Post-wildfire seedling colonisation patterns in a *Eucalyptus delegatensis* (Myrtaceae) windthrow site at Snowy River National Park, Victoria

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Summary

During June 1998, a severe windstorm caused significant damage to a sub-alpine stand of *Eucalyptus delegatensis* (Myrtaceae) at the Snowy River National Park. In 2002, about 4.5 y after the windstorm, a study documented the effects on *E. delegatensis* and early understorey succession. In February 2003, wildfire burnt across the windthrow site and we examined the seedling recruitment patterns at windthrow–burn and burn-only sites. Our aim was to document the regeneration of the canopy-dominant *E. delegatensis* and to confirm that *Acacia dealbata* is a pioneer species that potentially interferes with or prevents regeneration of *E. delegatensis*. Permanent transects were established within the windthrow–burn and burn-only sites. The data suggest that the heavily disturbed (mounded) soil at the windthrow site had a strong positive influence on regeneration of both species. By providing favourable growing conditions, the disturbed soil appears to have assisted seedling survival and subsequent growth of the *E. delegatensis*, despite competition from dense, concurrently established *A. dealbata*.

Keywords: windthrow; fire; seedbeds; regeneration; survival; mortality; topography; *Acacia dealbata; Eucalyptus delegatensis*

Introduction

During June 1998, a severe windstorm within the Snowy River National Park near Mt Gelantipy caused significant damage to a stand of *Eucalyptus delegatensis* (Myrtaceae). In 2002, about 4.5 y after the windstorm, Florentine and Westbrooke (2004) examined the effects of windthrow on *E. delegatensis* and early understorey succession. This study found that high winds had toppled virtually all trees, damaging 99% of the *E. delegatensis*, and that very few *E. delegatensis* seedlings were recruited in the windthrow plots. The authors proposed that the windthrow site should be burnt and *E. delegatensis* seed broadcast to accelerate seedling recruitment. By coincidence, in February 2003, wildfires burnt across the Snowy River National Park including the windthrow site. This current study reports a follow-up assessment conducted in January 2004 and January 2005. It compares seedling recruitment patterns at windthrow–burnt and burnt-only sites.

Florentine and Westbrooke (2004) proposed several reasons for the lack of *E. delegatensis* seedling recruitment following the 1998 windthrow: absence of a soil-stored seed bank, limiting microclimate and unsuitable seedbed conditions. *E. delegatensis* seedlings normally flourish where seed falls onto a burnt seedbed, or a seedbed where the litter layer, grass and other understorey, and the mineral soil have been mechanically disturbed (Grose 1957, 1960). In the windthrow area, soil disturbance associated with uprooting of the larger trees of the stand may have adversely affected the seed which had already fallen onto the site. Even small-scale disturbance can hinder the germination of *E. delegatensis* seed already in the soil (Battaglia and Reid 1993). The seedbed conditions would also have been affected by the large amount of woody debris created by the snapping and uprooting of trees and the thick cover of early colonising species. Another factor could be microclimate: germination of *E. delegatensis* seed requires particular microclimatic conditions; fully ripened seed will successfully germinate within the range of 17–21°C (Grose 1960, 1963).

Grose (1960) pointed out that a burnt seedbed or bare soil is necessary for the establishment of *E. delegatensis* and the closely related *E. regnans*. Seedlings established in the bare ground will have less competition and there will be increased light and more soil moisture after fire (Gill 1997). Other eucalypt species may be more tolerant of site conditions: for example, Barker (1988) and Ashton and Williams (1989) found that sub-alpine *E. pauciflora* seedlings recruited without fire, although seedling recruitment is generally greater after fire (Barker 1988; Wimbush and Forrester 1988).

Studies in other countries have demonstrated that at a windthrow site the uprooting of trees results in small-scale variations in topography — termed pits and mounds — and consequently of soil properties (Peterson *et al.* 1990). Pits and mounds may persist for centuries, maintaining their shape and structure (Stephens 1956). A number of ecological soil-related characteristics — soil temperatures (Dwyer and Merriam 1981; Schaetzl 1990), accumulation of litter (Schaetzl 1990), thickness and distribution of mineral soil horizons (Veneman *et al.* 1984; Schaetzl *et al.* 1989, 1990) and exposure of buried seeds (Putz *et* *al.* 1983) — may vary between these topographic features. These micro-topographic variations may create conditions ideal for the recruitment of some plant species in the northern hemisphere (Sousa 1984; Uhl *et al.* 1988). *E. delegatensis* stands, however, are confined to altitudes around 1200 m asl, where windthrow is not common; consequently, treefall pits and mounds are not common landscape features and their possible importance for *E. delegatensis* recruitment remains unknown.

In 2003, a wildfire provided an opportunity to examine whether this event assisted recruitment of *E. delegatensis* seedlings. The overall aim of this study was to compare the post-fire response of *E. delegatensis* and competing vegetation on a windthrow site with that on a site that had not been windthrown. More specifically, the aim was to document the regeneration of *E. delegatensis*, the canopy dominant, and a potential competitor, *Acacia dealbata*, an abundant sub-canopy pioneer species. We were also interested in the way pit and mound structures assisted the recruitment of these different species.

Method

The study site

The Snowy River National Park (SRNP) is located in the Far East Gippsland region of Victoria and covers about 98 700 ha. The study site is at Mt Gelantipy, which is about 1200 m asl. (Fig. 1). This part of SRNP is dominated by even-aged *E. delegatensis* with a sub-canopy of *A. dealbata*. Fires of only low intensity have been recorded at the study site, and the area has never been harvested. The height of *E. delegatensis* on a control site (undisturbed) was about 35–40 m, and the mean diameter was 42 cm.

About 3.5 ha, at the highest part of the SRNP near Mt Gelantipy, were affected by high winds during June 1998. Possibly a combination of shallow soil, and tall older trees fully exposed on an open slope, rendered this site particularly susceptible to windthrow. Treefall direction in all plots indicates that the winds were from the south-east. Some 90% of the *E. delegatensis* trees were windthrown, and sub-canopy species such as *A. dealbata* and shrub layer species were either damaged or snapped (Florentine and Westbrooke 2004). Soil pits and mounds were created by the windthrow, the ground was covered with fallen twigs and leaves, and tree boles were piled up. Five years after the windthrow, only a small number of *E. delegatensis* seedlings were recorded, none in areas unaffected by windthrow; the exotic *Rubus fruticosa* (blackberry) was colonising the windthrow site but not undisturbed sites.

Methods

To assess the effects of windthrow and fire on seedling recruitment, ten and seven permanent transects respectively were established to monitor seedling recruitment within sites which were windthrown and burnt (WB) and burnt only (B) (Fig. 1). Each transect consisted of 25 contiguous sample quadrats measuring 2 m × 1 m. These transects were oriented in an east-west direction. Within each sample quadrat, seedlings were identified and their topographic location recorded (mound, pit or flat). In addition, for each species, density and life form were recorded. For each sample quadrat, the height of the tallest *E. delegatensis* and *A. dealbata* seedlings and whether those seedlings occurred on a mound, in a pit or on the flat were recorded. The assessment was made in January 2004 and again in 2005. As WB and B were not under experimental control, nor spatially replicated, we present only totals and ignore variation between sample quadrats.

The square-root transformed heights of the tallest *E. delegatensis* and *A. dealbata* seedlings per sample plot were summarised according to fire and windthrow history. The sample distributions of the tallest plants in the B and WB plots were compared by Kolmolgorov–Smirnov (K–S) tests.

Results

Recruitment of *E. delegatensis* and *A. dealbata* seedlings in the windthrow–burn and burnt areas

At the 2004 assessment, 9360 and 10 029 *E. delegatensis* seedlings were recorded per hectare at the windthrow–burn and burn-only sites respectively (Table 1). A year later, the *E. delegatensis* seedling stocking had declined sharply on the burn-only site (to 1457 ha^{-1}). Seedling mortality was considerably less on the windthrow–burn site (declining to 5720 ha^{-1}). This pattern is also seen in the seedling frequency data. There was a decline at the burn-only site (from 50% to 20%) while there was an increase in frequency at the windthrow–burn site (from 35% to 44%).

The seedling stocking of *A. dealbata* was much greater than that of *E. delegatensis* at both windthrow–burn and burn-only sites: 98 580 and 22 571 seedlings ha^{-1} respectively in 2004. The pattern in seedling mortality was similar to that of *E. delegatensis*: a substantial decline from 22 751 to 4143 ha^{-1} at the burn-only site, and only a slight decline from 98 580 to 92 580 ha^{-1} at the windthrow–burn site.

Height growth of the tallest seedlings of both *E. delegatensis* and *A. dealbata* was substantially greater on the windthrow–burn than on the burn-only site (Fig. 2, Table 1). Within the windthrow–burn site, micro-topographic location appears to have had a strong influence on seedling growth. Most of the tallest *A. dealbata* seedlings (89% in 2004 and 98% in 2005) were on 'flats', while for *E. delegatensis* 66% of the tallest seedlings in 2004 were on mounds, dropping to 41% in 2005.

Discussion

There have been many studies of the response of *E. delegatensis* and other forests to wildfire or to clearfelling followed by intense slash burning (e.g. Ashton 1981, 2000; Adams and Attiwill 1984; Wang 1997). While the responses we have observed are consistent with these studies, they contribute some additional background to the regeneration process. This is shown by comparing the responses of regeneration to the three disturbance events: windthrow in 1998, the 1998 windthrow followed by the fire in 2003, and the fire alone in 2003.

Regeneration of *E. delegatensis* and *A. dealbata*

Very little *E. delegatensis* regeneration was recorded on the 1998 windthrow plots (49 seedlings ha^{-1}) and none in intact control plots in 2002. Florentine and Westbrooke (2004) suggested three

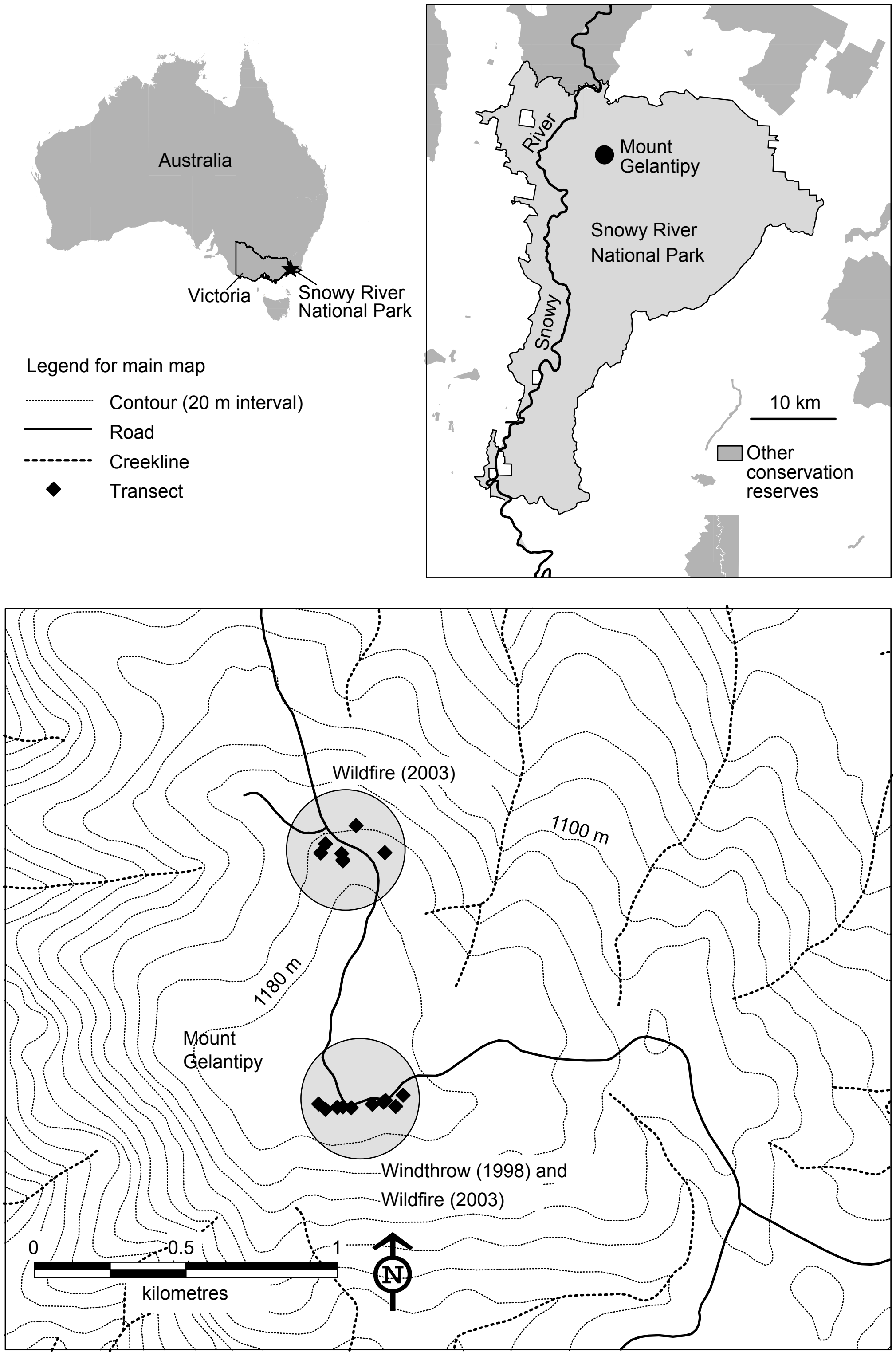

Figure 1. Location of the study site in the Snowy River National Park, Victoria

reasons for this: (i) lack of seed, as 99% of mature *E. delegatensis* trees had been uprooted; (ii) non-receptive seedbed; and (iii) inappropriate microclimate. As the subsequent February 2003 fire produced a high seedling stocking at the same site, the first of these proposals (lack of seed) does not seen valid. In 2003, seed appears to have come from trees carrying seedcrops which survived the fire, and which were located, for example, some 50 m from the northern edge of the windthrow–burn area and also within the burn-only area. The near failure of regeneration at the 1998 windthrow site may be more appropriately attributed to a non-receptive seedbed, that is the thick mat of wood debris which accumulated following the windstorm.

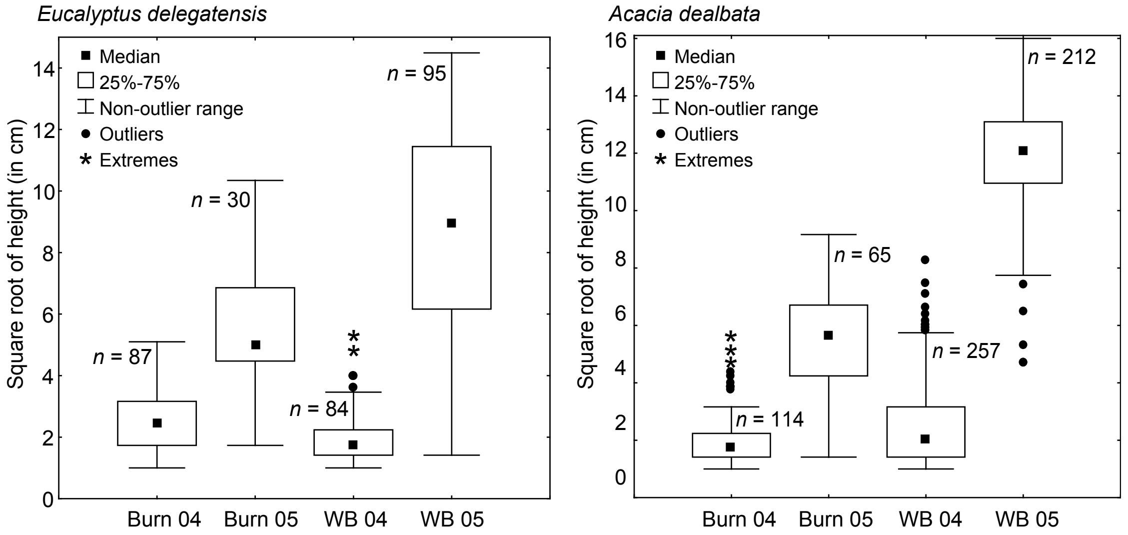

Figure 2. Height distribution of tallest *Eucalyptus delegatensis* and *Acacia dealbata* seedlings recorded per sample plot in the windthrow and burnt (WB) and burnt (B) sites in 2004 and 2005

Table 1. Density and frequency of seedlings in sample plots; the outcome of K–S test for differences in maximum height distribution in windthrow and burnt (WB) and burnt sites; and the relative distribution of tallest seedling per plot in flat, pit and mound locations

Attribute and site	*Eucalyptus delegatensis*		*Acacia dealbata*	
	2004	2005	2004	2005
Density (no. ha^{-1})				
Burnt	10 029	1 457	22 571	4 143
WB	9 360	5 720	98 580	92 540
Frequency (%)				
Burnt (n = 175)	50	19	69	43
WB (n = 250)	36	45	90	89
K–S test of data on tallest plant per plot	$P < 0.001$	$P < 0.001$	$P < 0.005$	$P < 0.001$
Fraction of tallest seedlings per WB plot (%)				
Flat	25	54	89	98
Pit	9	5	2	0.2
Mound	66	41	9	2

The 2003 fire completely incinerated the woody debris and created a seedbed suitable for *E. delegatensis* at both the burn-only and windthrow–burn sites. Sufficient seed fell from scattered mature trees to establish some 10 000 *E. delegatensis* seedlings ha^{-1} by 2004 at each site.

There was a far greater germination of the pioneer species *A. dealbata*. Almost 100 000 seedlings ha^{-1} were recorded in 2004 at the windthrow–burn site, and 22 000 seedlings ha^{-1} at the burn site. The heat from the 2003 fire triggered the germination of soil-stored seed of this species, and subsequent suitable soil moisture ensured seedling survival and growth. Mass regeneration of this and other pioneer species is consistent with many observations on the response of pioneer species to intense fire.

Seedling survival at the windthrow–burn and burn sites

Just over 60% of the *E. delegatensis* seedlings recorded in 2004 at the windthrow–burn site were still present in 2005. In contrast, only around 15% of seedlings at the burn-only site were still present. The survival pattern (2004–2005) for *A. dealbata* at both sites is similar to that of *E. delegatensis*, that is there was a much greater survival on the windthrow–burn (94%) than on the burn-only site (18%).

There may be a number of reasons for the greater survival of both *E. delegatensis* and *A. dealbata* on the windthrow–burn site. Grose (1957) identified factors that could affect the survival of *E. delegatensis*: seedling root exposure, soil desiccation and snow. While the seedbed in our study may have been ideal at both sites, the greater survival on the windthrow–burn site might be attributed to the way half-burnt uprooted trees and the uneven ground surface provided greater shelter for new recruits, while seedlings on the burn site were more exposed to open sunlight and frost. The latter condition may have helped eliminate a much greater proportion of both *E. delegatensis* and *A. dealbata* seedlings on the burn-only site.

The effect of site conditions on seedling mortality and growth

A decline in the stocking of *E. delegatensis* will normally be related to competition for light and soil resources exerted by concurrently-establishing fire successional species such as *A. dealbata.* In our study, however, mortality of *E. delegatensis* was considerably less at the windthrow–burn site despite the far greater survival of *A. dealbata* at this site. This again suggests that site resources may have been in greater supply where the soil had been heavily disturbed by near-total windthrow and that this greatly advantaged the survival and development of regrowth on this site.

Analysis of the height of the tallest *E. delegatensis* and *A. dealbata* in 2004 and 2005 (Fig. 2) illustrates the more vigorous development of both species on the windthrow–burn site. And within the windthrow–burn site, mounds created by the windthrow appear to be much more important for *E. delegatensis* than *A. dealbata* (Table 1). An uneven windthrow surface has been shown elsewhere to favour the germination and survival of seedlings (Clinton and Baker 2000). In the southern Appalachians of the US, more seed germinated on the warmer soils of mounds than in the pits. If this translated to our study, it is possible that *E. delegatensis* seed germinated earlier on the mounds and seedlings developed more rapidly on the 'cultivated' soil, hence being less susceptible to adverse environmental factors and competition from *A. dealbata*.

Disturbances such as fire or windthrow can mould the structure and composition of vegetation. As Putz *et al.* (1983) indicated, the scale and scope of natural disturbances can determine the time and type of the response by vegetation. The situation we have described in this study is rather unusual —one natural disturbance followed another within a short period. One might speculate that the large quantities of fuel present after the windthrow might result in a relatively high probability an intense subsequent wildfire. While these disturbances may appear to be severe catastrophic events, our results show that windthrow followed by wildfire in the *E. delegatensis*-dominated stand in Mt Gelantipy is probably an appropriate sequence for vegetation recovery. This sequence may be particularly relevant where the soil and environmental conditions of a site are marginal for *E. delegatensis*. The abundant stocking of *E. delegatensis* and *A. dealbata*, and some seedling recruitment of native ground cover species, indicate that the 1998 windthrow event followed by the February 2003 wildfire led to rapid recovery of canopy and sub-canopy species. It is essential that these sites continue to be monitored to document the medium- and long-term changes in vegetation following these two catastrophic events.

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