Drought-related dieback in four subalpine shrub species, Bogong High Plains, Victoria

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Abstract: Subalpine shrubs on rocky slopes on the Bogong High Plains, Victoria (36° 53' S, 147° 19' E), were observed to be severely desiccated over the summer of 2002/03 after a 50 day period when only 1.2 mm of rainfall was recorded. Moderate to severe canopy dieback was noted in shrubs growing on rocky north- and west-facing slopes. Four shrubs were assessed for their drought tolerance on west-facing slopes at Basalt Hill. Soils were rocky and uniformly shallow across the site (mean depth = 11.32 ± 0.69 cm). *Prostanthera cuneata* was the most drought tolerant species (as evidenced by the least amount of canopy dieback observed) followed by *Hovea montana*, *Pimelea axiflora* var. *alpina* and *Epacris glacialis*. All *Epacris glacialis* plants (n = 16) had died at the study location whereas no *Prostanthera cuneata* plants (n = 45) had canopy dieback that exceeded 60%. The amount of dieback observed was not significantly associated with either local soil depth or shrub canopy area. Hence, very small plants were not more susceptible to drought nor were shrubs found on the shallowest of the soils at the site. This suggests that drought effects are possibly dependent on local influences such as topography, drainage and competition intensity. Drought has only rarely been considered a major factor affecting the abundance and distribution of subalpine shrub species in Australia but this study suggests that it should be added to the list of abiotic factors governing the local dynamics of subalpine vegetation. In particular, the high mortality of *Epacris glacialis* observed in the study area suggests that non-equilibrium dynamics are likely to be the 'norm' for some shrubs in subalpine areas.

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Introduction

The effects of infrequent climatic events such as drought, on the composition of plant communities in south-eastern Australia may be long-lasting (Bureau of Meteorology 1993), but has only rarely been documented. Clearly there is a need to document these effects on Australian vegetation given the propensity for El Nino Southern Oscillation-driven droughts (Fensham & Holman 1999, Rice et al. 2004). Previous studies have used drought-induced dieback to assess the moisture tolerance of tree species at individual sites (Fensham & Holman 1999). Pook et al. (1966) described the effects of drought in forest trees of the Australian Capital Territory and Monaro region during a severe drought in 1965; dry sclerophyll forests were the most severely affected, especially on shallow stony soils on northerly and westerly aspects. Ashton et al. (1975) documented the response of woodland vegetation at Mount Towrong, Victoria during the drought of 1967/8 and found severe damage in vegetation on hot rocky western slopes. Kirkpatrick (1970) assessed the drought resistance of two co-occurring eucalypts in coastal forests at Aireys Inlet, Victoria after the 1967/68 drought, and found one of the species, *Eucalyptus globulus*, was much more impacted than the other, *Eucalyptus tricarpa*. Kirkpatrick and Marks (1985) found that a large number of shrubs and trees suffered drought damage near Hobart, Tasmania during a prolonged drought and observed that damage was most common on shallow soils and gully margins on dolerite soils. All four studies highlight the differing drought resistance of native species, and suggest that explanations for current vegetation patterns need to consider the effects of infrequent extreme events such as drought, more so than has previously been done.

This may be particularly true in alpine and subalpine areas where climatic variability is a noted feature (Costin 1968). While exposure to wind and frost, depth and duration of snow, drainage and disturbance are well known to influence plant community distribution in alpine areas (Williams & Ashton 1987, Costin et al. 2000), the effects of summer drought on local community composition are generally less well-appreciated. Summer drought appears to be relatively common in high mountain areas. Wimbush and Costin (1979) document droughts that occurred in the summers of 1965 and 1978, while Williams (1990) documented drought during the 1982/83 growing season when precipitation was 36% of average, and soil moisture was usually below permanent wilting point.

The effects of drought on subalpine plants are poorly understood. In subalpine grasslands, drought adversely affected the survival and growth of snowgrasses, *Poa* spp., leading to their partial replacement by herbs (Wimbush & Costin 1979, Costin et al. 2000). Williams (1990) reported the effects of drought following severe frost on the growth of four subalpine shrubs, *Grevillea australis*, *Hovea montana*, *Phebalium squamulosum*, *Prostanthera cuneata*. He found that drought sensitivity varied with species, *Hovea* > *Grevillea* > *Phebalium* = *Prostanthera*, and that the impacts of drought differed according to plant size i.e. old 'senescent' plants were more sensitive than young 'building' plants. Pook et al. (1966) also observed that drought effects were evident in subalpine and alpine heaths during the 1965 drought. They found that shrubs on stony ridges e.g. *Podocarpus lawrencei*, *Kunzea muelleri*, were more susceptible to wilting than were shrubs and herbaceous species on deeper, relatively stone-free soils. These studies suggest that infrequent climatic events in alpine areas may play an important role in the distribution of plant species and the structure and composition of plant communities.

Between October 2002 and February 2003, when rainfall was well below-average, shrubs on rocky slopes at Ruined Castle and Basalt Hill on the Bogong High Plains, Victoria were observed to be suffering severe moisture stress. Leaves of severely affected shrubs were browned-off, dry and brittle and contrasted sharply with unaffected leaves. This led the author to undertake field observations to contribute to the sparse literature on drought impacts on subalpine shrubs.

Methods

Study area

The study was conducted within open grassy-heath and closed-heath on west-facing slopes at Basalt Hill on the Bogong High Plains, approximately 4 km east of Falls Creek, Victoria (36° 53' S, 147° 19' E). The site is at 1680 m asl; slopes are short (100 m) and steep (20–30°). Dominant species in the open-heath were *Hovea montana* (Fabaceae) and *Poa costiniana* (Poaceae) while *Prostanthera cuneata* (Lamiaceae) dominated the closed-heaths. Soils were mostly rocky, shallow (range <1– 40 cm), acidic, alpine humus soils developed on a parent material of Tertiary basalt. Surface rocks were frequent (>20% cover) across the site. Average rainfall for the area is 1298 mm (Falls Creek recording station, 4 km west of study site; Bureau of Meteorology unpublished data). Mean maximum temperatures are 18.0 °C (March) and mean minimum temperatures are -3.0 °C (July). From October 2002 to February 2003, precipitation was 41% of average (Fig. 1), with no rain recorded for 27 consecutive days (9 January to 6 February). After 1 January, when 18 mm of rainfall was recorded, the following 50 days (to 21 February) had only 1.2 mm of rainfall (Bureau of Meteorology unpublished data). Maximum and minimum temperatures were also well above-average during this period (Fig. 2).

Since the 1850s, summer-grazing of domestic cattle has occurred on the Bogong High Plains but the rocky and steep nature of the study site suggests that grazing pressure is lower there than elsewhere in the region (author pers. obs.). During January 2003, bushfires occurred in subalpine vegetation on the Bogong High Plains and surrounding forests, but did not burn the study area.

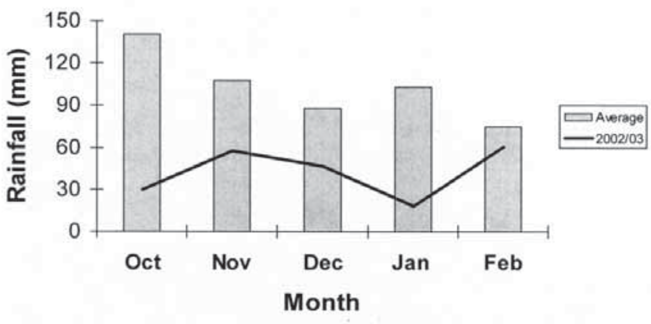

Fig. 1. Monthly rainfall from October 2002 to February 2003 versus the long-term average rainfall for the Falls Creek meteorological recording station.

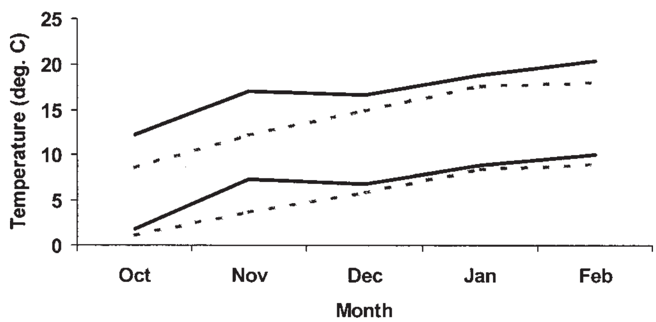

Fig. 2. Mean monthly minimum and maximum temperatures (solid lines) from October 2002 to February 2003 versus the long-term average (dashed line) for the Falls Creek meteorological recording station.

Table 1. Description of the study species, their distribution and the sample sizes used in the study.

Species (Family)	Description and distribution	Sample size (*n*)
Epacris glacialis (Epacridaceae)	Prostrate to decumbent shrub to 30 cm high; common in and around the margins of bogs and in other wet sites such as fens, short alpine herbfield and wet stony areas in sod tussock grassland.	16
Hovea montana (Fabaceae)	Spreading, multistemmed shrub to 0.5 m high; stems ascending or the outer decumbent, sometimes rooting. Usually in open alpine heath and on grassy slopes in subalpine heath at altitudes between 1200 and 1830 m.	88
Pimelea axiflora var. *alpina* (Thymelaeaceae)	Shrub or subshrub, 0.2–1.0 m high. Found in alpine and subalpine habitats above 1500 m, usually in rocky areas.	31
Prostanthera cuneata (Lamiaceae)	Compact dense shrub to 1 m high. Locally common or dominant in alpine closed heathlands between 1500 and 2000 m altitude, mostly in rocky sheltered sites.	45

Study species

The four main shrub species at the site, *Prostanthera cuneata*, *Hovea montana*, *Pimelea axiflora* var. *alpina* and *Epacris glacialis* were selected for study (Table 1). Nomenclature follows Ross (2000). *Prostanthera cuneata* appears to be commonest on deeper soils of lower slopes while *Hovea montana* appears to be common on upper slopes in shallower soils. *Pimelea axiflora* var. *alpina* is found in similar locations to *Hovea montana* while *Epacris glacialis* is confined to shallow soils on lower slopes. All four species produce discrete individuals and population-level responses to drought can be attributed to individuals for each species. Williams (1990) suggested that while *Hovea montana* produces discrete individuals, individuals of *Prostanthera cuneata* are rare or difficult to observe in closed-heath since plants expand by layering of stems. This was not evident at the study site.

Assessment of drought damage

In March 2003, two 75 m long transects were haphazardly located on mid-slope positions on west-facing aspects after reconnaissance of the area. These transects passed through major areas of visible canopy dieback and were used to estimate the relative effects of drought on the four major shrub species present. The line intercept method was used; all shrubs that were intercepted by the transect were recorded and their position noted, their canopy area estimated (using the product of the maximum and minimum widths to obtain a canopy area) and the amount of canopy dieback was estimated by eye using a cover-abundance scale (1 = <10% dieback, 2 = 10–30% dieback, 3 = 31–60% dieback, 4 = 61–99% dieback, 5 = dead). At 1 m intervals, a 5 mm metal pin was pushed into the soil and the depth to bedrock was recorded to the nearest centimetre. Each plant recorded was assigned a soil depth according to the nearest measurement location. This method provides an indication of the local soil depth on which plants were growing rather than an absolute measure.

Data analysis

Data collected from the two transects were pooled for each species to increase sample size. Across species, the association between species and frequency of individuals in each canopy dieback category was analysed using the G-test of independence (Sokal & Rohlf 1981; Quinn & Keough 2003). This tests the goodness of fit of the observed cell frequencies to their expectations (Sokal & Rohlf 1981). Within individual species, the association between the frequency of canopy dieback and (a) canopy size-class (for *Prostanthera*, <10 000 and >10 000 cm^2; for *Hovea* and *Pimelea*, <1000 and >1000 cm^2) and (b) soil depth (<10 cm, >10 cm) was also examined using the G-test of independence.

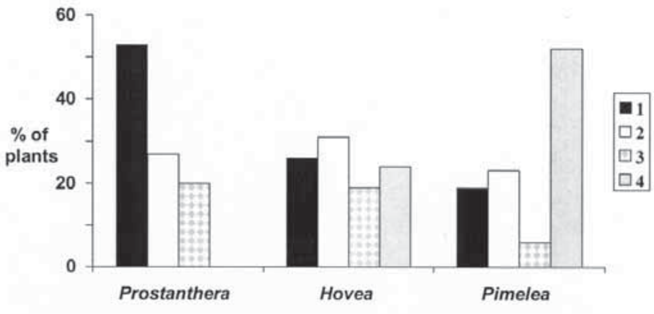

Fig. 3. Frequency of plants observed in canopy dieback categories (1= <10% dieback, 2 = 10–30% dieback, 3 = 31–60% dieback, 4 = >60% dieback) for *Prostanthera cuneata*, *Hovea montana* and *Pimelea axiflora* var. *alpina* at Basalt Hill, Victoria after drought during the 2002/03 growing season.

Results

All *Epacris glacialis* plants (*n* = 16) recorded were dead at the time of the survey. Leaves were brown and shrivelled but remained on the plant. Drought-induced death occurred regardless of the canopy area of individual shrubs (mean = 1740 cm^2, range = 170– 4420 cm^2) and the soil depth on which shrubs occurred (mean = 10.1 cm, range = 4–18 cm).

No mortality was recorded for the other three shrubs. The amount of canopy dieback, however, was not independent of species (G = 40.74, df = 6, p<0.001, Fig. 3). All *Prostanthera cuneata* plants had less than 60% canopy dieback whereas 52% of *Pimelea axiflora* var. *alpina* plants exhibited more than 60% canopy dieback. *Hovea montana* had an intermediate response to drought i.e. 24% of plants had >60% canopy dieback. For these three species, the amount of dieback was independent of canopy size (*Prostanthera*: G = 0.76, p>0.05; *Hovea*: G = 3.40, p>0.05; *Pimelea*: G = 5.66, p>0.05) and soil depth on which plants were growing (*Prostanthera*: G = 0.50, p>0.05; *Hovea*: G = 2.24, p>0.05; *Pimelea*: G = 1.78, p>0.05).

Discussion

Over the 2002/03 growing season (October to February) rainfall was 41% of the long-term average, but while this is similar to the rainfall deficit reported by Williams (1990) during 1982/83, it is suspected that the plant responses observed during the present study were most likely the result of the almost complete absence of rain during the warmest months of the year. Over a 50 day period (i.e. most of January and February), only 1.2 mm of rainfall was recorded. Hence, soil moisture stress was likely to have been extreme, particularly given that shallow soils characterise the area. Plant responses are likely to have been determined by the extreme dryness over that period rather than the below-average rainfall for the entire growing season.

The effects of drought on subalpine shrubs were species-specific (as found by Williams 1990), suggesting that the ability to withstand moisture stress is a species trait, and generalisations about drought sensitivity of subalpine shrubs will be unlikely. *Epacris glacialis* was the most drought-sensitive species and *Prostanthera cuneata* the most resilient. *Hovea montana* and *Pimelea axiflora* var. *alpina* showed an intermediate response. Williams (1990) has shown *Prostanthera cuneata* to be drought-resistant elsewhere, while the sensitivity of *Epacris glacialis* is not surprising given that it is mostly found in wet heathland communities (Costin et al. 2000). At Basalt Hill, the distribution of *Epacris glacialis* may reflect its ability to colonise and establish in areas where moisture stress was not severe during most years, perhaps because the basalt-derived soils retain high soil moisture. Only when extreme soil moisture stress was encountered was the species pushed back to more favourable or core habitat (i.e. closer to wetland communities). Similar patch dynamics have been reported for *Eucalyptus obliqua* at Mount Towrong (Ashton & Spalding 2001). Hence, drought has the potential to alter the floristic composition of subalpine communities but the extent of the change will depend on the density and cover of the particular drought-sensitive species present.

It is likely that differences between species in root/shoot ratio, water-use efficiency, ability to withstand severe dehydration and low relative moisture content of leaves may help explain the dieback patterns observed at Basalt Hill (Pook et al. 1966, Ashton et al. 1975). However, no research has been conducted on Australian alpine plants to understand these mechanisms and, although they appear to be important factors elsewhere in Australia (Pook et al. 1966), much work needs to be done to determine their significance in alpine environments.

In subalpine areas, shrubs growing on soils that are the shallowest across the landscape appear to be the most susceptible to drought (Pook et al. 1966, Costin et al. 2000), as they are in other plant communities (Kirkpatrick 1970, Ashton et al. 1975, Kirkpatrick & Marks 1985). This response suggests that drought sensitivity on shallow soils is greatest because plants are growing in areas of the landscape with the least soil moisture storage. Hence, when soils remain below wilting-point for an extended period, shrubs on shallow soils would be expected to show the effects of moisture stress well before shrubs on deeper soils. Given the shallow nature of soils at Basalt Hill (mean = 11.3 cm) and other rocky out-crops such as Ruined Castle, it was perhaps not surprising that drought impacts were observed there, and not elsewhere on the Bogong High Plains, where the soils are generally deeper (Williams & Ashton 1987).

That no significant association between local soil depth and the amount of canopy dieback was found for any species was unexpected, since it was predicted that shallowest soils at Basalt Hill have less capacity to buffer rain-free periods than locally deeper soils. However, it may simply reflect the fact that soils were shallow across the entire site, and deep soil pockets were rare. When previous studies have found that drought effects are moderated by soils, it has usually been because of texture, rather than depth (Pook et al. 1966, Lamb & Florence 1973, see Ashton & Spalding 2001 for an exception). However, texture effects may be moderated by the volume of stones and rocks in the soil profile, as they reduce available water storage. Hence, plants on stony soils may be more susceptible to drought than those plants on stone-free soils, regardless of their texture.

Similarly, no significant association was found for any species between shrub size and the extent of dieback. Canopy area was used as a surrogate for plant age in this study (i.e. small canopy areas were presumed to represent younger plants) as has been done in many studies (e.g. Watt 1947, Williams 1990). Size (and by extension, age) has previously been seen to be an important predictor of drought impacts. Williams (1990) found that senescent shrubs were more susceptible to drought than smaller ‘building’ shrubs while Pook et al. (1966) found larger diameter trees to be more susceptible to drought effects than smaller trees. By contrast, Kirkpatrick and Marks (1985) found that the smallest individuals of *Eucalyptus pulchella* and *E. viminalis* were the most drought-sensitive, while Fensham and Holman (1999) found that tree dieback during drought in tropical savanna was largely independent of stem size. That no effects of canopy size on drought sensitivity were observed in the present study suggests that the factors that influence local persistence of plants e.g. drainage, microtopography, intra- and inter-specific competitive effects, are also likely to effect the response of individual plants to drought. Local factors are also likely to interact with landscape-scale processes to determine local community composition (Fensham & Holman 1999, Ashton & Spalding 2001).

Conclusion

Summer drought in subalpine areas appears to be relatively frequent at the decadal scale and a potentially important influence on vegetation. Sensitivity to drought will be a species-specific trait, but it appears to be capable of affecting plant community composition and contributing to local patch dynamics. Such patch dynamics in alpine areas have usually been attributed to disturbance events (Williams & Ashton 1988). Indeed, the complete mortality of *Epacris glacialis* in the study area suggests that non-equilibrium population dynamics are likely to be common in some plant communities. Further work, such as that conducted by Ashton et al. (1975) for forest species, is needed to determine the factors that make plants susceptible or resistant to drought in subalpine areas. It will be interesting to observe the length of time it takes plant populations of susceptible species to recover from drought. The preliminary results of the 2002/03 drought event reported here for four shrub species, however, should be treated with caution and be seen within the context of longer-term vegetation dynamics in alpine areas.

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