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Comparative changes in *Eucalyptus pauciflora* (Myrtaceae) stand structure after bushfires in Victoria

[1]*Fiona Coates*

Arthur Rylah Institute for Environmental Research,
Department of Environment and Primary Industries, Land, Water and Planning (DELWP) Victoria;
[1]Currently Woods to Water Plant Ecology, North Fitzroy, Victoria 3068 AUSTRALIA; Email: fiona@woodstowater.com.au

***Abstract*:** The recent frequency and extent of landscape-scale fires in subalpine areas of Victoria have led to almost all *Eucalyptus pauciflora* (snow gum) forests and woodlands being burnt, to the extent that old growth stands are now rare. A comparison of *Eucalyptus pauciflora* stand structure at three mountains with comparable geology, altitude, topography and grazing history but with different fire histories revealed three regeneration syndromes: (i) long-unburnt stands consisting of few-stemmed trees at Mt Baw Baw and recently-burnt stands at Lake Mountain, both characterised by a single establishment phase in response to fire disturbance; (ii) long-unburnt stands consisting of few-stemmed trees at Mt Buffalo, characterised by continuous regeneration and ongoing seedling recruitment independent of major disturbances, and (iii) multi-burnt stands with high tree density and thin stems at Mt Buffalo, with multiple stem establishment phases.

At some sites with very high fire frequency and/or short inter-fire intervals, multi-or thin-stemmed architecture may have become entrenched. Post-fire seedling recruitment is high but seedlings are likely to be outcompeted and remain in a suppressed state. Snow gum is a tenacious niche persistor with capacity to resprout after multiple fires but the current outlook is one of a radical demographic shift in population structure in subalpine landscapes. It is crucial that remaining long-unburnt *Eucalyptus pauciflora* stands are protected from fire as far as is practicable to allow stand development and to preserve the unique quality and function of mature snow gum woodlands.

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Introduction

Recent high fire frequencies in mountainous terrain in south-eastern Australia have provided many opportunities to improve our understanding of post-fire vegetation recovery. However, opportunities to gather information on unburnt or rarely burnt subalpine vegetation are now exceedingly rare. High fire frequency is expected to continue into the future (Parry *et al.* 2007), including in areas with a history of infrequent fire. The response of species to repeated perturbations poses a number of challenges for predicting thresholds beyond which recovery to a previous state may not occur (Westman 1986).

Eucalyptus pauciflora Sieber ex Spreng. occurs in south-eastern Queensland, eastern New South Wales (NSW), the Australian Capital Territory (ACT), south-eastern South Australia, Tasmania and Victoria (Williams & Ladiges 1985). Snow gum forests occupy a range of altitudes between sea level and 2000 m but are most often associated with alpine and subalpine treelines on shallow rocky soils (Boland *et al.* 1984; Williams & Ladiges 1985; Brookhouse *et al.* 2008). Vegetation dominated by snow gum in Victoria is usually confined to mountains with elevations generally above about 1100 m ASL. Since 2003, all except one of these mountains (Mt Baw Baw) have been burnt in bushfires. In the most recent landscape-scale fire in 2009, some of the last remaining long-unburnt subalpine vegetation at Lake Mountain was burnt at extremely high severity. This was the first fire to have reached the plateau since 1939. Mires, shrublands and extensive tracts of snow gum forest were all affected.

Snow gum is considered a resilient, long-lived tree, with stems likely to persist for at least 325 years (Barker 1988). Lignotuber ages are unknown but are likely to be much older since these are generally protected from fire (Rumpff 2008) . Resprouting following fire-induced canopy removal is initially prolific but over time, stem thinning occurs as the upper branches extend and shade lower branches (Barker 1988; Noble 2001). Climate-related stress, such as drought or frost may induce low level resprouting at other times (Bell & Williams 1997). Adult mortality resulting from the death of the lignotuber after a single fire is rare but has been observed after repeated fires (Banks 1986; Noble 2001). Snow gums can also regenerate from seed following fire and after about six months of age, seedlings have well-developed lignotubers (Leigh & Holgate 1979; Carr *et al.* 1984; Noble 1984; Barker 1989), although grazing by domestic livestock and feral herbivores has reduced the rate of post-fire seedling survival at many locations (Wimbush & Forrester 1988; Wearne & Morgan 2001; Pickering & Barry 2005). Nevertheless, snow gum characteristically has dual reproductive mechanisms and therefore the 'best of both worlds' (Bond & Midgley 2001).

Since European occupation, widespread stock grazing, increased deliberate burning and extensive bushfires have affected much of the alpine and subalpine landscapes of south-eastern Australia (Rumpff 2008). This is thought to have led to the conversion of mature snow gum woodlands to dense stands of multi-stemmed mallees at some localities (Costin 1967; Good 1982 in Pickering & Barry 2005; Barker 1989; Pickering & Barry 2005; Rumpff 2008). At many of these, there has been insufficient time between fires (<100 years) to allow self-thinning of regrowth stems and a return to more open stand structure (Rumpff 2008).

The majority of studies which have examined the relationship between fire frequency and stem structure have focussed on alpine areas above 1700 m ASL (e.g. Banks 1986; Barker 1988; Barker 1989; Rumpff 2008) but there is comparatively little work at sites at lower elevations (e.g. Ashton & Hargreaves 1983). At these climatically more favourable locations, trees would be expected to tend toward a single-stemmed habit (Lacey & Johnston 1990). However, multi-stemmed trees also dominate sites which are known to have been burnt in one or more fires, or occupy a range of topographies with varying environmental and climatic limitations (e.g. soil depth, aspect and rockiness), which also promote multi-stemmed architecture (Lacey & Johnston 1990; Rumpff 2008).

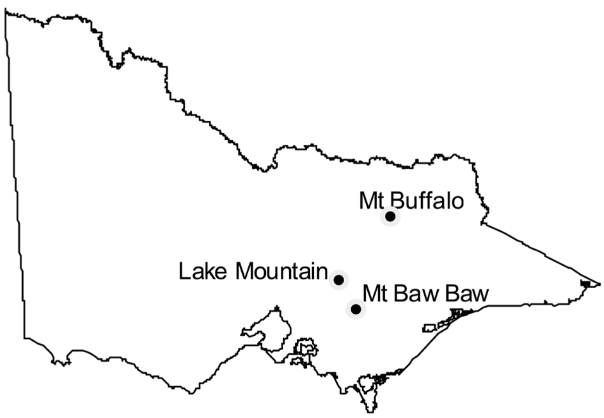

Fig. 1. Locations of Lake Mountain, Mt Baw Baw and Mt Buffalo.

The regime of widespread, high-intensity fire which has prevailed in south-eastern Victoria since 2003 has caused considerable changes to the structure of snow gum forest. As yet, the exact nature of these changes is uncertain. Most trees have vigorously resprouted and in this respect, snow gum is a "niche persistor" and is typical of slow growing plants in low productivity environments able to efficiently re-occupy a site after disturbance (Bellingham & Sparrow 2000; Bond & Midgley 2001; Bellingham & Sparrow 2009). It is often assumed that *Eucalyptus pauciflora* has a more or less unlimited capacity for continuous resprouting because lignotubers comprise a bud bank formed during the early stages of development which is retained throughout the life of the tree (Carr *et al*. 1984). To test this capacity and to examine the degree to which a regime of recurrent fire influences above ground stand structure, snow gum forests and woodlands were compared on three subalpine mountains with different fire frequencies – Lake Mountain after a single fire, a long-unburnt stand at Mt Buffalo, stands unburnt since 1939 at Mt Baw Baw and stands burnt in recurrent fires since 1970 at Mt Buffalo.

Study areas

The three study areas consist of dissected plateaux below 1700 m ASL and isolated from the more contiguous and extensive alpine and subalpine areas of the Great Dividing Range (Rowe 1970; Ashton & Hargreaves 1983; McDougall & Walsh 2007) (Figure 1). The Lake Mountain plateau is the smallest of the three and Mt Baw Baw plateau the most extensive, although average plateau height is similar (Table 1). All three mountains are composed of granitic parent material: granite at Mt Buffalo, granodiorite at Mt Baw Baw and rhyodacite at Lake Mountain.

Table 1. Maximum and average elevations and area of plateaux on each of the three mountains.

Mountain	Max height (m ASL)	Average height (m ASL)	Plateau area (ha)
Lake Mountain	1,482	1,348	2,352
Mt Baw Baw	1,565	1,378	6,941
Mt Buffalo	1,693	1,395	5,757

Livestock grazing occurred from the early days of European settlement until leases were terminated in 1958 (Mt Buffalo), 1964 (Lake Mountain) and 1978 (Mt Baw Baw). Mt Buffalo has the longest and most intense history of land use by Europeans and various areas of the plateau have experienced a range of disturbances since the mid-19th century (Webb & Adams 1998).

The three mountains represent a climate gradient from southern areas subject to oceanic influences, to more continental northern and inland areas. All have high annual rainfall which persists as snow at upper elevations for up to about four months during winter and early spring. Mean annual precipitation is around 1600–1900 mm (Ashton & Hargreaves 1983; McKenzie 1997). BIOCLIM estimates (Nix 1986) of mean annual temperatures indicate a range between 6.5°C and 10.4°C (McKenzie 1997). At Mt Baw Baw, mean annual precipitation is around 1540 mm and mean annual temperatures are 5.7°C to 6.2°C (Kershaw *et al.* 1993). Mean annual precipitation at Mt Buffalo is 1856 mm and strongly seasonal relative to the other two mountains. Mean annual minimum and maximum temperatures are 5°C and 11.7°C respectively, although lower temperatures would be expected in the high valley plains owing to cold air drainage from the adjacent slopes (Rowe 1970).

Numerous bushfires have been recorded throughout the study areas since 1850 (Zylstra 2006) but in many cases their precise localities are not known and it is not possible to reconstruct fire histories prior to 1939. However, parts of Mt Baw Baw National Park were probably burnt in 1923/24 and extensively burnt in 1939. Parts of Mt Buffalo appear to have been burnt in 1923/24 or 1926 and to a minor extent in 1939 (Hodgson 1927; Rowe 1970; Zylstra 2006). Lake Mountain plateau was burnt in 1939 (Ashton & Hargreaves 1983; Zylstra 2006; Shannon & Morgan 2007). Graziers are also believed to have lit fires to promote ‘green pick’ but these fires are not documented and their frequency, severity and extent are unknown.

Recent fire histories since 1970 differ markedly between mountains. Lake Mountain was burnt at high fire severity during the 2009 bushfires. The Mt Buffalo plateau was entirely burnt in 2003 and parts were burnt in 1972, 1985, and 2006/07 (Coates et al. 2012). Mt Baw Baw has remained unburnt since the 1939 bushfires and is currently the only substantial subalpine area in Victoria that has not been burnt since 2003 (Shannon & Morgan 2007; Coates *et al*. 2012).

Snow gum forests dominated by *Eucalyptus pauciflora* subsp. *pauciflora* or *Eucalyptus pauciflora* subsp. *acerina* Rule (endemic to Mt Baw Baw; Rule 1994) occur on upper slopes, crests and rocky rises but occupy similar niches and display similar physiognomy. Lower strata composition varies within and between sites according to degree of rockiness and soil depth, aspect, cold air drainage and time since fire. Shrubs are dominant on shallow soils, while grasses dominate on deeper soils.

Methods

Study design and field methods

The Point-Centred Quarter method (Cottam & Curtis 1956) was used to estimate stem density, stem frequency and total basal area of *Eucalyptus pauciflora* trees at each mountain along 300 m transects which were either continuous or segmented depending on the terrain.

Table 2. Site names, locality, fire history, number of transects and number of trees measured at each mountain.

Stem age is calculated from known fires.

LM1=Lake Mountain Site 1; LM2=Lake Mountain Site 2; BB1=Mt Baw Baw Site 1; BB2=Mt Baw Baw Site 2; PVO=Parks Victoria Office; Mt Dunn=Mt Dunn area; Mt McLeod=Mt McLeod area; 5 Acre Plain=Five Acre Plain area.

Mountain	Site	Latitude	Longitude	Fire history	Altitude (m)	Number of fires since 1938	Time since fire (y)	Number of transects	Number of trees measured	Alive stem age (y)	Dead stem age (y)
Lake Mountain	LM	37° 28’ 44” S	145° 52’ 37” E	1939	1440	2	2	2	200	–	70
	LM2	37° 29’ 28” S	145° 52’ 55” E	2009							
Mt Baw Baw	BB1	37° 50’ 17” S	146° 15’ 58” E	1939	1500	1	72	2	200	72	–
	BB2	37° 50’ 6” S	146° 16’ 23” E		1500						
Mt Buffalo	PVO	36° 43’ 30” S	146° 48’ 7” E	unknown	1400	0?	unknown	1	100	>70	–
Mt Buffalo	Mt Dunn	36° 43’ 52” S	146° 46’ 44” E	2003 2006	1410	2	5	1	100	5	3
Mt Buffalo	Mt McLeod	36° 41’ 28” S	146° 46’ 55” E	1972 2003	1410	2	8	1	80	8	31
Mt Buffalo	5 Acre Plain	36° 44’ 10” S	146° 45’ 47” E	1972 1985 2003 2006	1430	4	5	1	100	5	13 19 3

At Lake Mountain and Mt Buffalo, transects were located between 1400 m and 1440 m ASL (Table 2). Two sites were sampled at Lake Mountain west of Triangle Junction (Table 2). Sites sampled at Mt Buffalo were near the Parks Victoria Office (PVO), Mt Dunn, Mt McLeod and Five Acre Plain (Table 2). Fire frequency count ranged from no fires to four fires since 1970 (Table 2). Two sites with a fire frequency of 2 were sampled at Mt Buffalo because the inter-fire interval differed markedly at each site and no suitable sites were located with a fire frequency of 1 or 3. None of the sites selected at Mt Buffalo were known to have been burnt in 1939. The Mt Baw Baw transects were at higher elevations (1500 m–1550 m), located north-east of the Baw Baw Ski-village (Table 2). Transects were selected randomly within burnt areas so that aspect varied within sites. Fieldwork was carried out in February and March 2011.

One hundred trees were randomly sampled along each of two transects per fire frequency class, except at Mt Buffalo where one transect was sampled per fire frequency class. No two points were <10 m apart, to avoid the same tree being measured repeatedly. Fifty points (=200 trees) were sampled at Mt Baw Baw and at Lake Mountain. At Mt Buffalo 25 points (=100 trees) were sampled at each site, except at Mt McLeod where 20 points were sampled (=80 trees) owing to extremely dense vegetation (Table 2).

The distance from the sample point centre to the closest tree and seedling in each of four quarters was measured to the nearest 0.1 m. Where trees were multi-stemmed, distance was measured from each point to the centre of the lignotuber. On each tree, stem diameter at breast height over bark (D_{130} – approximately 130 cm above ground level) was recorded for all live and dead stems greater than 1 cm diameter. Dead stems which had broken away from the main clump and were lying on the ground were also measured. The diameter measures on dead stems were under bark diameters, as burnt bark had fallen from the trees after the fires. This is not expected to impact results to any serious extent as snow gum bark is relatively thin and the diameter classes used in the data analysis are relatively coarse. A general linear relationship between diameter and age was assumed for the present study although this is likely to have varied to some degree (Barker 1988; Wimbush & Forrester 1988; Wearne & Morgan 2001; Rumpff *et al*. 2009).

Some multi-stemmed trees at Mt Buffalo had arisen from extremely large lignotubers (1–2 m diameter), or the remains of lignotubers where parts had decayed and divided into separate clumps. This has been previously recorded in multi-stemmed trees (Barker 1988; Lacey & Johnston 1990; Dahdouh-Guebas & Koedam 2006). In these cases, an attempt was made to detect whether there was a connection between lignotuber sections by excavation and the clump closest to the sample point centre was measured, although in some cases this was not precise.

At Lake Mountain, 100% of trees were burnt in 2009, so measurements were an estimate of pre-fire population structure. Unburnt trees at Mt Baw Baw were an estimate of post-1939 population structure.

Seedlings were recorded as present if they occurred within twice the distance from the sampling point to the nearest tree in each quarter. Given the density of vegetation at some sites it was not practical to search beyond this distance. It was not possible to estimate seedling density using the Point-Centred Quarter method as seedlings were not found at each sample point. Hence, only the frequency of occurrence of seedlings per sample point was calculated. Presence or absence of fruits was recorded for each tree as an estimate of the frequency of reproductive adults.

Analytical methods

Stand structure and demography (tree density, mean number of stems, mean stem diameter, total basal area and relative basal area) were analysed according to the methods of Cottam & Curtis (1956). The percent frequencies of occurrence of seedlings and reproductive adults were the total number recorded divided by the number of quarters. Sites at Mt Baw Baw contained trees with only living stems and at Lake

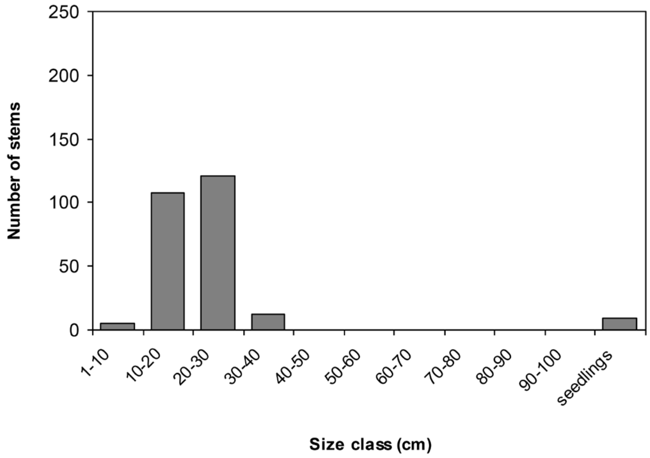

Fig. 2. Frequency of stem diameter size classes and seedlings at Mt Baw Baw (BB1). The site was last burnt in 1939.

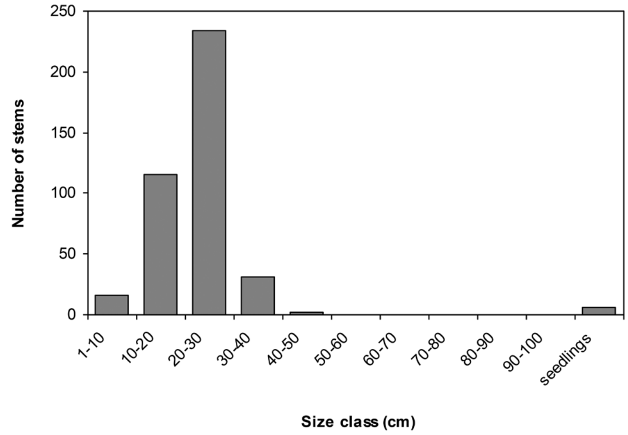

Fig. 3. Frequency of stem diameter size classes and seedlings at Mt Baw Baw (BB2). The site was last burnt in 1939.

Table 3. Tree density, mean number of stems and mean stem diameter of alive and dead stems as an estimate of pre-fire and post-fire stand structure at sites burnt since 2003, compared with unburnt sites. Tree density is the number of trees per hectare. Unburnt sites occurred at Mt Baw Baw (BB1, BB2) and Mt Buffalo (PVO). Fire frequency is calculated since 1938 to include the 1939 fires. LM1=Lake Mountain Site 1; LM2=Lake Mountain Site 2; BB1=Mt Baw Baw Site 1; BB2=Mt Baw Baw Site 2; PVO=Parks Victoria Office; Mt Dunn=Mt Dunn area; Mt McLeod=Mt McLeod area; 5 Acre Plain=Five Acre Plain area.

Site	Number of fires since 1938	Fire history	Tree density (trees/ha)	Pre-fire total basal area (dead stems m^2/ha)	Relative pre-fire basal area (%)	Post-fire total basal area (alive stems m^2/ha)	Relative post-fire basal area (%)	Mean (±SD) number of pre-fire stems/individual (dead stems)	Mean (±SD) number of post-fire stems/ individual (alive stems)	Frequency of seedlings (%)	Frequency of fruiting adults (%)
LM1	2	1939 2009	651	83	31	0	0	2±1	0	100	0
LM2	2	1939 2009	678	54	20	0	0	2±2	0	87	0
BB1	1	1939	445	0	0	70	33	0	4±2	6	91
BB2	1	1939	638	0	0	55	28	0	3±2	9	87
PVO	0?	unknown	821	0	0	33	16	0	1±0.4	77	81
Mt Dunn	2	2003 2006	1,468	48	18	2	1	3±2	4±4	3	44
Mt McLeod	2	1972 2003	1,333	54	20	26	14	7±6	17±11	35	33
5 Acre Plain	4	1972 1985 2003 2006	2,246	32	14	13.7	7	4±4	9±8	56	65

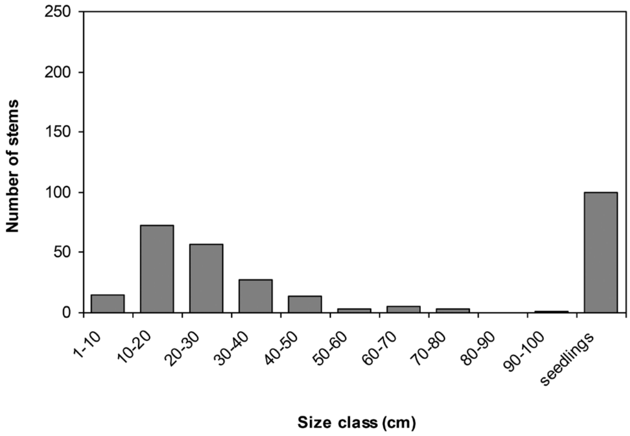

Fig. 4. Frequency of stem diameter size classes and seedlings at Lake Mountain (LM1). The site was burnt in 1939 and 2009.

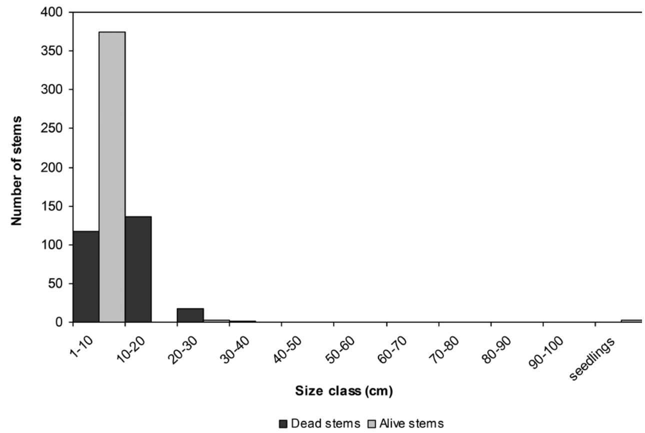

Fig. 7. Frequency of stem diameter size classes and seedlings at Mt Buffalo – Mt Dunn site. The site was burnt in 2003 and 2006.

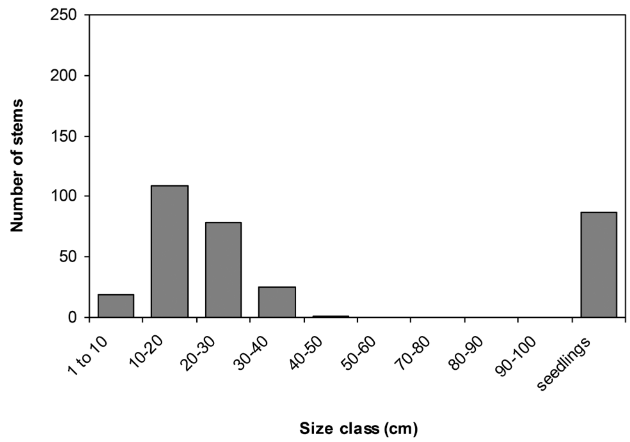

Fig. 5. Frequency of stem diameter size classes and seedlings at Lake Mountain (LM2). The site was burnt in 1939 and 2009.

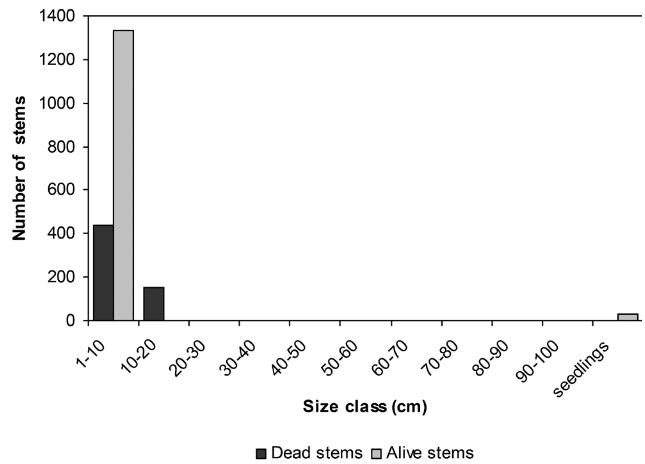

Fig. 8. Frequency of stem diameter size classes and seedlings at Mt Buffalo – Mt McLeod site. The site was burnt in 1972 and 2003.

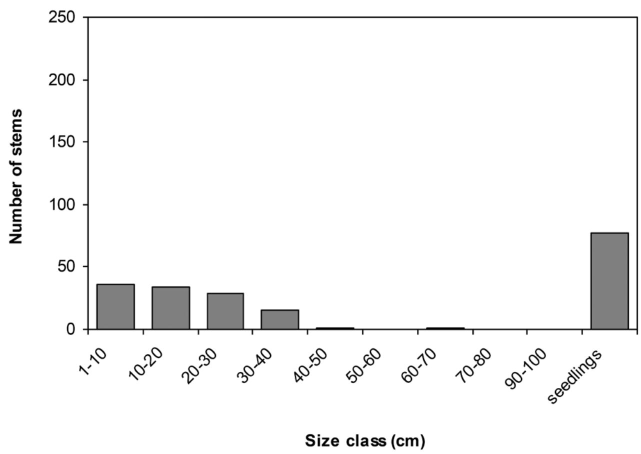

Fig. 6. Frequency of stem diameter size classes and seedlings at Mt Buffalo PV Office site (PVO). There is no recorded history of fire.

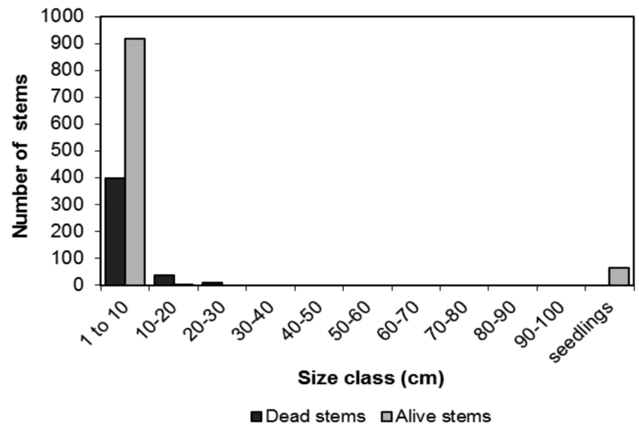

Fig. 9. Frequency of stem diameter size classes and seedlings at Mt Buffalo – Five Acre Plain site. The site was burnt in 1972, 1985, 2003 and 2006.

Mountain, only dead stems >D_{130}. At Mt Buffalo, multi-stemmed trees consisted of both dead and living stems. Dead stems were assumed to have arisen after one fire and then been killed by a subsequent fire (i.e. had clearly been burnt). The age of stems was calculated as the time between one fire and the next, or the time elapsed since the last fire. Separate calculations were carried out for dead and live stems at each site to estimate pre- and post-fire structure, respectively.

For each transect, stems were allocated to 10 cm D_{130}, size classes. Histograms of the frequency distributions of classes were compiled for each stand, representing pre-fire and post-fire population structure. The Kruskal-Wallis test was used to compare pre- and post-fire stem density, mean stem diameter and total basal area at each site, using Minitab® 16.1.0 Statistical Software (Minitab Inc. 2010). Results were considered significant if P <0.05.

Results

Tree density, basal area, stem density and stem size

Long-unburnt sites (Mt Baw Baw, Mt Buffalo PVO) and Lake Mountain

Tree density was broadly similar at Mt Baw Baw and Lake Mountain and slightly higher at the long-unburnt Mt Buffalo PVO site (Table 3). Tree density at Lake Mountain was considerably lower than recorded by Ashton and Hargreaves (1983) at 23 years after fire (1072 trees ha^{-1}).

Total basal area at Mt Baw Baw was roughly equivalent to pre-fire total basal area at Lake Mountain (Table 3). However, total basal area at Mt Buffalo PVO was about half that of stands on the other two mountains (Table 3).

Mean number of stems at Mt Baw Baw and Lake Mountain was 2 to 4 (Table 3) although occasionally up to nine stems were recorded at Mt Baw Baw. At the long-unburnt Mt Buffalo PVO site, trees were single-stemmed (Table 3) and occurred with *Eucalyptus dalrympleana* as an occasional co-dominant. Pre-fire mean number of stems at Lake Mountain was lower than recorded 43 years after the 1939 fires (2 *cf.* 2.9) by Ashton & Hargreaves (1983).

Stand structure at Mt Baw Baw indicated recruitment following a major disturbance. The majority of stems were 20–30 cm D_{130} at BB1 and in the 10–20 cm D_{130} and 20–30 cm D_{130} classes at BB2 (Figure 2). Variability in tree and stem density across sites suggests differing disturbance histories. There were large trees (30–40 cm D_{130}) at both sites as well as a few very large trees (> 40 cm) recorded at BB1. There were few stems below 10 cm D_{130} at both BB sites (Figure 2).

Pre-fire structure at LM1 consisted of a range of size classes including some very large trees (>40 cm D_{130}) which were mostly absent from LM2. Most stems at both sites fell within classes 10–20 cm D_{130} or 20–30 cm D_{130} (Figure 3).

Stand structure at Mt Buffalo PVO comprised mostly single-stemmed trees and was consistent with its history of no recorded fire, although fire scars at the base of some trees suggested that the site had been burnt at some time in the past. Size classes were more or less evenly distributed (Figure 4). There were a couple of very large trees (>40 cm D_{130}), suggesting that this stand has been established for a very long time.

Multi-burnt sites (Mt Buffalo)

Tree density was up to five times higher at the three multi-burnt sites compared with Lake Mountain and the long-unburnt sites at BB and PVO and was particularly high at Five Acre Plain (Table 3).

In the short time that had elapsed since the last fires in 2003 and/or 2006, post-fire total basal area was significantly lower than pre-fire total basal area at all three sites (P <0.05; Table 3). Total basal area had recovered to roughly half pre-fire levels at Mt McLeod and Five Acre Plain but was still very low at Mt Dunn (Table 3). Mt Dunn and Five Acre Plain, both burnt twice within three years, had the lowest pre-and post-fire total basal areas (Table 3).

At Mt McLeod and Five Acre Plain, the mean number of post-fire stems was significantly higher than the number of pre-fire stems (P <0.0001) but numbers were higher at Mt McLeod (Table 3). There was a great deal of variation between trees at both of these sites, with stem numbers ranging from one to 49.

Pre- and post-fire stand structure at the most frequently-burnt site, Five Acre Plain, both consisted of numerous small stems (<10 cm $D_{130;}$ Figure 7). Very few larger burnt stems (>20 cm D_{130}) were measured. Pre-fire stems were assumed to be a mix of resprouts from 1972, 1985 and 2003, although it is possible that some stems killed in earlier fires had since been completely incinerated by 2006 and were no longer detectable. Thus, multiple regeneration events may not be completely represented and pre-fire estimates may mostly reflect 2003 structure.

At Mt McLeod, living stems which had resprouted after the 2003 fire were all <10 cm D_{130} (Figure 6). Stems which had resprouted after the 1972 fire and were burnt by the 2003 fire were also small (<10 cm D_{130}) although some larger stems were also measured (10–20 cm D_{130}).

There was little change between the low number of pre- and post-fire stems at Mt Dunn (Table 3). Dead stem numbers per tree at Mt Dunn ranged from one to 10 whilst live stem numbers ranged from one to 21 but only 10% of the trees measured had more than five living stems. Overall stand structure implied stems from three generations. Most post-2003 resprouts were killed in the 2006 fire and the current stand was composed almost entirely of thin stems <10 cm D_{130} which had resprouted after 2006 (Figure 5). A small number of burnt and living stems was recorded in size classes 20–30 and 30–40 cm D_{130} (Figure 5). The large, living stems had survived both the 2003 and 2006 fires, suggesting patchy fire coverage at this site. However, in comparison with the other sites, there was a higher number of burnt stems in the

10–20 cm D_{130} class than would be expected after only three years growth (between 2003 and 2006). This suggests that pre-fire structure may have included stems burnt in some unrecorded fire prior to 2003.

Reproduction

Seedlings were most frequent at Lake Mountain and Mt Buffalo PVO (Table 3; Figures 2, 3 and 6). Continuous recruitment was occurring at Mt Buffalo PVO in long-unburnt snow gum forests with a high number of reproductive adults, whilst at Lake Mountain a pulse of recruitment occurred following the 2009 fire. In spite of a high proportion of fruiting adults at Mt Baw Baw, seedling recruitment was very low (Table 3; Figures 4 and 5). Seedling recruitment was highest in stands with high stem numbers (Mt McLeod and Five Acre Plain; Table 3; Figures 8 and 9) and lowest at Mt Dunn (Table 3; Figure 7), even though the frequency of fruiting adults was substantial at the latter site.

Discussion

Stem density at Lake Mountain was consistent with the prediction of Ashton & Hargreaves (1983) that stem thinning would occur in the absence of fire. Stem density was slightly higher at Mt Baw Baw but still within expected ranges 70 years after fire. Similar total basal areas at Lake Mountain and Mt Baw Baw imply that stand structure developed along similar trajectories until the most recent fire in 2009 and it is almost certain that pre-fire stand structure will not be restored at Lake Mountain for at least another 70 years. Predicted climate change impacts of lower rainfall and higher fire frequency (Parry *et al.* 2007) may mean that recovery of pre-fire structure may take longer.

Stand structure at Mt Buffalo PVO was consistent with a long fire-free period but mean stem diameter was lower compared to trees at other sites. This is most likely a consequence of faster stem growth owing to more favourable site conditions (e.g. climate, water availability, soil depth or fertility) and hence taller, more slender trunks consistent with tree physiognomy at lower altitudes. *Eucalyptus dalrympleana* was an occasional co-dominant, indicating that frost and snow cover are lighter relative to sites where snow gum is the sole dominant (Farrell and Ashton 1973). However, since the time of the last fire is unknown, thinner stems may also be a consequence of a more recent, unrecorded fire.

In addition to recent high fire frequency, escaped fires from deliberate burning by graziers prior to 1958, as well as shallow soils, may have contributed to current high stem numbers and high tree density at Five Acre Plain. More recently, control of rabbits, known to kill basal shoots through ringbarking (Wimbush & Forrester 1988), may also have promoted multiple stem development.

At Five Acre Plain, stems were all within the smallest size class and pre- and post-fire total basal area was low in spite of high post-fire stem numbers, suggesting that above ground carbon storage may be constrained when there is investment in numerous small stems. Since at least 1970, trees at this site have probably remained in the ‘proliferative’ growth phase characteristic of post-fire coppicing (Noble 2001). High tree density at this site also suggests that intraspecific competition may constrain biomass accumulation (Bellingham & Sparrow 2000), since natural thinning in stands with high stem densities and a mallee habit seems to occur at a lower rate than within open forest (Barker 1988).

Grazing by cattle, sheep and rabbits has been credited with suppressing post-fire stem and seedling regeneration in alpine snow gum forests in some more elevated locations on deeper soils such as in Kosciusko National Park and the Bogong High Plains (Bryant 1971; Wimbush & Forrester 1988; Rumpff 2008). Prior to 1958, cattle probably occupied the area around Five Acre Plain, where salt was left for cattle before the autumn muster (Webb & Adams 1989). However, it is doubtful that stock accessed the relatively dry, rocky terrain at the site, or preferentially grazed the shrubby strata over more herbaceous vegetation around low lying terrain. There is no record of sheep grazing at Mt Buffalo.

Pre-2006 fire structure at Mt Dunn consisted of few-stemmed trees but relatively high total basal area. The grassy stratum at this site is suggestive of deeper soils and higher site productivity. Some large stems (burnt and living) were recorded. However, there were a number of burnt stems recorded in the 20–40 cm D_{130} classes and total pre-fire basal area was comparable with LM2. The most likely explanation for stems of this size is patchy fire history at this site and that stand structure includes stems which originated after one or more unrecorded fires prior to 1958, around the time o f cattle grazing.

The mallee form and numerous thin stems at Mt McLeod suggest that this site was also burnt in unrecorded fires prior to 1972. Its location on the northwest part of Mt Buffalo would expose this site to bushfires, which typically occur on days of strong northerly winds, such as the severe fires of 1972 and 2003 (Dexter 1973; Coates *et al.* 2006). Soils are relatively shallow and rocky, which would also promote a mallee growth form. Lignotubers of most trees that were measured were very large (up to 2 m diameter), suggesting long-term dominance of lignotuber growth over stem growth, as can occur when secondary lignotubers fuse laterally (Carr *et al.* 1984). Stem clumps were distributed in wide rings, consistent with descriptions in the literature of repeated resprouting after the upper lignotuber surface is killed and new growth is initiated at the periphery (Lacey & Johnston 1990). The lack of stems in size classes greater than 10–20 cm D_{130} adds further weight to the notion that multi-stemmed trees have prevailed at this site for a long time.

There is no record in the available literature to confirm that Mt McLeod was ever grazed (e.g. Rowe 1970; Binder 1978; Stephenson 1980; Webb & Adams 1998) and it is unlikely that cattle occupied this remote site, where access is difficult.

Thus, the influence of cattle grazing on stand structure is likely to have been insignificant.

Stand regeneration

With the exception of the stand PVO, all the stands measured show pre-fire size/age structures which indicate pulse regeneration following a major disturbance. In contrast, stand PVO has a size/age structure which appears to indicate more or less continuous regeneration.

At Lake Mountain and Mt Baw Baw stand structure is indicative of regrowth after the 1939 fire. The very large/old individuals present at LM1 tend to suggest that these stems were not destroyed in the previous fire in 1939, unlike in 2009 when 100% of trees were burnt at extremely high intensity. In contrast with a relatively heterogeneous pre-fire structure, snow gum forest at Lake Mountain will comprise stands of even-aged stems for the foreseeable future.

At Mt Dunn, the few trees recorded in the 10–20 cm and 20–30 cm D_{130} size classes imply that this site may have been burnt in 1939 but regeneration has since been poor and there are no living stems which pre-date the 1939 fire. At other multi-burnt Mt Buffalo sites, there were almost no stems >20 cm D_{130}. The size-class range of dead stems at these sites suggests that stems of all diameters can be killed during a fire so that stem size is unlikely to be useful for re-constructing fire severity. Large stems which had survived some fires were occasionally recorded but these were rare. Because snow gum bark is thin throughout the lifespan of the tree (Williams & Ashton 1988), snow gum stems may be more vulnerable to low intensity fires than most other eucalypt species.

Seedling recruitment

Ashton & Hargreaves (1983) reported high seedling densities 23 years after fire at Lake Mountain. These densities later diminished with natural thinning and interspecific competition. The current cohort of seedlings on Lake Mountain is expected to decline with regrowth of competing understorey vegetation and natural attrition. Seedling frequency was low at Mt Baw Baw in forest with dense shrubs but was relatively high at PVO where the lower strata are open. However, the lack of individuals in the mid-storey at PVO implies that these seedlings are likely to persist in a suppressed state (Ashton & Williams 1989; Loehle 2000) until canopy disturbance creates growing space.

The very low seedling frequency at Mt Dunn is most likely a result of the short time between the two recent fires. However, the grassy ground stratum at this site also implies that seedlings which have been unable to compete effectively for resources may have been more vulnerable to frost or drought in the absence of an intact canopy in the years after fire (Wearne & Morgan 2001; Loveys *et al*. 2010). Seedling recruitment was moderate at Five Acre Plain and Mt McLeod. Given patchy fire coverage in 2006 at Five Acre Plain and high rock cover at both of these sites, seedlings are likely to have been better protected.

How persistent is snow gum under a changed fire regime?

The ability to repeatedly resprout certainly suggests that snow gum is a tenacious 'niche persistor' (Bond & Midgley 2001). Such adaptation might have derived from limited opportunity for populations to expand in an environment where seedling establishment is constrained by snow and extreme frosts (Billings 1969; Loveys *et al*. 2010; Green & Venn 2012). Resprouting is an extremely effective means of replacing biomass after damage to adults (Loehle 2000) and as a long-term site occupancy strategy, even when intervals between disturbances are short (Bellingham & Sparrow 2000). In this study, we detected capacity for resprouting after four fires within four decades at one site. However, until recently snow gum has occupied landscapes with infrequent large-scale fires (Wahren *et al*. 2001) so that historically, complete destruction of above ground biomass and replacement of the entire crown by resprouting is likely to have been rare.

The results of this study demonstrate structural differences between long unburnt and frequently burnt snow gum stands, both within and between mountains. The two sites with the shortest inter-fire intervals (Mt Dunn and Five Acre Plain) also had the lowest post-fire total basal areas in spite of an increase in the mean number of stems, at least partly explained by the relatively short growth time between the last fire and the timing of the survey. However, at Five Acre Plain and Mt McLeod, the results also imply that multi-stemmed architecture has become entrenched as numerous small stems assume equal apical dominance and that large stems may never fully develop, even after a long fire-free period (Lacey & Johnston 1990).

The potential for snow gum stands to persist in the longer term under this switch in disturbance frequency is uncertain. Not examined in this study was the resprouting ability of very old trees which may already have sustained damage from previous fires, insects and pathogens. The response of such trees is currently unknown. Field observations suggest that there has been a trade-off between resources allocated to growth and reproduction rather than starch storage in lignotubers and a reduction in resprouting ability (Bond & Midgley 2001), also observed in some *Eucalyptus camaldulensis* populations under regimes of infrequent disturbance (Jahnke et al. 1983). As a consequence, with increasing age, trees may be allocating an increasing proportion of their resources to growth and reproduction (by seed) than to starch storage and resprouting ability. The implications are that some old trees may never be replaced after fire and that niche persistence is size/age limited, or can only be maintained under low frequency and low severity disturbance regimes. The current outlook is one of a radical demographic shift in snow gum population structure in subalpine landscapes.

Open snow gum stands provide the most effective means of water collection and regulation and repeated fire substantially impacts on their ability to sustain snow accumulation and persistence, retain soil moisture, prevent erosion (Costin 1967) and possibly to store carbon owing to reduced total basal area. Some of the only long-unburnt snow gum forests in Victoria occur at Mt Baw Baw and to a limited extent, at Mt Buffalo. Excluding fire from these areas is imperative to maintain these old growth stands.

Recent severe and widespread bushfires between 2003 and 2009 have seen the introduction of mandatory targets for fuel reduction burning across Victoria's public lands to mitigate the scale and impact of future unplanned fires. Fire severity data were not available to this study and stands burned by low-severity fuel reduction fires were not investigated. Conversely, the impact of stands with higher stem numbers and hence increased elevated fuel (Lentile *et al*. 2006) on fire severity has not been studied in subalpine forests in Victoria. Further work is also needed to determine these possibly unforeseen and additional consequences of changes in fire frequency in snow gum woodlands.

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References

Ashton, D. H. & Hargreaves, G. R. (1983) Dynamics of subalpine vegetation at Echo Flat, Lake Mountain, Victoria. *Proceedings of the Ecological Society of Australia* 12**:** 35–60.

Ashton, D. H. & Williams, R. J. (1989) Dynamics of subalpine vegetation in the Victorian region. In: Good, R. (Ed.) *The Scientific Significance of the Australian Alps* pp. 143–169. The Australian Alps National Parks Liaison Committee and the Australian Academy of Science, Canberra.

Banks J. C. G. (1986) Fire and stand histories in subalpine forests on the Thredbo ski slopes, Kosciusko National Park, NSW, Australia. In: Jacoby, G. C. (Ed.) *Proceedings of the International Symposium on Ecological Aspects of Tree Rings* pp. 163–174. Columbia University Press, Palisades, New York.

Barker, S. (1988) Population structure of snow gum (*Eucalyptus pauciflora* Sieb. ex Spreng.) subalpine woodland in Kosciusko National Park. *Australian Journal of Botany* 30**:** 483–501.

Barker, S. (1989) Snow gum woodland: past, present and future. In: Good, R. (Ed.) *The Scientific Significance of the Australian Alps* pp. 359–369. The Australian Alps National Parks Liaison Committee and the Australian Academy of Science, Canberra.

Bell, D. T. & Williams, J. E. (1997) Eucalypt ecophysiology. In: Williams, J. & Woinarski, J. (Eds.) *Eucalypt Ecology: Individuals to Ecosystems* pp. 168–196. Cambridge University Press, Cambridge.

Bellingham, P. J. & Sparrow, A. D. (2009) Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409–416.

Bellingham, P. J. & Sparrow, A. D. (2000) Multi-stemmed trees in montane rain forests: their frequency and demography in relation to elevation, soil nutrients and disturbance. *Journal of Ecology* 97: 472–483.

Billings, W. D. (1969) Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. *Plant Ecology* 19: 192–207.

Binder, R. M. (1978) *Stratigraphy and Pollen Analysis of a Peat Deposit, Bunyip Bog, Mt Buffalo, Victoria*. Monash Publications in Geography No 19. Department of Geography, Monash University, Australia.

Boland, D. J., Brooker, M. H., Chippendale, G. M., Hall, N., Hyland, B. P. M, Johnston, R. D., Kleineg, D. A. & Turner, J. D. (1984) *Forest Trees of Australia*. Nelson, CSIRO.

Bond, W. J. & Midgley, J. J. (2001) Ecology of sprouting in woody plants: the persistence niche theory. *Trends in Ecology and Evolution* 16: 45–51.

Brookhouse, M., Lindesay, J. & Brack, C. (2008) The potential of tree rings in *Eucalyptus pauciflora* for climatological and hydrological reconstruction. *Geographical Research* 46: 421–434.

Bryant, W. G. (1971) Grazing, burning and regeneration of tree seedlings in *Eucalyptus pauciflora* woodlands. *Soil Conservation Journal* 27: 121–134.

Carr D. J., Jahnke, R. & Carr S. G. M. (1984) Initiation, development and anatomy of lignotubers in some species of *Eucalyptus*. *Australian Journal of Botany* 32: 415–437.

Coates, F., Sutter, G. & Mavromihalis, J. (2006) *Regeneration of treeless subalpine vegetation after recurrent fires at Mt Buffalo National Park*. Arthur Rylah Institute for Environmental Research Technical Report No. 160. Department of Sustainability and Environment, Heidelberg, Victoria.

Coates, F., Cullen, P., Zimmer, H. & Shannon, J. (2012) *How snow gum forests and subalpine peatlands recover after fire: Black Saturday Victoria 2009–Natural values fire recovery program*. Department of Sustainability and Environment, Heidelberg, Victoria.

Costin, A. B. (1967) Management opportunities in Australian high country mountain catchments. In: Sopper, W. E. & Lull, H. W. (Eds.) *Forest Hydrology* pp. 565–577. Pergamon Press Ltd.

Cottam, G. & Curtis, J. T. (1956) The use of distance measures in phytosociological sampling. *Ecology* 37: 451–460.

Dahdouh-Guebas, F. & Koedam, N. (2006) Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM): solutions to ambiguous field situations and description of the PCQM+ protocol. *Forest Ecology and Management* 228: 1–18.

Dexter, B. D. (1973) *A history of the Mt Buffalo fire, 14th December–26th December 1972*. Forests Commission Victoria.

Farrell, T. P. & Ashton, D. H. (1973) Ecological Studies on the Bennison High Plains. *Victorian Naturalist* 90: 286–302.

Good R. B. (1982) The impact of prescribed burning on subalpine woodlands. MSc Thesis, University of New South Wales, Sydney.

Green, K. & Venn, S. (2012) Tree-Limit Ribbons in the Snowy Mountains, Australia: Characterization and Recent Seedling Establishment. *Arctic, Antarctic, and Alpine Research*, 44: 180–187.

Hodgson, L. L. (1927) On the Buffalo Plateau. *Victorian Naturalist* 44: 188–196.

Jahnke, R., Carr, D. J. & Carr, S. G. M. (1983) Lignotuber development and growth parameters in *Eucalyptus camaldulensis* (Dehnh.): effects of phosphorous and nitrogen levels. *Australian Journal of Botany* 31: 283–292.

Kershaw, A. P., Reid, M., Bulman, D., Aitken, D., Gell, P., McKenzie, M. & Hibberd, J. (1993) *Identification, classification and evaluation of peatlands in Victoria*. Report to the Australian Heritage Commission, Canberra.

Lacey C. J. & Johnston R. D. (1990) Woody clumps and clumpwoods. *Australian Journal of Botany* 38: 299–334.

Leigh, J. H. & Holgate, M. D. (1979) The responses of the understorey of forests and woodlands of the Southern tablelands to grazing and burning. *Australian Journal of Ecology* 4: 25–45.

Lentile, L. B., Smith, F. W. & Shepperd, W. D. (2006) Influence of topography and forest structure on patterns of mixed severity fire in ponderosa pine forests of the South Dakota Black Hills, USA. *International Journal of Wildland Fire* 15: 557–566.

Loehle, C. (2000) Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *The American Naturalist* 156**:** 14–33.

Loveys, B. R., Egerton, J. J. G., Bruhn, D. & Ball, M. C. (2010) Disturbance is required for CO_2-dependent promotion of woody plant growth in grasslands. *Functional Plant Biology* 37: 555–565.

McDougall, K. L. & Walsh, N. G. (2007) Treeless vegetation of the Australian Alps. *Cunninghamia* 10: 1–57.

McKenzie, G. M. (1997) The late Quaternary vegetation history of the south-central highlands of Victoria, Australia. *Australian Journal of Ecology* 22: 19–36.

Minitab Inc. (2010) *Minitab® statistical software release 16.1.0*. Minitab Inc., State College, Pennsylvania.

Nix, H. A. (1986) 'A biogeographic analysis of Australian Elapid Snakes'. In: Longmore, R. (Ed.) *Atlas of Elapid Snakes of Australia* pp. 4–15. Australian Flora and Fauna Series Number 7. Australian Government Publishing Service: Canberra.

Noble I. R. (1984) Mortality of lignotuberous seedlings of *Eucalyptus* species after an intense fire in montane forest. *Australian Journal of Ecology* 9: 47–50.

Noble J. C. (2001) Lignotubers and meristem dependence in mallee (*Eucalyptus* spp.) coppicing after fire. *Australian Journal of Botany* 49: 31–41.

Parry, M. L., Canziani, O. F., Palutikof, J. P., van der Linden, P. J. & Hanson, C. E. (2007) *Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Pickering, C. M. & Barry, K. (2005) Size/age distribution and vegetative recovery of *Eucalyptus niphophila* (snowgum, Myrtaceae) one year after fire in Kosciusko National Park. *Australian Journal of Botany*, 53: 517–527.

Rowe, R. K. (1970) *A study of the land in the Mount Buffalo National Park*. Soil Conservation Authority, Melbourne.

Rule, K. (1994) Three new endemic subspecies of snow gum for Victoria and notes on the taxonomy of the informal superspecies *pauciflora* L.D. Pryor and L.A.S. Johnson. *Muelleria* 8: 223–233.

Rumpff, E. J. (2008) The influence of climate and disturbance on alpine tree-line dynamics in the Victorian Alps, Australia. PhD Thesis, University of Melbourne.

Rumpff, E. J., Cutler, S. C., Thomas, I. & Morgan, J. W. (2009) An assessment of the relationship between tree-ring counts and basal girth of high-altitude populations of *Eucalyptus pauciflora* (Myrtaceae). *Australian Journal of Botany* 57: 583–591.

Shannon, J. M. & Morgan, J. W. (2007) Floristic variation in *Sphagnum*-dominated Peatland communities of the Central Highlands, Victoria. *Cunninghamia*, 10: 59–76.

Stephenson, H. (1980) *Cattleman and Huts of the High Plains*. Graphic Books, Armadale, Victoria.

Wahren, C-H. A., Papst, W. A. and Williams, R. J. (2001) Early post-fire regeneration in subalpine heathland and grassland in the Victorian Alpine National Park, south-eastern Australia. *Austral Ecology* 26: 670–9.

Wearne, L. J. & Morgan, J. W. (2001) Recent forest encroachment into subalpine grasslands near Mount Hotham, Victoria, Australia. *Arctic, Antarctic and Alpine Research* 33: 369–377.

Webb, D. & Adams, B. (1998) *The Mount Buffalo Story 1898–1998*. Melbourne University Press, Carlton South.

Westman, W. E. (1986) Resilience: concepts and measures. In: Dell, B., Hopkins, A. J. M. & Lamont, B. B. (Eds.) *Resilience in Mediterranean-type ecosystems* pp. 5–19. Dr W. Junk Publishers.

Williams J. & Ladiges P. (1985) Morphological variation in Victorian, lowland populations of *Eucalyptus pauciflora* Sieb. ex Spreng. *Proceedings of the Royal Society of Victoria* 97: 31–48.

Williams, R. J. & Ashton, D. H. (1988) Cyclical patterns of regeneration in subalpine heathland communities on the Bogong High Plains, Victoria. *Australian Journal of Botany* 36: 605–19.

Wimbush, D. J. and R. I. Forrester (1988) Effects of rabbit grazing and fire on a subalpine environment II. Tree vegetation. *Australian Journal of Botany* 36: 287–298.

Zylstra, P. (2006) Fire history of the Australian Alps. Prehistory to 2003. Australian Alps Liaison Committee. http://www.australianalps.environment.gov.au/publications/research-reports/fire-history.html. Accessed 25 May 2011.

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