

Density-dependent effects on tree survival in an old-growth Douglas fir forest

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Summary

1 We mapped the locations of live and dead trees in a large forest plot dominated by pioneer Douglas fir (*Pseudotsuga menziesii*) with an understorey of the invading late-successional species western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) on Vancouver Island, British Columbia, Canada, to test for intra- and interspecific density-dependent effects on tree survival.

2 We analysed both the spatial patterning of trees in the plot and the relationships between neighbourhood density and tree survival. We also examined the effects of additional variables (principally elevation) as covariates in our neighbourhood analyses.

3 Both the spatial and initial neighbourhood analyses suggested strong intra- and interspecific density-dependent effects on tree survival. Douglas fir survival was significantly higher in less dense patches of conspecifics and non-random tree death led to regularly spaced survivors, as expected from intraspecific competition. The significantly lower survival of western hemlock in denser patches of Douglas fir and the resulting negative spatial association between surviving trees of these two species were consistent with interspecific competition.

4 However, having controlled for the influence of elevation on tree survival (probably mediated by variation in soil moisture) in neighbourhood analyses, although the survival of the pioneer Douglas fir trees was still subject to strong density-dependent effects, variation in its density in the overstorey no longer appeared to influence the survival of the invading late-successional species. There was, however, evidence for asymmetric interspecific density dependence between the two late-successional species since western hemlock mortality tended to be higher in denser patches of western red cedar.

5 Our results emphasize the importance of considering confounding factors in studies that seek evidence for density dependence.

Key-words: competition, confounding effect, neighbourhood analysis, population dynamics, Ripley's *K* function; logistic regression, spatial pattern, stand mapping.

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Introduction

Density-dependent effects are widely hypothesized, and in many instances have been shown to play an important role in the population dynamics of forest trees. There is, for example, abundant evidence that intraspecific competition affects the growth and survival of pioneer trees that initially colonize large disturbance openings. Trees of many pioneer species

undergo self-thinning, with higher rates of mortality in denser patches of conspecifics, often leading to regularly spaced survivors (Ford 1975; Yeaton 1978; Cannell *et al.* 1984; Weiner 1984; Peet & Christensen 1987; Kenkel 1988; Duncan 1991; Newton & Jolliffe 1998). Negative density-dependent effects have also been documented within species for recruitment, growth and survival in tropical forest trees, and such processes could contribute to high species diversity in these areas (Augspurger 1984; Connell *et al.* 1984; Condit *et al.* 1994; Wills *et al.* 1997).

The extent to which density-dependent interactions between species plays a role in the dynamics of tree populations is however less clear. It is frequently hypothesized, for example, that interspecific competition affects the rate of replacement of pioneer by late-successional species in forest succession (Connell & Slatyer 1977; Oliver 1980; Peet & Christensen 1980; Finegan 1984; Pickett *et al.* 1987). Pioneer trees may capture resources in disturbance openings to a sufficient extent that they prevent late-successional species from recruiting to the canopy by lowering their growth rate or survivorship in the understorey. Late-successional species can thus only recruit successfully in openings formed by the death of pioneer trees. Indeed, late-successional species are often observed to be spatially clumped in canopy gaps and negatively spatially associated with overstorey pioneer trees (Williamson 1975; Veblen *et al.* 1980; Stewart 1986a; Taylor & Zisheng 1988). However, although many of the investigations into the role of interspecific competition in driving successional change have been conducted in communities of annuals and herbaceous perennials, an overall picture emerges of mixed outcomes, with evidence both for and against density-related effects (Abul-Fatih & Bazzaz 1979; Uhl & Jordan 1984; Armesto & Pickett 1986; Chapin *et al.* 1994; Peterson & Squiers 1995a; Halpern *et al.* 1997).

A significant challenge in evaluating the importance of density dependence is finding methods suitable for detecting such effects. This is particularly problematic for forest trees, which are typically large, long-lived individuals whose populations are not readily amenable to direct experimental manipulation. Consequently, the importance of density dependence in tree population dynamics is often inferred from field studies that either investigate correlations between some measure of plant performance (e.g. growth or survival) and the density of neighbouring plants (Weiner 1984; Penridge & Walker 1986; Peterson & Squiers 1995a; Wills *et al.* 1997) or investigate the spatial arrangement of individuals in a population (Pielou 1960, 1961; Yeaton 1978; Kenkel 1988; Duncan 1991; Peterson & Squiers 1995b). Nevertheless, a potential problem with these approaches is that patterns consistent with density dependence can be confounded with or masked by variation in other factors that influence the spatial distribution or performance of plants (Pielou 1960; Chapin *et al.* 1989; Wilson 1991; Duncan 1995). Most field studies have indeed failed to consider variation in these factors, although several have minimized local site variation by selecting sites that are environmentally homogeneous (Kenkel 1988; Biondi *et al.* 1992; Peterson & Squiers 1995a) or have controlled statistically for variation in such factors (Duncan 1991; Wilson 1991).

Our aim in this study, is to quantify the importance of density-dependent effects on tree survival in

an old-growth Douglas fir forest and to highlight the extent to which patterns consistent with density dependence can be confounded with other processes. The study was carried out in forests of the Pacific North-west, North America, that are dominated by Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). In these forests a predictable sequence of species replacement occurs in large disturbance openings formed by wildfire. Douglas fir, a shade-intolerant pioneer tree, usually establishes first and forms dense, nearly monospecific stands. Subsequently, late-successional species such as western hemlock and western red cedar (*Thuja plicata* Donn ex D. Don) establish beneath the Douglas fir and eventually grow to dominate the canopy (Franklin & Hemstrom 1981). Light is considered to be a key resource limiting the rate of colonization and growth of species in these forests (Spies & Franklin 1989).

We took advantage of the slow decomposition rate of dead stems in our study area to reconstruct the spatial patterning of live and dead individuals in a single large study plot. We then tested if tree mortality had been spatially non-random and whether it was consistent with the patterns expected if both intra- and interspecific density-dependent effects had contributed to tree death. Specifically, we predicted that: (i) intraspecific competition should have resulted in higher rates of Douglas fir mortality in denser patches of conspecifics, causing the surviving individuals to be more regularly spaced than expected from random mortality, and (ii) asymmetric interspecific competition should have resulted in higher mortality of the late-successional species in denser patches of Douglas fir, so that the surviving late-successional trees would be more negatively associated with surviving Douglas fir than expected due to random mortality and would be spatially clumped in canopy openings.

Our study plot was located on a hillside with the highest and lowest points differing in elevation by about 33 m. Local variation in site conditions across such elevation gradients could influence tree growth and survival (e.g. Becker *et al.* 1988). We therefore examined the extent to which survival was correlated with elevation in our plot, and the extent to which patterns consistent with density dependence could be confounded by environmental heterogeneity.

Methods

STUDY SITE AND DATA COLLECTION

The study site is in an old-growth forest that forms part of a larger coastal forest chronosequence that is being used by the Canadian Forest Service to study the changes caused by converting old-growth coastal

temperate forests to managed forests (Trofymow & Porter 1998). It is located in the Greater Victoria Watershed District on southern Vancouver Island (48°38', 123°43') and is biogeoclimatically classified as within the Coastal Western Hemlock Zone, Very Dry Subzone (Klinka *et al.* 1991). This region is characterized by mild, wet winters and warm, dry summers, with a mean annual temperature of 9.3°C and mean annual precipitation of 1505 mm. The forest is dominated by pioneer Douglas fir with significant components of the late-successional species western hemlock and western red cedar, and minor components of western white pine (*Pinus monticola* Dougl.) and red alder (*Alnus rubra* Bong.). The understorey is overwhelmingly dominated by Salal (*Gaultheria shallon* Pursh).

In the summer of 1997, a 102 × 87 m (0.8874 ha) plot was established in an old-growth forest stand that had regenerated following a catastrophic fire more than 250 years ago. The plot was located at average elevation of 382 m a.s.l. on a south facing hillside with a slope of about 20° and an elevational range of 33 m from the lowest to the highest point. Four tree species, Douglas fir (Df), western hemlock (Hl), western red cedar (Rc) and western white pine (Wp), occurred in the plot. All live trees in the plot had their diameter measured at 1.4 m above the ground (diameter at breast height, d.b.h.) or were counted if they were less than 1.4 m tall. All dead trees were allocated to one of three classes: snag/log (snags are standing dead trees and logs are dead trees recently fallen on the ground with identifiable stumps or roots), high stump (> 0.5 m tall or decay class ≤ 3, according to Sollins 1982) and low stump (< 0.5 m tall or decay class > 3). The d.b.h. of dead trees was recorded at 1.4 m (or their highest point if less than 1.4 m tall). Each live and dead tree was identified to species and its geographical coordinates (*x*, *y* and elevation) were recorded relative to a reference point using a survey station (Nikon DTM-310; Melville, New York, USA).

Logs can be an important establishment substrate for late-successional species in forests of the Pacific North-west (Harmon *et al.* 1986) and, at least for western hemlock, it has been shown that the growth rate and survivorship of individuals is related to whether or not they establish on logs (Christy & Mack 1984). However, logs are not an important regeneration substrate in the very dry region of the Coastal Western Hemlock Zone that we worked in; very few western hemlock and western red cedar established on fallen logs in our plot (Wells & Trofymow 1998) and consequently we did not record this factor.

(Sternier *et al.* 1986; Kenkel 1988; Duncan 1991; Haase 1995), was used to quantify the spatial patterns of Df, Hl and Rc in the plot. It is usually more convenient to use the *L* function, a transformation of the *K* function, when comparing an observed pattern to a random pattern. The definition and form of the *L* function can be found in Ripley (1977) and the publications cited above. The estimate of the *L* function, $\hat{L}(h)$ at a given distance *h*, is expected to be zero when trees are randomly distributed. A departure from zero indicates that the observed pattern is non-random, with positive values of $\hat{L}(h)$ indicating clustering and negative values indicating regularity. The significance of departures from zero is tested using Monte Carlo simulation since the sampling distribution of $\hat{L}(h)$ is unknown.

We tested two null hypotheses concerning the univariate spatial distribution of trees in the plot. The first was the hypothesis that the trees of each species were randomly distributed in the plot, both pre-mortality (i.e. including both live and dead trees) and post-mortality (live trees only). Random coordinates of the same number of trees as were present in each empirical data set were generated 25 times. Approximate 95% confidence envelopes were estimated from the highest and lowest $\hat{L}(h)$ values obtained from these 25 simulations of the random point process; empirical values that lie outside these confidence envelopes indicate significant departure from spatial randomness. The second hypothesis was that of random mortality (Sternier *et al.* 1986; Kenkel 1988; Duncan 1991), i.e. that the spatial distribution of live trees does not differ from that expected if tree mortality had occurred at random. For each of 25 runs, random mortality was simulated by selecting and removing trees at random from the pre-mortality (live + dead trees) data set. The number of trees removed was set to equal the number of dead trees and departure from random was tested as above. The computations were done using S+SpatialStats (MathSoft 1996).

The *L* function can be extended to analyse bivariate spatial patterns, i.e. the spatial association between two species. We used the variance reduction bivariate estimate, $\hat{L}_{12}(h)$, given by Lotwick & Silverman (1982). $\hat{L}_{12}(h)$ provides evidence of spatial association between species 1 and 2: $\hat{L}_{12}(h) = 0$ indicates spatial independence of the two species, while positive and negative values indicates positive and negative association, respectively. Statistical evidence of a departure from zero can be evaluated by Monte Carlo simulation as in the univariate case. Here, approximate 95% confidence intervals were estimated from high and low values of the function $\hat{L}_{12}(h)$ generated from 25 toroidal shifts of one species with respect to the other (Diggle 1983). Values of $\hat{L}_{12}(h)$ were calculated between species pairs of Df, Hl and Rc both pre- and post-mortality to test for changes in spatial pattern. $\hat{L}_{12}(h)$ was computed

SPATIAL PATTERN ANALYSIS

Ripley's *K* function, now a standard method for analysing univariate mapped point patterns in ecol-

using a BASIC program which is available in the *Journal of Ecology* archive on the World Wide Web (see the cover of a recent issue of the journal for the WWW address).

ELEVATION

For each species, we tested if the probability of mortality varied with elevation by comparing the mean elevation of live and dead trees in the plot. We also investigated how tree density varied with elevation both pre- and post-mortality. To do this, we estimated the elevation at each intersection of a 10×10 m grid overlaying the plot. The elevation at each grid intersection was estimated by interpolating from all of the recorded tree coordinates (x , y and elevation) using the default interpolation procedure in PROC G3GRID in SAS version 6.11 (SAS Institute 1990). At each grid intersection we also counted the number of live and dead trees of each species within a 5-m radius to avoid overlap sampling and then correlated tree density with elevation for the 80 grid intersections that were 10 m or more away from the plot boundaries.

NEIGHBOURHOOD ANALYSIS

Negative intra- or interspecific density dependence should be evident as lower survival (higher mortality) of trees in denser patches of surviving trees of their own or other species, respectively. We tested if dead trees tended to occur in locally denser patches than live trees by counting the number of live trees of each species within a prescribed radius of each live and dead tree. Because density effects could potentially vary with the radius used to define the local neighbourhood, we present results from analyses using three neighbourhood radii: 5, 7.5 and 10 m. Furthermore, because trees close to the plot edges had neighbours outside the plot, only those trees a distance equal to the neighbourhood radius or more away from the plot edges were included in these analyses.

We used logistic regression to test for a relationship between tree survival and neighbourhood density. However, the significance of this relationship cannot be tested in the usual way because our data violate the assumption of independence. The response variable (whether a tree is alive or dead) may have been affected by the density of live neighbours but in turn may have affected that density (Firbank & Watkinson 1987). We therefore used the randomization approach of Mitchell-Olds (1987) to test the null hypothesis of no association between survival and neighbourhood density. One randomization consisted of randomly assigning values of the response variable (alive or dead) to the values of the predictor variable (neighbourhood density) and then calculating the change in deviance from the logistic

regression between survival and density. This randomization procedure was repeated 1000 times to generate a null distribution of the change in deviance assuming that tree survival was random with respect to neighbourhood density. The observed change in deviance was then compared with this null distribution to determine the significance of the observed relationship.

We conducted two types of analysis using logistic regression. The first tested for a significant relationship between tree survival and the density of a neighbouring species by including the neighbourhood density of that species alone as a predictor in logistic regression. The second tested for a significant relationship between tree survival and the density of a neighbouring species by including the neighbourhood density of that species last in a multiple logistic regression that already included elevation and the neighbourhood density of the remaining species as predictor variables. This second analysis tests for a significant relationship between survival and the density of a neighbouring species having statistically controlled for factors that could potentially confound such a relationship. For both types of analysis, we used the method of significance testing described above.

Although we were interested in density effects on tree survival, survival may be influenced not only by the density but also by the size of neighbours. In competition for resources, we would expect a tree surrounded by large neighbours to have a lower probability of survival than a tree surrounded by an equivalent number of small neighbours (Weiner 1984; Thomas & Weiner 1989). The larger trees in the plot were almost exclusively Df, although there was considerable variation in their size (Fig. 1). Most Hl and Rc trees were < 10 cm d.b.h. To test for an effect of neighbour size on target tree survival, we calculated the neighbourhood density of both large (> 50 cm d.b.h.) and small (≤ 50 cm d.b.h.) Df and analysed their effects separately.

Results

COMPOSITION AND SIZE STRUCTURE

A total of 2054 individual trees were mapped in the plot of which 62.5% (1284) were alive at the time of census (Table 1). For live and dead trees combined, Hl, Df and Rc were dominant in order of abundance, but for live trees the order of Rc and Df were reversed. Despite its lower numbers, Df dominated the stand, comprising 90% of the total live basal area and forming the main canopy with Hl and Rc occupying the mid-canopy and understorey. The diameter-distribution of Df was symmetrical with a lack of small trees (Fig. 1); this is a pattern typical of pioneer species that establish as approxi-

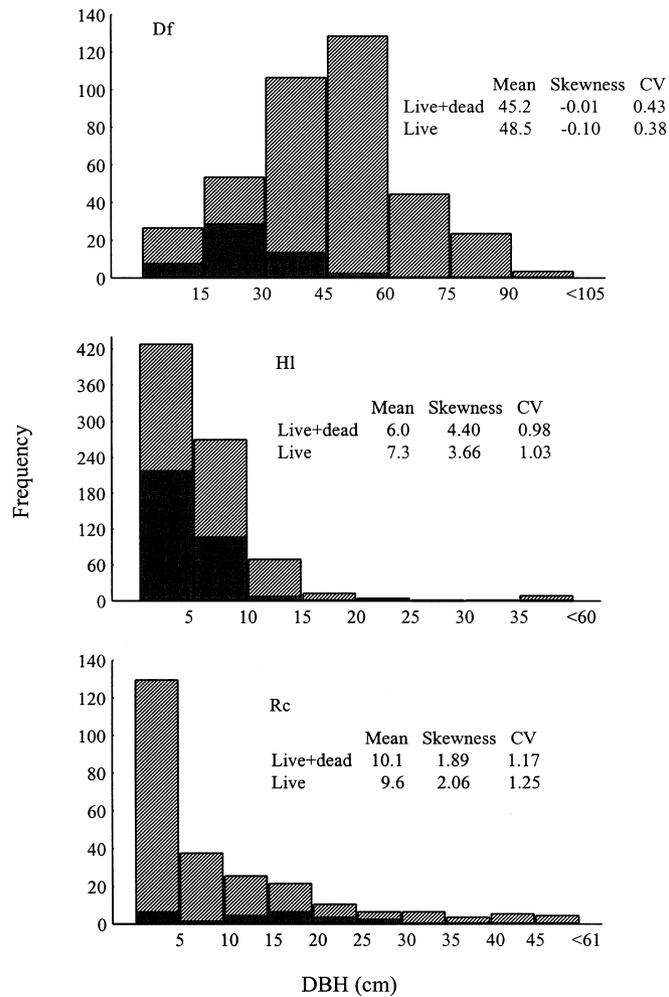


Fig. 1 Frequency distribution of d.b.h. of Douglas fir (Df), western hemlock (Hl) and western red cedar (Rc). The shaded areas represent dead trees. The inserts compare the d.b.h. distributions of live and dead trees combined (Live + dead) and live trees (Live).

mately even-aged cohorts in large disturbance openings. In contrast, the diameter-distributions of Hl and Rc were strongly right-skewed with most trees less than 10 cm d.b.h., suggesting that most individuals had established recently in the stand.

Western red cedar had a much lower proportion of dead trees in the plot (10.6%) compared with Hl

(42.2%) and Df (47.8%). In both Hl and Df, dead trees were concentrated in the smaller diameter classes (Fig. 1). Most dead Df were low, well decayed stumps while dead Hl were mostly snags or logs (Table 1). In contrast, mortality of Rc was approximately evenly distributed across trees up to 30 cm d.b.h.

Table 1 Two-way contingency table showing the number of trees in the study plot assigned to each category for Douglas fir (Df), western hemlock (Hl), western red cedar (Rc) and western white pine (Wp), and the total basal area of live trees > 0.5 cm d.b.h. of each species in the plot

Species	Live	Snag/log	High stump	Low stump	Total basal area (m ²)
Df	341	16	78	218	70.9
Hl	568	359	52	3	4.0
Rc	372	15	22	7	4.2
Wp	3	0	0	0	0.0
Sum	1284	390	152	228	79.0

Pre-mortality (live + dead) trees of Df were significantly regularly distributed at distances of up to 4 m, and were randomly distributed between 4 and 8 m, and were significantly clustered at distances greater than 8 m (Fig. 2a). Post-mortality live trees were even more strongly regularly distributed over short distances than combined live and dead trees had been.

In contrast, combined live and dead HI and Rc were strongly clustered at all distances up to 20 m (Fig. 2b, c). Mortality in these species was also non-random (Fig. 3). However, unlike Df, whose survivors shifted significantly toward a more regular distribution, HI and Rc became more aggregated post-mortality.

Mortality also changed the spatial associations between species (Fig. 4). Pre-mortality, HI and Df were spatially independent but post-mortality they

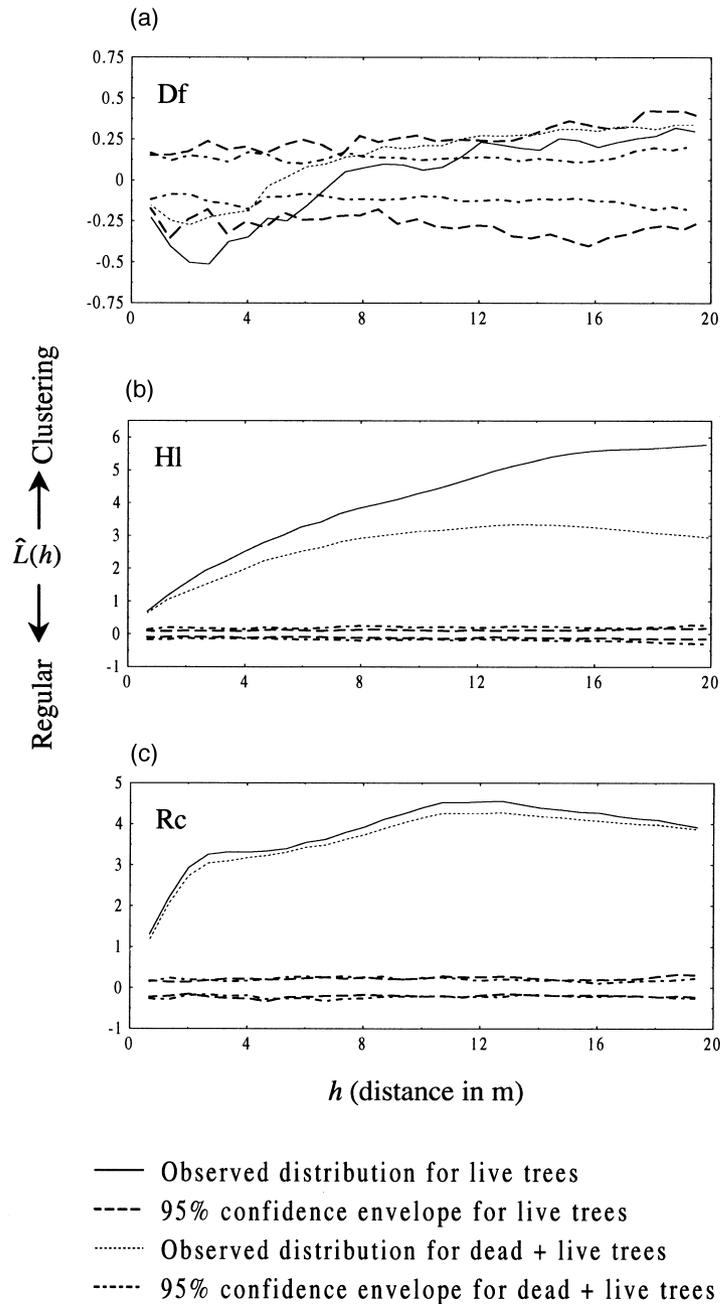


Fig. 2 $\hat{L}(h)$ showing the spatial distributions of both live trees and live+dead trees for three dominant species. Approximate 95% confidence envelopes obtained from 25 random simulations of the random point process are shown for both live and live + dead trees. Observed $\hat{L}(h)$ lines that fall below the confidence envelopes indicate significant regularity; $\hat{L}(h)$ lines that fall above the confidence envelopes indicate significant aggregation.

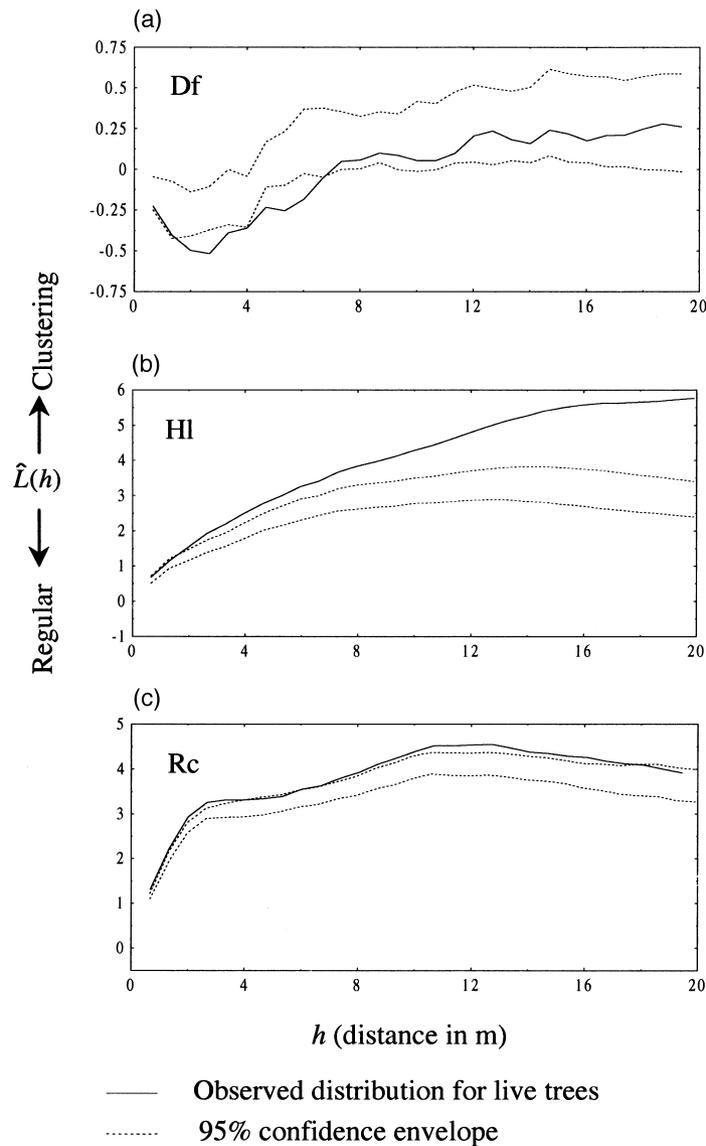


Fig. 3 Test of random mortality: conventions as in Fig. 2.

were significantly negatively associated at short distances (< 5 m). Pre-mortality, Rc and Df were significantly negatively associated at short distances and became more so post-mortality. HI and Rc were positively associated at short distances pre-mortality but were spatially independent post-mortality.

NEIGHBOURHOOD EFFECTS

Compared with live Df, dead Df were found in significantly denser patches of live conspecifics, but only at a neighbourhood radius of 5 m with no significant effect at greater distances (Table 2). However, when live Df of different sizes were included separately as predictors of Df mortality, only large trees (> 50 cm d.b.h.) showed a significant relationship. This effect was most pronounced for

the smallest neighbourhood radius (5 m) but remained significant at greater neighbourhood distances. Hence, the probability of Df mortality was most strongly related to the number of live conspecifics > 50 cm d.b.h. within a 5-m radius of a target tree. Compared with live Df, dead Df also had significantly more live Rc neighbours.

Compared with live HI, dead HI were found in significantly denser patches of live Df at all of the neighbourhood distances we examined (Table 2). However, the significant negative relationship between HI survival and overall Df density was due primarily to a negative relationship between HI survival and the density of small (≤ 50 cm d.b.h.) Df trees. The density of large Df trees (> 50 cm d.b.h.) was significantly related to the probability of HI survival only at the largest neighbourhood radius (10

Table 2 Results of logistic regressions modelling the response of the target species (alive or dead) with the density of neighbours of each of three species at three neighbourhood radii. The results are the change in deviance associated with adding each predictor variable alone to a logistic regression model. The significance of the observed change in deviance was tested with a randomization procedure (see Methods). * $P < 0.05$, ** $P < 0.01$, *** $P \leq 0.001$. Where effects were significant, a negative sign (-) under the Direction column indicates that larger values of the predictor (i.e. higher neighbourhood density) are associated with a lower probability of survival in the target species; a positive sign (+) indicate the reverse

Target species	Predictor variable	Direction	5 m	7.5 m	10 m
Df	Live Df	-	12.9***	0.03	2.0
	Live Df > 50 cm d.b.h.	-	18.4***	6.4*	8.9 **
	Live Df ≤ 50 cm d.b.h.		0.9	2.1	0.2
	Live Hl		3.2	2.5	0.9
Hl	Live Rc	-	5.7*	3.3	3.1
	Live Df	-	29.8***	39.4***	34.2***
	Live Df > 50 cm d.b.h.	-	0.2	2.6	8.5**
	Live Df ≤ 50 cm d.b.h.	-	33.4***	32.1***	21.8***
	Live Hl	+	83.9***	83.9***	58.4***
Rc	Live Rc	-	39.7***	41.0***	37.4***
	Live Df		1.0	0.04	0.02
	Live Df > 50 cm d.b.h.		1.5	0.2	0.4
	Live Df ≤ 50 cm d.b.h.		0.03	0.01	0.3
	Live Hl		0.01	0.01	0.06
	Live Rc		0.07	1.3	3.5

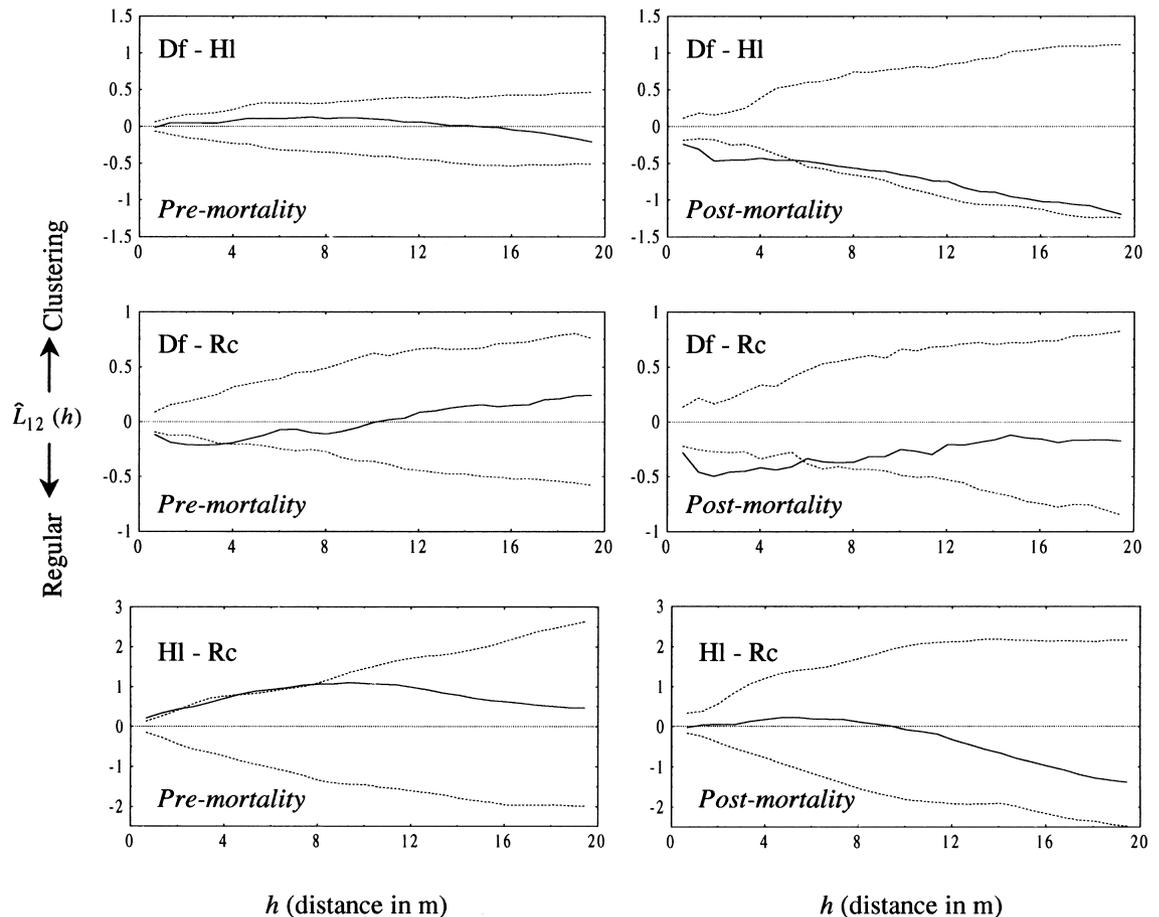


Fig. 4 $\hat{L}_{12}(h)$ showing spatial associations between species pairs: Df-Hl, Df-Rc and Hl-Rc.

m). Survival of H1 was significantly higher in denser patches of conspecifics but significantly lower in denser patches of Rc. The probability of Rc survival was not significantly related to the density of neighbouring trees of any species (Table 2).

ELEVATION

The probability of Df and Rc survival was independent of elevation as the mean elevation of live and dead trees of each species were not significantly different (Table 3). In contrast, the probability of H1 survival varied with elevation; live trees of H1 were found on average at significantly lower elevations than dead trees. This pattern of survival was evident in the correlation between H1 density and elevation (Table 4). Pre-mortality, H1 tree density was not significantly correlated with elevation, but post-mortality live tree density decreased significantly with elevation, reflecting the lower rate of H1 survival at higher elevations in the plot. The overall density of Df trees increased with elevation both pre-mortality and among the surviving trees post-mortality. However, the correlation between live Df density and elevation was due entirely to an increase in the density of small (≤ 50 cm d.b.h.) Df trees with increasing elevation. The density of large (> 50 cm d.b.h.) Df trees was unrelated to elevation.

ADJUSTING FOR CONFOUNDED VARIABLES

Our results suggest that several variables in our data set were confounded. The probability of H1 survival, for example, was related to both the density of Df neighbours and to elevation, but Df density and elevation were themselves correlated. To assess the degree to which these intercorrelated variables could independently predict survival, we fitted multiple logistic regression models in which we controlled for the influence of confounding variables (see Methods).

Table 3 The mean elevation (m above a reference point) and the 95% confidence intervals around the mean (in parentheses) for live and dead trees of each species in the study plot

Species	<i>n</i>	Mean elevation (m)
Live trees		
Df	341	18.1 (17.2–18.9)
H1	568	11.9 (11.1–12.6)
Rc	372	17.2 (16.4–18.0)
Dead trees		
Df	312	17.6 (16.7–18.5)
H1	414	20.6 (19.9–21.4)
Rc	44	17.6 (15.2–20.1)

Table 4 Pearson correlation coefficients (*r*) between elevation and counts of the number of live and dead trees of each species within a 5-m radius circle. Elevation was estimated, and tree counts were made at each intersection of a 10 × 10 m grid overlaying the study plot. Only the 80 grid intersections that were ≥ 10 m from the plot boundaries were used in calculating the correlation coefficients. Significance level: * $P < 0.05$, ** $P < 0.01$

Species	Status	<i>r</i>
Df	Live + dead	0.380***
	Live	0.362***
	Live (> 50 cm d.b.h.)	0.008
	Live (≤ 50 cm d.b.h.)	0.361***
H1	Live + dead	−0.101
	Live	−0.450***
Rc	Live + dead	0.022
	Live	0.048

Having adjusted for the influence of other variables, the probability of Df mortality remained significantly higher in denser patches of live conspecifics, with the effect being due primarily to the presence of large (> 50 cm d.b.h.) trees (Table 5). Dead Df were also associated with higher densities of live H1 and, more strongly, with live Rc, as before. The probability of Df survival had previously been independent of elevation, but having adjusted for the density of neighbours within 10 m the probability of Df survival increased significantly with elevation.

As before, the probability of H1 survival decreased significantly with elevation. However, having adjusted for the influence of other variables, the previously strong negative correlation between H1 survival and Df density was no longer significant at any neighbourhood radius. The probability of H1 survival remained significantly lower in denser patches of Rc up to a neighbourhood radius of 7.5 m, but was no longer related to the density of live conspecifics. Having adjusted for the influence of other variables, the probability of Rc mortality remained uncorrelated with elevation and the number of neighbours of any species.

Discussion

We hypothesized that both intra- and interspecific density-dependent processes would influence tree survival in our study area. First, intense intraspecific competition should lead to self-thinning of the colonizing Douglas fir, resulting in low survivorship of this species in the understorey following canopy closure. Subsequently, self-thinning as well as other forms of Douglas fir mortality, should progressively open up the forest canopy, creating light gaps that promote the recruitment of late-successional trees. Asymmetric interspecific competition for light

Table 5 Results of logistic regressions modelling the response of each target species (alive or dead) with the density of different neighbouring species at three neighbourhood radii. The results are the change in deviance associated with adding each predictor variable last to a multiple logistic regression model that already includes the remaining predictors listed beside each target species in the model. The significance of the observed change in deviance was tested with a randomization procedure (see Methods). * $P < 0.05$, ** $P < 0.01$, *** $P \leq 0.001$

Target species	Predictor variable	Direction	5 m	7.5 m	10 m
Df	Elevation	+	2.8	1.6	8.3**
	Live Df > 50 cm d.b.h.	-	29.0***	8.7**	15.7**
	Live Df ≤ 50 cm d.b.h.	-	8.2**	0.2	5.3*
	Live Hl	-	4.1*	0.9	0.1
	Live Rc	-	11.4 **	4.9*	8.2**
Hl	Elevation	-	100.1***	47.7***	25.2***
	Live Df > 50 cm d.b.h.		1.4	0.2	0.2
	Live Df ≤ 50 cm d.b.h.		3.7	1.8	2.7
	Live Hl		0.02	2.5	3.4
	Live Rc	-	7.9**	6.0*	3.1
Rc	Elevation		0.07	0.0	0.0
	Live Df > 50 cm d.b.h.		1.9	0.4	0.3
	Live Df ≤ 50 cm d.b.h.		0.3	0.02	0.07
	Live Hl		0.07	0.06	0.01
	Live Rc		0.2	1.3	2.3

between Df and these species should result in higher survival of late-successional trees in less dense patches of Douglas fir (Spies & Franklin 1989).

Prior to considering the effects of elevation, our spatial and neighbourhood analyses appeared to give strong support to these hypotheses. The non-random pattern of Df mortality, with a higher rate of survival in less dense patches of conspecifics leading to a significantly more regular spatial distribution of trees (Figs 2 & 3, Table 2), is consistent with the outcome expected from the process of self-thinning. Three lines of evidence pointed consistently to interspecific density-dependent effects of Df on Hl and Rc survival. First, both Hl and Rc mortality was non-random such that the survivors became more strongly aggregated than expected (Fig. 3); an observation consistent with higher tree survival in favourable canopy openings. Second, this non-random mortality resulted in significant negative spatial associations between live Hl and live Df and between live Rc and live Df at small spatial scales (Fig. 4); an observation consistent with higher survival of Hl and Rc in openings away from the surviving Df. Third, for Hl, although not for Rc, the probability of survival was significantly higher in less dense patches of Df (Table 2). In addition, denser patches of live Rc were significantly associated with dead Df, suggesting that Rc had established preferentially in openings formed by the death of Df trees.

Nevertheless, several results of the neighbourhood analyses were altered substantially by controlling for the confounding influence of elevation (and other variables) on tree survival (Table 5). In particular, the probability of Hl survival was no longer significantly higher in less dense patches of Df. Hence, the

initial results of the spatial and neighbourhood analyses, which could have been interpreted as showing a strong density-dependent effect of Df on Hl survival, appeared to be spurious. Patterns consistent with negative density dependence arose because both the probability of Hl survival and the density of small Df trees covaried independently with elevation such that Df density was lower and Hl survival was higher at lower elevations (Tables 4 & 5). The fact that elevation remained a highly significant predictor of Hl survival having controlled for Df density (Table 5) suggests that some factor(s) that covaries with elevation, other than Df density, exerted a major influence on Hl survival in the plot. We do not know what this factor is, but data from four neutron probes located at different elevations in the plot showed that there was a strong moisture gradient related to elevation at soil depths of 30 cm and 50 cm (but not at 10 cm or 20 cm depth), such that deeper soils were drier at higher elevations (Table 6). Hence, within the plot, the probability of Hl mortality and the density of small Df tended to be greater in soils that were drier at depths of more than 30 cm. Western hemlock are susceptible to conditions of low moisture in summer (Kotar 1972) and the tendency for Df to achieve higher density on drier sites within our study plot is consistent with how these species separate along moisture gradients at larger spatial scales (Franklin 1988). Western hemlock is mostly absent from extremely dry sites in the Pacific North-west where Douglas fir forms apparently stable, self-perpetuating populations (Franklin & Hemstrom 1981).

Neighbourhood and spatial pattern analyses are widely used to test for patterns consistent with density dependence in plant populations (e.g. Mack &

Table 6 Pearson correlation coefficients (r) between mean soil moisture taken at four depths (per cent water by volume measured monthly from May 1993 to June 1994 using a neutron probe; sample size = 14 months) and elevation at four sites of differing elevation in the study plot

Soil depth (cm)	r	P
10	-0.043	0.755
20	-0.063	0.643
30	-0.392	0.003
50	-0.608	<0.001

Harper 1977; Firbank & Watkinson 1987; Kenkel 1988; Condit *et al.* 1994). Because the emphasis in such studies is on detecting density dependence, additional factors that influence plant performance are often not explicitly measured and controlled for, although some studies attempt to minimize the confounding influence of such factors by selecting environmentally homogenous areas for study. At most sites, however, there is local heterogeneity in abiotic factors related to variation in elevation, topography, soils and microhabitat. Our results show that failing to control for the influence of such local variation on plant performance could lead to incorrect inferences about the importance of density-dependent effects, an outcome that reinforces previous warnings about the potential for studies investigating density dependence to be misled by confounding factors (Pielou 1960; Chapin *et al.* 1989; Wilson 1991; Duncan 1995).

Given this caveat, we nevertheless found evidence for some density-related effects on tree survival in our plot. Having controlled for elevation and the density of other neighbouring tree species, the probability of Df mortality was higher in denser patches of conspecifics (Table 5) and mortality of Df resulted in more regularly spaced survivors than would be expected from random (Fig. 3); these are both outcomes consistent with intraspecific competition affecting tree survival. Indeed, there is no obvious mechanism other than intraspecific competition that could result in more regularly spaced Df survivors in these forests. Furthermore, the probability of Df mortality was most strongly correlated with the density of large (> 50 cm d.b.h.) conspecifics. This suggests that, relative to small neighbours, the presence of large neighbours had a stronger influence on the likelihood of tree death, as would be expected if these density effects were due to intraspecific competition. Competition from overstorey trees was also most likely to be responsible for the lack of recent Df recruitment into the small diameter classes (Fig. 1).

Having controlled for the influence of other variables, there was no evidence that the local density of Df trees affected the probability of survival of the

invading late-successional species. This suggests that, at the stage of forest development in our plot, density-dependent interactions play little role in the replacement of Df by Hl and Rc. Succession may not therefore be due to local pre-emption of space by Df and its competitive exclusion of other species, with late-successional trees recruiting only into openings vacated by Df. Rather, it may be as a result of differences in the species life-histories (see also Walker *et al.* 1986), so that Df, a rapidly colonizing, fast growing, shade-intolerant species, is being replaced by slower colonizing, slower growing species that tolerate the low-resource conditions under the Df canopy. Nevertheless, we found a higher density of Hl and, more strongly, Rc around dead compared to live Df trees (Table 5). This could have resulted from a higher rate of establishment of these late-successional species in openings around dead Df trees (see also Stewart 1986b), even though there was no evidence that their subsequent survival was higher in those areas. Finally, having adjusted for the effects of other variables, the probability of Hl mortality was slightly higher in denser patches of Rc, but not vice versa, a pattern that could be due to asymmetric competition between the two late-successional species.

Because of the effort involved in detailed mapping, our study was confined to a single large study plot, as are many similar studies (Sterner *et al.* 1986; Kenkel 1988; Chapin *et al.* 1989; Duncan 1991). Hence, we do not know if our results generalize to other Douglas fir stands or to what extent the lack of strong interspecific density-dependent effects on tree survival apply to other forest successions. Few other studies have sought evidence for interspecific density-dependent effects on tree survival in forest successions involving long-lived trees. It is likely that the factors influencing tree survival during forest succession, including the role of density-dependent effects, will vary with aspects of the site, the species and the stage of succession (Pickett *et al.* 1987; Walker & Chapin 1987; Chapin *et al.* 1994; Rejmánek & Lepš 1996). Stewart (1986b, 1989), for example, found that Hl rapidly replaces pioneer Df trees in succession following wildfire in the Cascade Mountains, suggesting that, as at our site, the overstorey Df trees impose few constraints on the growth and survival of invading Hl. In contrast, regeneration of Hl appears to be inhibited by the overstorey trees when Hl itself forms a pioneer canopy following wildfire, perhaps as a consequence of the much deeper shade cast by Hl compared to Df trees. Spies & Franklin (1989) likewise hypothesize that the importance of competition between Df and late-successional species may change through the course of stand development. They suggest that the survival of late-successional trees is likely to be related to overstorey density in young, crowded stands of Df where light levels in the understorey

are low, but that density-related effects are less likely to be important in stands of older, less dense Df where a more open canopy results in higher understorey light levels, as was probably the situation in our plot. Consequently, conclusions regarding density effects are likely to vary if age and density of the Df are taken into account. What is clear from our study is that attempts to detect and ultimately generalize about the importance of density-dependent effects in regulating plant populations will require careful consideration of the role of additional factors that can influence plant performance and that can confound the results of studies that seek evidence for density dependence.

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