

Spatio-temporal structure of multi-storied, multi-aged interior Douglas fir (*Pseudotsuga menziesii* var. *glauca*) stands

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Summary

1. We used replicated, repeated-measures data to examine the spatio-temporal structure of multi-storied, multi-aged interior Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco) stands growing on dry sites under more than 50 years of fire protection. Along with the univariate and bivariate Ripley's *K* and related functions, we used a random coefficients mixed model to investigate the variation in these functions over replicates and time.

2. The spatio-temporal analyses revealed that trees greater than 1.3 m in height were clustered over space, and clustering was more evident for small trees (i.e. diameter at breast height (d.b.h.) ≤ 7.0 cm).

3. Bivariate functions indicated that small trees were spatially aggregated with large trees, indicating higher germination success and early survival near large trees. For these dry sites, moisture is more limiting than light and large trees provide moister microsites.

4. Dead trees were clustered, more commonly smaller in size and aggregated near large trees, indicating competition for moisture.

5. For the 16-year period of the study, there was very little evidence that the spatio-temporal patterns changed from a clustered to a more regular arrangement over time, unlike evidence from studies in other forest types.

6. Using the random coefficients mixed model approach, the majority of spatio-temporal variation was due to differences among replicates, with little variation over time.

7. Under fire protection, interior Douglas fir stands on dry sites might be expected to have lower mortality but any increase in density will be limited by moisture availability. Since interior Douglas fir is moderately shade-tolerant, this may result in an approach to a steady state of regeneration and death over the long term.

8. *Synthesis.* Spatio-temporal analysis using replicated, repeated-measures data, including a random coefficients mixed model approach, gave useful insights into mortality and recruitment in multi-storied and multi-aged stands. Similar patterns might be expected in other naturally occurring multi-storied and multi-aged stands. The use of replicated, repeated-measures data rather than chronosequence data allows for the examination of true changes in spatial patterns over time.

Key-words: competition, mortality, pair correlation, random coefficients mixed models, regeneration, replicated and repeated-measures data, spatial point processes, spatial-temporal analysis, stand structure

Introduction

Interior Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco) is a common species in the southern and central

interior of British Columbia (BC), Canada. The species extends to mountainous areas of Alberta in Canada and is also found in Montana, Idaho, Oregon and Washington in the United States and in parts of Mexico (Hermann & Lavender 1990). The dynamics of the interior variety of Douglas fir differ from the more-often-studied coastal variety (*Pseudotsuga*

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menziesii var. *menziesii* (Mirb.) Franco), which extends from Alaska to California along the Pacific Ocean. The coastal variety is shade intolerant and is often found in even-aged mixtures with other conifers (Hermann & Lavender 1990). Conversely, the interior variety is moderately shade-tolerant and often appears in multi-storied and multi-aged stands.

Analysis of spatial patterns can be used to give insight on processes of stand development over time (e.g. Moeur 1993, 1997; Goreaud, Courbaud & Collinet 1999; Mast & Veblen 1999; Getzin *et al.* 2006). Changes in spatial patterns of trees over time are determined by a number of factors, including regeneration mechanisms, as impacted by seed availability, substrate characteristics, moisture and light availability and competition among tree species and with other vegetation. Initial seed dispersal may result in clumped patterns of regenerating trees, but this may shift towards a random or even regular pattern as mortality due to inter-tree competition occurs (Oliver & Larson 1990; Moeur 1997). For species that are light-demanding, such as coastal Douglas fir, large gaps must be created through mortality of overstorey trees before regeneration can take place; as a result, stands tend towards being even-aged. Where gaps are created, smaller trees are often clustered and distanced from large trees. Getzin *et al.* (2006) examined fine-scale spatial characteristics using a chronosequence in coastal stands of Douglas fir, western red cedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). They found that these species tended towards spatial resource partitioning, and long-term existence of Douglas fir relied upon spatial heterogeneity.

In the multi-aged stands of the more shade-tolerant interior Douglas fir (IDF), spatial patterns have not been generally studied. Regeneration on sites that are moisture-limited may occur near larger trees where soils are moister, resulting in clustering of small trees and a pattern of attraction between large and small trees. Conversely, on moister sites where light is the limiting factor, regeneration may occur in gaps, again resulting in clustering of small trees, but with a pattern of repulsion between large and small trees. Over time, expected differential mortality of smaller trees and ingress will alter these patterns, but it is not known whether patterns will tend towards regularity.

Commonly, Ripley's K function ($K(r)$) or related functions, including the $L(r)$ function and the pair correlation function, $g(r)$ (Ripley 1981; Stoyan & Penttinen 2000), have been used to examine spatial point patterns in forest environments (Perry, Miller & Enright 2006). In practice, the spatial point process is observed only for a spatial window (i.e. a plot area), resulting in estimates of these measures calculated as (Ripley 1981; Illian *et al.* 2008):

$$\hat{K}(r) = \frac{\sum_{i=1}^n \sum_{j=1}^{n-1} I_{ij}(r)}{n\hat{\lambda}}, \hat{L}(r) = \sqrt{\frac{\hat{K}(r)}{\pi}}, \hat{g}(r) = \frac{\hat{K}'(r)}{2\pi r}$$

where r is the radius from the event i (i.e. tree), $I_{ij}(r)$ is 1 for each tree j within radius r of the event and 0 otherwise, n is the number of trees in the sample window with area A , λ is the expected number of events per unit of

area, $\hat{\lambda}$ is an estimate of λ , and $\hat{K}'(r)$ is the first derivative of $\hat{K}(r)$. Normally, a correction for edge effects is also applied. For all three functions, all possible event-to-event neighbours are used, allowing for interpretation of patterns at near-to-far (i.e. fine-to-coarse) spatial scales. For a completely spatially random (CSR) point process, $K(r) = \pi r^2$, $L(r) = r$ and $g(r) = 1$, indicating that the expected density under a random process within radius r from the event is equal to the observed density. Often, $L(r)-r$ is calculated, with an expected value of 0 under a CSR process. Values larger than these indicate a tendency towards clustering (i.e. attraction of trees), whereas values smaller than these indicate regularity (i.e. repulsion or separation of trees). These functions can highlight different spatial patterns at different scales and are particularly useful in forest environments with a variety of tree sizes, since interactions among sizes can occur at a variety of scales. Although $L(r)$ is perhaps the most commonly used function, if a non-Poisson pattern is indicated for smaller values of r , the function may continue to indicate a clustered or regular pattern at larger distances. Conversely, $g(r)$ does not have this tendency and has a limit of 1 as r increases (see description of $g(r)$ in Illian *et al.* 2008, p. 220).

Bivariate versions of these functions allow interpretation of interactions of two types of events (i.e. types 1 and 2) which are qualitative marks for each point. These bivariate functions indicate attraction if more than the expected number of type-2 events occur near type-1 events, or repulsion where the reverse is true. For forest environments, bivariate functions can give insights on relationships among species as well as other cohorts of trees within the stand such as small versus large trees.

Ripley's K , univariate and bivariate functions and derivations of these functions were developed under the assumption of a common density over the area of interest, termed a homogeneous point process (Illian *et al.* 2008). However, in stands with very high vertical and horizontal variability, the density may be inhomogeneous, reflecting smaller scale site variability coupled with regeneration processes (Getzin *et al.* 2008). As an alternative, Baddeley, Møller & Waagepetersen (2000) suggested an inhomogeneous $K(r)$ function, and associated $L(r)$ and $g(r)$ functions. The application of these functions requires estimates of densities over the spatial window as a first step, which is more computationally intensive and introduces an additional level of uncertainty in the determination of functions. Under a homogeneous point process, the densities would be the same over the spatial window. As a result, the inhomogeneous K function simplifies to the homogeneous K function if the process is homogeneous (Baddeley, Møller & Waagepetersen 2000). However, it is often difficult to determine whether the process is inhomogeneous since a particular realization of a homogeneous process may appear inhomogeneous (Ripley 1988, p. 7).

Extension of spatial analyses to include changes in time (spatio-temporal analysis) allows the examination of changes in stand structure due to mortality, regeneration, growth and competition. Because of cost and time constraints, only a

limited number of studies have included spatio-temporal analysis; many of these studies have used chronosequences rather than true time series (i.e. repeated measures) resulting in some difficulties in interpreting trends over time. Where repeated-measures data have been used, often there are no or only a few replicates (e.g. Biondi, Myers & Avery 1994). Therefore, most research has relied upon graphical approaches to display changes in spatial functions over time for the few sites in the study. For larger numbers of replicates of repeated-measures data, graphical approaches are informative but become cumbersome. Bell & Grunwald (2004) noted that there is very limited research into methods for analyzing replicated spatial processes. Diggle, Lange & Benes (1991) proposed the K -function analysis of variance. Bell & Grunwald (2004) proposed the use of generalized linear or generalized linear mixed models; this approach was used by Hampe *et al.* (2008) in their study of recruitment over time. Diggle, Rowlingon & Ting-li Su (2005) used a spatio-temporal model to predict disease. As an alternative to these approaches, a random coefficients mixed model (e.g. Schabenberger & Pierce 2002; Chapter 7; Littell *et al.* 2006; Chapter 8) might be useful for gaining insights into variations in spatial patterns over replicates and over time. Before mixed models algorithms became generally available, this was termed a parameter prediction approach and was used for longitudinal data (e.g. Meredith & Stehman 1991). In this approach, the spatial function, $K(r)$, $L(r)$ or $g(r)$ could be modelled using a flexible-form equation. Then, each coefficient of this flexible-form equation is considered a random coefficient varying with replicate and with time, allowing examination of variation over replicates and over time.

In this article, we examined the spatio-temporal structure of multi-storied, multi-aged IDF stands on drier sites of the Interior Douglas fir (IDF) biogeoclimatic ecological classification (BEC) zone of British Columbia (BC) that had little or no recent harvest activity and under the prevention of large-scale fires. Our hypotheses are that:

1. The spatial pattern for all trees is clustered as a result of localized regeneration of small trees and competition among large trees; and
2. The spatial pattern for small trees is initially clustered in space, as a result of seed dispersal and substrate availability, including the need for moisture, but becomes more regularly dispersed over time because of competition-based mortality.

In terms of the relationships between small and large trees, there are two alternative hypotheses:

- 3A. Small trees tend towards attraction to large trees, seeking moister microsites; or
- 3B. Small trees tend towards repulsion from large trees, seeking gaps with more light and less competition.

For these dry sites, we expected that the first of these competing hypotheses regarding small versus large trees would more likely occur. In terms of mortality, the hypotheses are that:

4. Mortality is higher for small trees; and
5. Mortality will be more common in areas of higher competition, indicating that competition-based mortality is more prevalent than mortality due to other biotic (e.g. disease, insects and animal damage) or abiotic (e.g. wind damage) causes.

To conduct the spatio-temporal analysis, initially separate spatial analyses in time and for each replicate were used to examine the spatial patterns of all trees, small trees only and spatial correlations between small trees and large overstorey trees. The assumption of an inhomogeneous process was examined by also calculating inhomogeneous spatial measures. Following this, a random coefficient mixed model approach was used to examine variation in spatial patterns among replicates and among times. This mixed model approach is suggested as a possible mechanism for spatio-temporal analysis where there are a number of replicated measures over time.

Materials and methods

SPECIES IMPORTANCE

Interior Douglas fir grows in dry to moist environments on higher elevations (Hermann & Lavender 1990). It is moderately shade-tolerant, growing to a maximum height of 42 m (British Columbia Ministry of Forests and Range 2008). In contrast, the coastal variety of Douglas fir exists in a maritime climate, with precipitation occurring mostly as rain, a long frost-free season and narrow diurnal fluctuations of temperature (6–8 °C) (Hermann & Lavender 1990). It often is found in even-aged stands in mixtures with other conifers (Hermann & Lavender 1990), it is very long-lived (> 400 years) and can reach heights up to 85 m (British Columbia Ministry of Forests and Range 2008); it is light-demanding (i.e. shade-intolerant), requiring a larger-scale disturbance to regenerate.

In BC, IDF is the dominant species in the IDF BEC zone (Meidinger & Pojar 1991), which covers approximately 5% (4.3 million ha) of BC forests (British Columbia Ministry of Forests 1995) in central and south-eastern BC. In this zone, IDF grows in pure stands or in mixtures with interior spruce (*Picea engelmannii*, *Picea glauca* and their crosses) and other species (Hope *et al.* 1991). Interior Douglas fir also occurs in the Interior Cedar–Hemlock and sub-Boreal Spruce BEC zones, generally in diverse mixtures with several tree species. Interior Douglas fir stands in BC are important as recreation areas and winter habitat for Rocky Mountain mule deer (*Odocoileus hemionus hemionus* Raf.) (Armleder *et al.* 1994). Management of these stands involves a balance among recreation, wildlife, timber and other uses. The prevention of large-scale fires for more than 50 years has altered the natural regeneration regime of these forests, resulting in changes to the vertical and horizontal structures.

On the driest sites of the IDF BEC zone, IDF stands are commonly multi-aged, fire-dominated and subclimax, with variable vertical and horizontal structures. The IDF BEC zone is characterized by warm, dry summers and cool winters (Hope *et al.* 1991), has a mean annual precipitation between 300 and 750 mm, except for a few wetter areas, and precipitation occurs mostly as snow (Vyse, Smith & Bondar 1991). Contributing to the structural complexity are insect attacks and small-scale fires as well as a history of single-tree selection partial harvest. Because of dry summers, fire occurred frequently historically.

Table 1. Numbers of live trees and statistics for diameters (d.b.h.) and heights by plot and date of measurement

Plot	Year	Size ha	No. live trees (Trees per ha)	d.b.h (cm)			Height (m)		
				Mean	Minimum	Maximum	Mean	Minimum	Maximum
1	1988	0.10	160 (1600)	10.7	0.3	87.8	8.2	1.4	32.6
	1992		145 (1450)	9.8	0.3	66.3	8.2	1.4	33.1
	1997		142 (1420)	10.8	0.3	67.0	8.6	1.3	33.7
	2004		140 (1400)	12.0	1.1	68.3	9.8	1.8	33.7
2	1988	0.10	116 (1160)	14.8	0.3	79.5	10.3	1.4	30.8
	1992		112 (1120)	15.6	0.5	79.5	11.0	1.4	32.3
	1997		110 (1100)	16.5	0.5	79.5	11.4	1.4	31.3
	2004		107 (1070)	17.7	0.8	80.2	12.7	1.9	36.0
3	1988	0.10	252 (2520)	8.5	0.6	67.0	7.8	1.4	30.1
	1992		244 (2440)	9.2	0.6	67.0	8.4	0.9	30.1
	1997		234 (2340)	10.1	0.7	67.2	8.8	1.5	29.7
	2004		226 (2260)	10.3	0.7	52.1	9.6	1.8	29.9
4	1988	0.10	152 (1520)	14.3	1.5	54.6	12.4	1.8	27.1
	1992		148 (1480)	15.0	1.5	54.8	13.0	1.8	27.7
	1997		145 (1450)	15.8	1.5	55.2	13.3	1.5	27.8
	2004		141 (1410)	16.8	1.9	56.5	14.4	2.2	28.3
5	1988	0.05	280 (5600)	6.0	0.3	51.7	5.6	1.3	27.1
	1992		261 (5220)	6.4	0.3	52.0	6.0	1.3	29.8
	1997		249 (4980)	6.9	0.6	53.4	6.4	1.6	26.7
	2004		219 (4380)	7.7	0.6	54.0	7.1	1.6	27.2
6	1988	0.05	213 (4960)	6.4	0.8	48.0	5.9	1.3	27.6
	1992		205 (4100)	6.8	0.8	49.0	6.3	1.5	27.7
	1997		198 (3960)	7.4	0.9	50.6	6.7	1.5	26.9
	2004		177 (3540)	8.3	0.9	52.4	7.6	1.5	28.4

STUDY AREA AND FIELD DATA

The data used in this study are part of a larger ongoing study of IDF stand dynamics (see Marshall & Wang 1996). The study area is located in the Knife Creek Block of the University of British Columbia, Alex Fraser Research Forest (52°3' N, 121°52' W) in the dry cool Interior Douglas fir subzone (IDFdk), one of seven IDF subzones (Hope *et al.* 1991). The landscape is generally rolling, with an average elevation of approximately 1000 m a.s.l., a mean daily temperature of 4.2 °C, extreme temperatures of -42 to 36 °C and annual precipitation (rain in summer and snow in winter) of 450 mm¹.

In 1988, six plots were established in dry, multi-aged, pure IDF stands that were without recent harvest and under large-scale fire suppression for the last half of the last century. Four of these plots were 0.10 ha in size (31.62 × 31.62 m; plots 1 to 4), and because of high density, two plots were 0.05 ha in size (15.81 × 31.62 m; plots 5 and 6). The locations of all trees above 1.3 m in height were recorded, and each tree was measured for diameter outside bark at breast height (1.3 m above ground; d.b.h.) and total tree height (m). Generally, trees above 1.3 m were not in competition with non-tree vegetation. All trees were measured again in 1992, 1997 and 2004.

SPATIAL ANALYSES OVER TIME

For all plots and times, translation and rotation of points was used to obtain positions relative to coordinates of (0,0) for the lower-left corner of the plot. Spatial positions of trees in each plot and time mea-

surement were then graphed along with frequency distributions of d.b.h. and height values. The spatial patterns of trees were then examined for all trees by plot and remeasurement time using the commonly used $L(r)$ transformation of Ripley's K univariate function as well as the pair correlation function, $g(r)$ (Illian *et al.* 2008), as implemented in the SpatStat package of the Freeware Software R, version 2.8.0 (<http://www.r-project.org>, accessed July 9, 2009). For all functions, an isotropic edge correction was applied (Ripley 1988, pp. 32–33). For the pair correlation function, the default the Epanechnikov kernel recommended by Stoyan & Stoyan (1994) (page 285) within $[-h, h]$, where $h = 0.2/\sqrt{\lambda}$ was used. This was repeated for small trees, defined as trees with d.b.h. ≤ 7.0 cm. Mast & Veblen (1999) defined small trees as those with d.b.h. ≤ 4.0 cm; however, we considered a limit of 7.0 cm to be more appropriate for these structurally complex stands. The inhomogeneous $K(r)$ measure was also estimated for all trees, as well as for small and large trees separately, based on estimated densities using a polynomial trend surface, and converted to an equivalent $g(r)$ inhomogeneous measure for comparison. The bivariate $K_{12}(r)$, $L_{12}(r)$ and $g_{12}(r)$ functions were calculated for small versus large trees, along with the inhomogeneous bivariate $K_{12}(r)$ and $g_{12}(r)$. In all cases, the functions were calculated over a range of distances around each tree and these distances truncated to a maximum radius of 10 m to avoid spurious results caused by fewer observations at longer distances. These analyses were used to graphically examine the proposed hypotheses 1 through 3.

For hypotheses 4 and 5, spatial maps of dead trees over the 16-year period were used to indicate mortality trends for small versus large trees and also mortality relative to competition at the beginning of the period. The competition measure was based on Adler (1996) (see also Illian *et al.* 2008, p. 435), as follows:

¹www.climate.weatheroffice.ec.gc.ca/climate-normals/ (accessed October, 2008).

$$c_i = \sum_{j=1}^4 dbh_j^\alpha \times \exp(-\delta \times dist_{ij}) / dbh_i^\beta$$

where c_i is the measure of competition for tree i ; dbh_j is the d.b.h. of a neighbouring tree, j , respectively; $dist_{ij}$ is the distance between trees i and j . Estimates of the parameters α , δ and β were chosen as part of a system of equations used to predict diameter increment using the sampled data (unpublished data). This competition measure was calculated for each live tree in 1988 using the four nearest neighbours to each tree. Also, the bivariate $L_{12}(r)$ and $g_{12}(r)$ functions were used to examine the relationship between cumulative mortality for the 16-year period (i.e. from 1988 to 2004) and large trees at the first time of measurement (i.e. 1988). Since mortality rates are commonly low for many stand types, density estimates over the spatial window would be very poor. Only the homogeneous bivariate $L_{12}(r)$ and $g_{12}(r)$ functions were used.

For all spatial point process functions, changes over time were shown by plotting all functions for all times on the same graph. As a result, no confidence envelopes were displayed. For modelling stand dynamics, additional trees that reached 1.3 m during the time period

of the study would need to be included in any analyses. However, in this analysis, only trees that were greater than 1.3 m in height in 1988 were included. This resulted in a clearer view of the spatial arrangements of these trees over time.

RANDOM COEFFICIENTS MIXED MODEL

As noted, spatial point process analyses were often represented as graphs illustrating changes in relationships over distance. However, as the number of replicates in time and space increased, interpretation becomes more difficult. As an alternative to graphical presentation of all replicates at all times, estimates of $g(r)$ and $L(r)$ for r from 0 to 10 m in 0.2-m increments were obtained for each of the six plots at four measurement times (i.e. 24 measures). Then, polynomial models with $g(r)$, $L(r)$ or $L(r)-r$ as the dependent variable and powers of r as the predictor variables were fit using all measures (i.e. population-averaged model). The coefficients of the polynomial model were then allowed to vary by replicate and by repeated measure resulting in the random coefficients model. In addition, a second random coefficients mixed model was fit, where coefficients were allowed to vary with replicate only. A residual

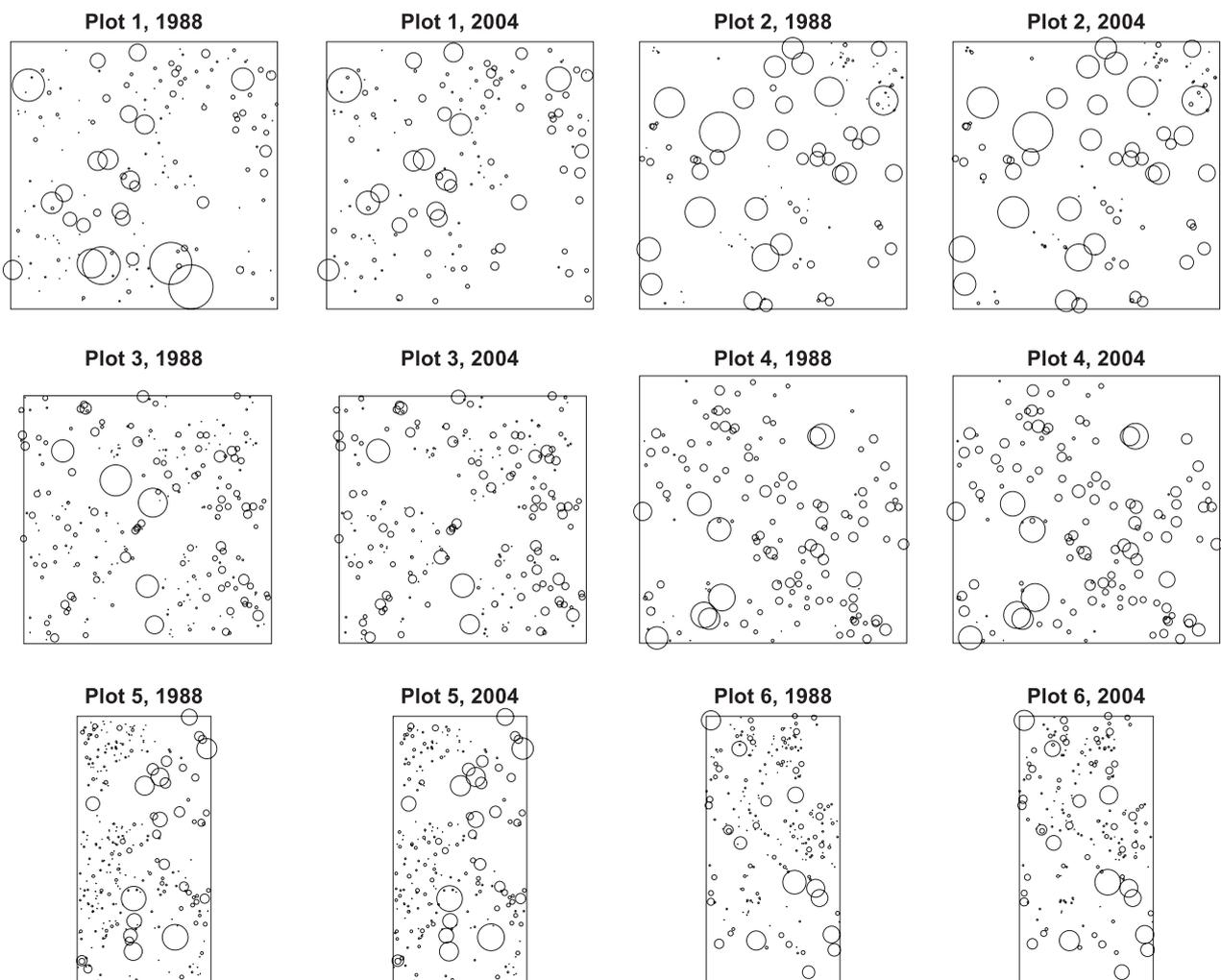


Fig. 1. Map of tree locations by plot for the first (1988) and last (2004) measurements. Sizes of circles indicate relative diameters (d.b.h. values). Plot 1 indicates loss of large trees (ranging in size from 9 to 27 cm d.b.h., bottom of plot) in the 1988 to 1992 period. All plots had a wide range of tree sizes dispersed over space, diameter increases over time and had gap areas with no trees.

information (also called restricted information) maximum likelihood (REML) approach was used to fit the population average and random coefficients models (PROC MIXED, SAS Version 9.1.3, SAS Institute Inc., Cary, NC, USA). In the first step of REML, a least squares method was used to find coefficients for the fixed effects, which, in this case, were the population average coefficients. In the second step, residuals from this model were used to find the maximum likelihood estimates of: (i) the residual variance, in the case of the population average model; (ii) variances in coefficients over space (i.e. replicate) and time (i.e. repeated measure), and the residual variance for the first random coefficients model; and (iii) variances in coefficients over space, and the residual variance for the second random coefficients model. The residual log likelihood was used to indicate model fit (-2 Res LL), with a smaller value indicating a better fit. Also, reduction in the estimated residual variance for the random coefficients mixed models relative to the population average model was used to indicate the impact of time and/or space on the $g(r)$, $L(r)$ and $L(r)-r$ functions. This approach facilitated the interpretation of spatio-temporal patterns by allowing for comparisons of variability in coefficients over time versus over the replicates. Although not used in this study, random coefficients modelling could also be used to group similar replicates and times by clustering the estimates of coefficients for each time and space measure in the sample dataset.

Results

STAND CHARACTERISTICS

Plots 1, 2 and 4 had the lowest densities (trees per ha), followed by plot 3, and then plots 5 and 6 with the highest densities (Table 1). As noted earlier, plots 5 and 6 were established as 0.05 ha in size because of the higher densities. The changes in density over time were largely due to mortality, with more than 1000 trees per ha dying over the 16-year measurement period in plots 5 and 6. However, in plot 1, nine trees were cut in the period from 1988 to 1992, four of which were very large ($> 50 \text{ cm d.b.h.}$). In plot 3, one live and two dead trees were cut in the same period.

Mean d.b.h. and height values were similar for plots 1 to 4 and smaller for plots 5 and 6, which were denser than the other plots (Table 1). Maximum d.b.h. values were also larger for plots 1 to 4 but maximum heights were similar across all plots. Mean d.b.h. increased over time, except for plot 1 from 1988 to 1992, when the large trees that were cut resulted in a decrease in mean d.b.h. Mean heights also increased over time for all plots,

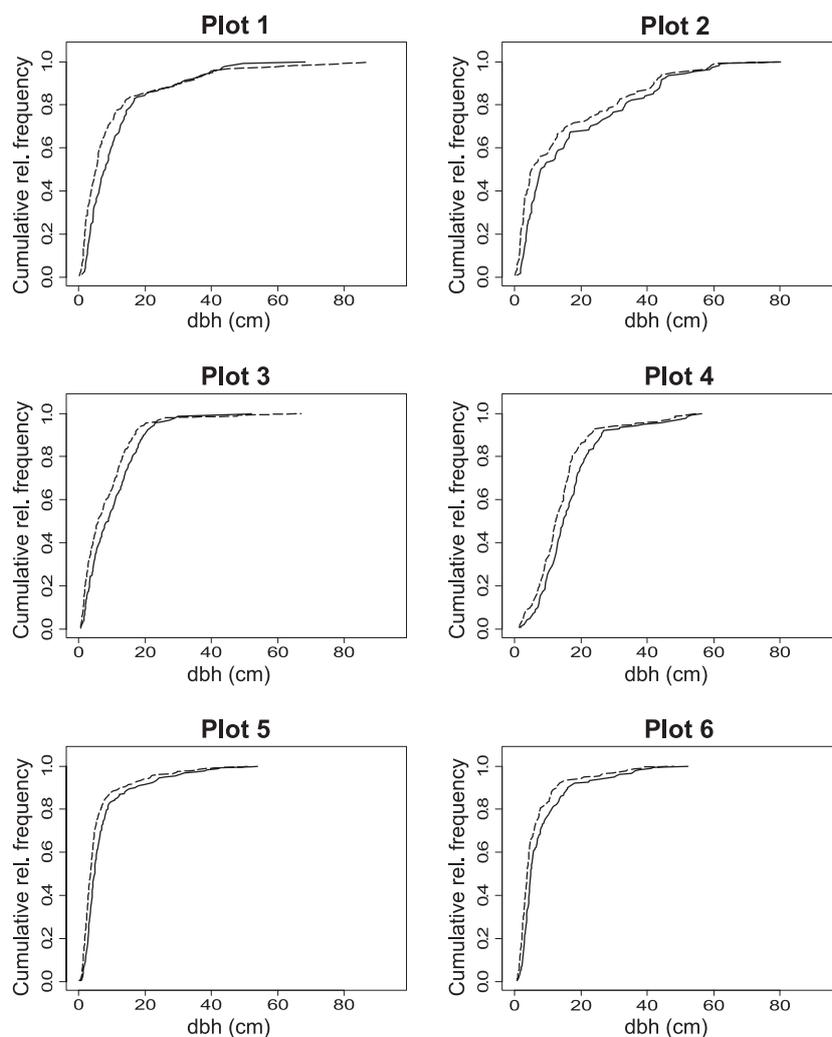


Fig. 2. Changes in the cumulative relative (Rel.) frequency for diameter (d.b.h.) at the beginning of the 16-year measurement period in 1988 (dashed line) and at the end in 2004 (solid line) showing a shift towards larger sizes and therefore fewer small trees over time. Plot 4 has fewer small trees, plots 5 and 6 have more small trees, and plot 5 has a more uniform distribution of tree sizes.

including plot 1. Maximum heights showed little change over time, indicating very little height growth for the largest trees on each plot.

The map of trees in plot 1 showed few very large trees, particularly after 1992, and these appeared to be somewhat clustered in space (Fig. 1). Small trees were more numerous and appeared to be more randomly dispersed, except for a gap in the lower right. No obvious changes over time were shown for plot 2, and the stems appeared to be randomly dispersed. Similar patterns were shown for plots 3 to 6, although plot 4 had fewer smaller trees and showed a shift towards larger trees over time.

Changes in the empirical distributions (i.e. cumulative relative frequency of stems) for d.b.h. and for height indicated decreasing steepness over time, as small trees increased and moved into larger size classes (Figs. 2 and 3). Plots 5 and 6 had a larger proportion of smaller trees (steep distribution), whereas plot 2 had a more even distribution of tree sizes (i.e. the empirical distribution is closer to a 45° line). Plots 5 and 6 which were denser showed more change in height distribution than in d.b.h. distribution over time, particularly for smaller trees.

SPATIAL PATTERNS OVER TIME

The assumption of a homogeneous process may not hold for these multi-aged, structurally diverse IDF stands. Therefore, univariate and bivariate inhomogeneous functions were estimated, along with homogeneous functions. As noted in Materials and methods, the first step in the analyses for inhomogeneous functions was to estimate the densities around each tree or, conversely, over the small spatial windows (i.e. a density map), leading to an increase in uncertainty. In comparison with homogeneous functions, differences were minimal, and for the plot sizes used in this study, the estimated density maps might not be sufficiently accurate. Also, as noted by Ripley (1988, p.7), it is often difficult to determine whether the process is inhomogeneous since a particular realization of a homogeneous process may appear inhomogeneous. As a result, all interpretations were based on the homogeneous functions.

For all trees combined, a tendency towards clustering at very short distances was indicated by $g(r)$ for plots 1 (Fig. 4a), 3, 4 and 5 (not shown). No marked changes in the spatial point pattern of all trees over time were detected. For plots 2 (Fig. 4b)

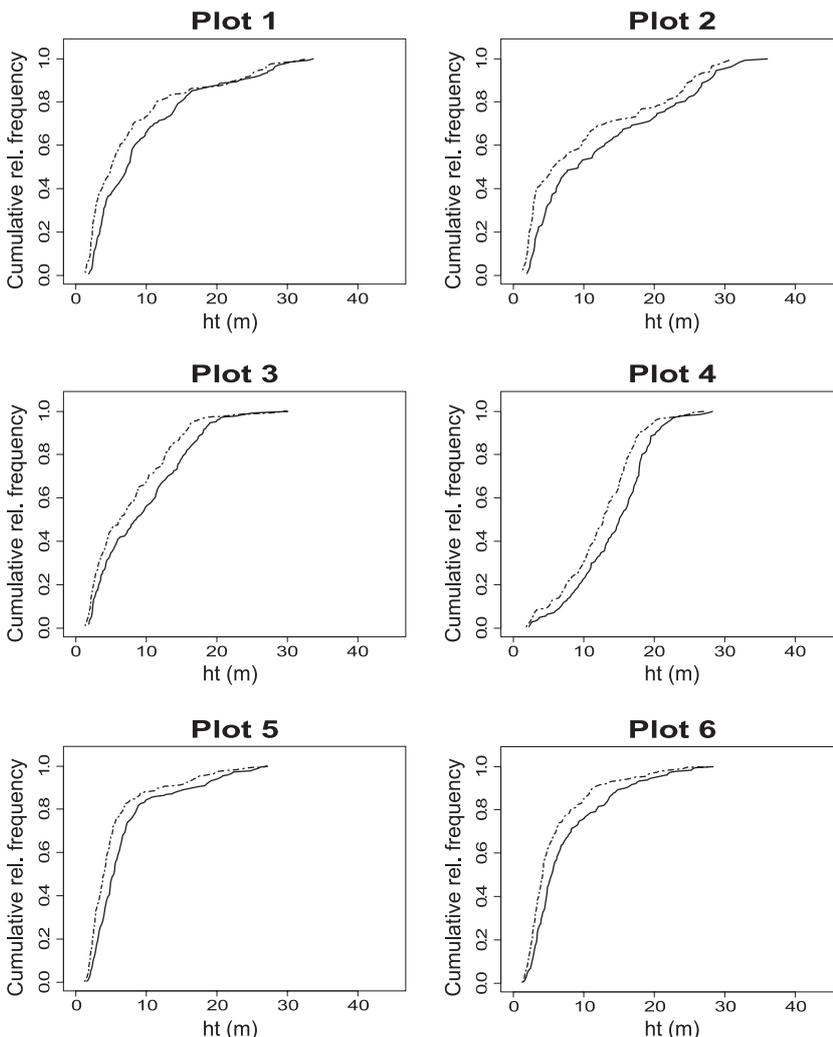


Fig. 3. Changes in the cumulative relative (Rel.) frequency for height (ht) at the beginning of the 16-year measurement period in 1988 (dashed line) and at the end in 2004 (solid line) showing movement towards larger sizes and therefore fewer small trees over time. Changes in height distribution over time are similar to those noted for diameter, except that these changes are greater for height.

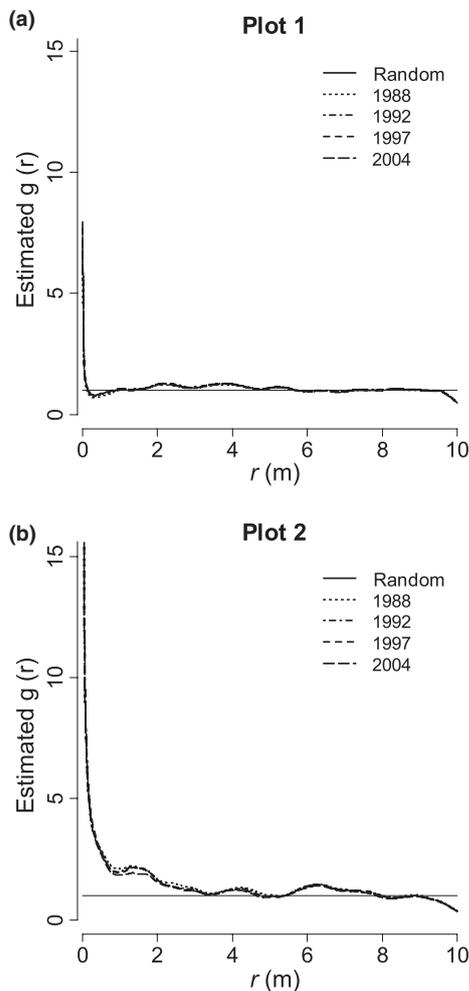


Fig. 4. Pair correlation function, $g(r)$, for: a) Plot 1 over time using the isotropic (e.g. Ripley's) correction for edge effects versus the spatial distribution under a random process. The function indicates possible clustering at very short distances. Plots 3, 4 and 5 are similar and are not shown; and b) Plot 2 over time using the isotropic (e.g. Ripley's) correction for edge effects versus the spatial distribution under a random process. The function indicates clustering at very short distances. Plot 6 is similar and is not shown.

and 6 (not shown), a tendency towards clustering of all trees was shown for distances to 2.0 m, without any obvious changes over time.

Clustering of small trees for short distances was detected for plots 1 (Fig. 5a) and 5 (not shown), with an increase in $g(r)$ over time for short distances. Since only trees present in 1988 were included in the analysis, this result was unexpected and is later discussed. For plot 2 (Fig. 5b), $g(r)$ indicated clustering of small trees up to 5 m with no noted changes over time. A similar result was obtained for plots 3 (Fig. 5c) and 6 (not shown) but for distances < 1.5 m. For plot 4, $g(r)$ indicated clustering at short distances with an approach to a more Poisson (random) distribution in time (Fig. 5d). However, plot 4 had very few small trees as shown in Figs. 1 and 2.

Small trees were generally attracted to large trees, based on the bivariate $g_{12}(r)$, with variations in the distances at which this occurred from < 0.5 m for plot 1 (Fig. 6a), to < 1 m for

plots 2 (Fig. 6b), 3 and 4 (not shown) and to < 3 m for plots 6 (Fig. 6c) and 5 (not shown).

Mortality over the 16-year period is as follows: plot 1, 12 trees; plot 2, 9 trees; plot 3, 27 trees; plot 4, 12 trees; plot 5, 62 trees; plot 6, 37 trees. As expected, dead trees were more commonly smaller trees and tended to cluster (Fig. 7). Mortality was higher in areas of higher competition for all plots, with no mortality in areas of very low competition (Fig. 8).

The bivariate $g_{12}(r)$ function also indicated attraction between dead trees and large trees (as of 1988), except for plot 1 which indicated repulsion (Fig. 9). However, because of the tendency towards clustered spatial patterns, the outcomes for mortality illustrated in Figs. 7–9 were difficult to interpret and will be later discussed.

RANDOM COEFFICIENTS MIXED MODEL

The fit of the polynomial models with $g(r)$, $L(r)$ or with $L(r)-r$ as the dependent variable for each of the 24 sets of data (i.e. six plots each with four measurements) and using powers of r as the predictor variables indicated that a fourth-degree polynomial represented the functions well. Based on variances in coefficients, only the intercept and the slopes of the first two polynomials (i.e. r and the square of r) varied greatly with replicates by time. Using the $L(r)-r$ function values as the dependent variable, the common population average model was fitted using a fourth-degree polynomial of r , resulting in a -2 residual log likelihood (-2 Res LL) value of 268.6 and an estimated residual variance of 0.0700. A random coefficients mixed model was then fit allowing these three coefficients to vary with time and replicate (i.e. plot) resulting in a much-improved (i.e. lower) -2 Res LL value of -3042.9 and an estimated residual variance reduced to 0.00334. A second random coefficients mixed model was then fit allowing the three coefficients to vary by replicate only, resulting in a -2 Res LL value of -2718.5 and an estimated residual variance of 0.005351, quite similar to that resulting from the model where coefficients varied with both time and replicate. For all three models, conditional residuals were approximately normally distributed and showed no obvious trends with time, indicating that assumptions of REML were met. Based on these results, it is apparent that more of the variation in the spatial patterning of all trees was due to replicates than to time.

Discussion

Stands of IDF growing as the dominant species on dry sites of the IDF BEC zone of BC are structurally complex, largely because of the moderate shade tolerance of this Douglas fir variety and the disturbance history of the stands. In this study, plots were established in stands that had little or no recent harvest and which had been protected from fire for much of the last half century. The structural complexity was evidenced by the range of negative d.b.h. values and heights. However, variation in the relative frequencies did occur over the six plots of the study, with some sites having relatively more small trees and higher densities.

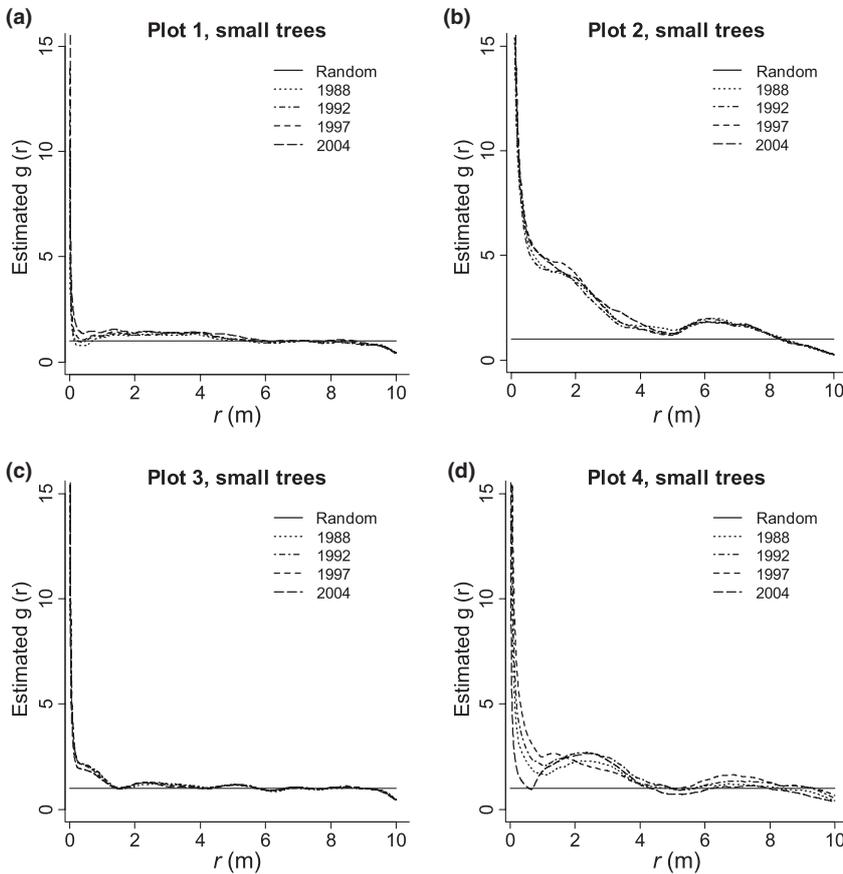


Fig. 5. Pair correlation function, $g(r)$, for small trees (d.b.h. ≤ 7.0 cm) over time using the isotropic (e.g. Ripley's) correction for edge effects versus the spatial distribution under a random process (random) showing: a) clustering for plot 1 at very short distances only, and no noticeable changes over time. Plot 5 is similar and is not shown; b) a tendency towards clustering at short distances (less than 5 m) for plot 2, with no noticeable changes over time; c) a tendency towards clustering at distances less than 1.5 m for plot 3, with no noticeable changes over time. Plot 6 is similar and is not shown; and d) a tendency towards clustering at distances less than 1 m for plot 4. However, because of the low numbers of small trees in plot 4, particularly for 2004, results may not be reliable.

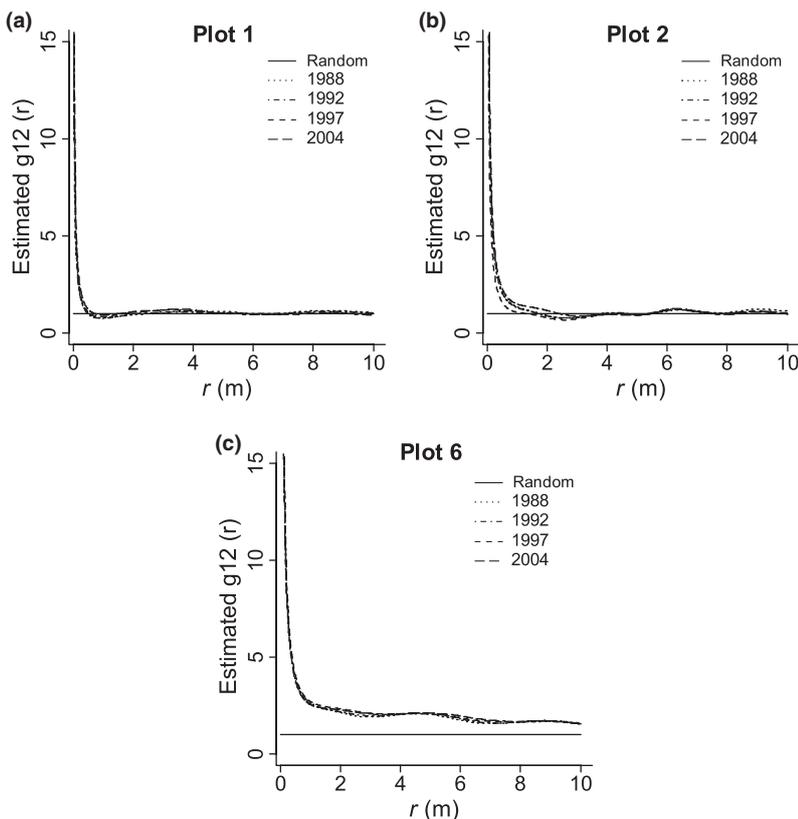


Fig. 6. Bivariate partial pair correlation function, $g_{12}(r)$, for small trees (d.b.h. ≤ 7.0 cm) versus large trees (d.b.h. > 7.0 cm) over time using the isotropic (e.g. Ripley's) correction for edge effects versus the spatial distribution under a random process (random) showing a tendency for attraction: a) between small and large trees at very short distances for plot 1, with no marked changes over time; b) between small and large trees at short distances (< 1 m) for plot 2; and c) between small and large trees at particularly at short distances (< 3 m), with no marked changes over time for plot 6. Results (not shown) for plots 3 and 4 are similar to plot 1, and plot 5 was similar to plot 6.

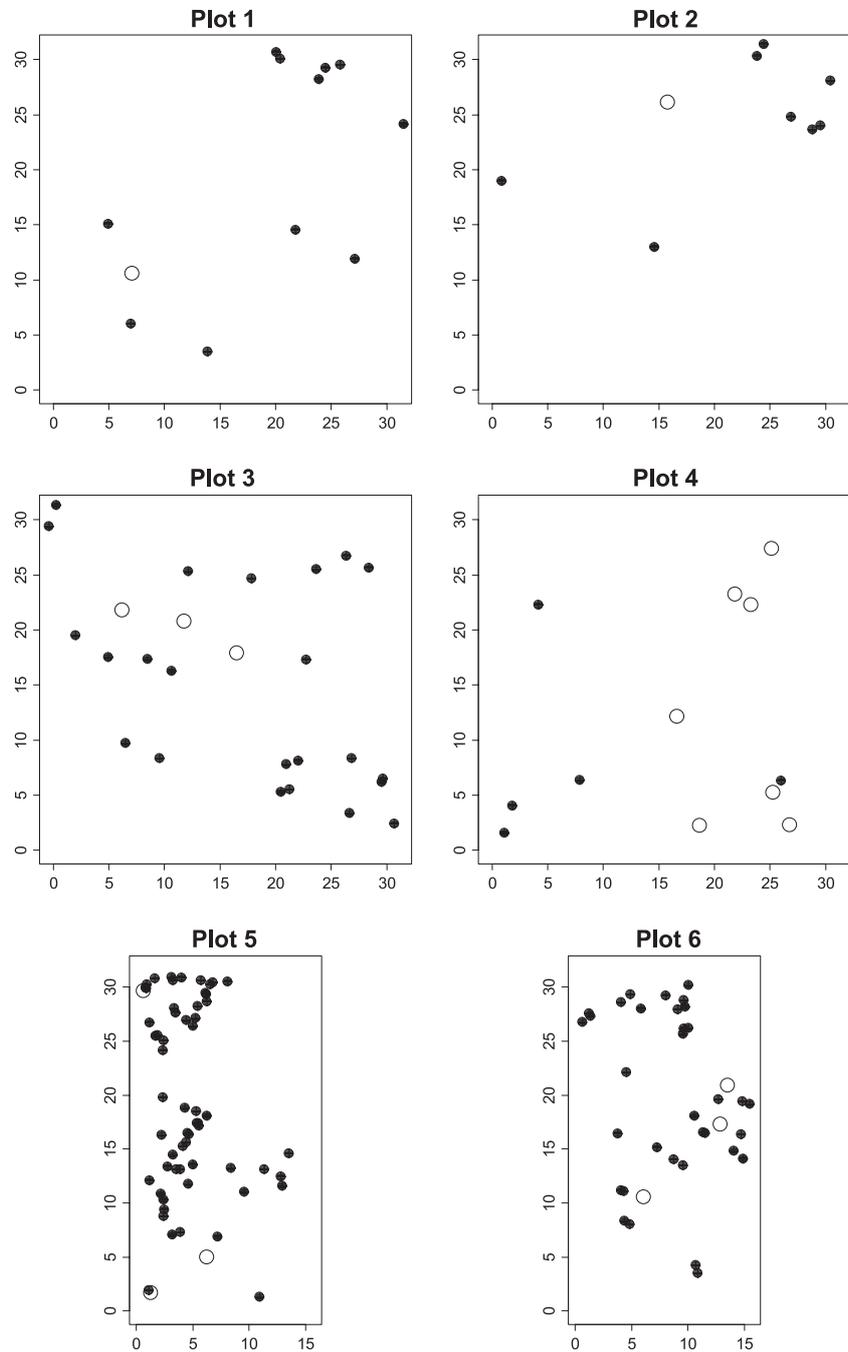


Fig. 7. Spatial pattern for dead trees over the 16-year period. Large trees (>7 cm d.b.h.) are shown as open circles, whereas small trees (≤ 7 cm d.b.h.) are shown as dots. All plots except plot 4 had greater mortality of small trees. Plot 4 had fewer small trees at the beginning of the period in 1988. There is some evidence of clumping at short distances for all plots.

Measures of spatial pattern were used to investigate the spatial complexity of these multi-aged stands. The common assumption of a homogeneous process over the spatial window might not be met for these and other structurally complex forests. For example, Getzin *et al.* (2008) used both homogeneous and inhomogeneous spatial metrics, along with a case studies approach recommended by Diggle *et al.* (2007). Therefore, inhomogeneous functions were also calculated for this study. However, differences between inhomogeneous and homogeneous spatial metrics were small. Also, given the plot sizes, the density estimates over the spatial window required for inhomogeneous functions were not precise. Finally, as noted earlier, Ripley (1988, p. 7) indicated that apparent inhomogeneity

might be a result of a single realization of a homogeneous process. Therefore, interpretations of all spatial patterns were based on the more commonly used homogeneous spatial point process functions.

Using all trees, we found evidence of clustering at shorter distances. This result was consistent with the first hypothesis proposed for these forests and with other studies. For example, Hanewinkel (2004) compared spatial patterns of coniferous uneven-aged and even-aged stands in the central Black Forest area of Germany and found that even-aged stands showed regular distributions of standing volume, whereas uneven-aged stands were more clustered. Druckenbrod, Shugart & Davies (2005) also found clustering at shorter distances, particularly

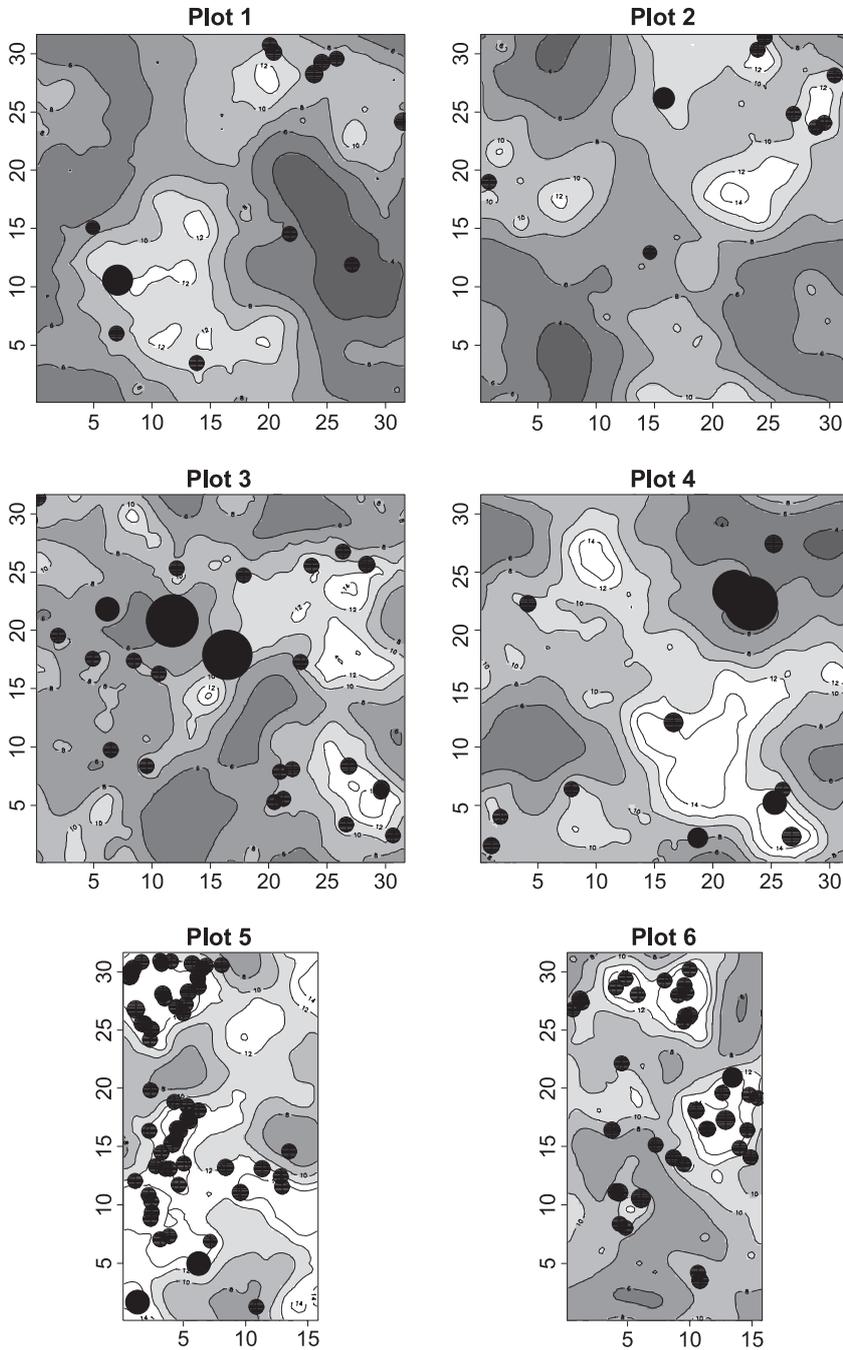


Fig. 8. Spatial pattern for dead trees over the 16-year period (dots, size increase with d.b.h.), along with competition at the beginning of the period (1988). Competition is shown in grey scale with white as very high competition and dark grey as very low competition.

for understorey trees, in complex forests of the Virginia, Piedmont, USA, based on measures of five plots at one point in time.

When trees were separated into two size groups, small trees with negative d.b.h. values ≤ 7 cm were clustered in this study. These results were consistent with the second hypothesis we proposed for these stands. Regeneration is more likely to have occurred in groups because of more favourable microsite conditions. For tree species with large heavy seeds, clusters of regeneration also occurred as a result of localized seed dispersal. However, the lighter-winged seeds of IDF could travel longer distances and clustering is less likely due to localized seed rain.

A number of studies have reported a trend towards a more regular distribution over time, as a result of competition among trees (e.g. Oliver & Larson 1990; Moer 1997). Conversely, Peterson & Squiers (1995) found that aspen (*Populus tremuloides* L.) growing in mixed aspen – white pine (*Pinus strobus* L.) stands became more clumped over time and attributed this result to high levels of vegetative reproduction. For these IDF stands, there was little change in the measures of spatial patterns over the 16-year period covered in this study for all trees and for small trees separately. Since these forests are multi-aged with a continuous distribution of tree sizes over a wide range, changes in spatial patterning as a result of competition-based mortality are more complex.

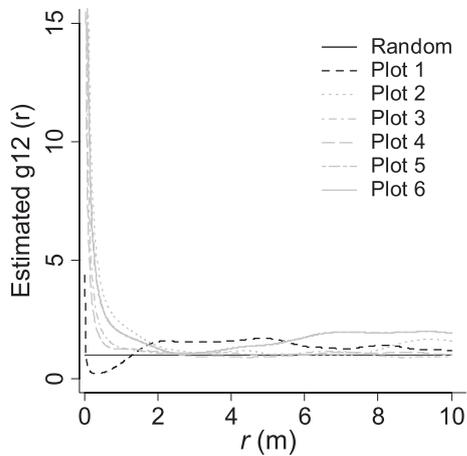


Fig. 9. Bivariate partial pair correlation function, $g_{12}(r)$, between trees that died in the 16-year period from 1988 to 2004 relative to large (> 7.0 cm d.b.h. based on 1988 measures) trees that were alive at the end of the period, using the isotropic (e.g. Ripley's) correction for edge effects for all plots. The spatial distribution under a random process (random) is shown for comparison. For short distances (1 to 2 m depending upon the plot), the $g(r)$ function shows a tendency for an association between trees that died and large trees present at the end of the measurement, except for plot 1 (shown in black), which shows a tendency towards repulsion.

In terms of the third hypothesis, there were two possible spatial arrangements proposed. In coastal Douglas fir and in other species that are light-demanding, seedlings regenerate in gaps (Daniels & Gray 2006). However, for IDF on the dry sites in this study, small trees were located closer to large trees than expected under random chance. This indicated that regeneration is likely to have occurred on moister microsites near larger trees, rather than in gaps with higher light away from large trees. However, on moister sites than those included in this study, it is possible that IDF may be more commonly found in gaps away from shading of large trees.

The numbers of dead trees over the 16-year period varied by plot, but there was evidence of clustering for all plots, as has been noted for other complex stands (e.g. Druckenbrod, Shugart & Davies 2005). On all plots, dead trees were predominantly small. Also, there was evidence that dead trees were closer to large trees than expected under a random spatial distribution and that mortality was more common in areas of high competition. For larger dead trees this seems to support competition-based mortality. However, for smaller trees, the mortality process is easily explained. Small trees were shown to be aggregated with large trees. Therefore, germination success and early survival was likely higher on moister microsites around large trees. The greater mortality of smaller trees near large trees might be the result of this early germination and survival success, which resulted in increased competition-based mortality over time.

As expected, dead trees were more commonly smaller trees and tended to cluster (Fig. 7). Mortality was often higher in areas of higher competition for all plots, with no mortality in areas of very low competition, particularly for plots 5 and 6 (Fig. 8). The bivariate $g_{12}(r)$ function also indicated attraction

between dead trees and large trees (as of 1988), except for plot 1 which indicated repulsion (Fig. 9). However, because of the tendency towards clustered spatial patterns, these three outcomes are difficult to interpret.

Because of the number of replications and remeasurements in this study, an alternative approach to examine variations in spatial patterns over plots and times was used. Based on the random coefficients mixed modelling approach, variation among replicates was higher than among times. Changes in local site conditions as well as in seed availability would have contributed to differences in spatial arrangements of trees among plots. However, over a longer period of time, increased differences in spatial arrangements due to time would be expected. The random-coefficients mixed-modelling approach used in this study provided an effective mechanism for comparing changes in spatial patterns over time, particularly as the number of replicates and times increased. Clustering of estimates of coefficients for each replicate and repeated measure obtained using mixed models could also be used to group similar spatio-temporal patterns which might give further insights into stand dynamics.

The prevention of large fires in these stands is expected to alter the stand structure, relative to what would occur under a natural fire regime. For example, Keeling, Sala & DeLuca (2006) noted increased tree densities in mixed Ponderosa pine (*Pinus ponderosa* Laws.) and IDF stands in the USA as a result of lower mortality under fire prevention. For mixed conifer forests in Arizona, USA, Mast & Wolf (2006) found increased densities for some species, which they hypothesized as being at least partially due to fire suppression. Similarly, these IDF stands on dry sites might be expected to increase in density under fire protection, as fire-related mortality was reduced or removed and regeneration of this moderately shade-tolerant species occurred. However, mortality as a result of other agents (e.g. insects) may be expected to increase as less robust potential host trees that might have been lost to fire survive under fire suppression. Also, any increase in density would be limited by moisture availability. The dynamics of these forests may approach a steady state of regeneration and mortality over the long term. Because of the moisture limitations of these dry sites, clumped spatial patterns are likely to continue, rather than approach a more regular spatial distribution as found particularly in more even-aged stands.

Conclusions

The spatio-temporal patterns of pure, multi-storied, multi-aged IDF stands on dry sites of interior BC were studied using replicated, repeated-measures data, using analysis at each point in time and using a random coefficients mixed-model approach. Trees, particularly small trees, were clustered, with larger differences in spatial patterns between replicates than between times. Over the 16-year measurement period, no approach towards a more regular spatial distribution was found. Because IDF was moderately shade-tolerant, smaller trees were associated with large trees, likely because large trees provided moister microsites. Under continued fire suppression,

these stands may increase in density, but further increases are likely to be low because of moisture limitations to regeneration and may be counterbalanced by mortality due to other agents. Also, spatial patterns are expected to remain clumped, as the stands approach a steady state of mortality and regeneration. Similar results might be expected for other naturally multi-storied, multi-aged stands, including other mixed species forests in south-eastern BC. The use of a random coefficients mixed model approach for examining the spatial and temporal variation in these and other stands shows promise, separating the variance in spatial patterns over replicates from the variance in time.

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Received 6 March 2009; accepted 18 June 2009
Handling Editor: James Cahill