

The East Gippsland Silvicultural Systems Project. II: Germination and early survival of eucalypt regeneration

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Summary

A major silvicultural experiment has been established in lowland forest in East Gippsland to evaluate alternative silvicultural systems. A range of harvesting and site preparation treatments was applied in a replicated design over two seasons. Harvesting treatments consist of a series of gap sizes (0, 0.03, 0.25 and 1-ha gaps, 4- and 10-ha clearfells) and retained overwood (clearfell and 7, 22, 35 and 100% retained basal area). Results of site preparation by slash burning and mechanical disturbance were compared.

A primary criterion for evaluation of these treatments was the successful establishment of eucalypt regeneration. Eucalypt germination and seedling establishment was monitored bi-annually for 3 y. Germination, survival, seedling stocking and height growth were significantly influenced by gap size or the amount of overwood retained. Total germination was largely a function of seed supply, increasing with increasing overwood retention and decreasing gap size. Its response to site preparation method was confounded by seasonal effects. Total stocking at age 3 y generally reflected these germination results, although percent survival increased with increasing gap size and decreasing retained overwood. Mean height of seedlings at age 3 y also increased with increasing gap size and decreasing retained overwood. All treatments had successfully regenerated at 3 y, although survival and growth were significantly lower in the less intensively harvested treatments.

Keywords: silvicultural systems; clearcutting; shelterwood system; regeneration; seed sources; seed germination; survival; stocking density; growth; site preparation; fire; surveys; *Eucalyptus*; Victoria

Introduction

The background to the Silvicultural Systems Project (SSP) is described by Squire *et al.* (2006). The project was initiated to test the hypothesis that a better balance between economic and environmental concerns regarding wood production from native forests could be achieved with systems other than clearfell. A primary objective of the field experiments was to determine

whether silvicultural systems other than clearfell would achieve successful eucalypt regeneration. Key variables affecting regeneration success are seed supply (timing, quantity and distribution), seedbeds (type, quantity and distribution) and the subsequent conditions for the germination, survival and growth of seedlings.

This paper reports seedling germination and survival to 3 y in the lowland forest experiment, at Cabbage Tree Creek, East Gippsland, Victoria. Aspects of seed crop development and seed supply have been reported by and Bassett and White (1993) and Bassett (1995), and seedbed characteristics by Stucken and Hajek (1993). Species dynamics to 3 y are reported by Lutze (1998) and development to 12 y by Lutze and Faunt (2006).

Methods

Silvicultural treatments

Details of the study area, experimental design, conduct of harvesting, site preparation and aerial seeding operations are given in Squire *et al.* (2006). The SSP experiment at Cabbage Tree Creek trialled nine harvesting treatments, as distinct from silvicultural systems, that represent points along the continua of increasing gap size and decreasing overwood retention. Their arrangement in time and space is not being examined. Two site preparation treatments were also trialled in conjunction with each of the nine harvesting treatments. About half of the coupes for each harvesting treatment were prepared by fire, and the remainder by mechanical disturbance (Table 1). Nil site preparation was not trialled because the seedbed conditions necessary for successful regeneration could not be expected without some site preparation in addition to harvesting disturbance.

All coupes were harvested for sawlogs and residual roundwood (Government of Victoria 1986). Trees were generally felled by chainsaw and the merchantable timber was snigged to a landing by bulldozer. Coupes regenerated in 1989 were harvested between December 1988 and May 1989, and those regenerated in 1990 were harvested between January and June 1990 (Fig. 1).

Table 1. Replication of harvesting and site preparation treatments by regeneration year, and sampling design for the study of eucalypt germination, survival and early growth in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

Harvesting treatment	Replicates (coupes) per treatment				Total no. of coupes	Germination study	
	Site preparation treatment					No. plots per coupe	Spacing (m)
	Burnt		Disturbed				
	1989	1990	1989	1990			
Unharvested forest	–	2	2	2	6	5	5 × 5
0.03-ha gap	3	8	3	8	22	8	4 × 4
0.25-ha gap	3	5	3	5	16	20	10 × 8
1-ha gap	3	4	3	4	14	30	16 × 14
4-ha clearfell	2	2	2	2	8	34	30 × 30
35% overwood*	–	2	2	2	6	20	16 × 14
22% overwood*	2	3	2	3	10	20	16 × 14
7% overwood*	2	2	2	2	8	32	18 × 18
10-ha clearfell	2	2	–	–	4	40	30 × 30
Total	17	30	19	28	94	1894	–

*The nominal fraction of basal area retained in these treatments was 50%, 30% and 10% respectively (Squire *et al.* 2006)

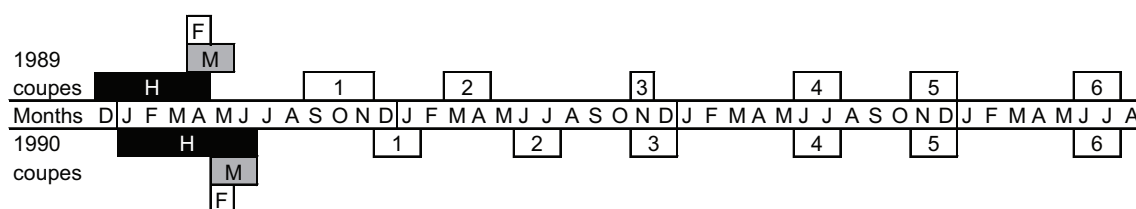


Figure 1. Timing of harvesting (H), site preparation by fire (F) or by mechanical disturbance (M) and germination monitoring (1–6 germination monitoring periods) for each regeneration year in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

Site preparation by fire took place in April–May in 1989 and May–June in 1990 (Fig. 1). Site preparation by mechanical disturbance occurred during April–May in 1989 and May–July in 1990 (Fig. 1). Bulldozers fitted with root rakes were used to push logging slash into rough heaps, with care being taken to include as little topsoil as possible and to ensure that the heaps were compact and well clear of retained trees.

Aerial seeding of the clearfell coupes took place on 9 May in 1989 and 30 May in 1990, using raw seed at the sowing rate of 50 000 viable seeds ha⁻¹. The species composition of the seed mixture matched that of the five main species in the original forest: 35% *E. sieberi*, 24% *E. globoidea*, 24% *E. baxteri*, 13% *E. consideniana* and 4% *E. botryoides*.

Germination study

Design and monitoring

Eucalypt germination and establishment were monitored on 1 m plots located systematically within each coupe following site preparation. The number and spacing of plots differed between harvesting treatments (Table 1), as coupe size and density of seedlings were expected to vary. Edge effect was avoided in treatments where it was not a function of the treatment effect. Thus, in the 10-ha clearfell and the 7%, 22% and 35% retained

overwood treatments, plots were placed a minimum of 50 m distant from coupe boundaries. Plot positions were mapped to determine the distance to the nearest coupe edge in gap size treatments, and distance to the nearest retained tree in retained overwood treatments.

Seeds of all eucalypt species occurring in lowland forest will normally germinate readily without pre-treatment (Boland *et al.* 1980), hence field germination may occur throughout the year (Campbell *et al.* 1984). However, three major germination events can usually be expected, with peaks in autumn and spring and mortality in summer due to drought. Monitoring was timed to follow these events, with a November–December measurement to assess spring germination prior to mortality over summer, and a June–July measurement to assess summer mortality and autumn germination. Monitoring thus occurred at intervals of about 6 mo for 3 y after site preparation, but the first two measurements differed from this timing and were not synchronised between the two regeneration years (Fig. 1).

During monitoring, each plot was searched thoroughly and each newly-observed eucalypt was tagged, and its species, height and germination period recorded. Subsequent monitoring recorded the height growth or mortality of each seedling (Table 2). About 21 000 seedlings were recorded in 1894 plots (Table 1) during the 3 y following site preparation.

Table 2. Seedling characteristics assessed in the study of eucalypt germination, survival and early growth in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

Characteristics	Description
Germination period	The measurement period in which the seedling was first observed
Mortality period	The measurement period in which the seedling was found dead. Missing seedlings were recorded as missing and the record amended to dead if the seedling was still missing or found dead at the following measurement.
Species	Nine eucalypt species occur at the study area. Identification of these at the cotyledon stage was difficult, but was confirmed where possible as the seedling grew.
Height	The height the highest growing tip of each seedling measured to the nearest centimetre
Health	Comments regarding seedling health and any evidence of browsing were recorded

Data analysis

Analytical model

The highly unbalanced and multi-level nature of the experimental design presented problems for statistical analysis. The Restricted Estimation of Maximum Likelihood (REML) model (Searle *et al.* 1992) was chosen as the most efficient means of analysing this design. REML is ideal for analysis of multi-level data that includes both fixed (harvesting and site preparation treatments, and regeneration year) and random (coupe and plot) effects. It empirically finds appropriate weighting of the coupe and plot data, and is not compromised by the non-orthogonal design. The statistical model examines the isolated and interactive effects of harvesting and site preparation treatments and regeneration year.

Germination, mortality and seedling density

Cumulative germination and mortality, and the corresponding seedling density, were calculated at the plot level for each of the six measurements. The calculation of seedling density included newly-observed germinants at the cotyledon stage. Each of these count data sets were transformed to the natural log scale to redress skewed distributions and analysed using REML.

Effect of distance from forest edge on germination and seedling density

Data from the 0.25 and 1-ha gap and 4-ha clearfell treatments in the gap size continuum were examined further for the effect of distance from coupe edge on germination and seedling density. The 0.03-ha gaps were deemed too small for the effect to be evident. The relationship between total germination at 3 y on each plot, and distance (m) from the plot to the nearest coupe edge, was examined with REML covariate analysis (with both variables transformed to the natural log scale). The isolated and interactive effects of the three harvesting treatments, two site preparation treatments and two regeneration years were examined. Edge effect was found to vary with harvesting treatment; thus the three treatments were analysed separately to quantify the individual gradients. The process was repeated for seedling density at 3 y.

Effect of distance from nearest retained tree on germination and seedling density

Data from the 7%, 22% and 35% overwood treatments were likewise analysed for the effect of retained overwood on germination and seedling density. The relationship between total germination and seedling density at 3 y on each plot, and distance from the plot to the nearest retained tree, was examined with

REML covariate analysis following transformation of each variable to the natural log scale.

Germination cohorts in total germination and seedling density

Over the 3 y of monitoring, each six-monthly measurement recorded new germination, collectively termed a cohort. Thus, total germination and seedling density at age 3 y are made up of six germination cohorts. The relative contributions of each cohort, and the effects of harvesting and site preparation treatments on them, were investigated at the coupe level. The number of seedlings in each cohort was considered in comparison to the total number in each coupe, and the cohort to which each seedling was assigned considered as an ordinal response.

The proportional odds model was used to evaluate the cumulative probabilities γ_k , $k = 1, \dots, 5$, where

$$\gamma_1 = P \{ \text{seedling in cohort 1} \},$$

$$\gamma_2 = P \{ \text{seedling in cohort 1 or 2} \},$$

$$\gamma_3 = P \{ \text{seedling in cohort 1, 2, or 3} \},$$

$$\gamma_4 = P \{ \text{seedling in cohort 1, 2, 3, or 4} \}, \text{ and}$$

$$\gamma_5 = P \{ \text{seedling in cohort 1, 2, 3, 4 or 5} \},$$

and relate them to the covariates harvesting treatment, site preparation treatment and regeneration year. After examining various combinations of covariates, the final model indicated that the cumulative probability of a seedling belonging to at least a given cohort changed with the harvesting treatment and that the pattern of that change depended on the site preparation treatment. Explicitly, the final model can be written as

$$\log \left(\frac{\gamma_k}{1 - \gamma_k} \right) = \theta_k - \mu \quad (k = 1, \dots, 5),$$

where θ is the cohort estimate and μ is the harvest \times site preparation effect. The cumulative probabilities were used to determine the probability of a seedling belonging to each cohort.

Cohort survival

Survival for each cohort was assessed 3 y after site preparation. Thus the survival periods assessed were 2.5 y for the first cohort, 2 y for the second, and so on. Survival percentage for each cohort was calculated from counts of the total number of seedlings in the cohort and the number surviving at 3 y. This count data was

first aggregated at the coupe level due to the disproportionate number of plots with zero survival. The data were treated as having a binomial distribution and analysed using the logistic regression model.

Height

The height at 3 y of ‘taller’ first-cohort seedlings was analysed with REML. Taller seedlings were those ranked 75th percentile by height at the plot level. This measure was used to focus the analysis on those seedlings more likely to become the final crop trees, and in preference to the tallest seedlings, which represent extremes in the sample distribution and have undesirable statistical properties. The data were first transformed to the natural log scale to redress a skewed distribution.

Stocking surveys

Eucalypt stocking surveys were conducted on each coupe using the method of Squire *et al.* (1991). The proportion of four-milacre sampling plots containing an ‘acceptable’ eucalypt seedling was determined at 1–3 y after regeneration treatment. Regeneration surveys used the standard operational sampling approach in the larger treatment areas, sampling plots being located at 20-m intervals along transects spaced 80 m apart. The sampling procedure was modified to suit the small areas in the unharvested and selection openings up to 1.00 ha in size, using two transects perpendicular to each other and the opening boundary, thus intersecting in the centre of the opening. Surveys were carried out at age 1 y in the 1989 and 1990 coupes (in April 1990 and May 1991). In the 1989 replication a large number of coupes did not meet the standard of 73% of plots stocked and thus surveys were conducted again at age 3 y in the 1989 replication (August–September 1992).

Understorey study

The cover and height of plant life forms (acacias, other shrubs, climbers, ferns, grasses, eucalypts, total of all life forms) and slash cover were assessed in the same plots used for the eucalypt germination and survival study. At 1.5 y after site preparation in the 1989 replication, and at 1.5 and 2.5 y after site preparation in the 1990 replication, plots were assigned a visually-assessed cover/abundance value for each life form, using the same system as Stuwe and Mueck (1990). The distribution of the life-form cover classes was used to derive an equivalent percentage cover on each coupe, which provided a measure of seedbed receptivity and competition for protracted eucalypt germination and subsequent survival over the 3-y study period.

Results

Germination

Germination and harvesting treatment

Harvesting treatment significantly influenced levels of eucalypt germination ($P < 0.001$) throughout the study period. From the outset, the amount of germination increased with increasing levels of retained overwood and decreasing gap size (Figs 2 and 3). At 3 y, total germination for both the gap size and retained overwood continua ranged from 133 000 germinants ha^{-1} in unharvested forest

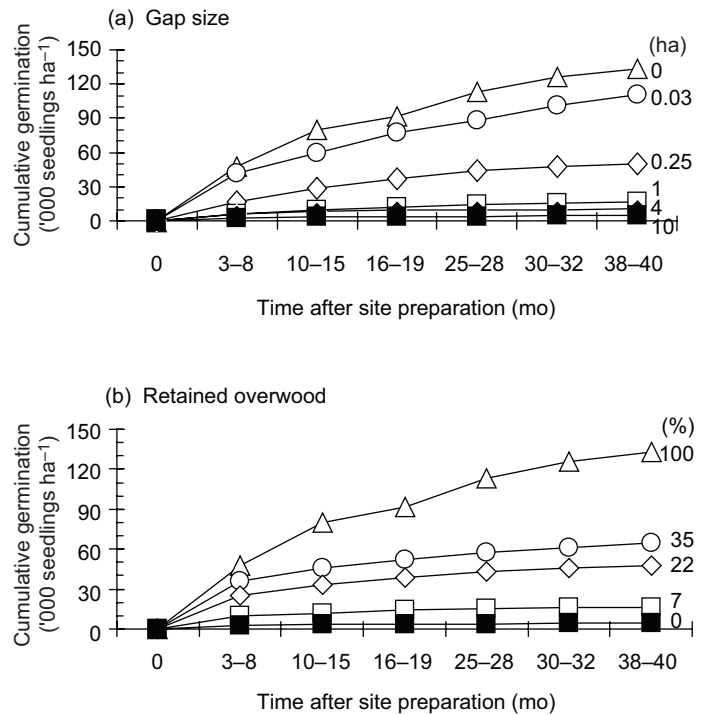


Figure 2. Cumulative germination to 3 y after site preparation versus (a) gap size and (b) retained overwood in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

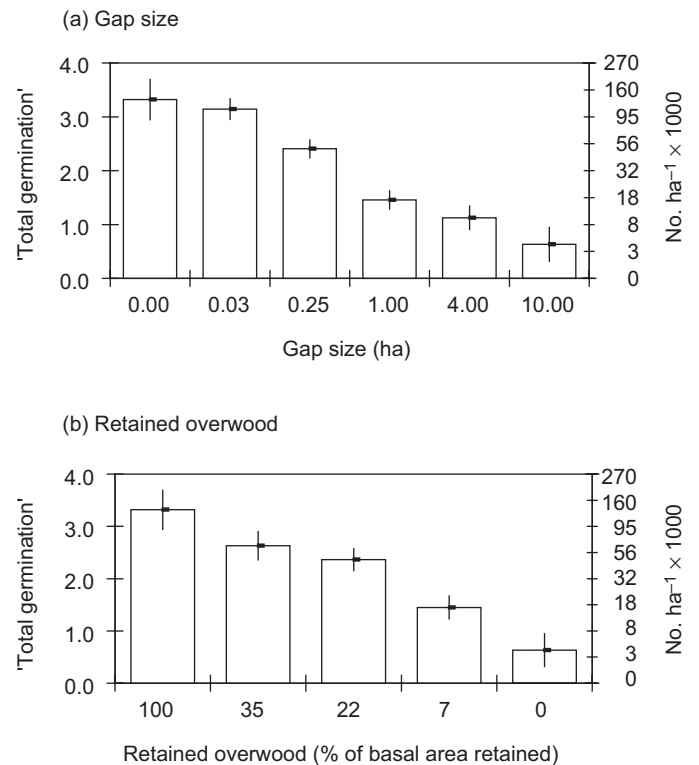


Figure 3. ‘Total germination’, 3 y after site preparation, versus (a) gap size and (b) retained overwood in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria. Vertical bars indicate 95% confidence intervals on the natural log scale. ‘Total germination’ = $\ln(\text{total germination})$.

to 4500 ha⁻¹ in the 10-ha clearfell (Table 3). Germination in 10-ha clearfells had virtually ceased by this time (Fig. 2), indicating a germination percent of 9% for the 50 000 viable seeds ha⁻¹ applied to that treatment. The rate of germination in other treatments had also declined steadily (Fig. 2) but continued to be greatest where gap size was smallest and retained overwood was greatest.

Germination and site preparation treatment

The effect of site preparation treatment on total germination differed between the two regeneration years. Treatments disturbed in 1989 produced greater germination than those burnt, while for 1990 treatments the reverse occurred (Fig. 4a). This interaction was significant from the outset (*P* = 0.008). Similarly, differences between the two regeneration years were dependent upon site preparation treatment. In burnt coupes there was no year effect, despite the burns being of different intensity in the two years, but in disturbed treatments 1989 produced significantly greater germination than 1990. For both regeneration years, rates of germination declined more rapidly over time in the burnt treatments than in their disturbed counterparts.

Effect of distance from forest edge and retained tree on germination

In the 0.25 and 1-ha gap and 4-ha clearfell treatments, total germination to age 3 y decreased as distance from the nearest coupe edge increased (Fig. 5). As the response varied between harvesting treatments, they were analysed individually. In the 0.25-ha gap, total germination varied with distance from coupe edge (*P* = 0.001) and with site preparation × regeneration year combination (*P* = 0.014; Fig. 5a). The regression equation for this relationship is:

$$\ln(\text{germination} + 1) = (\mu + \delta_i + \gamma_i + \delta_i \times \gamma_i) + \beta (\ln(\text{distance} + 1) - \phi)$$

where μ = mean $\ln(\text{germination} + 1) = 2.206$; β = slope = -0.3194 ; ϕ = mean $\ln(\text{distance} + 1) = 2.444$; and γ , δ and $\gamma \times \delta$ values are:

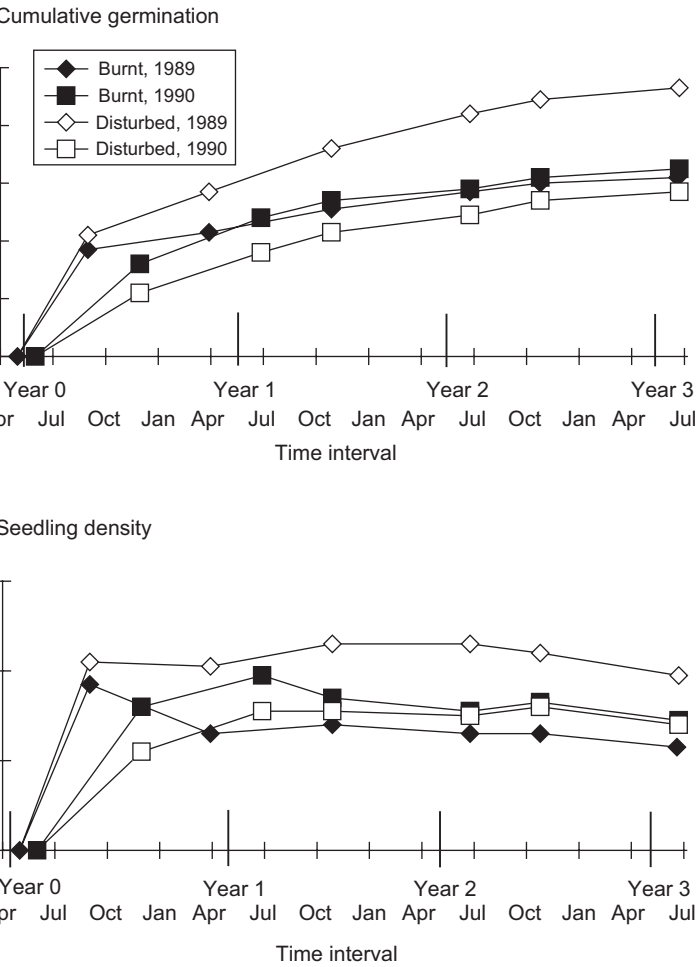


Figure 4. Interactive site preparation × regeneration year effect over time on (a) cumulative germination and (b) seedling density in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

		Site preparation treatment (δ)	
		Burnt	Disturbed
		0.0000	0.7919
Regeneration year (γ)	1989	0.0000	0.0000
	1990	0.5095	-1.2720

Table 3. Total germination, seedling density, survival of first cohort seedlings and height of taller first cohort seedlings at 3 y in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

Harvesting treatment	Total germination (seedlings ha ⁻¹)	Seedling density (seedlings ha ⁻¹)	Survival (%)	Height (cm)
Unharvested forest	133000	31000	14	13.1
0.03-ha gap	111000	36000	19	15.6
0.25-ha gap	50500	21000	29	41.7
1-ha gap	16500	8000	38	52.4
35% overwood	64500	25000	28	27.1
22% overwood	48000	19500	34	32.9
7% overwood	16500	9000	44	72.1
4-ha clearfell	10500	6500	43	60.3
10-ha clearfell	4500	3000	47	69.6

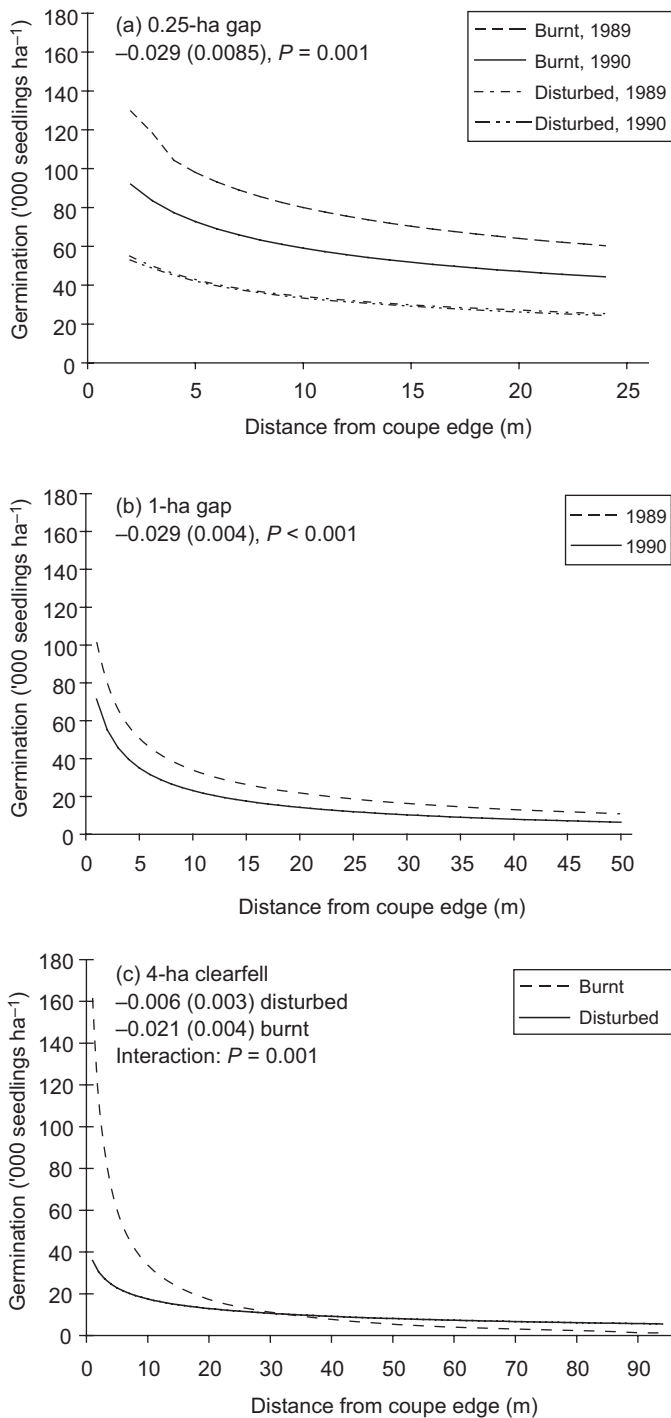


Figure 5. Regression relationships between total germination, 2 y after site preparation, and distance from coupe edge for germination plots in the (a) 0.25-ha gap, (b) 1-ha gap and (c) 4-ha clearfell treatments. Site preparation treatments are shown separately in (c). The slope, its standard error (in brackets) and *P*-value are shown for each regression.

In the 1-ha gap, total germination varied with distance from coupe edge (*P* = 0.000) and with regeneration year (*P* = 0.048; Fig. 5b). The regression equation for this relationship is:

$$\ln(\text{germination} + 1) = (\mu + \gamma_i) + \beta(\ln(\text{distance} + 1) - \phi),$$

where μ = mean $\ln(\text{germination} + 1) = 1.636$, β = slope = -0.5874 ,

ϕ = mean $\ln(\text{distance} + 1) = 3.107$, and γ values are 0.0000 for 1989, and -0.3271 for 1990.

In the 4-ha clearfell, total germination varied with distance from coupe edge by site preparation treatment (*P* = 0.000; Fig. 5c). The regression equation for this relationship is:

$$\ln(\text{germination} + 1) = (\mu + \delta_i) + (\beta + \gamma_i) \times (\ln(\text{distance} + 1) - \phi),$$

where μ = mean $\ln(\text{germination} + 1) = 1.094$; β = slope = -0.3507 ; ϕ = mean $\ln(\text{distance} + 1) = 3.526$; δ = 0.0000 for burnt and 0.0146 for disturbed; and γ = -0.5001 for burnt and 0.0000 for disturbed.

In the retained overwood treatments, no effect of distance from the nearest retained tree on total germination was detected.

Germination cohorts

The relative contributions of each germination cohort to total germination at age 3 y varied with harvesting and site preparation treatment (Fig. 6). The first cohort provided the major contribution in all treatments. However, the proportional contribution of this cohort varied with site preparation treatment. In all harvesting treatments except the 0.25-ha gap and the 4-ha clearfell, the proportion of seedlings in the first measurement was greater in slash-burnt treatments than in their disturbed counterparts.

Subsequent cohorts made progressively smaller contributions to total germination so that the sixth cohort provided an average of 5% of the total (Figs 2 and 6). This declining rate of germination was greatest in burnt, more intensively felled and aerially seeded treatments (Figs 2, 4a and 6).

Mortality

Patterns of eucalypt mortality followed those of germination to age 3 y (Figs 2 and 7). Total mortality decreased as gap size increased and as levels of retained overwood decreased (*P* < 0.001). Again, there was a significant interaction between site preparation treatment and regeneration year (*P* = 0.005). Total mortality in treatments disturbed in 1989 was greater than in their slash-burnt counterparts, but vice versa in 1990. Treatments disturbed in 1989 also suffered higher mortality than those disturbed in 1990. Initial mortality in treatments burnt in 1989 was greater than in those burnt in 1990, but by the second measurement cumulative mortality was similar. No peak mortality events were recorded during the 3-y measurement period (Fig. 7).

Survival

Both harvesting and site preparation treatments influenced survival of the first and second germination cohorts, but no significant effects were detected for the remaining cohorts (*P* > 0.05). Survival of the first cohort increased as gap size increased and as levels of retained overwood decreased (*P* < 0.001; Fig. 8 and Table 4). Survival of this cohort was better in the disturbed than in burnt treatments by an average 6% (*P* = 0.025), and was higher in 1990 coupes than in 1989 coupes by about 17% (*P* < 0.001).

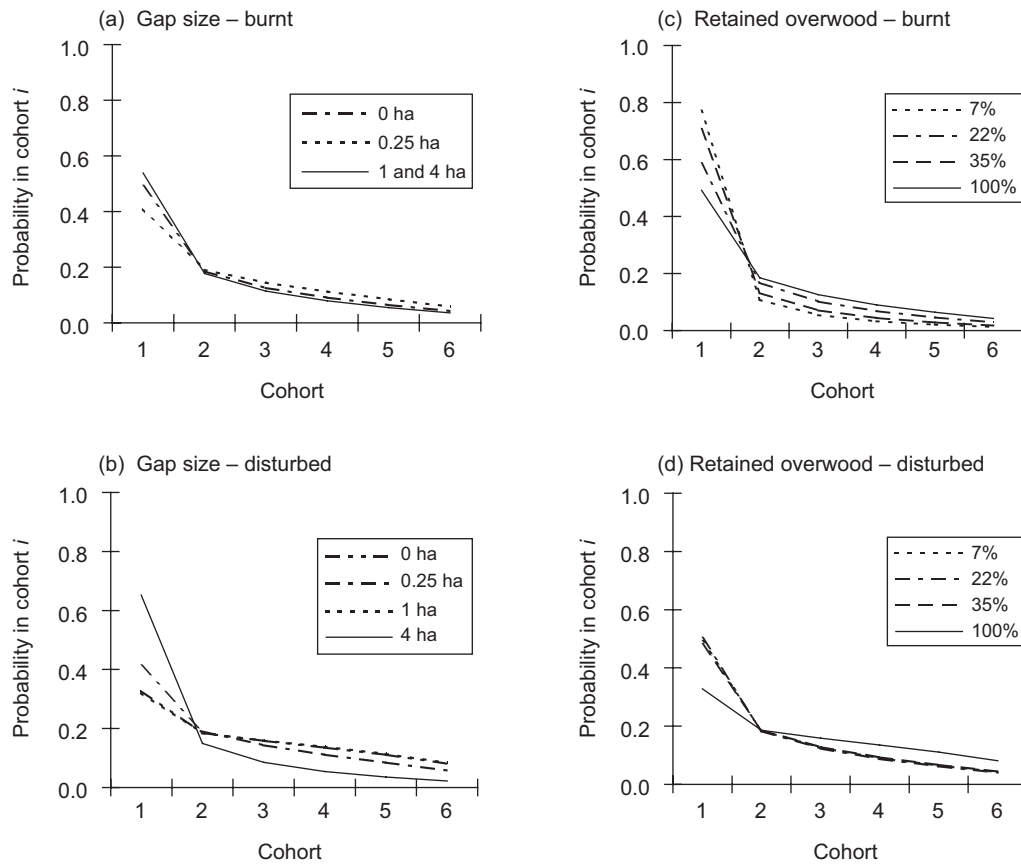


Figure 6. Cohort contribution to total germination, 3 y after site preparation, versus gap size treatment in sites prepared by (a) fire and (b) mechanical disturbance; and retained overwood treatment in sites prepared by (c) fire and (d) mechanical disturbance in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

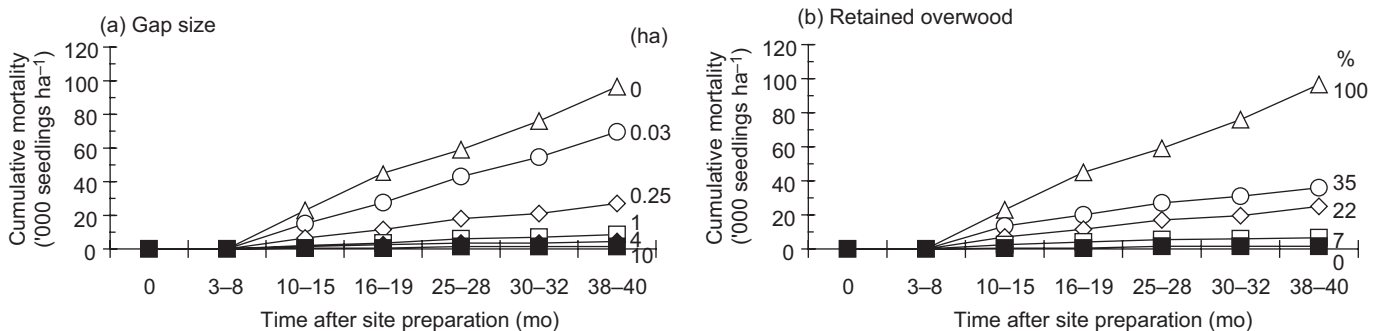


Figure 7. Cumulative mortality, to 3 y after site preparation, versus (a) gap size and (b) retained overwood in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

This pattern differed slightly for the second germination cohort. Survival of this cohort was also positively related to increased gap size and reduced overwood retention, but differences between site preparation treatments varied with harvesting treatment ($P = 0.009$; Fig. 9). In the gap size continuum, survival was greater in disturbed than burnt treatments for all gap sizes except the 1-ha gap, where the reverse occurred. In the overwood continuum, survival was greater in disturbed than burnt 100% retained overwood treatments, but was the reverse in the 35%, 22% and 7% treatments. The year effect was the opposite to that of the first cohort. Survival was greater in 1989 coupes than in

1990 coupes by an average of 12% ($P < 0.001$). Survival of the first cohort was considerably less than of the second and subsequent cohorts (Figs 8 and 9).

Seedling density

Seedling density and harvesting treatment

Seedling density remained relatively constant following the first measurement in the more intensively-harvested treatments and declined in the less intensively-harvested treatments (Fig. 10).

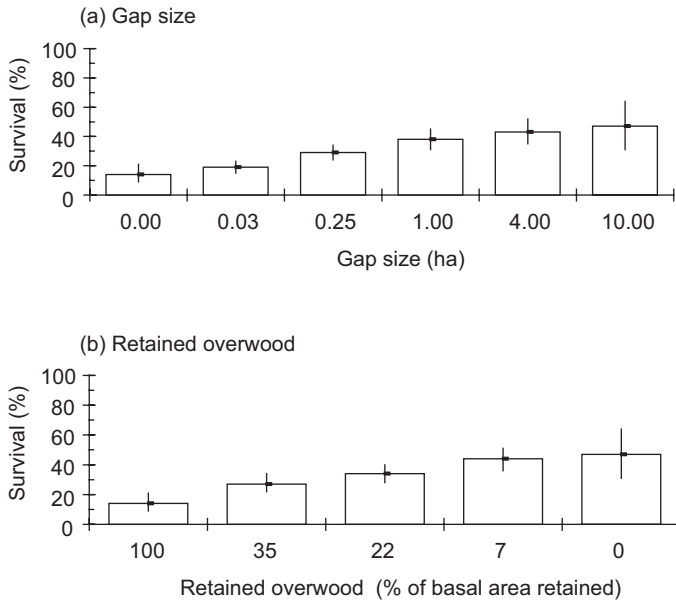


Figure 8. Survival of the 1st germination cohort to 3 y after site preparation versus (a) gap size and (b) retained overwood in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria. Vertical bars indicate 95% confidence intervals.

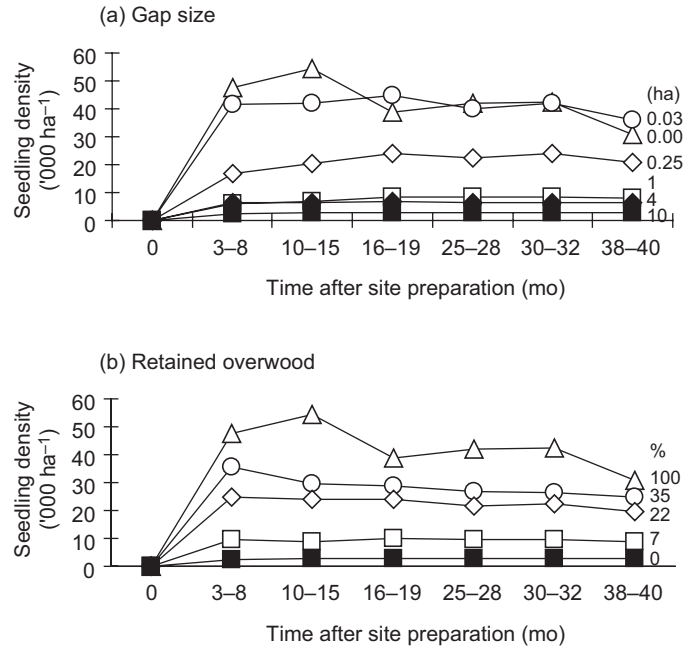


Figure 10. Seedling density, 3 y after site preparation, versus (a) gap size and (b) retained overwood in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

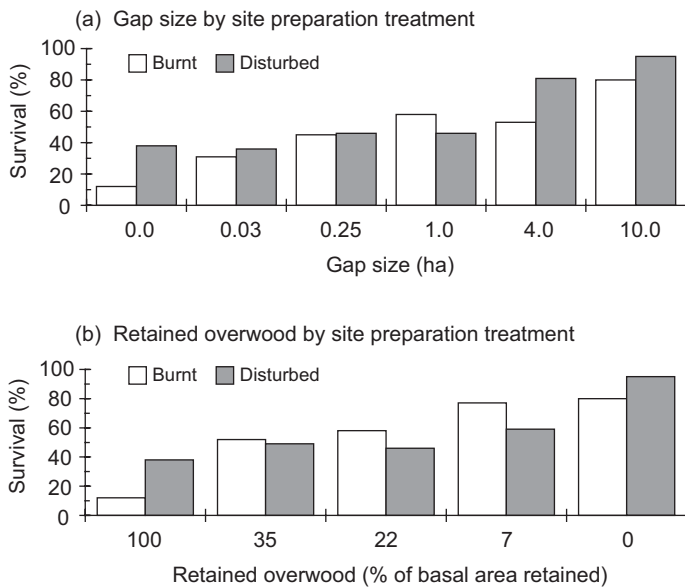


Figure 9. Survival of the 2nd germination cohort, 3 y after site preparation, versus (a) gap size and (b) retained overwood, by site preparation treatment, in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

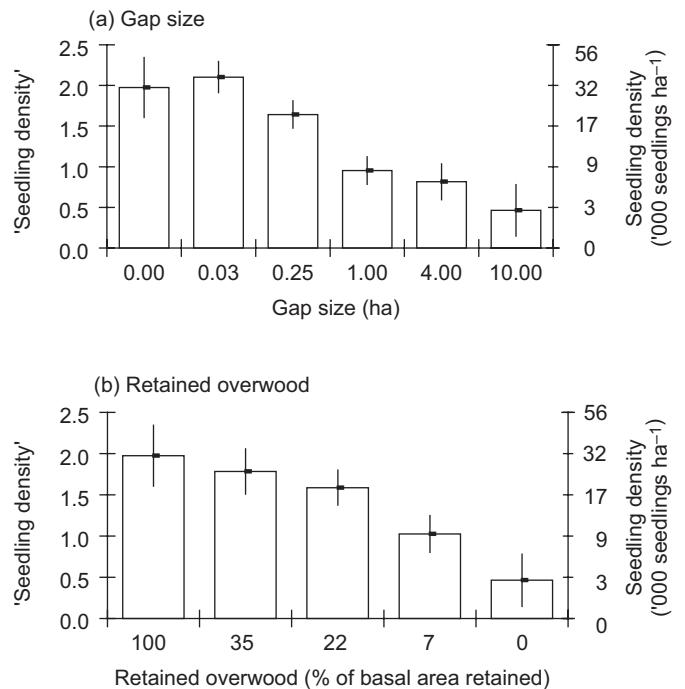


Figure 11. 'Seedling density', 3 y after site preparation, versus (a) gap size and (b) retained overwood in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria. Vertical bars indicate 95% confidence intervals on the natural log scale. 'Seedling density' = ln(seedling density).

At age 3 y, seedling density (Fig. 11; Table 3) largely reflected the results for total germination (Fig. 3; Table 3), generally decreasing with increasing gap size and decreasing levels of retained overwood ($P < 0.001$). The exception was where seedling density in the 0-ha gap (unharvested forest) had fallen below that in the 0.03-ha gap ($P > 0.05$).

Seedling density and site preparation treatment

As with cumulative germination and mortality, the effect of site preparation treatment on seedling density altered with regeneration year ($P = 0.006$; Fig. 4b). Seedling density in

disturbed treatments regenerated in 1989 was consistently greater than in burnt treatments from either year. For coupes regenerated in 1990, burnt treatments had initially greater seedling densities than disturbed treatments but, by age 2 y, there was no difference due to site preparation treatment. Similarly, differences between the two regeneration years were dependent upon site preparation treatment: 1989 disturbed treatments had greater seedling densities than 1990 disturbed treatments, but 1989 burnt treatments had lower seedling densities than their 1990 counterparts.

Seedling density and germination cohorts

The relative contribution of each germination cohort to seedling density at age 3 y varied with harvesting and site preparation treatment. The first germination cohort has remained the major contributor in all harvesting treatments (Fig. 12). As with total germination (Fig. 6), the proportional contribution of this first cohort varied with site preparation treatment. In all harvesting treatments except the 0.25-ha gap and the 4-ha clearfell, the proportion of seedlings observed in the first measurement was greater in slash-burnt treatments than in their disturbed counterparts. However, unlike the pattern of germination, the proportional contribution from subsequent cohorts did not decline steadily in all treatments. In the less intensive harvesting treatments, unharvested forest in particular, the contribution of

later cohorts to seedling density was higher. Germination continued to occur in these less intensive treatments but mortality was higher (Figs 2 and 7), resulting in a turnover of seedlings and the higher contribution from the later cohorts. In all harvesting treatments, the contribution of the final cohort was greater than the previous because no time had elapsed over which mortality of this cohort could occur.

Effect of distance from forest edge and nearest retained tree on seedling density

The distribution of seedlings within gaps reflected the trends established by germination. In the 0.25 and 1-ha gaps and the 4-ha clearfell, seedling density at age 3 y decreased as distance from the nearest coupe edge increased. This trend was apparent, but was not significant, in the 0.25-ha gap ($P > 0.05$). In the 1-ha gap, seedling density varied with distance from coupe edge ($P = 0.014$; Fig. 13a), the regression relationship being:

$$\ln(\text{seedling density} + 1) = \mu + \beta(\ln(\text{distance} + 1) - \varphi),$$

where $\mu = \text{mean } \ln(\text{seedling density} + 1) = 0.9523$, $\beta = \text{slope} = -0.3960$, and $\varphi = \text{mean } \ln(\text{distance} + 1) = 3.107$.

The effect of regeneration year, apparent for germination in the 1-ha gaps, was not detected for seedling density.

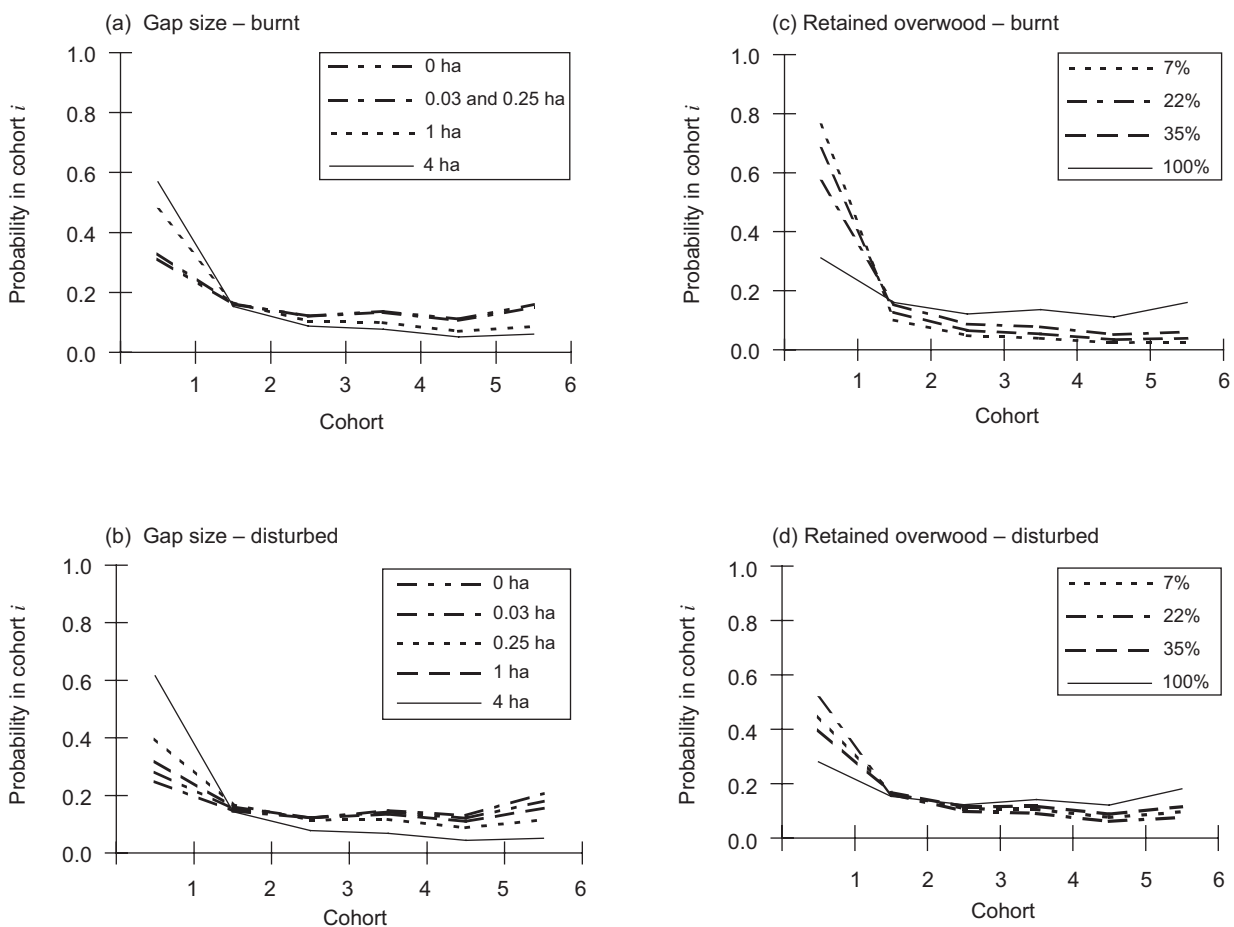


Figure 12. Cohort contribution to seedling density, 3 y after site preparation, versus gap size treatments in sites prepared by (a) fire and (b) mechanical disturbance; and retained overwood treatments in sites prepared by (c) fire and (d) mechanical disturbance in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

Table 4. Four-milacre stocking and seedling density at age 1 y, and seedbed receptivity post-site preparation (after Stucken and Hajek 1993), for 10-ha clearfell coupes in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria

Regeneration year	Coupe	Four-milacre stocking (%)	Seedling density (seedlings ha ⁻¹)	Seedbed receptivity (%)
1989	510/01	43	2500	64
	510/20	71	4200	52
1990	510/56	76	3700	88
	511/02	78	4100	95

In the 4-ha clearfell, seedling density varied with distance from coupe edge × site preparation treatment ($P = 0.008$; Fig. 13b). The regression equation for this relationship is:

$$\ln(\text{seedling density} + 1) = (\mu + \delta_i) + (\beta + \gamma_i) \times (\ln(\text{distance} + 1) - \phi),$$

where $\mu = \text{mean } \ln(\text{seedling density} + 1) = 0.7895$; $\beta = \text{slope} = -0.3136$;

$\phi = \text{mean } \ln(\text{distance} + 1) = 3.526$; $\delta = 0.0000$ for burnt and 0.0364 for disturbed; and $\gamma = 0.0358$ for burnt and 0.0000 for disturbed.

In the retained overwood treatments, no effect of distance from the nearest retained tree on seedling density was detected.

Stocking

Four-milacre stocking for each of the 10-ha clearfell coupes at age 1 y is presented in Table 4, along with average seedling densities at age 10–15 mo, derived from the germination study (Fig. 10), and seedbed receptivities post-site preparation, derived from the raw data of Stucken and Hajek (1993) and defined as the proportion of four-milacre plots containing at least 80% receptive seedbed. Four-milacre stocking was acceptable in each coupe except 510/01 (Squire *et al.* 1991) and correlated well with the seedling density data. The lower stockings achieved in 1989 are directly attributable to the impaired conditions for slash-burning that year and the correspondingly lower seedbed receptivities.

In the 1989 replication a number of other coupes did not meet the standard of 73% stocking; three of the 4-ha clearfells, two of the 7% retained overwood coupes and three of the 1.00-ha gaps were in the range of 50% to 73% stocking. By age 3 y all these coupes met the minimum stocking standard of 65%.

Height

The height of taller first cohort seedlings at age 3 y was positively related to harvesting intensity. Height generally increased as gap size was increased and retained overwood decreased ($P < 0.001$; Fig. 14 and Table 3). The method of site preparation also influenced height growth ($P < 0.001$); seedling heights, adjusted for harvesting treatment, were taller in burnt treatments (40.6 cm) than in disturbed treatments (33.2 cm). No effect of regeneration year was found.

Recolonisation by understorey

The mean covers (total of all life forms) of mechanically-disturbed retained overwood treatments at 1.5 y after site preparation were less than 20% (Table 5), which indicates that these treatments may still have met the minimum seedbed receptivity standard of 75% of plots with 80% of the plot being uncompacted bare soil or uncompacted ashbed. In the burnt treatments, which had the greatest recolonisation of understorey, 35–50% of the ground remained free of cover 2.5 y after site preparation (Table 5).

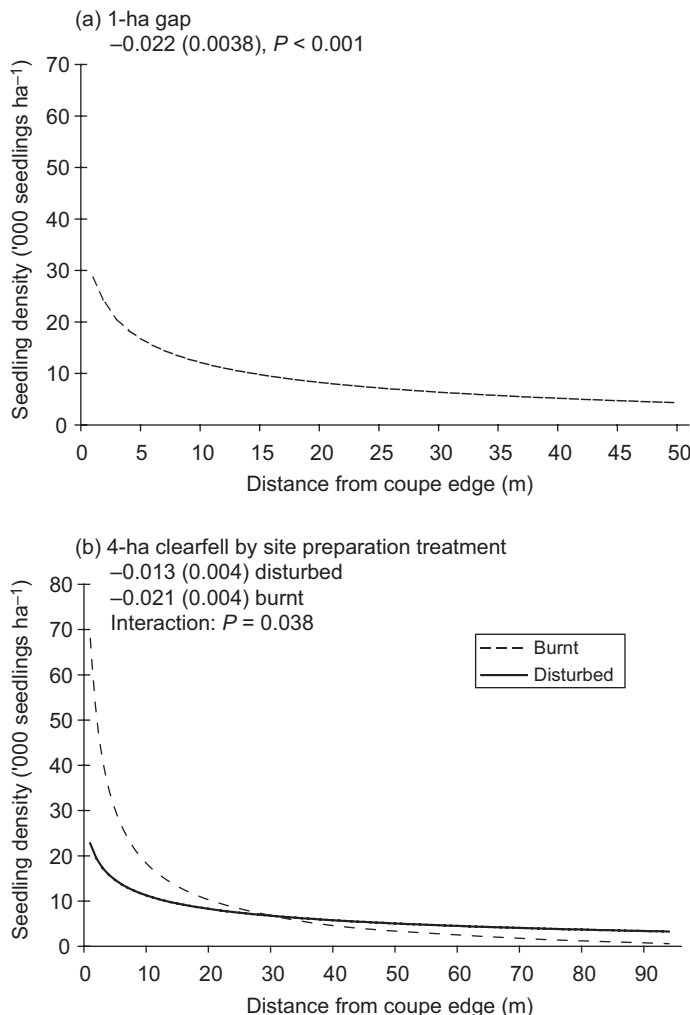


Figure 13. Regression relationships between seedling density, 2 y after site preparation, and distance from coupe edge for seedling plots in the (a) 1-ha gap and (b) 4-ha clearfell treatments in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria. Data are for all site preparation treatments and regeneration years combined for (a). Site preparation treatments are shown separately in (b). The slope, its standard error (in brackets) and P -value, is shown for each regression.

Discussion

A primary objective of the Silvicultural Systems Project was to determine whether silvicultural systems other than clearfelling would achieve successful eucalypt regeneration. The results reported here demonstrate that, for the lowland forest studied, regeneration can be established under the entire range of harvesting treatments trialled. At age 3 y, seedling density ranged from 3000 seedlings ha⁻¹ for the 10-ha clearfell, to 36 000 ha⁻¹ for the 0.03-ha gap (Table 3), most of which, in all treatments, originated from the first germination cohort (Fig. 12). In Victoria, the prescribed optimum seedling density for even-aged regeneration with a clumped distribution is 2500 seedlings ha⁻¹ at age 2–4 y (Squire *et al.* 1991).

Further objectives of this study were to evaluate and compare eucalypt germination, establishment and early growth in the treatments trialled. Germination and seedling density were strongly influenced by the effect of retained overwood and gap size on seed supply. Survival and early height growth were also strongly influenced by retained overwood and gap size, to the extent that the long-term productivity of regeneration in the less-intensively harvested treatments is expected to be considerably reduced. Site preparation treatment had far less influence and its effects were often confounded by regeneration year. These influences are discussed below, and the need to take them into account when prescribing silvicultural treatments or systems to achieve particular management objectives is made apparent. The regularity of the results obtained here provide a sound basis for doing so. Nevertheless, continued monitoring and data analysis will be required to examine longer-term trends which may differ from those currently apparent.

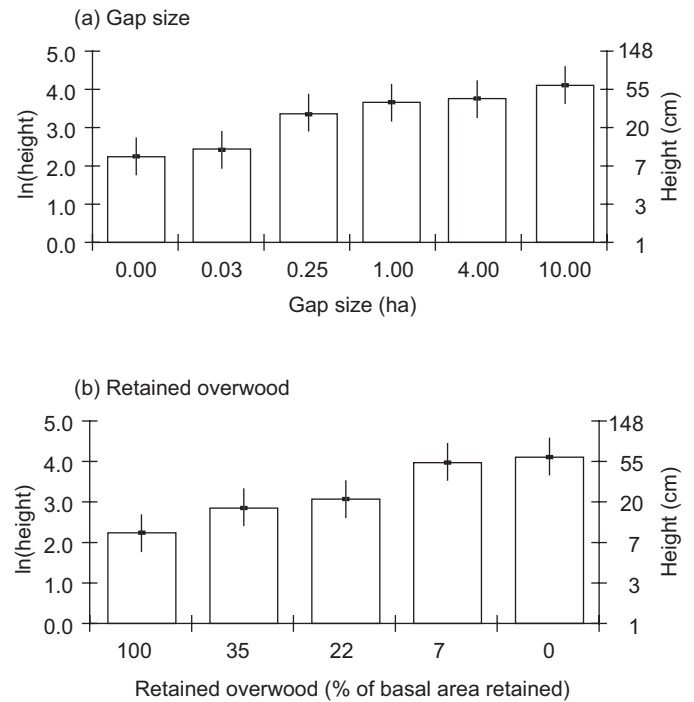


Figure 14. Height of seedlings from the 1st germination cohort, 3 y after site preparation, versus (a) gap size and (b) retained overwood in the Silvicultural Systems Project at Cabbage Tree Creek in East Gippsland, Victoria. Vertical bars indicate 95% confidence intervals on the natural log scale.

Table 5. Cover by vegetation at 1.5 and 2.5 y after site preparation in the harvesting and site preparation treatments at the Silvicultural Systems Project at Cabbage Tree Creek, East Gippsland, Victoria

Harvesting treatment	Site preparation treatment	Cover (%)		
		1990 replication		1989 replication
		1.5 y	2.5 y	2.5 y
Large clearfell	Burnt	40	63	64
	Disturbed	36	61	60
Small clearfell	Burnt	31	55	48
	Disturbed	29	62	58
Large gap	Burnt	18	40	39
	Disturbed	27	56	65
Medium gap	Burnt	27	56	65
	Disturbed	27	56	65
Small gap	Burnt	25	53	53
	Disturbed	28	53	63
7% retained overwood	Burnt	40	66	47
	Disturbed	15	37	45
22% retained overwood	Burnt	38	59	53
	Disturbed	18	41	27
35% retained overwood	Burnt	28	53	
	Disturbed	17	43	44
Unharvested forest	Burnt		50	
	Disturbed		45	

Germination

The quantity, distribution and timing of germination strongly reflected the influence of harvesting treatment on seed supply. Regeneration of all treatments except the 4- and 10-ha clearfells relied upon seed crops in the retained overwood or edge trees. Thus the quantity of seed available for regeneration varied between harvesting treatments, depending on gap size and the amount of retained overwood. Bradshaw (1992) argued that the essential difference between gap size treatments lies in the proportion of the gap that is influenced by edge effect. Bassett and Geary (unpublished data) monitored seedfall for about 6 mo after site preparation in the retained overwood treatments and found that total seedfall decreased with levels of retained overwood. Total germination to age 3 y was primarily a function of this manipulation of seed supply by harvesting treatment, increasing as gap size decreased or retained overwood increased (Table 3; Figs 2 and 3). The contribution of seed from logging slash was comparatively small (K. Faunt, unpublished data).

The effect of harvesting treatment on seed supply was also apparent in the distribution of germination within harvesting treatments. Total germination within the 0.25 and 1-ha gaps and 4-ha clearfells decreased as distance from the nearest coupe edge, and therefore from seed supply, increased (Fig. 5). The differences evident between the gradients for these treatments is similarly explained; seed from edges other than the nearest edge will have made a greater contribution to germination in the progressively smaller gaps. Cremer (1966) has previously demonstrated such gradients for *E. regnans* forest, and Cremer *et al.* (1978) noted that effective seeding distance for regeneration purposes will depend upon species, seed crops, local wind climates and seedling percents. In this study, total germination declined rapidly over the first 25 m from the nearest edge (Fig. 5), but was still sufficient at 50 m in the 1-ha gap treatment to give acceptable seedling densities at 3 y (Fig. 13a). Data for distances beyond that in the 4-ha clearfells is confounded by the aerially-applied seed (Fig. 13b). No gradients were identified in the distribution of germination in the retained overwood treatments. This is largely consistent with the results of the seedfall studies, which reported that seedfall was evenly distributed in open unharvested forest (Bassett 1995).

Germination continued throughout the 3-y study period, but steadily declined in all treatments (Fig. 2) as seedbeds were recolonised and receptivity decreased. At 3 y, it had virtually ceased in the 10-ha clearfall, where there was negligible seed input following aerial seeding. Consequently, the first germination cohort was the major contributor to total germination for all harvesting treatments (Fig. 6). In most of these treatments, the proportion of germinants originating from the first cohort was greater in burnt treatments than in their disturbed counterparts (Fig. 6). It was also greater in the more intensively-burnt treatments than in those burnt less intensively. These effects are likely to have been a response to both more rapid recolonisation of burnt seedbeds by understorey plants (Table 5), and a comparative decline in seed supply following fire-induced seedfall (Bassett and White 1993).

Site preparation treatment had far less effect on total germination. Stucken and Hajek (1993) showed that both fire and mechanical

disturbance generally produced adequate levels of receptive seedbed in this experiment, and that the major seedbed type produced by both treatments was unburnt, topsoil disturbed and slash-free. They also showed that mechanical disturbance consistently produced a greater proportion of receptive seedbed than burning. Disturbed soil seedbeds have often been reported to produce higher germination percents than burnt seedbeds (e.g. Fagg 1987), but the influence of site preparation treatment on total germination in this study was confounded by differences between the regeneration years (Fig. 4a). In 1989, mechanically-disturbed treatments produced greater or similar levels of germination compared with their burnt counterparts, whilst in 1990 the reverse occurred. This may be explained by the delay in site preparation for some 1990 disturbed treatments until June, after the autumn conditions conducive to germination had passed. If this were the case, the site preparation effect on total germination detected for 1990 may not be a true reflection of the treatment effect. Burnt coupes, prepared by the end of May in both years, produced a similar level of germination each year.

Given the generally adequate level of seedbed preparation (Stucken and Hajek 1993), germination occurred under all conditions of gap size and retained overwood, despite the apparent effect of these factors on temperature, light, moisture and other environmental factors (e.g. Keenan 1986; Bradshaw 1992; Stoneman 1994). Faunt *et al.* (unpublished data) reported germination of 1.2–12.6% for seed sown by hand on to selected seedbeds in the coupes studied here, but found no significant difference between harvesting treatments. These germination percents, and the 9% calculated for the aerially-sown seed in the 10-ha clearfells, are consistent with data reported from other studies in this and similar forest types (Fagg 1987; Stucken *et al.* 1998). All of the above evidence indicates that the overriding influence on germination to 3 y in this study has been the quantity, timing and distribution of seed supply, as determined by harvesting treatment.

The lack of sensitivity of germination to site preparation is further highlighted by the occurrence of germination in coupes before site preparation was carried out. Although these coupes did not meet the seedbed receptivity standards, they were found to have acceptable levels of regeneration. Furthermore Bridges (1983) reported that *E. sieberi*/stringybark (that is, lowland forest) in south-eastern New South Wales was routinely regenerated without any site preparation other than that associated with harvesting. The evidence indicated that the standard for minimum receptivity was too high and that harvesting disturbance *per se* may create sufficient seedbed for regeneration (Stucken and Hajek 1993). Subsequent guidelines lowered the standard for seedbed receptivity and recommended that no site preparation be used on some coupes (Lutze and Geary 1998).

Mortality and survival

Total mortality at three years closely reflected the total germination results. Total mortality was highest where total germination was highest, and decreased with increasing gap size and decreasing overwood retention (Figs 2, 7). Within cohorts, mortality was highest soon after germination, but the overall rate of mortality was relatively constant during the 3-y monitoring

period and no episodic mortality events were recorded (Fig. 7). At 3 y, recruitment was still occurring (Fig. 6), although the rate of germination had declined below the rate of mortality, particularly in the less intensively harvested treatments (Figs 2, 7).

In contrast to mortality, survival percent improved with larger gap size and reduced overwood (Table 3; Figs 8 and 9). Survival of the first cohort to 3 y ranged from 14% in unharvested forest to 47% in the 10-ha clearfell, and of the second cohort from 12% in burnt unharvested forest to 80% in the burnt 10-ha clearfell. This is a critical result and it is anticipated that it will be exacerbated over time. Although germination percents were found not to vary with the range of retained overwood and gap sizes trialled (K. Faunt *et al.*, unpublished data), retained overwood and edge trees are known to affect establishing seedlings directly, through competition for site resources and the deposition of litter, and indirectly, through their influence on factors such as microclimate, development of fungi and the activity of browsing animals. Bradshaw (1992) discussed these effects in relation to gap size and Battaglia and Wilson (1990) showed that the survival of regeneration beyond the first or second year tended to decline with increasing overwood. It is also evident from the relationships between seed supply, harvest treatment and the amount and distribution of germination in this study that a further inherent harvest treatment effect will be the degree of inter-seedling competition experienced by seedlings in different treatments, and at different locations within treatments.

Survival of the first cohort was substantially different to that of the second and subsequent cohorts. Figures 8 and 9 illustrate this, although direct comparison of the two figures is not valid due to the adjustments for site preparation treatment and regeneration year in the REML analyses depicted. A proportion of the real difference between cohorts can be attributed to the first cohort enduring a more hostile environment for germinants (e.g. soil movement, pathogenic fungi), as well as an additional 6 mo to the calculation of survival at 3 y. Nevertheless, the large flush of germination contributed by the first cohort (Fig. 2) ensured that it comprised the bulk of seedlings surviving to 3 y in all harvesting treatments (Fig. 6). The effect of site preparation treatment and regeneration year on survival differed between cohorts, primarily as a result of the delayed mechanical disturbance in 1990 and the unsynchronised early measurements (Fig. 1). Survival of the later cohorts showed no effects of harvesting treatment, site preparation treatment or regeneration year.

Seedling density and stocking

Seedling density at any time was primarily a function of the germination results, as determined by the effect of harvest treatment on seed supply (Figs 2 and 10). At 3 y, seedling density ranged from 3000 seedlings ha⁻¹ in the 10-ha clearfells to 36 000 ha⁻¹ in the 0.03-ha gaps, and generally increased with increasing overwood and decreasing gap size (Table 3; Fig. 11). These density estimates encompassed all seedlings, including recent germinants. Most operational procedures for assessing eucalypt regeneration include a specification for acceptable seedlings that is appropriate to the silvicultural system being used (e.g. Squire *et al.* 1991; Dignan and Fagg 1997; CALM 1990). The standard applied in the regeneration surveys at the experimental site were intended for clearfell, seedtree or low

levels of shelterwood, and defined acceptable seedlings at age 1–3 y as at least 25 cm tall, with more than six leaves and with the vigour and potential to grow into saplings (Squire *et al.* 1991). Application of this standard would have excluded a lot of small seedlings in the small to medium gaps and the 35% and 100% retained overwood coupes, but it has provided a realistic measure of the spatial distribution of healthy seedlings.

Lowland forest has a record of reliable regeneration (Bridges 1983; Campbell *et al.* 1984; Wilson and Fagg 1994; Murphy and Fagg 1996). The seedling densities achieved across the range of treatments in this study reinforce this. A critical factor is that the volume and regularity of seed production by the major species make the forest type well suited to regeneration systems which rely upon natural seed sources (e.g. Bridges 1983; Campbell *et al.* 1984). Bassett (1995) recorded annual production of up to 2.2 million capsules ha⁻¹ and average annual seedfall of 1.7 million viable seeds ha⁻¹ at an unharvested forest site at the study area. Further, Bassett and White (1993) estimated average crops of 138 000 viable seeds tree⁻¹ on retained *E. sieberi*, and 418 000 viable seeds ha⁻¹ on retained trees overall, in two of the 7%-retained-overwood coupes. Subsequent seedfall over 6 mo following burning was 342 000 viable seeds ha⁻¹.

The seed tree system is consequently the dominant silvicultural system employed in this and similar forest types in East Gippsland (Lutze *et al.* 1999), and excessive seedling densities are frequently a problem (e.g. Fagg 1987; Loyn 1981; Stucken *et al.* 1998). The 9000 seedlings ha⁻¹ at age 3 y achieved for the 7%-overwood coupes in this study (Table 3; Figs 10 and 11) are also well in excess of the prescribed optimum of 2500 seedlings ha⁻¹ at age 2–4 y (Squire *et al.* 1991). Early spacing has been investigated as a means of redressing this problem and enhancing the productivity of large areas of over-stocked fire and harvesting regrowth (Kerruish *et al.* 1993; Hescocock 1995; Raison *et al.* 1995). The ability to manipulate seedling density through seed supply provides a more direct solution.

The 10-ha clearfell coupes indicate the degree of control that is possible in this reliably regenerated forest type. These coupes were aerially seeded at one-third of the recommended operational sowing rate of 150 000 viable seeds ha⁻¹ (Fagg 2001), with the target of achieving seedling densities of 3000 seedlings ha⁻¹ at age 2 y. A distinction must be made here, however, between seedling density and stocking. Average seedling density does not reliably portray whether regeneration is evenly distributed or if a coupe is fully occupied: hence the widespread use of stocked-plot methods for regeneration surveys. In Victoria, a four-milacre stocking of 73% is considered equivalent to 3000 seedlings ha⁻¹ (Squire *et al.* 1991). Seedling densities for the 10-ha clearfells at age 1 y ranged from 2500 to 4200 seedlings ha⁻¹, averaging 3600 seedlings ha⁻¹, and four-milacre stocking ranged from 43% to 78%, averaging 69% (Table 4). The lower seedling densities and stockings were directly attributable to the lower-intensity burns and reduced seedbed receptivities achieved in 1989. The results therefore indicate that broad control can be exercised over stocking and seedling density through seed supply, but that adequate distribution of receptive seedbed is essential and that sufficient margin should be allowed to ensure that the minimum stocking achieved is acceptable. Under such prescriptions, some

spacing work may still be warranted if the productivity of regrowth is to be maximized, but should be easier and less costly to implement. The extent to which control through seed supply can be applied to species composition is examined in Lutze (1998).

The first cohort remained the major contributor to seedling density at any time over the 3 y study period (Fig. 12). Seedling density declined in most treatments following the first measurement, as the rate of germination and recruitment fell below the rate of mortality (Figs 2, 7 and 10). Incoll (1974) has previously reported the decline in seedling density that occurs with time in dense, young *E. sieberi* regrowth. This has particularly been the case with the less-intensively harvested treatments in this study, reflecting the significant reductions in survival percent with increasing retained overwood and decreasing gap size (Table 3; Figs 8 and 9). Battaglia and Wilson (1990) and Kellas (1994) found a similar effect when evaluating shelterwood systems in *E. delegatensis* R.T.Baker (alpine ash) forest and messmate/peppermint forests respectively. It is anticipated that this process will eventually replace seed supply as the major influence on seedling density and cause the rankings of seedling density relative to gap size and retained overwood to be reversed.

The distribution of seedling density within treatments at 3 y reflected that established by seed supply for germination. In the gap size treatments examined, seedling density declined with distance from nearest edge (Fig. 13). In the 1-ha gap, it declined from 29 000 to 4300 seedlings ha⁻¹. The effect of edge trees on survival, evident at the treatment level (Figs 8 and 9), can also be expected to affect within treatment gradients and eventually replace seed supply as the dominant influence on the distribution of seedling density. No seedling density gradients were detected in the retained overwood treatments, confirming the germination results, but, similarly to the edge trees, the effect of retained trees on survival can ultimately be expected to affect seedling distributions. Incoll (1979) has previously found that few seedlings survive within the crown projection of retained *E. sieberi* overwood trees.

The effect of site preparation treatment on seedling density generally reflected that recorded for germination (Fig. 4), including the confounding effects of the un-synchronised early measurements. Other confounding factors are likely to have been the differences described in the timing and quality of site preparation, including burn intensity. A number of individual coupes did not meet minimum operational standards for seedbed receptivity following site preparation (Stucken and Hajek 1993), and seedling densities on those coupes tended to be reduced accordingly (e.g. Table 4).

Height

Retained overwood and edge trees were found to have a severe suppressive effect on the height of taller first-cohort seedlings (Table 5; Fig. 14). A number of other studies in a variety of eucalypt forests have produced similar results (e.g. Incoll 1979; Rotherham 1983; Battaglia and Wilson 1990; Kellas 1994; Bi and Jurskis 1996; Dignan *et al.* 1998; Van der Meer *et al.* 1999; Bauhus *et al.* 2000). There is a possibility in this study that the height results are due in part to the inherent harvest treatment effect on inter-seedling competition, but there is no direct evidence

to suggest that this is the case (K. Faunt, unpublished data), and a reduction in the height of taller seedlings need not necessarily be expected as a consequence of inter-seedling competition (Opie *et al.* 1978).

The clear implication of the height data presented is that competition from overwood and edge tree needs to be minimized if seedling growth is to be maximized. Incoll (1979) estimated the potentially large proportions of regrowth volume lost due to suppression by *E. sieberi* overwood, although his estimates exceed those of other authors on the subject (Bassett and White 2001). This study has confirmed that retained overwood and edge trees will reduce seedling survival and height growth, and it is these two harvest treatment effects combined that can ultimately be expected to have the greatest influence on the long-term persistence and productivity of the regeneration. Associated factors that also need to be considered when prescribing silvicultural systems or treatments are the potentially compensating growth of the overwood and edge trees (e.g. Ellis *et al.* 1987), and the ability of the regeneration to respond to release from competition (e.g. Kellas *et al.* 1987), wherever the retained overwood or edge trees are to be subsequently removed.

The response of seedling height growth to site preparation by fire has also been previously demonstrated (e.g. Lockett and Candy 1984) and attributed to changed soil conditions (e.g. Florence and Crocker 1962; Humphreys and Lambert 1965; Raison 1979; Launonen *et al.* 1999). At this study area, CSIRO (1991) found higher soil C : N ratios, lower soil N-mineralisation and lower N-uptake by plants in mechanically-disturbed coupes, and that seedling heights increased with burn intensity and were least where there had been major mixing of soil horizons during harvesting and site preparation.

Conclusions

This study has demonstrated that regeneration can be established under a wide range of gap size and retained overwood conditions in lowland forest. It has also illustrated the major processes affecting regeneration to 3 y. Given adequate site preparation, seed supply was the major determinant of levels of germination and seedling density. Seed supply can clearly be manipulated and, in this reliably regenerating forest type, could be used to achieve broad control over seedling densities. Site preparation had less influence on germination and seedling density, and its effects were often confounded by timing and regeneration year. Adequate levels of regeneration may be obtained without any additional site preparation other than that obtained through harvesting.

Although regeneration was achieved under a wide range of gap size and overwood conditions, the establishing seedlings were subject to the influence of the retained trees. Survival of seedlings was significantly less and the height growth of surviving taller seedlings was severely suppressed in the less-intensively-harvested treatments. These two treatment effects combined can be expected to be the major determinants of the long-term persistence and productivity of the regeneration. It is clear that the influence of retained overwood and edge trees needs to be minimized if the productivity of regeneration is to be maximized. Site preparation by fire had a positive effect on height growth.

Overall, the study has highlighted the need to take such effects into account when prescribing silvicultural treatments or systems to achieve particular management objectives. The regularity of the results obtained here provides a sound basis for doing so in lowland forest. Nevertheless, continued monitoring and data analysis is required to examine longer-term trends, which may vary from those currently apparent.

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*See Squire *et al.* (2006), p. 167, for a list.

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