

Experiments on tree and shrub establishment in temperate grassy woodlands: Seedling survival

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Abstract Experimental studies of the emergence of shrubs and trees in grassy woodlands on the New England Tablelands, New South Wales, Australia, showed that emergence of seedlings was determined by seed supply, seed predators and seed burial. The survival of these seedlings was then observed in an experiment to test the effects of previous land use, grazing by stock and grazing by other vertebrates. The fate of four eucalypts and six shrub species was followed over 5 years. Across all species more than 50% mortality occurred in the first 6 months prior to the imposition of grazing treatments. These deaths were attributed to the combined effects of insect defoliation, cold, and low soil moisture. Average mortality over all treatments showed two distinct trends: eucalypts and one unpalatable shrub (*Leptospermum*) had greater than 1% survival over 5 years, whereas *Acacia*, *Cassinia*, *Indigophera*, *Lomatia* and *Xanthorrhoea* either had very low or no survival after 5 years. The effect of livestock grazing on seedling numbers was rarely detected because of patchy emergence and mortality due to other causes. However, proportional hazard regression models showed that there was often an increased hazard associated with grazing or grazed landscapes. Overall, those species with high hazard coefficients associated with stock are rare in the landscape, whereas those with lesser risk are more common. Recruitment is likely to be an extremely rare event because the highest proportion of germinable seed sown that survived to a juvenile stage was 0.42% and the mean across all species was 0.12%. No natural recruitment of shrub species was observed over 5 years of observation, suggesting that recruitment is episodic and disturbance driven. Enhancing natural 'regeneration' of woody plants under these circumstances may be more challenging than simply fencing off remnants.

Key words: eucalypt woodland, grazing, herbivory, manipulative experiment, recruitment, seedling mortality, survival analysis.

INTRODUCTION

The recruitment of trees and shrubs in grassy ecosystems involves several stages that determine establishment success. In a companion paper (Clarke & Davison 2001), experimental studies of the emergence of trees and shrubs in grassy woodlands on the New England Tablelands, New South Wales, Australia, showed that the emergence of seedlings was limited by seed supply and microsite conditions when above average rainfall occurred. Burial of seeds also enhanced seedling emergence through escape from seed removers and/or enhanced moisture conditions (Clarke & Davison 2001). Although a lack of emergence appears to be a major constraint on recruitment in these woodlands, the combined demographic effects of seed supply, germination, emergence and seedling survival have been shown to influence recruitment patterns in temperate woodlands (Yates & Hobbs 1997).

Early mortality of seedlings at the cotyledon stage is a widespread phenomenon in woody plants but slows as cohorts age (Harper 1977). Climate, herbivores,

pathogens and competitors are all factors that will affect the survival of tree and shrub species in grassy woodlands (see reviews in Clarke 2000; Windsor 2000). A lack of adequate moisture is often reported as a controlling factor that reduces the survival of seedlings in eucalypts (Curtis 1989; Stoneman *et al.* 1994; Semple & Koen 1997; Yates & Hobbs 1997), although manipulations involving watering are rare. Competition from the grassy matrix in woodlands also appears to be important for seedling survival because removal of the ground stratum enhances seedling survival (Harrington 1991; Semple & Koen 1997). Intraspecific competition among seedlings may also regulate survival where seedling densities are high (Hodgkinson 1991), although this appears to be rare in temperate woodlands (Clarke 2000). Grazing is also often cited as having profound effects on the composition of woodland vegetation through the inhibition of recruitment and the transformation from woody into graminoid-dominated vegetation (Gibson & Kirkpatrick 1989; Cheal 1993; Pettit *et al.* 1995). Conversely, grazing is also associated with the conversion of semi-arid grassy woodlands into unpalatable shrub-dominated communities (Wilson 1990; Noble 1997). A lack of recruitment of trees and shrubs is widely perceived

Table 1. Total number of germinable seed sown, seedlings emerging and seedlings surviving summed across all treatment levels

Species	Growth form	Seed mass (mg)	Sites sown	Seed sown	Emergence	2 month	4 month	8 month	12 month	21 month	60 month
<i>Acacia dealbata</i>	Shrub	13.8	Granite	450	51 (11%)	44*	39*	17*	13*	0	0
<i>Cassinia quinquefaria</i>	Shrub	>0.1	Granite	2268	36 (2%)	0	0	0	0	0	0
<i>Eucalyptus blakeyi</i>	Tree	0.1	All	10800	1363 (13%)	406	215	108	45*	32*	22*
<i>Eucalyptus melliodora</i>	Tree	0.3	All	9288	925 (10%)	326	226	72	43	36*	29*
<i>Eucalyptus viminalis</i>	Tree	1.1	Basalt	3456	487 (14%)	198	117	41	22	11*	8*
<i>Eucalyptus youmanii</i>	Tree	2.2	Granite	2808	205 (14%)	117	82	67	22	8*	3*
<i>Indigophera australis</i>	Shrub	6.1	Sediments	3600	450 (13%)	243	171	58*	11*	11*	6*†
<i>Leptospermum polygalifolium</i>	Shrub	0.2	All	5184	96 (2%)	69	47	41*	24*	12*	8*
<i>Lomatia fraseri</i>	Shrub	7.2	Granite	3168	300 (9%)	123*	72*	54*	5*	2*	0
<i>Xanthorrhoea johnsonii</i>	Shrub	18.0	Sediments	3600	351 (10%)	78*	74*	46*	39*	32*	0

Variance heterogeneity ($P < 0.01$ using Cochran's test after angular transformation) for species survival across treatments shown by *. Data become increasing heterogeneous through time because of patchy mortality. †Two individuals flowered. Emergence is 3 months after seeds were sown.

as a major threat to the viability of temperate grassy woodlands in Australia (Yates & Hobbs 1997; Reid & Landsberg 2000). However, census data on the seedling survival of woody plant species in temperate Australian ecosystems are scarce (Leigh & Holgate 1979; Curtis 1989; Auld 1990, 1995; Stoneman *et al.* 1994; Keith 2002). In particular, the effects of spatial heterogeneity and grazing on survival are poorly known.

The aim of our study was to determine the factors limiting the recruitment of shrubs and trees in grassy woodlands and to quantify survivorship. We examined seedling survival in terms of: (i) the effects of spatial variation among plots; (ii) the presence of herbivores; and (iii) the presence of stock. These data were then combined with seedling emergence and seed germinability data from a previous study (Clarke & Davison 2001) to compare the overall survivorship patterns among species. The relationship between the relative abundance of species in the field and their survival functions was also explored to see if survival under stock grazing was correlated with abundance.

METHODS

Experimental designs

Spatio-temporal factors

The experimental sites were located on the New England Tablelands in remnant grassy temperate woodlands. Details of the 10 species used and sites have been described in a previous paper (Clarke & Davison 2001) and are listed in Table 1. The experiment was arranged at each of three study sites in four fenced plots measuring 5 m × 5 m on either flat or slightly sloping ground. Fencing excluded rabbits, kangaroos and livestock (sheep and cattle). Each of the 12 plots had a complete cover of grasses and forbs and a canopy cover of eucalypt trees ranging from 10 to 30%. Three species (*Eucalyptus blakeyi*, *Eucalyptus melliodora*, *Leptospermum polygalifolium*) were sown in all plots; the other seven were sown in sites where they are associated with a particular lithology (Clarke & Davison 2001; Table 1). Fifty seeds of each of the species listed in Table 1 were sown into an area of 5 cm × 5 cm for each replicate. Seeds were sown between December 1995 and April 1996. The spatial factors in the experiment were site (lithology), grazing history and paddock (patch) variation. There were three levels of site: high nutrient (basalt plots), medium nutrient (metasediment plots), and low nutrient (granite plots). Time of sowing and consequent season of mortality varied across sites. At the granite plots, seedlings emerged over summer and most mortality occurred

from February to May 1996. The metasediment plots followed next with maximum emergence in April and mortality from May to July 1996. Finally, the basalt plots had maximum seedling emergence by July and seedling mortality occurred from August to November 1996. Plots were located so as to provide two levels of grazing history: (i) recently grazed by stock; and (ii) stock grazing excluded for more than 5 years. Each of these levels was replicated in two independent fenced plots (i.e. two spatially distinct paddocks), thus there were four fenced plots at each site (Fig. 1). The survival of seedlings from three species (*E. blakelyi*, *E. melliodora*, *L. polygalifolium*) was followed in 18 replicate quadrats (5 cm × 5 cm) within each of the 12 plots (3 sites × 2 grazing × 2 patches), whereas the survival of seven species sown in single sites was followed with 18 replicates in four plots (2 grazing × 2 patches). Initial survival data followed the fates of seedlings after they had emerged at approximately 10 weeks from initial sowing (Clarke & Davison 2001). Censuses were undertaken at 0, 2 and 4 months after

emergence. Then, at 7 months, grazing treatments were imposed, as will be described later. Potential numbers of replicates in each plot were not achieved because of the absence of seedling emergence in some of the 18 sown replicates. Natural recruitment in and adjacent to plots was also recorded at sites but the fate of these seedlings was not measured.

Vertebrate grazing factors

At each site two levels of grazing were imposed when seedlings were approximately 7 months old. In plots where stock grazing had been excluded for at least 5 years, half the replicates were exposed to grazing by kangaroos and rabbits by the removal of fences (Fig. 1). In plots where stock grazing had recently occurred prior to the erection of fences, half the replicates were exposed to grazing by cattle, sheep, kangaroos and rabbits by the removal of fences. Stocking rates varied in space and time but ranged from 1 to 8 dry sheep equivalents (d.s.e.) ha⁻¹ prior to and after the removal of fences. Seedling survival was

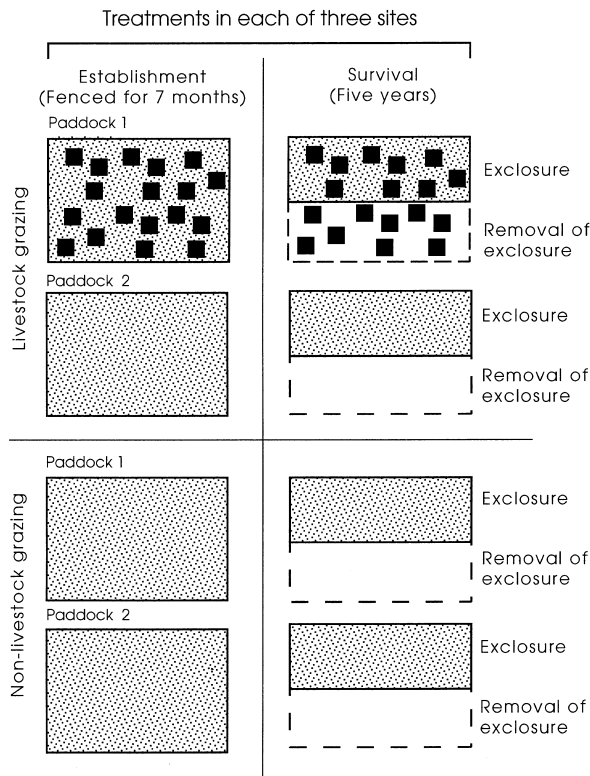


Fig. 1. Schematic arrangement of three sites (basalt, granite and metasediment) and (■) plots within them. Within each study site, two paddocks (patches) were selected in areas that were currently grazed by livestock and in areas where grazing had been excluded for at least 5 years. In each of the 12 fenced plots (3 sites × 2 paddocks × 2 previous levels of grazing) there were 18 replicate quadrats (5 cm × 5 cm) where seedlings had been established for approximately 7 months. Half of the replicates were exposed to grazing by removal of fences, the other half remained fenced. The fate of these seedlings was followed for 5 years.

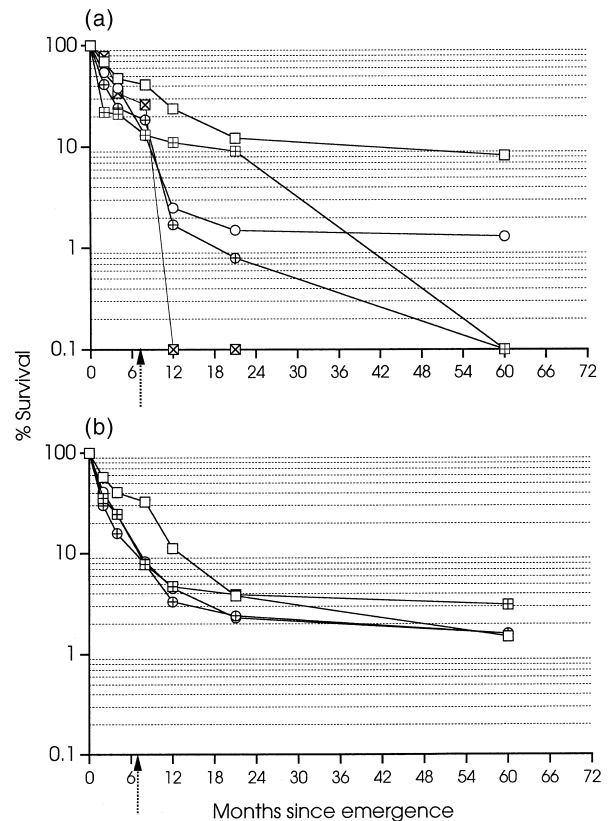


Fig. 2. Mean percentage survival of species from establishment (3 months since seeds were sown) to the end of the study averaged across all treatment effects. Most mortality occurred before removal of grazing exclusions at 7 months. *Cassinia quinquefaria* had no seedlings that could be followed. (a) (□), *Leptospermum*; (⊞), *Xanthorrhoea*; (⊕), *Lomatia*; (○), *Indigophera*; (⊗), *Acacia*. (b) (□), *Eucalyptus youmanii*; (⊞), *E. melliodora*; (⊕), *E. blakelyi*; (○), *E. viminalis*.

recorded after the fences were removed at 8, 12, 21 and 60 months.

Statistical analyses

Cumulative survival data were analysed starting 3 months after seedlings had emerged. Data were plotted at 0, 2, 4 (exclosures removed at 7 months), 8, 12, 21 and 60 months. The data describing per cent seedling survival at 4 months and prior to the removal of fences were analysed in two- and three-factor ANOVA. Site, grazing history and paddock (patch) variation were analysed for the three species sown in all sites. Site and grazing history were treated as fixed factors, whereas the two replicate plots were a nested factor. Grazing history and paddock (plot) were analysed for the other seven species sown in single sites.

The data from per cent seedling mortality 1 month after the removal of fences (8 months after seedling emergence) were analysed in two- and three-factor ANOVA. Site, exclosures, and paddock (plot) variation were analysed for three species. Site and exclosures were treated as fixed factors and the two replicate plots were a nested factor. Exclosures and paddock (patch) were analysed for the other seven species. Interactions between grazing history and exclosures were also examined but the number of missing cells precluded formal analyses. Where plot effects were not significant ($P > 0.25$) they were pooled with replicates. All per cent data were angular transformed (arcsine square root) and homogeneity of variances was tested using Cochran's test. Levels of power for the F -tests were also determined because of the low numbers of replicates in some plots and the high levels of mortality. Pearson correlation coefficients were also calculated between minimum and maximum monthly temperatures, monthly rainfall and mortality where species were sown at different times.

Survival analyses were also performed on right censored data using a proportional hazard regression model (Cox & Oakes 1984). In survival analysis, time to death is the variable of interest and regression models can be used (Cox & Oakes 1984). When an experiment 'ends' before all events have occurred then data for non events are right censored. Although

comparison of survival functions are useful, the number of census points precluded detailed parametric analyses of survival functions. However, differences in survival pattern among treatments (strata) can be undertaken where the underlying hazard functions are proportional (Cox & Oakes 1984). Initial plots of log cumulative hazard versus time for different treatment pairs (stock *vs* exclosure; other herbivores *vs* exclosure; recently grazed *vs* less grazed) were generally parallel, indicating proportionality. The likelihood ratio test was used to evaluate whether the levels of covariates make a significant contribution to the global model. Chi-squared tests were used to test for each level of covariates in expanded models after the hazard functions were examined for proportionality. The exponent of the regression coefficient (e^{β}) gives the relative risk of mortality for a seedling subjected to a hazard (grazing or grazed landscapes) compared with a seedling in an exclosure where no recent grazing has occurred. The relative hazard of treatments can be compared across species and against initial densities of seedlings arising from emergence studies (Clarke & Davison 2001). The relationship between hazard coefficients and abundance of species in the landscape was also explored by Pearson correlation coefficients.

Establishment index

An establishment index (EI) was derived from the product of the estimated relative amount of seed produced by each species (F) and the addition of the proportion of germinable seeds that emerged (E) (Clarke & Davison 2001) and survived after 5 years (S). Mean data were used across all treatments for comparative purposes.

RESULTS

Relative patterns of survival and natural recruitment

For all species, less than 1% of germinable seed sown survived to become juvenile plants after 5 years of

Table 2. Analysis of variance for the effects of grazing history and site on percentage of seedlings surviving for the three species sown at all sites

Source	d.f.	<i>Eucalyptus blakelyi</i>		<i>Eucalyptus melliodora</i>		<i>Leptospermum polygalifolium</i>	
		<i>F</i>	Power	<i>F</i>	Power	<i>F</i>	Power
Grazing history (G)	1	9.6**	0.9	1.0	0.1	0.8	0.1
Site (S)	2	12.2***	0.9	6.4**	0.9	0.7	0.1
S × G	2	0.1	0.1	0.2	0.1	3.1*	0.5
Residual	204	155	128	23			

Data collected 4 months after emergence and 3 months before exclosures were removed. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

growth and one species (*Cassinia*) had no seedlings surviving past the first month (Table 1). Between 2 and 14% of germinable seed sown emerged, following which 0–25% of emerged seedlings survived the first year of growth. In general, eucalypts had better emergence than the shrubs and with the exception of *Leptospermum* and *Indigophera* they also had greater overall survival. Initial post-emergence survival was low in all species, with more than 50% mortality occurring within 8 months of emergence (Table 1, Fig. 2). Average mortality over all treatments and spatial effects showed two distinct trends. All eucalypts and two shrubs (*Indigophera*, *Leptospermum*) had greater than 1% survival over 5 years, whereas *Acacia*, *Cassinia*, *Lomatia* and *Xanthorrhoea* either had very low or no survival up to 5 years (Table 1, Fig. 2). All eucalypts developed pronounced lignotubers greater than 1 cm in diameter and expressed a 'suppressed' growth form even in plots where grazing was excluded. After 3 years of growth, *E. youmanii* was the tallest species (approximately 80 cm high) followed by *E. viminalis*, *E. blakelyi* and *E. melliodora*.

Natural recruitment of *E. viminalis* was observed adjacent to plots at one site (basalt site) during the study where cotyledonary seedling densities often exceeded thousands per square metre, but after 5 years seedling densities were less than one per 0.1 ha. Nevertheless, this was a significant recruitment event, with thousands of juvenile trees still present in the landscape. Similar natural recruitment of other eucalypts was observed throughout the New England Tablelands following the rainfall events of January 1996. One *Acacia* recruit was also observed at one site but no other shrub or eucalypt recruits were observed.

Effects of previous grazing and spatial factors

Seedling emergence did not occur in many of the sown replicates and early mortality further contributed to high variability among treatments. Despite this, tests for variance heterogeneity on transformed data were generally not significant during the early survival phase (Table 1). Mortality often exceeded 50% of emerged seedlings prior to the imposition of grazing treatment and positive effects of past grazing history were only

detectable in one (*E. blakelyi*) of the nine species tested (Tables 2,4). Six species, however, showed pronounced spatial variation in seedling mortality (site and/or patch effects; Tables 2 and 4). The site-temporal effect was stronger than the patch (paddock) differences in those species (*E. blakelyi*, *E. melliodora*, *Leptospermum polygalifolium*) that were sown at two spatial scales (sites and paddocks within sites). The effect of site, with different emergence times, could not be correlated to differences in monthly rainfall ($r = +0.25$, $P > 0.5$). There was, however, a negative correlation between minimum monthly temperature and mortality of species sown in different sites ($r = -0.69$, $P < 0.01$).

Effects of vertebrate grazing

The effects of vertebrate grazing on seedling numbers was only detected in one species (*E. blakelyi*) after exclosures were removed (Table 3). Defoliation of all species was clear in the field with high levels of resprouting. Both stock and other vertebrate grazing increased mortality in *E. blakelyi* and this effect was more pronounced at some sites than others. All other species had patchy mortality associated with either site of treatments or patches (paddocks) within a site (Tables 3,5). This variability in mortality can also be seen in the increasing levels of heterogeneity of variance at 8 months (Table 1). In many cases all seedlings had died in treatment patches before measurements were made at 8 months (Fig. 2). Both the effects of patchy and complete mortality in some plots reduced the ability to detect the effects of grazing as shown in the power analyses (Tables 4,5). Analyses of data at 6 and 12 months after exclosures were removed also produced similar results but had decreased power because of greater variance heterogeneity.

Survival analyses

Survival analyses were performed on each species using demographic data up to 5 years after initial emergence. For the purposes of these analyses, only the

Table 3. Analysis of variance for the effects of immediate grazing and site on percentage of seedlings surviving for the three species sown at all sites

Source	d.f.	<i>Eucalyptus blakelyi</i>		<i>Eucalyptus melliodora</i>		<i>Leptospermum polygalifolium</i>	
		F	Power	F	Power	F	Power
Exclosures (G)	3	5.1**	0.9	0.8	0.2	0.4	0.1
Site (S)	2	10.1***	0.9	19.5***	1.0	1.6	0.3
S × G	6	2.4*	0.8	0.7	0.3	1.0	0.3
Residual	204	149	121	23			

Data collected 1 month after grazing exclosures were removed and 8 months after initial emergence. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 4. Analysis of variance for the effects of grazing history on percentage of seedlings surviving for species sown at single sites

Source	d.f.	<i>Acacia dealbata</i> F	Power	<i>Eucalyptus viminalis</i> F	Power	<i>Eucalyptus youmanii</i> F	Power	<i>Indigofera australis</i> F	Power	<i>Lomatia fraseri</i> F	Power	<i>Xanthorrhoea johnsonii</i> F	Power
Grazing history	1	<0.1	<0.1	0.2	0.1	<0.1	<0.1	0.9	0.1	3.3	0.4	2.7	0.3
Patch (paddock)	1	<0.1	<0.1	10.1**	0.9	<0.1	<0.1	13.6***	0.9	7.5**	0.8	11.2**	0.9
Residual	70	20	55	55	35	62	47	62	47	47	32	32	32

Data collected 4 months after emergence and 3 months before exclosures were removed. ** $P < 0.01$, *** $P < 0.001$.

Table 5. Analysis of variance for the effect of immediate grazing on percentage of seedlings surviving for species sown at single sites

Source	d.f.	<i>Acacia dealbata</i> F	Power	<i>Eucalyptus viminalis</i> F	Power	<i>Eucalyptus youmanii</i> F	Power	<i>Indigofera australis</i> F	Power	<i>Lomatia fraseri</i> F	Power	<i>Xanthorrhoea johnsonii</i> F	Power
Exclosures	2	0.3	0.1	0.9	0.2	0.2	<0.1	2.0	0.5	1.2	0.3	1.6	0.4
Patch (paddock)	1	NA	6.9*	6.9*	0.7	0.2	<0.1	1.2	0.2	5.1*	0.6	3.0	0.4
Residual	70	19	53	53	33	60	45	60	45	45	30	30	30

Data collected 1 month after grazing exclosures were removed and 8 months after initial emergence. * $P < 0.05$.

Table 6. Summary results of survival analyses of trees

	d.f.	<i>Eucalyptus blakebyi</i> e ^s	P	<i>Eucalyptus meliiodora</i> P	<i>Eucalyptus viminalis</i> e ^s	P	<i>Eucalyptus youmanii</i> e ^s	P
Likelihood ratio	3	-	***	*	-	NS	-	NS
Stock versus exclosure	1	0.95	NS	**	0.87	NS	1.28	NS
Other herbivores versus exclosure	1	1.4	***	*	0.93	NS	0.92	NS
Recent grazed versus less grazed	1	0.77	***	NS	0.85	NS	1.22	NS

Coefficients greater than 1 indicate increasing risk of mortality. NS, not significant. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 7. Summary results of survival analyses of shrubs

	d.f.	<i>Acacia dealbata</i> e ^s	P	<i>Indigofera australis</i> e ^s	P	<i>Lomatia fraseri</i> e ^s	P	<i>Leptospermum polygalifolium</i> e ^s	P	<i>Xanthorrhoea johnsonii</i> e ^s	P
Likelihood ratio	3	-	NS	-	*	-	**	-	*	-	***
Stock versus exclosure	1	1.57	NS	1.46	***	1.96	***	1.66	NS	1.51	*
Other herbivores versus exclosure	1	1.21	NS	1.27	*	1.14	NS	1.05	NS	0.99	NS
Recent grazed versus less grazed	1	1.26	NS	1.26	*	1.51	***	1.81	*	1.76	***

Coefficients greater than 1 indicate increasing risk of mortality. NS, not significant. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

effects of treatment on the relative hazard of mortality were determined as the patch and site effects were revealed through ANOVA. The likelihood ratio test, used to evaluate the contribution of covariates to the global model, was significant in six of the nine species tested (Tables 6,7). Four species (*E. melliodora*, *Indigophera*, *Lomatia*, *Xanthorrhoea*) had significant regression coefficients indicating an increased risk of mortality because of the introduction of stock (Tables 6,7). Three species (*E. blakelyi*, *E. melliodora*, *Indigophera*) had significant regression coefficients reflecting increased mortality because of the introduction of other herbivores, and four species (*Indigophera*, *Lomatia*, *Leptospermum*, *Xanthorrhoea*) had regression coefficients associated with increased mortality because of the effects of grazing prior to seedling emergence. One species (*E. blakelyi*) had a coefficient associated with a decreased risk with grazing prior to seedling emergence. These results were consistent with the outcome of the ANOVA where significant effects were detected. Log relative hazards, compared across species, suggest that the shrubs generally have a greater hazard than eucalypts for treatments of stock grazing and previous intensive grazing (Table 7). The legume shrubs (*Acacia* and *Indigophera*) also had greater hazard to non-stock grazing than other shrubs (Table 7). Correlations of increasing relative hazard of stock grazing and history of grazing and the abundance of species in the landscape were negative ($r = -0.64$, $P < 0.05$; $r = -0.74$, $P < 0.01$). However, no significant correlation was detected between non-stock grazing and landscape abundance of species ($r = +0.1$, $P > 0.8$).

Establishment index

Contrasting establishment patterns are reflected in the establishment index (Table 8). In general, eucalypt species had greater indices than the shrub species because of greater fecundity and emergence. Shrub species have lesser indices because of both low fecundity and very low mean survival.

DISCUSSION

Pattern of survivorship

Previous studies of seedling emergence suggest that recruitment was triggered by a disturbance event that buried seed, decreased seed theft and reduced competition in the presence of prolonged above-average rainfall (Clarke & Davison 2001). Such event-dependent recruitment of shrubs is also characterized by moderate mortality of seedling recruits (Deevey Type II), at least in fire-driven recruitment (Leigh & Holgate 1979;

Bond & Van Wilgen 1996; Clarke & Fulloon 1997). This pattern contrasts with the high post-emergence mortality (Deevey Type III) of all woody species found in our study. This difference may be attributable to the use of resprouting species (see Clarke & Knox 2002) that have slower growth rates than obligate seeding species (Pate *et al.* 1990).

Although the emergence of larger-seeded shrubs was poorer than the small-seeded species, seedling survival patterns appeared unrelated to seed size. Both small- and large-seeded shrub species failed to survive in plots over 5 years, but all eucalypts (small seeds) and some shrubs (small and large seeded) had some survivors. Survivorship from seed entry into the seed-bank to 5-year-old juveniles ranged from 0 to 0.4%. Comparative data for seed-to-seedling survival are rare and most studies have focused on emerged seedlings. Visual comparison of seedling survival curves of semi-arid shrubs (Crisp & Lange 1976; Auld 1990; Harrington 1991; Hodgkinson 1991) are comparable with ours, showing an approximately 1% survival of seedlings, a value that stabilizes over a few years. Survivorship curves are rare for subhumid eucalypts, because of the lack of emergence, but show massive initial mortality of cotyledonary seedlings (Curtis 1989; Stoneman *et al.* 1994; Semple 1997).

What factors influence early seedling survival?

Lack of soil moisture in subhumid environments is reported, or suggested, as being the cause of death in young eucalypt seedlings (Curtis 1989; Wellington 1989; Stonemann *et al.* 1994; Florence 1996). Curtis (1989) was only able to locate 270 natural eucalypt recruits in his study sites on the New England Tablelands and, of these, most died during a dry summer. Widespread mortality of all species across different sites and patches within sites suggested that lack of moisture resulted in early seedling losses. However, rainfall was only below average at one site for 2 months and no correlation could be found between rainfall at different sites and mortality. Most seedling emergence was completed by winter 1996 and mortality occurred during winter of that year when it snowed and frequent frosts occurred. Minimum monthly temperatures at different sites correlated with mortality, suggesting that a combination of freezing, cold-induced photoinhibition and lack of available moisture killed many seedlings. Wingless grasshoppers were also observed eating legume seedlings at one site and unknown invertebrates defoliated many seedlings that emerged on basalt soils. Similar effects of invertebrates have been reported for *E. albens* (Semple 1997). Overall, the interaction of cold, defoliation and micro-site moisture stress appeared to produce variable mortality among sites and patches within them.

Table 8. Relative establishment index (EI) for species used in the experiment

Species	Growth form	<i>F</i>	<i>E</i>	<i>S</i>	EI
<i>Acacia dealbata</i> [†]	Tall shrub	0.01	0.11	>0.001	0.001
<i>Cassinia quinquefaria</i>	Shrub	0.1	0.02	>0.001	0.002
<i>Eucalyptus blakelyi</i>	Tree	1.0	0.13	0.01	0.140
<i>Eucalyptus melliodora</i>	Tree	1.0	0.10	0.03	0.130
<i>Eucalyptus viminalis</i>	Tree	1.0	0.14	0.01	0.150
<i>Eucalyptus youmanii</i>	Tree	0.5	0.14	0.01	0.075
<i>Indigophera australis</i> [†]	Shrub	0.01	0.13	>0.001	0.001
<i>Leptospermum polygalifolium</i>	Shrub	1.0	0.02	0.04	0.060
<i>Lomatia fraseri</i> [‡]	Shrub	0.01	0.09	>0.001	0.001
<i>Xanthorrhoea johnsonii</i> [‡]	Shrub	0.01	0.10	0.04	0.001

The EI index equals the product of the estimated relative amount of seed produced (*F*) and the addition of the mean species emergence (*E*) (Clarke & Davison 2001) and the mean survival of species over 5 years (*S*) (the present study). Means are averaged over all treatments and expressed as a proportion. [†]Fire related germination cues; [‡]fire stimulated flowering and seed producing.

Effects of vertebrate herbivores on seedling survival

Low levels of initial recruitment and high mortality prior to the removal of grazing exclosures made the analyses and interpretation of experimental manipulations difficult but tractable. Field observation of plots after fences were removed showed that cattle and sheep moved into the long grass and grazed all plots, and sheep defoliated established seedlings. In particular, legume seedlings appeared to be selectively grazed by sheep. Similar, but more patchy patterns occurred in the plots open to non-stock grazing where grey kangaroos were observed in some plots. Analyses of the numbers of seedlings surviving were unable to detect grazing effects in most species because of the low numbers of survivors and spatial heterogeneity. However, survival analyses showed that the risk associated with stock grazing was significant in four species, whereas the risk associated with non-stock grazing was significant in three species. Sheep typically did the most damage, whereas cattle appeared only to trample and break stems. Grey kangaroos were also observed browsing where seedlings occurred and experiments using transplanted seedlings in the absence of stock showed pronounced shrub mortality (K. A. Wills & P. J. Clarke, pers. comm., 2001). Similar patterns of shrub seedling mortality through grazing by wombats have been reported, especially after postfire emergence (Leigh & Holgate 1979). If prior land use (grazing history) is used in the survival model, then in previously grazed landscapes there was also a significantly increased risk of mortality in four species. This may be explained by the occurrence of denser and more palatable grasses in previously grazed sites, resulting in increased grazing pressure when fences were removed. Increased competition from grasses may also explain reduced survival on ungrazed plots as has been found with shrubs in semi-arid habitats (Harrington 1991).

Overall, those species with high hazard coefficients (risk) associated with stocking are uncommon, whereas those with lesser risk are more commonly found species. Species with high coefficients tend to be more palatable shrubs, whereas those with lower coefficients are less palatable and resprout from lignotubers or below-ground buds. The formation of, albeit small, lignotuberous banks of recruits is consistent with observations of eucalypt recruitment in grassy landscapes (Curtis 1989). These suppressed seedlings have been termed 'Gullivers' (Bond & van Wilgen 1996), but the interactions of grazing, fire and competition allowing them to emerge from the herb layer requires study. Curiously, all eucalypt seedlings expressed a 'suppressed' growth form despite some never being grazed or trampled. This suggests that there may be a genetic basis for 'stunting' in these eucalypts.

Integration and conclusions

Integration of relative amounts of seed produced with emergence (Clarke & Davison 2001) and survival provides an estimate of the relative establishment of species when rainfall conditions stimulate germination (Table 8). Shrubs produce less seed and have poorer emergence than the eucalypts, resulting in a lower establishment index than the eucalypts (Table 8). Fire may also be required to break the dormancy of hard-seeded shrubs (legumes and epacrids) and stimulate flowering of shrubs (*Lomatia* and *Xanthorrhoea*) prior to a rainfall event that stimulates germination. The coincidence of these two events in remnant vegetation on the New England Tablelands is conservatively estimated to be one in 25 years. Under these conditions approximately 0.1% of germinable seed might be expected to establish to a juvenile stage. This suggests that at least 10^3 germinable seeds are needed for the replacement of shrub populations if their lifespan is less

than two events (50 years). In contrast, eucalypts live much longer, produce more seed, and the opportunities for establishment appear more frequent, although their survival may be similar to shrubs.

Establishment of both trees and shrubs appears to be a rare event in the grassy woodlands and forests of the New England Tablelands because the opportunities for recruitment are infrequent and survival is low. Adaptive management of remnant vegetation has been widely advocated (e.g. Clarke & Davison 1997), but rare establishment events give managers little opportunity for adaptive management. In these circumstances, modelling, based on empirical data, may be valuable in developing management guidelines (Harrington 1991).

Recruitment of woody plants on the New England Tablelands requires a supply of seed, bare ground, low levels of seed predation, seed burial, high rainfall, mild winters and low levels of seedling herbivory. It is therefore not surprising that little natural recruitment of eucalypts and no shrub recruitment was observed during our 5 year study. It is suggested that seed supply limits recruitment and that recruitment is episodic and disturbance driven. Enhancing natural 'regeneration' of woody plants under these circumstances in grassy woodland remnants may be more challenging than simply fencing remnant vegetation.

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