

Spatial distribution of regeneration in mixed-species forests of Victoria

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Summary

A study was carried out to describe the variation in the spatial distribution of regeneration in mixed-species forests of Victoria and examine its causes, as a basis for testing measures of regeneration success. Seedbed characteristics, stand history and spatial statistics based on quadrat counts and nearest-neighbour distances were determined for both intensively mapped stands and sparsely sampled coupes at case study sites. It was found that spatial distribution in stands established by clearfelling and artificial sowing, and by retention of seedtrees or shelterwood, were random to very aggregated.

Seedbed characteristics were the dominant factor contributing to seedling aggregation in high-elevation mixed-species forest. In low-elevation mixed-species forest the seedbed had an effect on aggregation, but the variation in seed supply also had a large influence on aggregation. Aggregation of regeneration within low-elevation mixed-species forest was not affected consistently by dominance class of the seedlings or the age of regeneration, but was affected by the source of regeneration (seedling or coppice). Aggregation of seedlings decreased or increased marginally with age in high-elevation mixed-species forest. There was variation in the degree of aggregation of different species in mixed-species stands, but there was a tendency for different species to occur together. It is recommended that further development of measures of regeneration success include a simulation study that tests measures with some proven performance in aggregated regeneration, and that the study should be on simulated stands that cover more than the full range of variation observed in the case study sites.

Keywords: mixed forests; regeneration; regeneration surveys; stand density; descriptors; distribution; occurrence; layout; standards; methodology; review; *Eucalyptus*; Victoria

Introduction

This paper examines the potential for a standardised measure for national reporting of regeneration success. Currently site occupancy, that is, the degree to which trees use the available space and resources of a particular site, is the main measure of regeneration success in Australia. A review of the measures of site occupancy recommended testing of the range of measures over the range of stand types that are usually encountered (Lutze *et al.* 2004). A useful approach is to simulate the range of stand

structures, which enables testing over a large number of stands at minimal cost. However, there is a need to characterise the stand structures with a range of spatial statistics. Characterisation should include the effect of the following potential sources of variation: forest type, silvicultural system, age, species composition, origin and dominance of regeneration (Lutze *et al.* 2004).

Few stand maps have been made at that stage of stand development when regeneration surveys are normally carried out. At the start of the project the only examples in Australian native forests were those from a 1-y-old dry mixed-species eucalypt forest in Tasmania (Lockett and Goodwin 1999), and some 4-y-old *Eucalyptus regnans*–*E. delegatensis* stands in the Central Highlands of Victoria (Hamilton 1984). Thus there was a need to prepare, for regeneration assessment, stand maps of seedling distribution over the range of forest types and silvicultural systems.

This paper is limited to studies on low- and high-elevation mixed-species forest types in Victoria. While these forests are important for sustainable timber production, there have been no reported studies on the spatial distribution of regeneration. Hence measures for assessing regeneration success need further development. A case study of the spatial distribution of regeneration and of the performance of site occupancy measures in spatially-variable forest is an important step in developing a standard indicator of regeneration success.

The low-elevation mixed-species forests cover about 78% of public land in Victoria, occurring at altitudes up to about 700 m on the coast and in the foothills of the Great Dividing Range (Lutze *et al.* 1999). These forests include two main species groups, the silvertop ash (*E. sieberi*)–stringybark species group and the messmate (*E. obliqua*)–peppermint species group. The silvertop ash–stringybark species group, which predominates in East and Central Gippsland, is routinely regenerated from seedtrees following harvesting disturbance, with or without slash burning. The regeneration of this forest type has been subject to intensive research through the Cabbage Tree Silvicultural Systems Project experiment (Lutze *et al.* 1999). This experiment examines the effect on regeneration of canopy gap size and the amount of retained overwood, and the use of either slash burning or mechanical disturbance for site preparation. The messmate–peppermint species group, which predominates in central and south-western Victoria, is routinely managed using a range of systems including group selection, shelterwood, seedtree and occasionally clearfell systems (Lutze *et al.* 1999). Typically seed

supply for regeneration is from retained trees, and the seedbed is generally created during harvesting with some supplementary seedbed preparation from top-disposal burning.

The high-elevation mixed-species forest generally occurs in the eastern highlands of Victoria (Lutze *et al.* 1999) and extends into south-eastern NSW where it is referred to as moist tablelands forest (SFNSW 2001). The main species are messmate (*E. obliqua*), cut-tail or brown barrel (*E. fastigata*), Errinundra shining gum (*E. denticulata*) and mountain grey gum (*E. cypellocarpa*). In Victoria, these forests are typically harvested in spring to summer followed by an intense slash burn or mechanical disturbance in autumn, with seed being supplied from retained seedtrees and supplementary sowing in winter.

Regeneration success is determined in all coupes in both forest types at 1.5–3 y after site preparation using the method of Dignan and Fagg (1997).

The objectives of this paper are to:

- describe the spatial pattern of seedlings at the time of regeneration surveys in mixed-species forests of Victoria under a range of even-aged silvicultural systems;
- describe the effect on the spatial pattern of forest type, silvicultural practice and stand attributes, dominance class of seedlings, age of regeneration and species associations; and
- define the spatial distributions to be simulated for testing measures of site occupancy.

Methods

Site and treatment details

Regeneration Reference Sites (RRSs) were selected, where the variation in spatial distribution of seedlings and its effect on measures of regeneration success could be studied. Three of these were low-elevation coupes (Bellbird Track, Steep Gully and

Mountain View) covering the range from low to high seedling density, and seedtree and shelterwood silvicultural systems. Two were high-elevation coupes, one clearfelled, slash-burnt and aerially sown (Clarkeville Road) and the other with seedtree retention, slash-burning and aerial sowing (Students Road). In addition, a previously-established experimental site, the Cabbage Tree Silvicultural Systems Project site (hereafter referred to as the Cabbage Tree site), was used as a source of data (Table 1). Treatments that had previously been applied to this site included harvesting by clearfelling, shelterwood retention, and seedtree retention, followed by site preparation by burning or mechanical disturbance. Clearfell coupes had been artificially sown from a helicopter, whereas shelterwood and seedtree coupes had been naturally sown from the retained trees.

Stand map study

Data based on seedling distribution maps were collected from large contiguous plots dispersed across the five coupes. Stand maps were prepared for three to six areas, each 20 m x 20 m, in each coupe. No stand maps were prepared for the Cabbage Tree site. The use of a few maps of large (400 m²) stands was considered to provide a better description of seedling pattern than a larger sample of maps of smaller stands or quadrats, as pattern could be responding to processes that operate at a range of scales up to and beyond the scale of the large plots. Both distance- and quadrat-based statistics may be applied to the stand maps to detect pattern. Stand maps were prepared about 2 y after site preparation. Plants were tagged and measured and attributes recorded (location, species, dominance, competitive position, height, growth stage, form, acceptability). Acceptable plants are generally vigorous new seedlings, coppice or lignotuberous seedlings of tree species native to the site, at least 40 cm in height and not suppressed by understorey, and free of any bole damage or impediment that may cause bole damage (Dignan and Fagg 1997).

Table 1. Details of experimental sites

Coupe/site name	Location	Forest type (important commercial species)	Silviculture system	No. of plots and plot size
Clarkeville Rd	East Gippsland	High-elevation mixed species (<i>E. fastigata</i> , <i>E. obliqua</i> , <i>E. denticulata</i>)	Clearfell	3 x 20 m x 20 m 72 x 4 m ² & 16 m ²
Students Road	East Gippsland	High-elevation mixed species (<i>E. fastigata</i> , <i>E. obliqua</i> , <i>E. denticulata</i> , <i>E. cypellocarpa</i>)	Clearfell and seedtree	3 x 20 m x 20 m 78 x 4 m ² & 16 m ²
Bellbird Track	East Gippsland	Low-elevation mixed species (<i>E. sieberi</i> , <i>E. globoidea</i> , <i>E. baxteri</i> , <i>E. cypellocarpa</i>)	Seedtree	3 x 20 m x 20 m 59 x 4 m ² & 16 m ²
Steep Gully	Midlands	Low-elevation mixed species (<i>E. obliqua</i> , <i>E. radiata</i> , <i>E. ovata</i> , <i>E. rubida</i>)	Shelterwood	6 x 20 m x 20 m 77 x 4 m ² & 16 m ²
Mountain View	Midlands	Low-elevation mixed species (<i>E. obliqua</i> , <i>E. radiata</i> , <i>E. ovata</i> , <i>E. rubida</i>)	Shelterwood	6 x 20 m x 20 m 44 x 4 m ² & 16 m ²
Cabbage Tree Silvicultural Systems Project	East Gippsland	Low-elevation mixed species (<i>E. sieberi</i> , <i>E. globoidea</i> , <i>E. baxteri</i> , <i>E. oliqua</i>)	Seedtree (8 coupes) Clearfell (4 x 10 ha & 8 x 4 ha coupes) Shelterwood 30% & 50% overwood (10 & 6 coupes)	27–35 x 2 m ² 24–46 x 16 m ² 29–44 x 2 m ² 17–72 x 16 m ² 14–28 x 2 m ² 13–34 x 16 m ²

Spatial analysis

The general approach to spatial analysis was to calculate a spatial index for the mapped seedlings and compare this with the value for a completely spatially random pattern. Quadrat-based indices of spatial distribution used the spatial statistics of intensity and frequency (Lutze *et al.* 2004). A map was subdivided into quadrats of equal area and the counts of seedlings (points) in the quadrats were used to indicate the variation in intensity. Seedling density, the number of seedlings per unit area, was calculated as the mean of the seedling (point) counts within a sample of quadrats. Frequency was calculated as the percentage of quadrats containing at least one seedling — often referred to as ‘stocking’ or ‘stocking percent’ in the forestry literature (Lutze *et al.* 2004). The following quadrat-based indices were used.

- *Variance: mean ratio of quadrat counts for a number of quadrat sizes.* Variance: mean = 1 for random, <1 for more uniform, and >1 for more aggregated distributions.
- *Green’s index (Ludwig and Reynolds 1988) for a number of quadrat sizes.* Green’s index = (variance:mean – 1)/(n – 1). Green’s index = 0 for random, <0 for more uniform, and >0 for more aggregated distributions.
- *Heterogeneity factor (Mount 1961) for a number of quadrat sizes.* The heterogeneity factor relates the count (i.e. seedling density) to the frequency of stocked quadrats (i.e. stocking per cent). Heterogeneity factor = $(d_o - d_m) / (d_r - d_m)$, where d_o is observed density, d_m is the minimum density for the measured frequency ($f\%$) of stocked plots, and d_r is the random density for the measured frequency ($f\%$); that is, $d_m = f/100$ and $d_r = \log_e(100/100-f)$ from the Poisson distribution. Heterogeneity factor = 1 for random, <1 for uniform, and >1 for aggregated distributions.

In addition to the quadrat-based statistics, the following distance-based statistics were calculated.

- *Pielou nearest-neighbour and point- (origin-) to-nearest-neighbour statistics (Pielou 1959):* $\alpha_i = \pi\rho\bar{w}_i$, $\alpha_p = \pi\rho\bar{w}_p$, where ρ is the estimated density in number of trees per unit area; \bar{w}_i is the mean of the squared distances from all seedlings to their nearest neighbours; \bar{w}_p is the mean squared distance from the n origins (points) to their nearest neighbours. Here, $\alpha_i = 1$ for random, >1 for uniform, and <1 for aggregated distributions. The inverse relationship applies to the point-to-nearest-neighbour (α_p) results.
- *Graphical analysis methods:* the empirical distribution functions of the nearest-neighbour distances and the K-function (Diggle 1983). When the empirical distribution functions of the nearest-neighbour distances are plotted against the nearest-neighbour empirical distribution function for a Poisson distribution, the function for uniform distribution shows a deficit of small distances and an excess of larger distances, whereas the aggregated distribution shows an excess of smaller distances and a deficit of larger distances. The K-function shows a similar trend, with aggregated distributions showing an excess density at small distances.

Statistical significance of departure from complete spatial randomness was determined by a Monte Carlo approach (Manly 1997). One hundred random distributions of the same density as the stand map were generated by the Poisson process and the 95% confidence interval determined from the 5th and 95th percentile

values of each statistic in the random set. Thence the statistics of the stand maps were compared to the upper and lower 95% confidence intervals of the random distribution of the same density.

The correlation matrix of all the quadrat and Pielou statistics across the entire set of stand maps was calculated, and on that basis a subset of the statistics was chosen for reporting of spatial pattern. The scale of spatial pattern was determined for each stand map by the blocked quadrat variance method (Greig-Smith 1952). Alternative methods of quadrat variance analysis have been recommended (Dale 1999), but they require a different sampling approach to that provided by the large square block of quadrats in the stand maps for 20 m x 20 m plots.

The degree of association between species was determined by chi-squared analysis of presence/absence of species pairs in quadrats of 16 m² (Zar 1984). A 2 x 2 contingency table of the following form was prepared (where a , b , c and d are frequencies of presence or absence):

Species 1	Species 2		Total
	Present	Absent	
Present	a	b	$m = a+b$
Absent	c	d	$n = c+d$
Total	$r = a+c$	$s = b+d$	$N = a+b+c+d$

The chi-squared test statistic, χ^2 , was calculated as $\chi^2 = N(|ad - bc| - 0.5n^2)^2 / mnrs$, and the significance of the statistic was determined by comparing it to the theoretical chi-squared distribution. Association or segregation was determined by comparing observed ‘ a ’ to expected ‘ a ’ if they were independent, $E(a)$; that is, $a - E(a) = (ad-bc) / N$. If positive then there was association; if negative there was segregation.

Sparse sampling study

An 80 m x 20 m sampling grid was applied to each RRS coupe to provide more than a minimum of 30 small plots (Table 1). At each sample point the numbers of all and acceptable eucalypt seedlings of each species were counted within radii of 1.13 m and 2.26 m to give stocking and density by 4 m² and 16 m² quadrats which are about equal to 1 and 4 milacre quadrats respectively. Sites were surveyed at 1–2.5 y after site preparation. A system of 2 m x 1 m (2 m²) and 2.26 m radius (16 m²) plots was used to monitor regeneration from 6 mo to 4 y after site preparation on coupes regenerated by the clearfell, seedtree and shelterwood systems on the Cabbage Tree site.

Two spatial statistics based on quadrat counts (the heterogeneity factor and Green’s index) were determined for the sparsely-sampled data. The relationship between the density of regeneration and seedbed type was analysed in two high-elevation reference site coupes. The heterogeneity of seedbed was related to the spatial pattern of seedlings at the two sites. The spatial distribution of the different seedbeds after slash burning was also determined by recording the distances of each seedbed type on 1500 m of continuous line transects at one of the high-elevation coupes.

Previously-reported data from the intensive regeneration studies at the Cabbage Tree site were used to analyse the effect of seed supply and seedbed on the spatial pattern of seedlings. The

Table 2. Correlation between measures of aggregation. Pielou point-to-nearest-neighbour (α_p), Pielou nearest-neighbour (α_i), variance:mean ratio for plots 2 m² to 100 m² (vm2 to vm100), heterogeneity factor for plots 2 m² to 16 m² (h2 to h16) and Green’s index for plots 2 m² to 100 m² (gi2 to gi100) in fully-enumerated plots with stand maps at age 2 y

Measure	Pielou		Variance:mean				Heterogeneity factor			Green’s index			
	α_p	α_i	vm2	vm4	vm16	vm100	h2	h4	h16	gi2	gi4	gi16	gi100
α_p	1												
α_i	-0.63	1											
vm2	0.75	-0.49	1										
vm4	0.77	-0.46	0.99	1									
vm16	0.78	-0.44	0.95	0.97	1								
vm100	0.76	-0.36	0.84	0.89	0.93	1							
h2	0.75	-0.5	0.79	0.75	0.68	0.58	1						
h4	0.85	-0.5	0.85	0.81	0.74	0.64	0.95	1					
h16	0.95	-0.55	0.90	0.91	0.92	0.91	0.72	0.82	1				
gi2	0.37	-0.23	0.57	0.50	0.44	0.32	0.85	0.70	0.34	1			
gi4	0.38	-0.15	0.57	0.52	0.46	0.35	0.85	0.73	0.37	0.97	1		
gi16	0.38	-0.17	0.55	0.51	0.50	0.38	0.79	0.72	0.39	0.90	0.95	1	
gi100	0.55	-0.18	0.72	0.70	0.68	0.65	0.86	0.80	0.62	0.86	0.90	0.89	1

relationship between seedling density and seedbed type (CSIRO 1993) and the heterogeneity of seedbed in each treatment (Stucken and Hajek 1993) and the variation in seedfall across treatment areas (Squire *et al.* 2004) were related to the spatial pattern of seedlings in each treatment.

The separate and combined effects of seedbed characteristics and seed supply were described by comparing the spatial pattern of seedlings across the range of silvicultural treatments at all the sites. The effects of the age of the regeneration, acceptability status and source of regeneration on the spatial pattern were also described where data were available. The effect of overwood competition was not analysed because it was not considered to have an influence on establishment or growth during the stage of stand development when regeneration measurement is carried out (Squire *et al.* 2004).

Results

The correlation between spatial statistics

The distributions of seedlings within plots within mapped stands of all forest types ranged from those showing no evidence of departure from complete spatial randomness to those showing great aggregation. Plots with aggregated distributions were more common than those with complete spatial randomness. The 95% confidence intervals for random seedling distributions obtained by simulation indicated that there was some inconsistency between statistics of spatial distribution. For example, a number of stands showed no evidence of departure from complete spatial randomness for one statistic, but were clearly aggregated. In contrast, in the lowest-density plots at three of the sites, there was no evidence of departure from complete spatial randomness for all but one statistic.

Regardless of these inconsistencies, there was a high degree of correlation between most of the statistics (Table 2). The Pielou nearest-neighbour statistic was an exception and hence an

unreliable indicator because, in a number of stands, it was the only statistic for which there was no evidence of departure from complete spatial randomness. A better test of the significance of departure from complete spatial randomness would be obtained if the analysis were to exclude any points that were closer to the boundary than to the nearest neighbour. Green’s index had a degree of correlation with other statistics similar to that of the Pielou nearest-neighbour statistic, but the low correlation of Green’s index was due to differences in the degree of aggregation shown by the statistic (see Table 5). Ludwig and Reynolds (1988) recommend Green’s index over other statistics based on the variance:mean ratio, because it is not dependent on total sample size.

The variance:mean ratio tended to increase at a greater rate with quadrat size than the heterogeneity factor. The heterogeneity factor was often greater than the variance:mean in plots of 2 m² or 4 m², but when plot size was increased to 16 m² the heterogeneity factor was less than the variance:mean ratio in most of the real stands. The key difference between the two statistics is that the variance:mean ratio is very sensitive to variation in density between plots, whereas the heterogeneity factor is sensitive to variation in density between plots only when plot density falls to zero. Green’s index increased with quadrat size at a greater rate than both the variance:mean ratio and heterogeneity factor. In order to simplify the interpretation of the degree of aggregation, a subset of statistics were considered to represent the degree of aggregation of stands. Considering the high degree of correlation between most statistics and the contrast provided by Green’s index, two statistics based on 16 m² quadrats were selected for characterising spatial distribution, the heterogeneity factor and Green’s index.

Sparse sampling results

Effect of seedbed variation in high-elevation coupes

The seedbed distribution was very different in the two high-elevation mixed-species coupes. At Students Road the slash burn had been at lower intensity than at Clarkeville Road, because

Table 3. Green's index and heterogeneity factors for all seedlings in 4 m² and 16 m² plots in sparsely sampled regeneration reference sites at about 1.5 y after site preparation

Forest type and coupe	Density (stems ha ⁻¹)		Stocking (%)		Green's index		Heterogeneity factor	
	4 m ²	16 m ²	4 m ²	16 m ²	4 m ²	16 m ²	4 m ²	16 m ²
<i>High-elevation mixed species</i>								
Clarkeville Road	5000	4045	47	69	0.041	0.034	9.16	11.76
Students Road	3942	3518	33	54	0.049	0.046	17.24	21.68
<i>Low-elevation mixed species</i>								
Bellbird Track	6958	5219	70	87	0.032	0.040	4.13	6.52
Steep Gully	23474	14635	88	99	0.016	0.007	3.14	6.68
Mountain View	2384	2689	42	65	0.056	0.054	7.71	9.08

climatic conditions became cool at Students Road on the day of the burn. Although similar proportions of the coupes remained unburnt (about 40% of quadrats), most Clarkeville Road seedbeds were burnt at high intensity, whereas most Students Road seedbeds were burnt at medium intensity. At Students Road 45% of the quadrats were classed as unreceptive; that is, less than 50% of the seedbed was friable soil or burnt ash. This contrasts with only 9% of unreceptive seedbed on the Clarkeville Road quadrats.

There was a similar mean seedling density associated with the seedbed types at the two sites at 2.5 y (i.e. high-intensity-burnt had 4 seedlings per quadrat; medium-intensity-burnt, 9 seedlings; unburnt, 12 seedlings; and unreceptive, 2 seedlings per quadrat). The high density of seedlings on the unburnt seedbed was a major factor contributing to the aggregation of seedlings at the two sites. Another major factor was the proportion of unreceptive seedbed. The difference in the proportion of unreceptive seedbed at the two sites resulted in a large difference in the percentage of plots with no acceptable seedlings (46% at Students Road vs 31% at Clarkeville Road), and in the degree of aggregation by the heterogeneity factor (22 at Students Road vs 12 at Clarkeville Road) and Green's index (0.046 at Students Road vs 0.034 at Clarkeville Road) (Table 3).

Effect of silvicultural treatments at Cabbage Tree Site

The seedling density and aggregation of seedlings in 16 m² plots by Green's index and heterogeneity factors were least in the large clearfell treatment (Table 4). The small clearfell had medium heterogeneity factors and high Green's index, whilst the seedtree and 30–50% shelterwoods had high heterogeneity factors and medium Green's index. The contrast between the large clearfell and small clearfell suggests that the spatial distribution of seed supply had an influence on spatial distribution of seedlings. Seedbed distribution, the other potential major factor influencing seedling establishment, was similar in the large clearfell and small clearfell treatments (Stucken and Hajek 1993). Although the artificial seed supply in both the large and small clearfell coupes was relatively uniform as a result of aerial sowing at a low rate (50 000 viable seeds per hectare) with a criss-cross pattern, the small clearfell coupes received additional natural seedfall from the surrounding unharvested forest (Squire *et al.* 2004). As a result of the additional seed supply, the seedling density and aggregation of seedlings was increased in the small clearfell coupes.

A seedfall study at the Cabbage Tree site showed there was large spatial variation in seedfall across the burnt seedtree coupes, due to the wide spacing of seedtrees, and that the variation in seedfall across the retained overwood coupes decreased with increasing level of retained overwood (Squire *et al.* 2004), thus tending to decrease the aggregation of regeneration. In contrast, the study of the relationship between seedbed type and seedling density and the heterogeneity of seedbeds suggests that the aggregation would tend to increase with the level of overwood retention. The seedling density was greatest on unburnt seedbeds and decreased with increasing intensity of the burn (CSIRO 1993). The proportions of the seedbeds with prolific regeneration (i.e. unburnt) and with little regeneration (i.e. burnt at high intensity) increased with the level of overwood retention (Stucken and Hajek 1993), which probably increased the aggregation of seedlings. Thus the seedfall and seedbed factors would tend to cancel one another and produce similar aggregation across the different levels of retained overwood (Table 4).

The seedbed study at the Cabbage Tree site showed that in burnt coupes there was not only variation in the intensity of fire over the burnt area, but 50–74% of the area remained unburnt because of concentrated soil disturbance and lack of slash accumulation (Stucken and Hajek 1993). In contrast, the seedbed was homogeneous in mechanically-disturbed coupes, with 90–96% of the area occupied by topsoil-disturbed seedbed (Stucken and Hajek 1993). The greater heterogeneity of seedbed in burnt coupes was associated with more aggregated regeneration in burnt than in disturbed coupes across the range of harvesting treatments (Table 4).

Spatial pattern at coupe level — variation with forest type, silvicultural system and age of regeneration

Collectively, the Cabbage Tree site (Table 4) and the 3 RRSs at low elevation (Table 3) indicate that the spatial distribution of seedlings in seedtree and shelterwood regeneration in low-elevation mixed-species forest is highly aggregated according to the heterogeneity factor (range of 5 to 9). However, Green's index indicated that one of the shelterwood coupes, with the highest seedling density, had a low degree of aggregation. Aggregation was greater at high elevation by the heterogeneity factor, but similar where based on Green's index (Table 3).

At the Cabbage Tree site there was an 8% reduction in Green's index over years 2 to 3 which corresponded to a 10% decrease in

Table 4. Variance: mean ratios and heterogeneity factors for all seedlings in 2 m² research plots and acceptable seedlings in 16 m² regeneration survey plots at 1–3 y after site preparation of coupes harvested by clearfelling or with overwood retention at the Cabbage Tree site, East Gippsland

Treatment	Density (stems ha ⁻¹)		Green's index		Heterogeneity factor	
	2 m ² plots	16 m ² plots	2 m ² plots	16 m ² plots	2 m ² plots	16 m ² plots
<i>Harvest treatment</i>						
LCF	3606	1399	0.032	0.022	2.78	1.77
SCF	12357	2503	0.076	0.065	5.64	3.49
O10	13949	4036	0.028	0.039	2.70	5.01
O30	32826	4509	0.032	0.037	4.16	4.80
O50	39081	4009	0.023	0.048	2.90	6.60
<i>Site preparation treatment</i>						
B	16622	3276	0.042	0.063	3.76	5.11
D	27134	3782	0.028	0.030	3.90	3.56

LCF = large clearfell (10.0 ha); SCF = small clearfell (4.0 ha); O10, O30 and O50 = 10% (seedtree), and 30% and 50% nominal retained overwood respectively;. B = burnt; D = mechanically disturbed

seedling density. Seedbed data from the site indicated that at 18 mo after site preparation there was still plenty of receptive seedbed as recolonisation by understorey had covered only about 30% of the seedbed (Squire *et al.* 2004), and germination was tending to balance mortality. In contrast, in the two high-elevation coupes there was a reduction in density of about 30% over the period 1.5–2.5 y. There was an associated reduction in aggregation as measured by a decrease in the heterogeneity factor and Green's index of 22% at Students Road, but a marginal increase in aggregation at Clarkeville Road. The seedbed data from these coupes indicated that most seedbed was recolonised quickly by a range of understorey species, and >75% of burnt seedbeds and about 65% of unburnt seedbeds were covered at 18 mo.

Stand map analysis: scale of pattern, variation in pattern with dominance, origin and species of regeneration

The mapped plots showed a larger range of spatial distribution (Table 5) than occurred in the small dispersed plots at the Cabbage Tree site (Table 4) and at the new RRSs (Table 3).

Graphical analysis illustrates the empirical distribution functions of nearest-neighbour distances and K-functions in three plots over the range of seedling density and aggregation (Fig. 1). As degree of aggregation increased (as indicated by the heterogeneity factor) the frequency of short nearest-neighbour distances increased relative to the 95% confidence envelope of random distributions of the same density. In the very highly aggregated stand of high density, about 100% of seedlings were outside the upper interval; that is, at shorter distances than complete spatial randomness. In the moderately aggregated stand of medium density, about 90% of seedlings were at shorter distances than complete spatial randomness. In the low-density stand with low degree of aggregation, all seedling probabilities fell within the 95% confidence envelope.

Scale of pattern

The scale of aggregation, as indicated by the block size at which the variance:mean ratio was maximised in the mapped stands (Table 5), did not appear to vary consistently with forest type or

silvicultural treatment. The variance: mean ratio tended to increase with plot size at two of the Bellbird Track plots, two of the Steep Gully plots, three of the Mountain View plots, the Clarkeville Road and the Students Road plots, which indicates that the scale of aggregation was greater than the largest sub-plot size tested (i.e. 100 m²). Other stand maps had variance: mean ratios peaking at the 2, 4 and 16 m² block sizes. The frequency distribution of distances across areas of uniform seedbed in transects established after slash burning at Students Road showed that the scale of variation of the three most common seedbed types was in the range of several metres to 90 m, with 90% of distances occurring in the range of 0 to 40 m (Fig. 2).

Variation with dominance and origin of seedlings

The comparison of acceptable seedlings with all seedlings in the low-elevation stand maps indicated that the heterogeneity factor was greater for all seedlings than for the acceptable seedlings. In contrast, at high elevation there was a lower heterogeneity factor for all seedlings than for the acceptable seedlings in 5 out of 6 stand maps. Although the 2 m² plot data from the Cabbage Tree site indicated a greater variance:mean ratio at 2 y for all seedlings than for the acceptable seedlings, that was not invariably the case. In the sparsely-sampled plots at the other RRSs, the heterogeneity factors for all seedlings and for acceptable seedlings were similar.

Coppice was shown to have an effect on spatial distribution by comparing seedling-plus-coppice regeneration with seedling-only regeneration at the Midlands mapped plots (Table 6). The coppice-plus-seedlings had a lower heterogeneity factor than the seedlings alone at 6 out of the 9 mapped plots.

Variation with species

There was variation in the spatial distribution of species in the mixed-species stand maps (Table 7). The difference in species spatial distributions occurred despite a lack of segregation between species. That is, species tended to be associated with each other according to the chi-squared analysis of presence/absence in quadrats of 16 m². As in the fully enumerated stands, the tests of association by chi-squared analysis of the sparsely-sampled plots

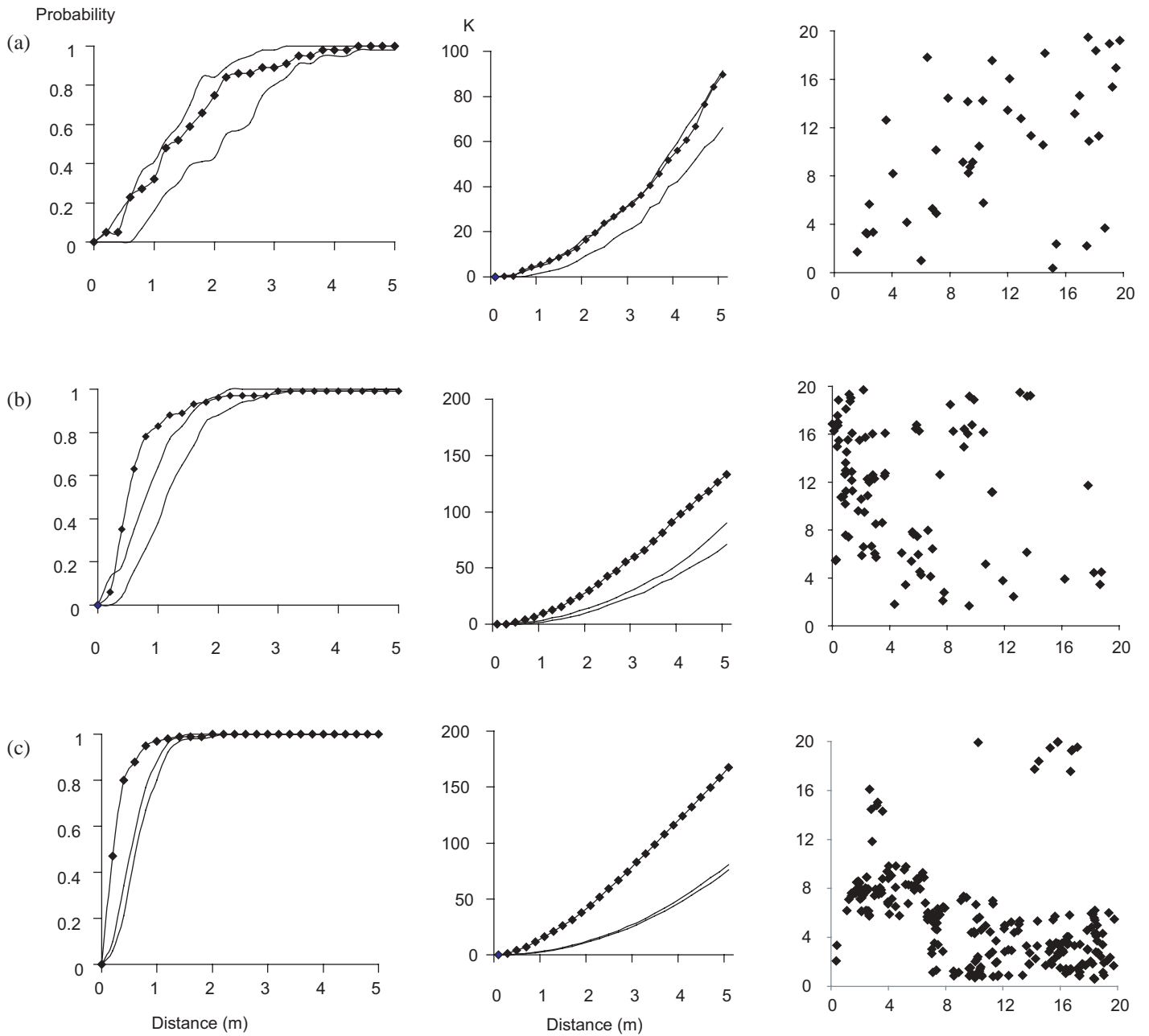


Figure 1. The empirical distribution functions of nearest-neighbour distances (points, left column) and the K-function (points, middle column) and 95% confidence envelopes of Poisson distributions with the same seedling density (solid lines), and seedling locations in three mapped plots of varying aggregation at age 2 y (right column). (a) Bellbird Track plot 2; (b) Students Road plot 2; (c) Clarkeville Road plot 3. Note that the functions for (b) and (c) occur outside and have higher values than the 95% confidence interval for the Poisson distribution.

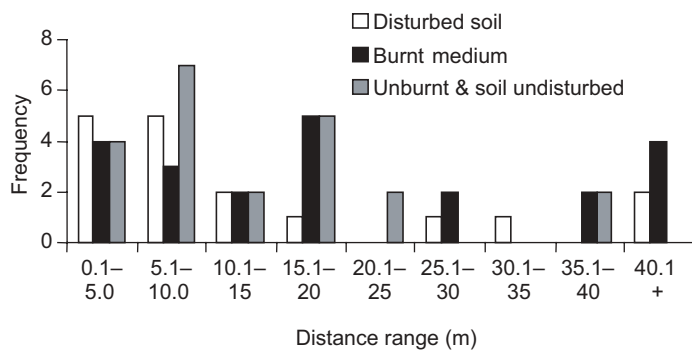


Figure 2. The frequency distribution of distances across seedbeds of the three most common types in transects established after slash burning at Students Road. Burnt medium = a seedbed prepared by a fire of medium intensity

at the RRSs showed that species were generally associated, but the association often was not statistically significant.

Discussion

Description of spatial pattern

The aggregated distribution of regeneration found in this study was not unusual; aggregated spatial distributions of woody plants, particularly in the young age class, have been widely reported (Couteron and Kokou 1997; Haase *et al.* 1997; Barot *et al.* 1999; Liu *et al.* 1999). Of most interest to the development of a standardised indicator of regeneration success is how the degree of aggregation varies with environmental and silvicultural factors.

Table 5. Density, stocking, Pielou point-to-nearest-neighbour (α_p), Pielou nearest-neighbour (α_i), variance:mean ratio (2 m² to 100 m²), heterogeneity factor (16 m²) and Green's index (16 m²) in fully-enumerated plots with stand maps at age 2 y

Forest type and coupe Density (no. ha ⁻¹)	Stocking (%) 16 m ²	Pielou statistics		Variance: mean ratios				Heterogeneity factor, 16 m ²	Green's index, 16 m ²
		α_p	α_i	2 m ²	4 m ²	16 m ²	100 m ²		
<i>Low-elevation mixed species</i>									
Bellbird Track 725–6175	56–100	*1.57–2.13	*1.08–0.72	*0.97–1.77	*1.02–2.34	*1.26–4.10	*0.44–5.86	*1.14–1.53	0.04–0.013
Steep Gully 8575–46700	84–100	1.69–10.57	*1.01–0.71	3.02–4.55	4.02–7.53	8.22–15.4	6.60–87.8	13.1–15.8	0.04–0.048
Mountain View 425–3650	40–100	*1.38–6.34	*1.03–*0.62	*0.92–4.44	*1.03–6.18	*1.42–14.0	*0.89–36.9	*1.17–10.6	0.04–0.163
<i>High-elevation mixed species</i>									
Clarkeville Road 1275–6600	68–76	2–13.7	*0.96–0.36	1.73–5.03	2.32–7.89	2.96–15.7	9.54–65.5	2.39–20.8	0.038–0.056
Students Road 750–4325	56–88	*2.01–3.49	1.56–0.84	1.32–2.81	1.72–4.55	2.64–9.27	5.47–12.4	2.45–5.13	0.048–0.055

*within 95% confidence interval of stands by Poisson process at the same density

Table 6. Stocking and heterogeneity factor (16 m²) of coppice-plus-seedlings, and seedlings only (all >15 cm tall) at age 2 y in mapped plots in the Midlands low-elevation mixed-species forest

Site	Coppice-plus-seedlings		Seedlings	
	Stocking (%)	Heterogeneity factor	Stocking (%)	Heterogeneity factor
Steep Gully	72–100	3.48–11.3	68–100	4.00–12.7
Mountain View	32–100	1.14–10.3	24–80	1.57–10.9

Table 7. Heterogeneity factor (16 m²) for all seedlings and by species and probability of species association of the most common and a minor species at the Regeneration Reference Sites plots. $P < 0.05$ indicates the association or segregation is significant. $a - E(a)$ is the observed minus the expected frequency of both species being present in plots; if positive then there was association, if negative there was segregation.

Forest type and coupe	Species association (a x b)	Heterogeneity factor			P	$a - E(a)$
		All	Species a	Species b		
<i>Low-elevation mixed species</i>						
Bellbird Track	sie x str	1.5	3.7	1.2	0.424	-2.24
Steep Gully	obl x rad	13.1–15.8	11.2–17.8	3.2–5.7	0.000–0.001	8.16–9.60
Mountain View	obl x rad	1.2–10.6	1.6–14.6	0.9–8.7	0.000–0.799	-13.6–12.6
<i>High-elevation mixed species</i>						
Clarkeville Road	fas x den	2.4–20.8	3.6–19.6	0.00–1.4	0.000–0.001	6.72–11.5
Students Road	fas x cyp	2.4–5.1	2.4–4.8	1.4–6.3	0.000–0.125	4.16–9.60

Species: sie = *E. sieberi*, obl = *E. obliqua*, fas = *E. fastigata*, den = *E. denticulata*, rad = *E. radiata*, cyp = *E. cypelloarpa*, str = stringybark (*E. globoidea* and *E. baxteri*)

Within low-elevation forests, coupe-level spatial distribution of seedlings in seedtree and shelterwood regeneration treatments was highly aggregated according to the heterogeneity factor (range of 5 to 9), the indicator that relates seedling density to frequency of stocked plots. The high-elevation regeneration established by artificial sowing showed greater aggregation, as measured by the heterogeneity factor, than low-elevation regeneration. Green's index also indicated that the regeneration was aggregated, but this index did not distinguish so clearly between forest types. The difference between indicators suggests that low-elevation regeneration may

be highly aggregated but the extent of voids may be less than in high-elevation regeneration. This would lead to better regeneration success in low-elevation forests, as reported by DSE (2003).

Cunningham (1960) reviewed the relationship between seedling density and frequency of stocked plots in coniferous forests of North America, and compared the relationship with that based on on1-milacre plots in *E. regnans* forest regenerated by seedtrees. He found that at lower stocking percentages there was similar seedling density in coniferous and *E. regnans* forest, but at higher

stocking percentages seedling density was greater in *E. regnans* in the Central Highlands, Victoria, indicating greater over-dispersion. Mount (1964) reported that seedling densities were even higher over a large range of stocking percentages in *E. regnans* forest in the Florentine Valley, Tasmania. Heterogeneity factors of about 2–3 were recorded on suitable seedbeds, but distributions with obvious clumpiness on a larger range of seedbeds had heterogeneity factors of 10 or more. Thus the range of aggregation in this study, with the exception of the large clearfell treatment at the Cabbage Tree site, was similar to that found in other studies in eucalypt forests established mainly through seedtrees. The large clearfell treatment at the Cabbage Tree site had regeneration with less aggregation than was found in the other reported cases, and was probably a result of the unusually low and uniform distribution of the seed provided by the criss-cross pattern of seed application.

Stand map data revealed more extreme uniformity and aggregation than is evident in coupe-level data, because infrequent areas of very high or low aggregation were 'averaged' at the coupe level, where data is sampled at grid points. The range of heterogeneity factors of 1–21 (Table 5) is higher than that reported in the few stand map studies in eucalypt forests. Results from stand maps in artificially-sown mixed-species eucalypt forest in Tasmania had heterogeneity factors of 1–14 (Lockett and Goodwin 1999). Hamilton (1984) showed that artificially sown *E. regnans*–*E. delegatensis* regeneration in the Central Highlands of Victoria had heterogeneity factors in the range of 1–8 (calculated from Hamilton's data). Regeneration in both of these studies had been established by artificial sowing and thus was likely to be less aggregated than in the stands regenerated from seedtrees as in this study. The scale of pattern indicated by the blocked quadrat variance in the stand maps was so inconsistent that it probably was confounded by the interaction of aggregation at a number of scales. It is also possible that, as in the study of Campbell *et al.* (1998), some variance peaks occurred by chance and were not biologically significant.

During the period when regeneration surveys are carried out in low-elevation mixed-species forest there may be little variation in aggregation of seedlings under seedtree or shelterwood systems, because mortality will be partly balanced by germination. K. Faunt (Department Sustainability and Environment, *pers. comm.*) found this to be the case in low-elevation forests, which may be explained by an ongoing seed supply from retained overwood and prolonged receptive seedbed, particularly on coupes prepared by mechanical disturbance (Squire *et al.* 2004). Where seedlings were established at low initial density in the large clearfells, there was limited mortality because competition was low. In contrast, on the two high-elevation coupes, there was a large reduction in density and aggregation over the period from 1.5 to 2.5 y. The reduction in density was accompanied by a large reduction in aggregation on one of the high-elevation coupes. This may be explained by a limited opportunity for ongoing germination as most seedbed was recolonised quickly by a range of understorey species, with high mortality occurring in the densest patches as a result of intense inter- and intra-species competition. Rapid recolonisation of seedbed and delay in most eucalypt germination until spring has been reported as a major limitation to regeneration in high-elevation mixed-species forest (Lutze *et al.* 1998).

The acceptable seedling criteria are designed to identify seedlings with greater capacity for survival and dominance, and to become crop trees at rotation age. There is evidence that naturally-regenerated eucalypt forest becomes more uniform over time (Hamilton 1984), and such trends have been observed in other woody vegetation communities. A number of alternative hypotheses of plant interaction have been developed to explain this (Wiegand *et al.* 2000). The acceptability criteria are based on the hypothesis that a clumped distribution of seedlings will lead to a random pattern of older trees through density-dependent mortality. Thus the seedlings that become dominant and survive should be less aggregated than the general seedling population. Application of the acceptability criteria to the stands in this study produced variable results, and in some cases the aggregation of acceptable seedlings was greater than the aggregation of all seedlings. The result suggests that the acceptability criteria do not identify the seedlings that will reach dominance and become final crop trees. However, they probably indicate the population from which the crop trees will be naturally selected. Perhaps the faster-growing trees occur in groups on the better seedbeds, and subsequently self-thinning within groups and then between groups produces a more uniform tree distribution.

It follows that forest types that regenerate well by coppice might exhibit a more uniform spatial distribution of regeneration than those that regenerate from seed only, because coppice forms on the more uniformly-distributed mature stems. The drier or lower-quality forests coppice more readily than wetter forests (Forrester *et al.* 2003), which is reflected in the lower aggregation in low-elevation mixed-species forests in this study. The negative effect of coppice on the aggregation of regeneration is supported by the comparison of seedling-plus-coppice with seedling-only regeneration in the Midlands stands.

The effect of species on the spatial distribution of regeneration may be expressed through varying patterns of germination (or coppicing), survival and growth. Studies of germination and early survival in low-elevation forest (Lutze 1998) and high-elevation forest (Fagg 1981; Lutze *et al.* 1998) have not indicated a large variation in the response of different species to different seedbed types. Thus differences in spatial distribution of species are probably related to differences in seed supply between species, and the competitive advantage given through the greater abundance of some species. Although there were differences in the degree of aggregation between species, there was a tendency for seedlings of different species to be associated. The association is consistent with association of seeds in the seed supply, as would occur in the mixed seedlots applied artificially or in the overlapping zones of seedtrees of different species. Interaction between seedlings, as reported for some vegetation communities (Haas *et al.* 1997; Eccles *et al.* 1999), may have had some small influence on species association over the short time since seedling establishment. As the regrowth ages, increasing competition could be expected to have a larger influence on the association between species. At the Cabbage Tree site the seedtree coupes could have contained areas where seed supply from different species did not overlap to any great extent, but this appears to have produced independence rather than segregation of the established species. That is, species occurred together frequently enough to be statistically independent, rather than segregated. Thus association or

independence of species occurrences apply to Victorian mixed-species forests at the time of regeneration assessment.

The main causes of variation in spatial pattern

The variation in scale of spatial pattern shown by the stand maps suggests that spatial pattern may be responding to a factor that operates over a large range of scales, such as seedbed characteristics. The increasing aggregation up to the scale of 100 m² is consistent with the larger pattern of disturbance, for example areas of convergence of snig tracks and landings. It is likely, however, that aggregation is occurring at a smaller scale than that because the distribution of favourable seedbeds, such as moderately burnt or disturbed soil, is often at a scale of several metres, and of favourable microsites such as beside logs and water-holding depressions at the scale of centimetres. The peak of variance: mean ratios at 2, 4 and 16 m² in some of the stand maps is consistent with smaller-scale seedbed factors. The absence of peaks in variance: mean ratio at the smaller scale on the remainder of the plots is probably a result of the interaction of patterns at a number of different scales.

The spatial variation observed in the high-elevation forest seedbed, and the relationship between seedling density and seedbed type, support the conclusion that the spatial pattern of seedlings is a result of variation in the seedbed at a range of scales. The relationship between seedling density and seedbed type in burnt high-elevation coupes in this study was similar to that reported by Featherston and Fagg (1983) for the same forest type. However, the spatial variation in seedbed type was different, with a much higher fraction of unburnt seedbed in this study.

Differences in seedling density between seedbed types have been reported in low-elevation forest (Fagg 1987; Kellas 1994), but they are generally less than those reported in high-elevation forest. At the Cabbage Tree site the difference in aggregation between the mechanically disturbed coupes, with relatively uniform seedbed, and burnt coupes, with more variable seedbed, suggests that the nature of the seedbed did have some effect on aggregation. This aggregation could have been partly due to poor survival on seedbed burnt at high intensity, as reported by CSIRO (1993).

Greater seedling aggregation occurred in low-elevation forest established under seedtree and shelterwood systems than from artificial seed supply alone. The seedfall studies at the Cabbage Tree site (Squire *et al.* 2004) indicate that variation in seedfall could have caused this greater degree of aggregation. The effect of variation in quantity of seedfall with distance from the seedtree (Cremer 1977) would be magnified by the difference in seedcrops between individual retained trees, particularly of different species (Squire *et al.* 2004).

Thus, based on information on variation in seedbed and seedfall, and their effects on regeneration processes, we conclude that the aggregation observed in low-elevation forest coupes was primarily a result of spatial variation in seedfall. In contrast, on the high-elevation coupes, the small number of, and small seedcrops on, retained trees, and the fact that the main seed supply was from relatively uniform aerial sowing, indicate that the type of seedbed was the main factor influencing aggregation.

Implications for indicator development

The simulation process proposed for developing and testing a standardised indicator of regeneration success should be guided by the results of this study. In particular, the various measures of regeneration success should be tested in simulated stands with aggregation at least as great as that identified in this study. The small number of stands sampled outside the Cabbage Tree site suggests that the full range of variation has not been identified, and that the sensitivity of the measures to more extreme spatial distributions should also be tested. The predominance of aggregation in the case study sites indicates that the measures to be tested should have some proven performance in aggregated regeneration.

The models for development of the simulated stands should be capable of reproducing the effect of environmental heterogeneity (i.e. seedbed variation) and clustering of offspring around parents (i.e. seed supply). A number of authors have demonstrated that heterogeneous or cluster processes produce similar distributions, and it may not be very useful to distinguish between them (Matern 1971; Diggle 1983).

Conclusions

Analysis of 20 m x 20 m mapped plots and small dispersed plots in mixed-species case study sites subject to a range of silvicultural systems indicated that, by a number of statistics based on nearest-neighbour-distance and quadrats:

- There was a high degree of correlation between the statistical measures of spatial distribution.
- Spatial distribution of regeneration established by clearfelling and artificial sowing or by retention of seedtrees was random to very aggregated. There was larger variation in the spatial distribution of seedlings after clearfelling or use of the seedtree system in low-elevation mixed-species forest than in high-elevation mixed-species forest. Regeneration in low-elevation mixed-species forest was highly aggregated, but there were fewer large voids than in high-elevation mixed-species forest, leading to better regeneration success in the low-elevation coupes.
- Seedbed type was the dominant factor contributing to aggregation in high-elevation mixed-species forest. Seedbed also had an effect on aggregation in low-elevation mixed-species forest, though seedlings were less aggregated on the relatively uniform seedbeds in mechanically-disturbed coupes. Variation in seed supply also had a large influence on aggregation in low-elevation mixed-species forest.
- The aggregation of more dominant seedlings was similar to that of all seedlings, which suggests that, at the time regeneration surveys are carried out, dominance may not be a reliable indicator of future crop trees in the mixed-species forests.
- Coppice regeneration was less aggregated than seedling regeneration, and as low-elevation mixed-species forests produce more coppice regeneration than the high-elevation forests, they may exhibit a less aggregated spatial distribution of regeneration.

- During the period when regeneration surveys were carried out, there was little variation in seedling aggregation in low-elevation mixed-species forests that had been regenerated by natural seedfall, because mortality was limited or balanced by germination. In high-elevation mixed-species forests, aggregation decreased or marginally increased as mortality occurred.
- The degree of aggregation of regeneration varied with species in mixed-species stands, but seedlings of different species tended to be associated rather than segregated.
- A proposed simulation study should test measures that have some proven performance in aggregated regeneration. The models for development of the simulated stands should cover more than the range of variation observed in the case study sites.

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