereby extending the utility of spatial pattern analysis. Our analyses (ANOVA) relating the strength of spatial association to the three habitat type groups (i.e., moisture availability levels) indicated significant differences according to habitat type in the bivariate association between saplings and medium-sized overstory trees (15–30-cm DBH) at small scales. Saplings were positively associated with these medium-sized overstory trees in plots belonging to dry and moderately dry habitat type groups, while negatively associated in plots belonging to moist

Table 5

F-values and probability values from the one-way ANOVA between the index of association (IA) and the habitat type groups

	Distances								PP vs. DF	
	5 m				10 m				5 m	10 m
	PP ^a		DF ^a		PP ^a		DF ^a			
	Medium ^b	Large ^b								
F-value	4.189	0.035	6.361	0.400	2.422	1.667	3.587	0.911	0.755	0.459
p-Values										
General	0.064	0.966	0.033	0.687	0.159	0.256	0.094	0.451	0.510	0.652
Comparisons ^c										
HT1 vs. HT2	0.682	0.906	0.849	0.742	0.822	0.111	0.962	0.815	0.279	0.432
HT1 vs. HT3	0.033	0.898	0.028	0.688	0.128	0.318	0.087	0.282	0.360	0.409
HT2 vs. HT3	0.047	0.799	0.018	0.405	0.076	0.523	0.047	0.299	0.875	0.919

The IA values are from the $\hat{L}_{1,2}(t)$ function up to 5 and 10-m (short and larger scale, respectively) for the spatial association between saplings and overstory trees in 10 plots (33 m × 33 m) of ponderosa pine and Douglas-fir in Western Montana.

^a Species for saplings only: PP, ponderosa pine (*Pinus ponderosa*); DF, Douglas-fir (*Pseudotsuga menziesii*).

^b Overstory tree size-class; large overstory trees represent trees with a DBH larger than 30-cm; medium overstory trees are trees with a DBH between 15–30-cm.

^c HT1: dry level habitat type group; HT2: moderate moisture level habitat type group; HT3: moist level habitat type group.

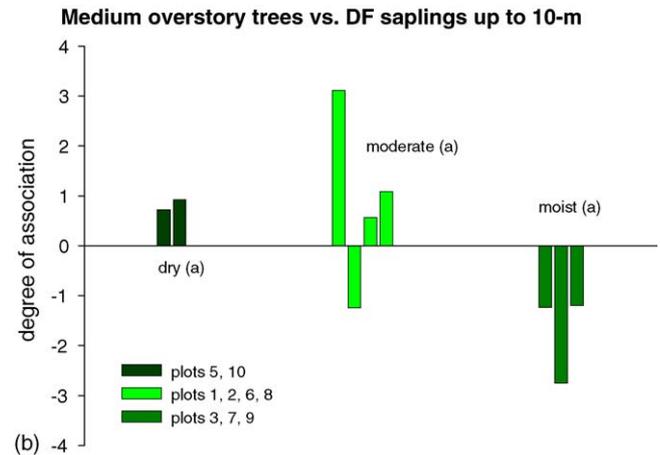
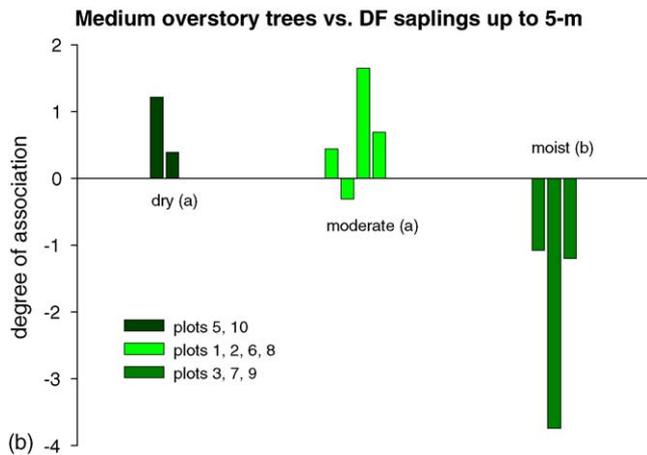
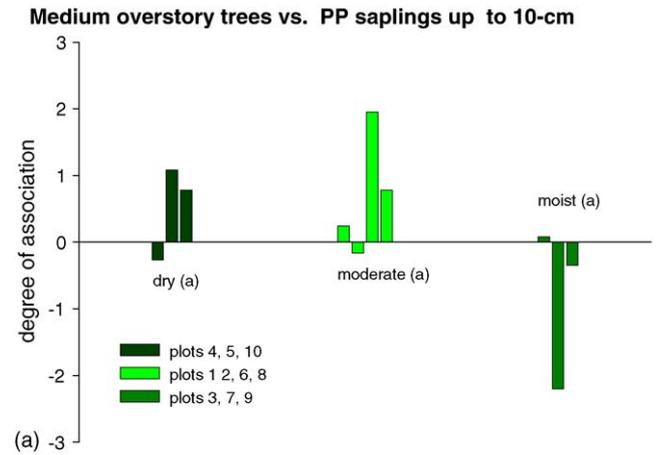
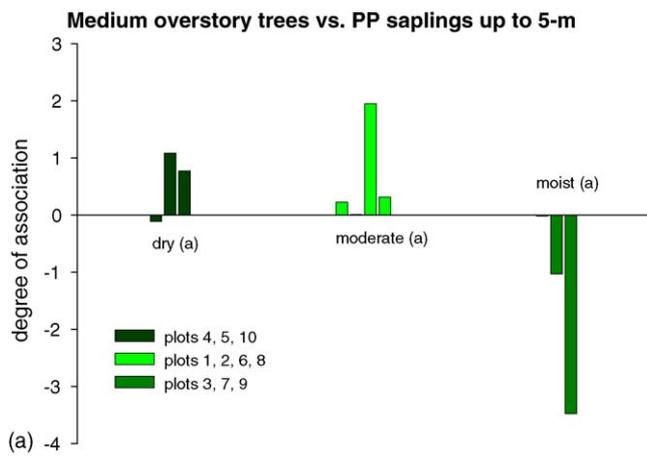


Fig. 4. Index of association (IA) among the three habitat-type groups at 5-m lag distance for the spatial association between medium overstory trees (DBH between 15 and 30 cm) vs. (a) ponderosa pine (PP) and (b) Douglas-fir (DF) saplings. Letters in brackets, when different, indicate significant differences between habitat type groups ($p < 0.05$).

Fig. 5. Index of association (IA) among the three habitat-type groups at 10-m lag distances for the spatial association between medium overstory trees (DBH between 15 and 30 cm) vs. (a) ponderosa pine (PP) and (b) Douglas-fir (DF) saplings. Letters in brackets, when different, indicate significant differences between habitat type groups ($p < 0.05$).

detected for spatial associations between saplings and medium-sized overstory trees only, and not when larger overstory trees (>30-cm DBH) were compared. Two explanations can be proposed for this difference between overstory size-classes. First, the positive association for saplings and medium-sized overstory trees could be related to a common dispersal process, such that saplings are later arriving recruits (or similar aged, but suppressed individuals) from the same regeneration event as larger pole sized trees and therefore continue to be spatially associated. But having anticipated the potential confounding effect of such an overlap in adjacent size-classes, we had decided to avoid bivariate analysis of saplings (<5-cm DBH) with small poles (5–15-cm DBH), and instead to examine only associations with overstory tree size-classes >15-cm DBH. A second explanation for the difference between overstory size-classes would be that medium-sized trees may be effectively providing more shelter to saplings than large overstory trees due to their having lower crown heights. It is possible that the ameliorating effect of larger “nurse trees” on temperature and moisture stress could be more pronounced for trees having the base of their live crown in closer proximity to the regeneration, such that the shade cast over young recruits is effective at short distances (i.e., smaller 5-m scale in our spatial analyses).

The results of this study have some interesting silvicultural implications for the establishment and release of regeneration in ponderosa pine/Douglas-fir forests managed under the individual tree selection system. While we found seedlings of both ponderosa pine and Douglas-fir tended to be clustered in patches, their establishment did not appear to be closely associated with locations under canopy gaps. It is one of the tenets of uneven-aged management under the selection system that recruitment of new age classes should be secured at each cutting as growing space is freed up by the harvested trees (Nyland, 2002; Smith et al., 1997). The available growing space is often conceptualized as being primarily within canopy openings (and associated root gaps) created by the removal of one or more mature trees, particularly when considering shade intolerant species that may require large gaps for successful recruitment into the overstory (Canham and Marks, 1985; McClure and Lee, 1993; Runkle, 1982). However, under the low reserve stocking levels typical of individual tree selection guidelines for various intolerant pine species (Baker et al., 1996; Fiedler et al., 1988; Palik et al., 2002; Shelton and Cain, 2000), initial establishment of regeneration is often more diffuse across the stand. In Western Montana, reserve basal area stocking levels for uneven-aged management of ponderosa pine are typically targeted between 9 and 13 m² ha⁻¹, a level which local permanent plot data suggest will capture the site’s growth potential while allowing for consistent regeneration of seral pine and larch (Becker, 1995; Fiedler et al., 1988). Our analysis suggested that the regeneration established under this management regime was no more likely to be found under canopy gaps than in association with overstory trees, particularly on drier sites. Given this potential for diffuse distribution, managers should plan for any site preparation treatments promoting natural regeneration (e.g., mechanical or prescribed fire) to be conducted throughout the stand, rather than limiting their focus

to canopy openings. Moreover, since the number of sapling recruits needed at each cutting cycle is relatively small (<100 ha⁻¹), securing broad distribution (i.e., full stocking) of desirable regeneration may be more important than the absolute density of saplings established (Becker, 1995).

Whereas our analysis of the distribution of sapling occurrence indicates that establishment may not be tied to canopy gaps, such openings are very likely important for the release of saplings once established. The microsite conditions that are suitable for initial establishment clearly differ from optimal conditions for sustained sapling growth, in part because the shade tolerance of tree seedlings tends to decrease with increasing size (Givnish, 1988; Messier et al., 1999). Any positive association we observed between young regeneration and adult trees would be expected to shift over time as the greater resource demands of larger saplings lead to more direct competition with the overstory layer (Holmgren et al., 1997). Subsequent selection harvests offer opportunities for releasing some of the saplings established in the previous cutting cycle. Given a diffuse distribution of regeneration across the stand, it may be more appropriate to consider canopy openings as areas where previously established saplings can be released, rather than as sites for establishing new regeneration. In locating new canopy openings, the presence of desirable saplings needing release would be taken into account along with which overstory trees might be selected for harvest.

One of the limitations of the current study is the focus on regeneration density within broad size-classes. Regeneration in these analyses included saplings ranging from 0.5-m tall up to large saplings at 5-cm DBH. We might arrive at different conclusions about spatial association between regeneration and medium-sized and overstory trees if we look at very small first year germinants versus well-established advance regeneration. In addition, we did not evaluate the effects of overstory tree competition on the growth rates of regeneration, or the potential for faster growth rates in canopy gaps to lead more rapidly to reduced density of regeneration due to natural self-thinning. Further work is needed, beyond descriptions of spatial point patterns, to examine the effects of spatial patterns on individual tree-growth performances (i.e., mean annual increment, survival, and growth efficiency) as well as on stand-level growth given different growing space allocation among cohorts (Woodall, 2000).

Given that this is a descriptive study, we cannot draw definite conclusions about causal relationships for the observed patterns; many possible variables may affect plant–plant interactions and thus be responsible for the observed patterns discussed above (Barot et al., 1999; Bazzaz, 1990; Wyszomirski et al., 1999). However, if we ignore spatial interactions, we may risk being unable to accurately predict the dynamics of even a very simple ecological system, regardless of how accurately we measure the underlying demographic rates (Hastings, 1993). Strategies such as quantifying the strength of association may allow us to extend inferences from observed patterns of spatial associations. The index of association strength introduced in this paper should be assessed in other studies involving bivariate spatial pattern analyses. We expect

that this or comparable indices could be useful for evaluating hypotheses regarding potential causes for observed spatial associations and thereby help to link functional and structural components of forest communities.

Acknowledgements

The USDA McIntire-Stennis program supported this research, which is a contribution of the University of Montana College of Forestry and Conservation. We would like to thank the Salish and Kootenai Tribes for access to sites on the Flathead Indian Reservation, and in particular Rolan Becker for his help in locating potential study stands. Christopher Vincent assisted with field data collection.

References

- Arno, S.F., 1980. Forest fire history in the Northern Rockies. *J. Forestry* 78, 460–465.
- Arno, S.F., Scott, J.H., Hartwell, M.G., 1995. Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relationship to fire history. U.S. Forest Service, Research Paper INT-RP-481. Intermountain Research Station, Ogden, UT.
- Baker, J.B., Cain, M.D., Guldin, J.M., Murphy, P.A., Shelton, M.G., 1996. Uneven-aged silviculture for the loblolly and short leaf pine cover types. USDA Forest Service, General Technical Report SO-118.
- Barot, S., Gignoux, J., Menaut, J.C., 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analysis. *Ecology* 80 (6), 1987–2005.
- Bazzaz, F.A., 1990. Successional environments: plant-plant interactions. In: Grace, J.B., Tilman, D. (Eds.), *Perspectives on Plant Competition*. American Press Inc., New York, pp. 139–263.
- Becker, R., 1995. Operational considerations of implementing uneven-aged management. In: O'Hara, K.L. (Ed.), *Uneven-Aged Management: Opportunities, Constraints and Methodologies*. School of Forestry, The University of Montana, Missoula, MT, pp. 67–81.
- Bertness, M.D., Callaway, R.M., 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9 (5), 187–191.
- Besag, J., 1977. Contribution to the discussion of Dr. Ripley's paper. *J. R. Stat. Soc. B* 39, 193–195.
- Brokaw, N.V.L., 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66, 682–687.
- Call, L.J., Nilsen, E.T., 2003. Analysis of spatial patterns and spatial association between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*). *Am. Midland Nat.* 150 (1), 1–14.
- Callaway, R.M., 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology* 73 (6), 2118–2128.
- Callaway, R.M., 1995. Positive interactions among plants. *Bot. Rev.* 61, 306–349.
- Camarero, J.J., Gutiérrez, E., Fortin, M.-J., 2000. Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. *Forest Ecol. Manage.* 134 (1–3), 1–16.
- Canham, C.D., Marks, P.L., 1985. The response of woody plants to disturbance: patterns of establishment and growth. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, FL.
- Chen, J., Bradshaw, G.A., 1999. Forest structure in space: a case study of an old growth spruce-fir forest in Changbaishan Natural Reserve, PR China. *Forest Ecol. Manage.* 120, 219–233.
- Chew, J.D., Stalling, C., Moeller, K., 2004. Integrating knowledge for simulating vegetation change at landscape scales. *West. J. Appl. Forestry* 19, 102–108.
- Choler, P., Michalet, R., Callaway, R.M., 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82, 3295–3308.
- Cooper, C.F., 1961. Pattern in ponderosa pine forests. *Ecology* 42, 493–499.
- Dale, M.R.T., 1999. *Spatial pattern analysis in plant ecology*. Cambridge University Press, New York, p. 326.
- Diggle, P.J., 1983. *Statistical analysis of spatial point patterns*. Academic Press, New York, p. 148.
- Dixon, P., 2002. Ripley's *K*-function. In: El-Shaarawi, A.H., Piergorsch, W.W. (Eds.), *The Encyclopedia of Environmetrics*. John Wiley & Sons Ltd., New York, pp. 1796–1803.
- Duncan, R.P., 1991. Competition and coexistence of species in a mixed podocarp stand. *J. Ecol.* 79, 1073–1084.
- Duncan, R.P., Steward, G.H., 1991. The temporal and spatial analysis of tree age distributions. *Can. J. Forest Res.* 21, 1703–1710.
- Fajardo, A., de Graaf, R., 2004. Tree dynamics in canopy gaps in old-growth forests of *Nothofagus pumilio* in southern Chile. *Plant Ecol.* 173 (1), 95–106.
- Fiedler, C.E., Becker, R.R., Haglund, S.A., 1988. Preliminary guidelines for uneven-aged silvicultural prescriptions in ponderosa pine. In: Baumgartner, D.M., Lotan, J.E. (Eds.), *Ponderosa Pine. The Species and its Management*. Washington State University, Pullman, WA.
- Fisher, W.C., Bradley, A.F., 1987. Fires ecology of western Montana forest habitat types, USDA Forest Service General Technical Report INT-223.
- Franklin, J.F., et al., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecol. Manage.* 155 (1–3), 399–423.
- Fröhlich, M., Quednau, H.D., 1995. Statistical analysis of the distribution pattern of natural regeneration in forests. *Forest Ecol. Manage.* 73, 45–57.
- Givnish, T.J., 1988. Adaptation to sun and shade: a whole-plant perspective. *Aust. J. Plant Physiol.* 15, 63–92.
- Goreaud, F., Courbaud, B., Collinet, F., 1999. Spatial structure analysis applied to modeling of forest dynamics: a few examples. In: Amaro, A., Tomé, M. (Eds.), *Empirical and Process Based Models for Forest Tree and Stand Growth Simulation*. Novas Tecnologias, Oeiras, Portugal, pp. 155–172.
- Goreaud, F., Pélissier, R., 2003. Avoiding misinterpretation of biotic interactions with the intertype *K*₁₂-function: population independence vs. random labeling hypotheses. *J. Veg. Sci.* 14 (5), 681–692.
- Gray, A.N., Spies, T.A., 1996. Gap size, within gap position and canopy structure effects on conifer seedling establishment. *J. Ecol.* 84, 635–645.
- Greig-Smith, P., 1979. Pattern in vegetation. *J. Ecol.* 67, 755–779.
- Guldin, J.M., 1996. The role of uneven-aged silviculture in the context of ecosystem management. *East. J. Appl. Forestry* 11 (1), 4–12.
- Gustafson, E.J., 1998. Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems* 1, 143–156.
- Haase, P., 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: introduction and methods of edge correction. *J. Veg. Sci.* 6, 575–582.
- Haase, P., 2002. SPPA EXE Statistical Program, <http://haasep.homepage.t-online.de/>.
- Haase, P., Pugnaire, F.I., Clark, S.C., Incoll, L.D., 1996. Spatial patterns in two-tiered semi-arid shrubland in southeastern Spain. *J. Veg. Sci.* 7, 527–534.
- Habeck, J.R., Mutch, R.W., 1973. Fire-dependent forests in the northern Rocky Mountains. *Q. Res.* 3, 408–424.
- Harrod, R.J., McRae, B.H., Hartl, W.E., 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. *Forest Ecol. Manage.* 114, 433–446.
- Hastings, A., 1993. Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology* 74, 1362–1372.
- He, F., Duncan, R.P., 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. *J. Ecol.* 88, 676–688.
- Holmgren, M., Scheffer, M., Huston, M.A., 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78, 1966–1975.
- Kenkel, N.C., 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69 (4), 1017–1024.
- Kikvidze, Z., et al., 2005. Linking patterns and processes in alpine plant communities: a global study. *Ecology* 86 (6), 1395–1400.
- Kunstler, G., Curt, T., Lepart, J., 2004. Spatial pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus pubescens* Mill.) seedlings in natural pine (*Pinus sylvestris* L.) woodlands. *Eur. J. Forest Res.* 123 (4), 331–337.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74 (6), 1659–1673.

- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
- Liebholt, A.M., Gurevitch, J., 2002. Integrating the statistical analysis of spatial data ecology. *Ecography* 25 (5), 553–557.
- Lotwick, C.G., Silverman, B.W., 1982. Methods for analyzing spatial processes of several types of points. *J. R. Stat. Soc. B: Methodol.* 44, 406–413.
- MacArthur, R.H., 1972. *Geographic Ecology: Patterns in the Distribution of Species*. Princeton University Press, Princeton, NJ.
- Mast, J.N., Veblen, T.T., 1999. Tree spatial patterns and stand development along the pine-grassland ecotone in the Colorado Front Range. *Can. J. Forest Res.* 29 (5), 575–584.
- McClure, J.W., Lee, T.D., 1993. Small-scale disturbance in a northern hardwood forest: effects of tree species abundance and distribution. *Can. J. Forest Res.* 23, 1347–1360.
- McClure, J.W., Lee, T.D., Leak, W.B., 2000. Gap capture in northern hardwoods: patterns of establishment and height growth in four species. *Forest Ecol. Manage.* 127, 181–189.
- Messier, C., et al., 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Can. J. Forest Res.* 29, 812–823.
- Minckler, L.S., Woerheide, J.D., 1965. Reproduction of hardwoods 10 years after cutting as affected by site and opening size. *J. Forestry* 63, 103–107.
- Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15, 278–285.
- Niering, W.A., Whittaker, R.H., Lowe, C.H., 1963. The saguaro: a population in relation to environment. *Science* 142, 15–23.
- Nyland, R., 2002. *Silviculture: Concepts and Applications*. McGraw-Hill Companies Inc., New York.
- O'Hara, K.L., 1996. Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. *Forest Sci. Monogr.* 33 (4), 1–44.
- Palik, B.J., Mitchell, R.J., Hiers, J.K., 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. *Forest Ecol. Manage.* 155, 347–356.
- Paluch, J., 2005. Spatial distribution of regeneration in west-carpathian uneven-aged silver fir forests. *Eur. J. Forest Res.* 124, 47–54.
- Pfister, R.D., Kovalchik, B.L., Arno, S.F., Presby, R.C., 1977. *Forest Habitat Types of Montana*. US Forest Service, General Technical Report INT-34. Intermountain Forest and Range Experiment Station, Ogden, UT.
- Plan Confederation Salish and Kootenai Tribes, 1999. Flathead Indian Reservation forest management plan: an ecosystem approach to tribal forest management, Pablo, MT.
- Ripley, B.D., 1977. Modeling spatial patterns. *J. R. Stat. Soc. B* 39, 172–212.
- Ripley, B.D., 1981. *Spatial Statistics*. Wiley, New York, p. 252.
- Rock, J., Puettmann, K.J., Gockel, H.A., Schulte, A., 2004. Spatial aspects of the influence of silver birch (*Betula pendula* L.) on growth and quality of young oaks (*Quercus* spp.) in central Germany. *Forestry* 77, 235–247.
- Runkle, J.R., 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62, 1041–1051.
- Runkle, J.R., 1982. Patterns of disturbance in some old-growth mesic forests of the eastern United States. *Ecology* 63, 1533–1546.
- Seymour, R.S., Kenefic, L.S., 2002. Influence of age on growth efficiency of *Tsuga canadensis* and *Picea rubens* trees in mixed-species, multiaged northern conifer stands. *Can. J. Forest Res.* 32, 2032–2042.
- Shelton, M.G., Cain, M.D., 2000. Regenerating uneven-aged stands of loblolly and shortleaf pines: the current state of knowledge. *Forest Ecol. Manage.* 129, 177–193.
- Skarpe, C., 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *J. Veg. Sci.* 2, 565–572.
- Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. *The Practice of Silviculture: Applied Forest Ecology*. Wiley, New York, p. 537.
- SPSS, 2000. SYSTAT SPSS Inc., Chicago, USA.
- Stoll, P., Bergius, E., 2005. Pattern and process: competition causes regular spacing of individuals within plant populations. *J. Ecol.* 93 (2), 395–403.
- Szwagrzyk, J., 1990. Natural regeneration of forest related to the spatial structure of trees: a study of two forest communities in Western Carpathians, southern Poland. *Vegetation* 89, 11–22.
- Szwagrzyk, J., 1992. Small-scale spatial pattern of trees in a mixed *Pinus sylvestris*–*Fagus sylvatica* forest. *Forest Ecol. Manage.* 51, 301–315.
- Szwagrzyk, J., Szewczyk, J., Bodziarczyk, J., 2001. Dynamics of seedling banks in beech forest: results of a 10-year study on germination, growth and survival. *Forest Ecol. Manage.* 141, 237–250.
- Uhl, C., Clark, K., Dezzeo, N., Maquirino, P., 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69, 751–763.
- Upton, G.J.G., Fingleton, B., 1985. *Spatial data analysis by example. Point pattern and quantitative data*, vol. 1. Wiley, New York, p. 410.
- Veblen, T.T., 1992. Regeneration dynamics. In: Glen-Lewin, D.C., Peet, R.K., Veblen, T.T. (Eds.), *Plant Succession: Theory and Prediction. Population and Community Biology Series*. Chapman & Hall, London, New York, pp. 135–145.
- Watt, A.S., 1947. Pattern and process in the plant community. *J. Ecol.* 35, 1–22.
- Webster, C.R., Lorimer, C.G., 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. *Ecol. Appl.* 15, 1245–1262.
- Wiegand, T., Moloney, K.A., 2004. Rings, circles and null-models for point pattern analysis in ecology. *Oikos* 104, 209–229.
- Woodall, C.W., 2000. Growth and structural dynamics of uneven-aged ponderosa pine stands in Eastern Montana. The University of Montana, Missoula, p. 137.
- Wyszomirski, T., Wyszomirska, I., Jarzyna, I., 1999. Simple mechanisms of size distribution dynamics in crowded and uncrowded virtual monocultures. *Ecol. Model.* 115 (2), 253–273.