Effects of windthrow on a stand of *Eucalyptus delegatensis* (Myrtaceae) and early understorey succession at Snowy River National Park, Victoria

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Summary

During June 1998 a very strong windstorm at the Snowy River National Park near Mt Gelantipy caused severe damage to a stand of *Eucalyptus delegatensis*. Little is known about the impact of windthrow on *E. delegatensis* and subsequent seedling recruitment. This study was undertaken 4.5 y later to examine (i) windthrow damage to *E. delegatensis* and the understorey *Acacia dealbata*, (ii) the influence of tree size on the pattern of tree damage, (iii) the undergrowth in the windthrow area compared with that in control plots, and (iv) species composition of the soil-stored seed-bank in windthrow and control plots.

We found that high winds toppled virtually all trees regardless of size and species, damaging 99% of the *E. delegatensis*. In windthrow plots there were 49 seedlings ha^{-1} of *E. delegatensis* and 2210 ha^{-1} of *A. dealbata*. No *E. delegatensis* or *A. dealbata* seedlings were recorded in the control plots. In the soil seed-bank study five species were recovered from soil samples collected from the control, and six from the windthrow-damaged sites. The canopy species *E. delegatensis* recruited only from the windthrow site**.** The exotic *Rubus fruticosus* was found to be colonising the windthrow site, but was not present in the control site. Results show that *E. delegatensis* recruitment is very poor in the damaged area, and species colonising within that area are light demanding or early succession species. It is proposed that seedling recruitment in the windthrow sites be accelerated by burning the site and broadcasting *E. delegatensis* seed, or transplanting seedlings.

Keywords: seedbeds; seedlings; regeneration; plant succession; plant colonisation; wind damage; alpine ash; *Eucalyptus delegatensis*

Introduction

Wind is one of the primary natural disturbances in terrestrial ecosystems and it has significant ecological effects on forest communities (Stephens 1956; Schaetzl *et al*. 1989; Clinton and Baker 2000). Generally, larger dominant canopy trees are most affected by this disturbance (Ulanova 2000). Barden (1981) reported that windthrow created about 97% of canopy gaps in a mature mixed-mesophytic forest. In another study, Clinton *et al*. (1993) found windthrow killed 11% of mixed hardwood forest trees. The effects are varied, but generally uprooting or tree fall is the major disturbance. This process may change the soil physical environment, exposing soil-stored seeds (Putz *et al*. 1983) and create a new pit and mound topography (Clinton and Baker 2000). The changes may modify the microenvironment (Collins *et al*. 1985) and hence affect recruitment of species (Collins and Pickett 1982).

Once canopy trees are damaged, seedling recruitment is essential. Yamamoto (1961) and Ulanova (2000) suggested that the size of windthrow patches and time are two major factors determining seedling recruitment and species composition. Regrowth may occur in three major ways: from the soil-stored seed-bank, from plants established prior to windthrow, and from lateral growth of branches of surviving trees (Collins *et al*. 1985). Removal of canopy strata by strong wind action may change soil temperature. Once the density of the canopy layer has been reduced, the changed microenvironment enables light-demanding species — especially small-sized species — to colonise the site (Bonan and Shugart 1989). The reduction of canopy density will also help colonisation by exotic species. The abundance of these early colonisers will decrease with time following the initiating disturbance. Ulanova (2000) found that early colonisers decreased from 55% in 1–5 y to 10% in an old uprooted site.

This paper reports the effects of a severe windstorm on *Eucalyptus delegatensis* forest during June 1998 within the Snowy River National Park (SRNP) near Mt Gelantipy in eastern Victoria. Little is known about windthrow effects on *E. delegatensis* stands and subsequent seedling recruitment. The major objectives of this post-windthrow study were to examine (i) windthrow damage to *E. delegatensis* and the understorey *Acacia dealbata*, (ii) the influence of tree size on the pattern of tree damage, (iii) the undergrowth in the windthrow area compared with that in control plots, and (iv) species composition of the soil-stored seed-bank in windthrow and control plots.

Method

Study site

Snowy River National Park (SRNP) is located in Far East Gippsland and covers about 98 700 ha. It is adjacent to the Alpine National Park, which gives additional protection to part of SRNP. The park was first proclaimed in April 1979 (26 000 ha) and additional surrounding lands (72 700 ha) were included between 1981 and 1991. SRNP is listed in Category II by the IUCN and managed mainly for conservation and recreation. It has 13 vegetation communities and about 900 native species, 61 of them

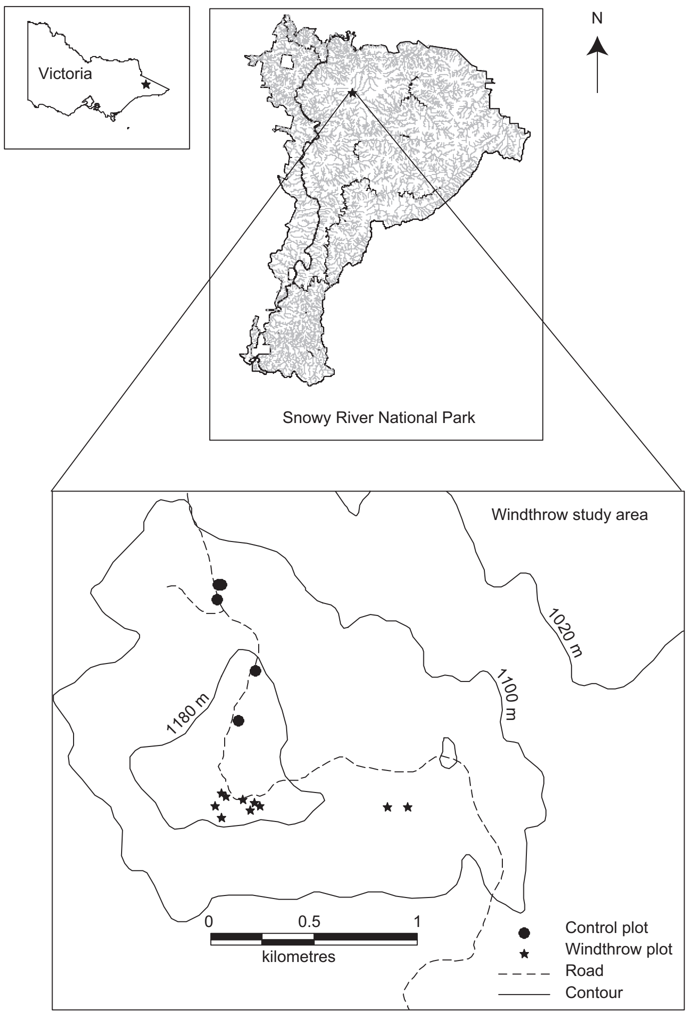

Figure 1. Location of the study site in the Snowy River National Park

listed as threatened. Similarly, over 250 species of native fauna have been recorded, 22 of them threatened in Victoria. Some areas of SRNP have been disturbed through past land use, including grazing and mining (Anon. 1995). The study site is located at Mt Gelantipy, which is about 1200 m a.s.l. (Fig. 1). This part of SRNP is dominated by even-aged *E. delegatensis* with a sub-canopy of *A. dealbata*. In the study site only low-intensity fire has been recorded, and the area has never been harvested. The height of *E. delegatensis* on the control site was about 35–40 m, and mean diameter was 41.8 cm. About 3.5 ha were affected by very strong winds during June 1998 near Mt Gelantipy, and this study was carried out between June and November 2002.

Sampling technique

Eleven sample plots (25 m x 25 m) were selected randomly within the windthrow area, and five within an undamaged stand some 300 m from the windthrow site. The north-east corner of each plot was marked with a numbered metal tag and spray marker. The diameter at breast height (1.3 m) was recorded for all trees found within the plots. In addition, the type of any damage — uprooted, snapped resprouted, or snapped dead — was recorded for each stem.

Each 25 m x 25 m plot was further divided into twenty-five 5 m x 5 m sub plots. Within each sub-plot all plants were counted and identified, including understorey and ground species. Diameters of all *E. delegatensis* seedlings were measured at 10 cm from the soil surface using a diameter tape.

Soil seed-bank

We collected 88 random samples from windthrow sites and 40 from control sites. The sites were sampled by throwing a 10 cm x 10 cm quadrat in the collection area and removing soil within the quadrat with a small trowel to a depth of 10 cm. Samples were put in separate labelled bags and transported to the University of Ballarat and stored in a glass house (20–25°C) until used.

The contents of the sample bags were thoroughly mixed within the bags to ensure that any seed was uniformly distributed throughout the soil. Punnets (8.5 cm x 14 cm x 5.5 cm) were lined with paper towel, filled with the mixed samples and placed into large trays (28 cm x 44 cm x 5.5 cm) on benches in a shade house. Trays were watered twice a day with an automatic sprinkling system. The germinable seed-bank was considered to be the seeds that germinated within 90 days (Bertiller 1996). The surface area of each punnet was taken to be about that of the sample quadrat (100 cm^2).

Statistical analysis

Data were analysed using the Super ANOVA software program (Abacus Concepts, Berkeley, California) for two-way ANOVA and pairwise multiple comparisons. Plots of residuals were obtained from each ANOVA to examine homogeneity of the variance.

Results

In the windthrow site, there were 1073 trees ha^{-1} of which 91% (980 ha^{-1}) were *E. delegatensis* and 9% (93 ha^{-1}) *A. dealbata*. Of the *E. delegatensis* trees, 67% were snapped and dead, 29% were uprooted, and only 4% were snapped and re-sprouting. Of the snapped and dead trees, 70% were *E. delegatensis* and 30% were *A. dealbata*. Most (95%) uprooted trees were *E. delegatensis*. The diameter class distribution shows that 78% of uprooted trees were >30 cm in diameter, and 98% of snapped and dead trees were <30 cm in diameter (Figs 2A and B).

One-way analysis of the diameter of the snapped dead, snapped resprouted, and uprooted trees shows significant differences in their diameter range ($F = 178$; $P < 0.0001$). Most large-diameter trees had been uprooted, medium-size trees had snapped but had resprouted, and the snapped and dead trees had smaller diameters (Fig. 3).

At the control site a total of 784 trees ha^{-1} were measured of which 62% (486 ha^{-1}) were *E. delegatensis* and 38% (298 ha^{-1}) were *A. dealbata*. The height class distribution showed an approximately normal distribution with a prominent single peak, suggesting a single recruitment event (Fig. 4).

In the control plots eleven species belonging to six families were found growing beneath the canopy species *E. delegatensis*. Within

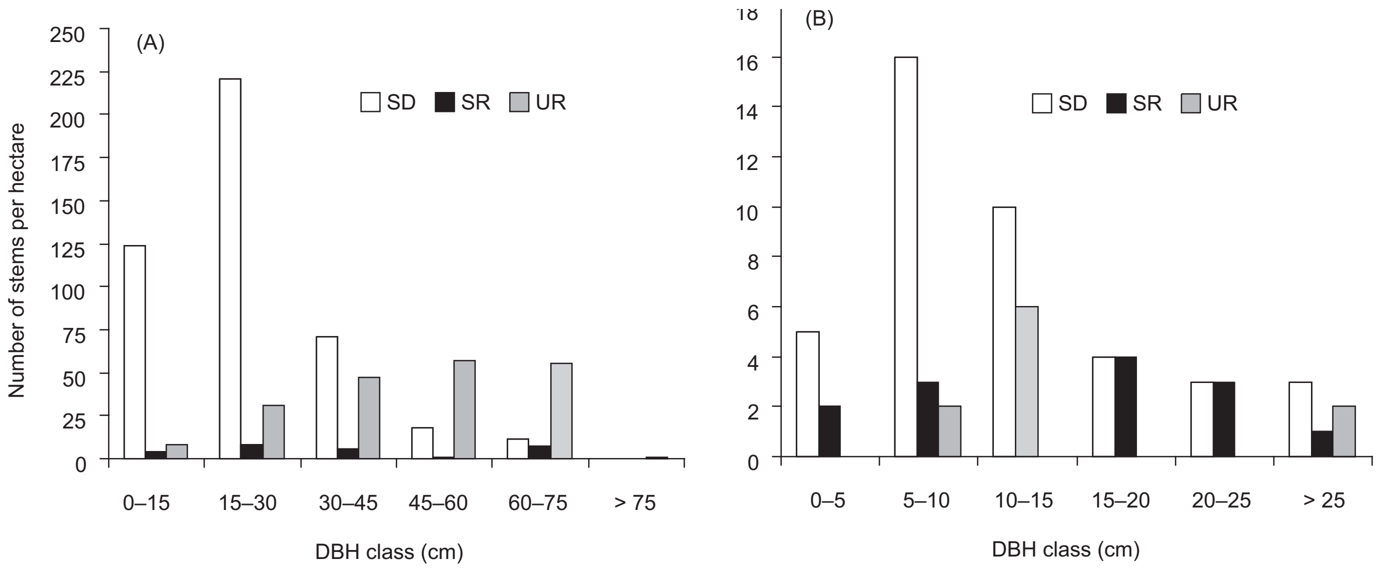

Figure 2. Diameter class distribution of *E. delegatensis* (A) and *A. dealbata* (B) trees found in the windthrow site. SD = snapped and dead; SR = snapped and resprouted and UR = uprooted.

the windthrow plots the species diversity was greater, with a total of 19 species from 15 families (Table 1). *Eucalyptus delegatensis* seedlings were found to have established in the windthrow plots (49 ha^{-1}) but no *E. delegatensis* seedlings were found in the control plots. There were 2210 seedlings ha^{-1} of *A. dealbata* in the windthrow plots. None was recorded in the control plots.

Seedlings of five species were recovered from soil samples collected from the control plots, and of six species from the windthrow plots. In samples from both control and windthrow sites the most frequent groundcover species recovered was *Stellaria flaccida* (Caryophyllaceae). *Eucalyptus delegatensis* seedlings (0.22 ha^{-1}) were recorded only from windthrow samples, but *A. dealbata* was found in both control and windthrow sites; stocking of *A. dealbata* seedlings at the windthrow site (4 m^{-2}) was greater than that at the control site (0.5 m^{-2})

Discussion

The 1998 windthrow devastated the *E. delegatensis* stands at SRNP. The strong wind toppled the trees regardless of size and species, and damaged 99% of *E. delegatensis* in affected stands. The type of damage varied with tree diameter (Fig. 2). Of 674 trees recorded, only 0.6% escaped windthrow damage. Characteristics of the trees that might influence windthrow include size and species (Webb 1988), root depth (Fowells 1965), trunk taper (King 1986), wood quality and flexibility (Putz *et al*. 1983) and prior wind stress (Mergen 1954). The damage occurred in the highest part of the SRNP near Mt Gelantipy, and possibly a combination of shallow soil, and tall and 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.

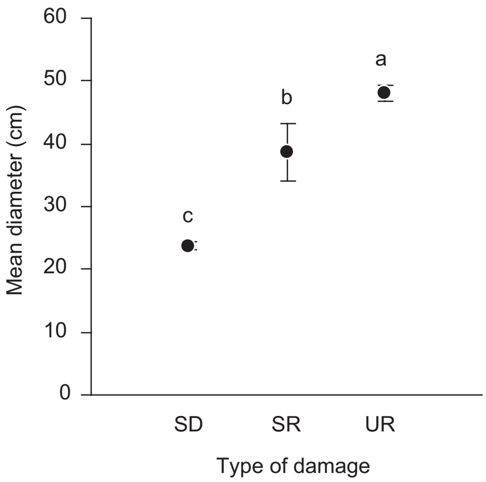

Figure 3. Mean diameter of *E. delegatensis* trees found in the windthrow plots. SD = snapped dead; SR = snapped resprouted and UR = uprooted. Vertical bars indicate standard errors. Different letters indicate means are significantly different.

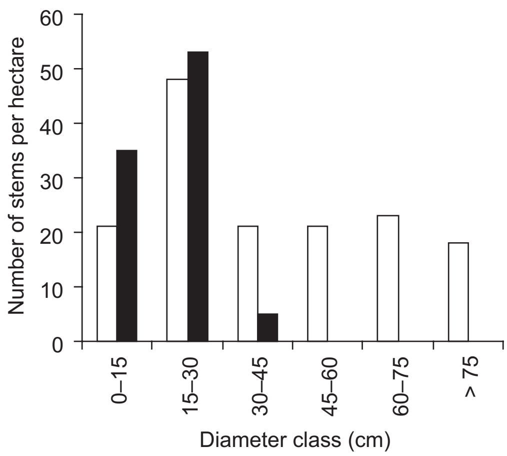

Figure 4. Diameter class distribution of *E. delegatensis* trees (white bars) and *A. dealbata* trees (black bars) found at the control site.

Table 1. Species recruited and population density (except *E. delegatensis* and *A. dealbata*) in the control and windthrow plots

Species	Family	Life form	Height (m)	Stocking (plants ha^{-1})	
				Control	Windthrow
Bedfordia arborescens Hochr.	Asteraceae	Tall shrub	3–7	118	Ab
Cassinia aculeata (Labill.) R.Br.	Asteraceae	Shrub	2–3	12	312
Clematis aristata R. Br. Ex Ker Gawl.	Ranunculaceae	Climber	NA	Ab	NA
Coprosma hirtella Labill.	Rubiaceae	Shrub	1–2	51	306
Coprosma quadrifida (Labill.) B.L.Rob.	Rubiaceae	Shrub	2–4	25	222
Cyathea sp.	Cyatheaceae	Fern	1–2	73	258
Dianella revoluta R.Br.	Phormiaceae	Grass	NA	6	129
Elaeocarpus holopetalus F.Muell.	Elaeocarpaceae	Tree	5–16	Ab	123
Olearia argophylla (Labill.) Benth.	Asteraceae	Tall shrub/small tree	3–8	38	138
Olearia lirata (Sims) Hutch.	Asteraceae	Shrub	1–2	Ab	29
Polyscias sambucifolia (DC.) Harms	Araliaceae	Shrub/small tree	1–6	Ab	97
Pomaderris aspera DC.	Rhamnaceae	Shrub/slender tree	3–8	48	119
Prostanthera lasianthos Labill.	Lamiaceae	Shrub/small tree	2–8	Ab	325
Rorippa dictyosperma (Hook.) L.A.S.Johnson	Brassicaceae	Herb	NA	Ab	34
Rubus fruticosus L.	Rosaceae	Prickly climber	NA	Ab	NA
Stellaria flaccida Hook.	Caryophyllaceae	Herb	NA	Ab	NA
Tasmannia lanceolata (Poir.) A.C.Sm.	Winteraceae	Shrub	2–3	41	93
Xerochrysum bracteatum (Vent.) Tzvelev	Asteraceae	Shrub	2–4	Ab	173
Grass sp. i (unidentified)	–	Grass	NA	48	142
Grass sp. ii (unidentified)	–	Grass	NA	25	119

NA = Not applicable, Ab = Absent

Analysis of the diameters of snapped dead, snapped resprouted and uprooted trees showed that trees of medium diameter (38.6 ± 4.5 cm) are more likely to resprout than those in smaller (23.7 ± 0.6 cm) or larger (48.1 ± 18.2 cm) diameter classes. Larger-diameter trees are more likely to be uprooted than those of smaller diameter. This is likely to be because, under stressed conditions, larger trees tend to exceed the soil shear strength (i.e. soil ability to resist torsional forces) (Putz *et al*. 1983).

The limited regeneration at the windthrow site (49 seedlings ha^{-1}) might be attributed to a number of factors. The first is seed supply: most seed of *E. delegatensis* is shed February–April, and most seed germinates in the following autumn and spring (Florence 1996). Consistent with the findings of Grose (1960) our soil seed-bank study shows that *E. delegatensis* does not accumulate as a soil seed store. It is possible that the seed crop maturing early in 1998 was light. Subsequently, some seed may have been disseminated from larger mature trees adjacent to the windthrow site, although this dispersal would be effective only within a radius more or less equal to tree height (Forestry Commission of Tasmania 1990). The new sprouts on snapped trees would not have produced seed within the period of observation.

A second factor is the seedbed conditions: if a reasonable amount of seed had fallen before the windthrow event, subsequent germination and seedling establishment may have been adversely affected by a non-receptive seedbed. The *E. delegatensis* seedling will normally thrive where seed falls onto a burnt seedbed or one where the litter layer, grass and other understorey and the mineral soil have been mechanically disturbed (Grose 1960). In the windthrow area, the uprooting of the larger trees of the stand may have created some soil disturbance, but 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 condition would also have been affected by the large amount of woody debris created by the uprooting and snapping of trees, and the thick cover of early colonising species.

A third factor is microclimate. A suitable temperature is critical for *E. delegatensis* seed. Fully ripened seed will successfully germinate within the range 17–21°C. The microclimate created by the large quantity of wood debris may have influenced seed germination and seedling establishment.

All species colonising the windthrow site are native to the study area except the exotic *Rubus fruticosus*, which was found only in plots close to the track. Seeds of this species may have been brought in and deposited in the soil during track maintenance, founding the resulting population which is slowly invading the gaps. Control measures should be taken immediately to prevent further infestation.

Windthrow hazard depends upon several biotic and abiotic factors including climate, topography, soil and stand characteristics (Ruel 2000). If we superimpose factors such as topography and stand characters of Mt Gelantipy (1200 m a.s.l.) on the Ruel (2000) windthrow hazards factors, we find that this site is particularly susceptible to windthrow. A major issue is how windthrow risk and effects on similar stands can be reduced. Silvicultural operations can minimise windthrow effects (Oke 1987), but thinning would also increase wind penetration into the stand and could increase the damage for some years after treatment (Cremer *et al*. 1982; Gardiner *et al*. 1997).

We conclude that the inadequate regeneration of *E. delegatensis* on the windthrow site is related to a combination of poor seed supply and a non-receptive seedbed due to the limited soil disturbance following seedfall and the cover of woody debris. To accelerate site regeneration, artificial restoration techniques are necessary including seedbed preparation (burning), followed by broadcasting *E. delegatensis* seed or transplanting *E. delegatensis* seedlings.

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