Mortality of Australian alpine grasses (*Poa* spp.) after drought: species differences and ecological patterns

Philippa C. Griffin* and Ary A. Hoffmann

Centre for Environmental Stress and Adaptation Research, Department of Genetics, Bio21 Institute, 30 Flemington Road,
University of Melbourne, Parkville 3010, Victoria, Australia
*Correspondence address. Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2000
Neuchâtel, Switzerland. Tel: +41 (0) 32 718 30 00; Fax: +41 (0) 32 718 30 01; E-mail: pip.griffin@gmail.com

Abstract

Aims

Australian alpine ecosystems currently experience high precipitation in the snow-free season, but they are predicted to experience drier conditions under climate change. We observed high mortality of the dominant alpine grasses following drought in 2007. Our aims were as follows:

  to test the involvement of plant-available water (PAW) and other environmental variables in grass mortality in the field;
  to detect possible species differences in drought response and
  to link soil moisture to precipitation using soil properties and climate data.

Methods

The dominant tussock grasses of the Australian alpine zone, *Poa hothamensis* var. *hothamensis* N.G. Walsh, *Poa hiemata* Vickery and *Poa phillipsiana* Vickery (Poaceae), all exhibited mortality following drought in the Bogong High Plains, Victoria, Australia in 2007. PAW was calculated using soil water potential measurements, and past drought occurrence was modelled using climate data. We then tested the effects of PAW and soil depth on grass survival both at

a large spatial scale spanning the elevational range of the alpine zone and at a smaller scale. *Poa hothamensis* and *P. phillipsiana* were compared in a common-garden experiment to test drought tolerance.

Important Findings

Poa hothamensis survival was predicted by dry-season PAW at the small spatial scale; at the large scale, soil depth and elevation were more important predictors of *P. hothamensis* survival, but dry-season PAW predicted *P. hiemata* survival. Common-garden experiments supported field observations that *P. hothamensis* is more drought-sensitive than is *P. phillipsiana*. We also present a simple polynomial relationship between rainfall and field soil moisture, which predicts that the alpine soils dry below wilting point several times a year. We suggest the timing of long rain-free periods may be more important than their duration.

Keywords: climate change • disturbance • drought adaptation • grassland

Received: 10 November 2010 Revised: 13 February 2011 Accepted: 27 February 2011

INTRODUCTION

Drought has been judged to have negligible impact on most alpine communities (Körner 1999), as alpine areas tend to receive high precipitation all year round. Several alpine areas, however, do experience frequent or periodic drought: tropical alpine areas (Rundel 1994; Smith and Young 1987), the Rocky Mountains (Aho and Weaver 2010; Dona and Galen 2006;

Galen 2000; Taylor and Seastedt 1994), the Mediterranean mountain ranges (Giménez-Benavides *et al.* 2007; Sanz-Elorza *et al.* 2003) and the Australian Alps (Costin *et al.* 2000; Good 1992). Precipitation regimes are predicted to become drier under climate change in several alpine regions, including the Central Swiss Alps (Gilgen and Buchmann 2009) and the southern part of the Australian Alps (Hennessy *et al.* 2003). Therefore, drought may become a new stress in some alpine

areas and is likely to be more frequent and severe in other areas where it already occurs.

Alpine plants respond to drought stress in the same way as other plants: by wilting, showing reduced growth (Sangtarash *et al.* 2009) and seed set (Galen 2000; Oberbauer and Billings 1981) and eventually dying (Galen 2000). Most alpine drought investigations have been performed at the level of single species (Dona and Galen 2006; Oberbauer and Billings 1981) without much characterisation of ecosystem-level responses beyond simple measures like total biomass (Gilgen and Buchmann 2009). Soil water availability, however, is known to be a major determinant of community composition in some alpine areas (Humphries *et al.* 1996; Isard 1986), and changing alpine soil moisture regimes under climate change may affect community composition (Taylor and Seastedt 1994).

The Australian alpine zone is currently characterized by a precipitation regime that is highly variable at seasonal, inter-annual and spatial scales (Bureau of Meteorology, http://www.bom.gov.au/climate/data; Carr and Turner 1959) although it is much wetter than the rest of south-eastern Australia, receiving ~1 200 mm/year (Bureau of Meteorology). The Australian Alps are relatively flat low mountains [maximum elevation 2 228 m above sea level (a.s.l.)], covered by soil and vegetation extending to the summit. The true alpine ecosystems of the Australian Alps cover only 700 km² (Good 1992) and harbour high biodiversity (Green and Osborne 1994); e.g. 30% of plant species in the region are endemic (McDougall and Walsh 2007). This region is also an important water catchment, largely protected by a network of national parks. Like mountain regions in general (Diaz *et al.* 2003), the Australian alpine zone has been judged especially vulnerable to climate change (Steffen *et al.* 2009). A temperature increase of between 0.6 and 2.9°C and a precipitation change of between +2.3 and −24.0% (relative to 1990 levels) are projected for this region by 2050 (Hennessy *et al.* 2003). For south-eastern Australia as a whole, projections indicate likely increases in drought occurrence, temperature and number of dry days as well as decreases in snow cover and stream flow (CSIRO and Australian Bureau of Meteorology 2007).

The true Australian alpine zone is dominated by free-draining highly acidic alpine humus soils typically derived from metamorphic rock (Costin *et al.* 2000) that have a low bulk density because of their high organic matter content (Good 1992). Alpine humus soil is deep in heathland and shrubland areas (Costin *et al.* 1964), but mountaintop soils are typically shallow (Morgan 2004). Physiological drought [shortage of plant-available water (PAW)] can occur at any time during the snow-free season in these soils, as they dry rapidly (Good 1992). The severity of drought experienced by plants depends on precipitation and water availability and can also depend on snowmelt timing and amount in alpine areas (Taylor and Seastedt 1994). Soil water-holding capacity is influenced by grain size, organic matter content and porosity (Jones 2007; Leeper and Uren 1993) and influences in turn both the ease with which water permeates the soil and its

availability for removal by evaporation or evapotranspiration (Eckhart *et al.* 2010).

Drought effects on individual plants depend on their physiological and structural adaptations to water deficit (Chaves *et al.* 2003; McDowell *et al.* 2008). Plant drought–response strategies are typically classified as drought tolerance, drought avoidance or summer dormancy, although many species use a combination of these (Norton *et al.* 2009). The *Poa* tussock grasses that dominate Australian alpine grassland are perennial and so seem unlikely to avoid drought by early flowering as occurs in many annual species (Norton *et al.* 2009). Many alpine species exhibit traits associated with low water demands (Körner 1999), as freezing and drought tolerance are mechanistically correlated. Both stresses reduce the amount of water available to cells (Beck *et al.* 2007; Block 1996; Verslues *et al.* 2006). Deep rooting systems (Oberbauer and Billings 1981), low specific leaf area (Brock and Galen 2005) and reduced reproductive resource allocation (Galen 2000) are associated with drought tolerance in various alpine species. The Australian alpine *Poa* species have leaf characters that have been shown to confer drought tolerance in other species, including rolled leaves (Balsamo *et al.* 2006) and a waxy leaf coating (Hadley and Smith 1989). Variation in leaf size, shape, rigidity and waxiness, growth habitat and habits (Vickery 1970; Walsh 1994) may indicate variation in drought response between and within these *Poa* species.

Previous research suggests drought is already a significant disturbance in Australian alpine plant communities (Green and Osborne 1994; Morgan 2004; Scherrer and Pickering 2005; Williams 1990; Wimbush and Costin 1979b). There exists relatively little information on species-level or community effects of drought even though it is regarded as a driver of succession in Australian alpine communities (Costin *et al.* 2000; Scherrer and Pickering 2005). Mortality of alpine snow-grasses (*Poa* spp.) (Green and Osborne 1994; Scherrer and Pickering 2005; Wimbush and Costin 1979b) and shrubs (Kirkpatrick *et al.* 2002; Morgan 2004) has previously been noted after drought. However, mortality levels were not quantified and details of how edaphic conditions and precipitation affect particular alpine species or communities remain poorly understood (McDougall and Walsh 2007).

In January 2007, at the end of a dry austral summer, extensive grass mortality was observed on the Bogong High Plains, Victoria, especially between 1 760 and 1 810 m a.s.l.. This provided an opportunity to investigate the following questions:

Can grass mortality be directly predicted by PAW, soil depth or elevation?
Do the dominant grass species differ in their drought response?

We then used climate data and soil water-holding content measurements to discover:

What is the relationship between precipitation and soil moisture in the Australian alpine environment?

MATERIALS AND METHODS

Study species

Poa species are the dominant grasses of true alpine ecosystems in Australia (Vickery 1970). The genus has about 300 recognized species worldwide, about 50 of which occur in Australia (Walsh 1994). The Australian alpine species are tussock forming and largely outcrossing (Byars *et al.* 2009) with little clonal growth (Vickery 1970). *Poa hiemata* Vickery dominates alpine tussock grassland and herbfield in mainland Australia. *Poa hothamensis* var. *hothamensis* N.G. Walsh (hereafter referred to as *P. hothamensis*) is endemic to Victoria above 1 200 m a.s.l. Although this species usually occurs in sheltered heath and woodland sites, it is common in alpine and subalpine grassland following fire (Vickery 1970). *Poa phillipsiana* (Vickery) occurs at lower elevations than most of the other alpine *Poa* species (Walsh 1994) and is locally common across a patchy distribution in Victoria, more prevalent in woodland than in open grassy sites (McDougall and Walsh 2007).

Sites

Three 1.5-km-long east-facing elevational mountainside transects were set up in the Bogong High Plains, Victoria, Australia [Mount Nelse Central (MNC), 1 760–1 890 m a.s.l.; New Country Spur (NCS), 1 735–1 885 m a.s.l. and Mount Cope, 1 710–1 850 m a.s.l.]. Mountainside transects all shared similar slope, soil type and vegetation, although Mount Cope reached only 1 850 m a.s.l. and therefore had little treeless grassland. Drought conditions may have been more severe on north-facing slopes, but previous genetic knowledge of the *P. hiemata* populations on these east-facing transects (Byars *et al.* 2007, 2009) meant they were suitable for this and an accompanying study (Griffin 2011). *Poa hiemata* was the dominant grass species on all three mountainsides, with *P. hothamensis* also common. By measuring grass mortality and environmental variables (described below) over the entire elevation range of alpine grassland, across these three replicate mountainsides, we examined drought effects at a broad spatial scale.

Initial observations revealed elevational patterns in grass mortality. To remove the potentially confounding factor of elevation and examine the patchy low-elevation mortality at a smaller spatial scale, we also chose a permanent grid site centred at 36°51.0′S, 147°21.1′E, 1 665 a.s.l. and 100 m east of Johnston's Hut in the Bogong High Plains (Fig. 1). Here, the understorey was dominated by *P. phillipsiana* and *P. hothamensis*. At the time of measurement, the community was in an early succession stage (Wimbush and Costin 1979a), as it had been burnt in the January 2003 bushfires. Snowgums (*Eucalyptus pauciflora* ssp. *niphophila*) dominated but most trees had experienced complete crown death and were re-sprouting from lignotubers. A grid of 55 points was permanently marked. Points were arranged in five 100 m east–west transects 20 m apart, with 11 points spaced 10 m apart along each transect. Each point was used as the centre of a 1 m² plot, oriented with sides square to the compass points.
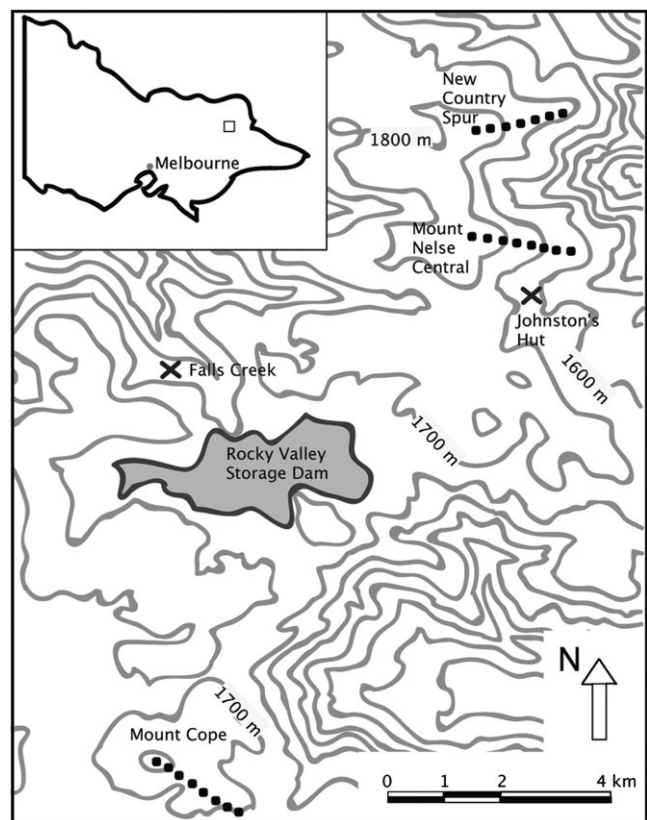

Figure 1: study locations. Inset. Victoria, Australia, showing the Bogong High Plains (indicated by square) in relation to Melbourne. Main figure. Location of mountainside transects (dotted lines) on Mount Cope, MNC and NCS on the Bogong High Plains and the permanent grid site at Johnston's Hut (cross). Falls Creek township is indicated by a cross. One hundred metres contour lines shown in grey.

Permanent grid plots were first placed in October 2007 (2 weeks after snow melt) and revisited in subsequent seasons.

Mountainside transects

Grass survival

Grass survival was measured along the mountainside transects in October 2007 (spring), January 2008 (summer) and April 2008 (autumn): dead plants could no longer be distinguished after this time. Quadrat plots of 1 m² were haphazardly chosen approximately every 25 m along each transect. Survival was recorded for the grasses *P. hiemata* and *P. hothamensis* in each season in each quadrat. Plants were scored as live or dead (no visible green leaves or new shoots). All dead tussocks were checked for re-sprouting in each measurement period.

Logistic regression models were used to test effects of soil depth (see below) and elevation on grass survival. The number of surviving plants was used as the response variable, weighted by the total number of plants, with a quasibinomial distribution. First, models were run for overall elevation patterns, including a squared term for elevation, using all plots measured in each of the three measurement periods when survival was

scored. A second set of models was run to test effects of soil depth, using just the April 2008 plots (when soil depth was measured). Modelling was repeated for each species and mountain separately.

To test the effects of PAW (see below) on grass survival, survival records for all quadrats falling within a 20-m elevational category centred on each bulk sample collection point were summed. Survival (as proportion) was plotted against PAW for each species over all mountains. Non-linear model parameters were estimated with the 'nls' command in R version 2.9.1 (R Development Core Team 2009) and then used in a linear model to investigate the model fit.

Soil water-holding capacity

Bulk soil samples were taken along the three mountainside transects in March 2009. Five sites were sampled evenly along each transect (by elevation rather than distance). At each site, 10 soil cores were taken within an area of 20 × 20 m spanning the transect line and bulked. Each core was 2 cm diameter and 10 cm deep (minimum 5 cm in shallow soil).

Standard methods were used to determine soil matric potential (Reynolds and Topp 2008). Volumetric water content was determined at four pressures: 0.01 MPa (field capacity), 0.1 MPa (readily available water), 0.5 and 1.5 MPa (wilting point). These pressures are commonly used as standards for plant water availability studies (Leeper and Uren 1993). For each of the 15 bulk samples described above, three replicate measurements were made at each pressure. Each bulk sample was sieved (0.85 mm) and mixed. Soil was tamped down in brass rings (12 mm high, 48 mm in diameter) and allowed to saturate in tap water. The fully saturated soil samples were weighed and placed on a ceramic pressure plate inside a pressure vessel (Soilmoisture Equipment Corp., Santa Barbara, CA, USA) which was sealed and subjected to the desired pressure for a minimum of 3 days (0.01 or 0.1 MPa) or 13 days (0.5 or 1.5 MPa). Samples were then removed, weighed and oven-dried at 105°C for 24 h. Finally, each sample was weighed again after drying.

Volumetric water content (θ) was calculated for each sample at each pressure using standard methods (Leeper and Uren 1993). For example, field capacity soil moisture (θ_{fc}) was the mean θ measured at 0.01 MPa. The soil samples were allowed to equilibrate for at least 13 days at a pressure of 1.5 MPa, a time longer than recommended in the literature (Reynolds and Topp 2008). However, the equilibration was not complete because the 1.5 MPa water content measurements were consistently higher than the 0.5 MPa measurements. For this reason, water content at wilting point was instead estimated by linear regression. First, pressures were converted to a logarithmic pF scale (Leeper and Uren 1993). The wilting point (pF = 4.2) volumetric water content (θ_{wp}) was then interpolated from a line joining the measured mean θ at pF = 3.69 (0.5 MPa) and θ = 0 at pF = 6.9 (~8 000 MPa, oven-dry) for each bulk sample.

To test for Bonferroni-corrected significant differences in water-holding capacity between the 15 bulk samples, the glht command in the 'multcomp' package (Hothorn et al. 2008) in R was applied to a generalized linear model with θ as the response variable and sample as the explanatory variable for each pressure. The θ_{wp} means were compared using t-tests on the interpolated mean and the measured standard deviation for each bulk sample.

Plant-available water

Volumetric soil moisture (θ) was measured at the same times as grass survival (see above), in the same 1 m² plots. Additional measurements were taken in October 2008 and January 2009. A ThetaProbe ML2x (Delta-T Devices) connected to a TP-Handheld Reader (Measurement Engineering Australia) was used to make six θ measurements in each plot (minimum two readings in especially rocky plots), inserting the probe to its full extent (60 mm). All readings were used to calculate the mean θ for each plot.

For calculations of PAW, plots that fell within 10 m elevation of each bulk soil sample collection site were selected. Volumetric soil moisture was converted to PAW for these plots by subtracting the appropriate wilting point value from the plot mean. To provide a dry-season PAW value, the overall average January 2008 and April 2008 PAW values were then averaged for each bulk soil sample collection site.

Soil depth

In April 2008, soil depth was measured using a sharpened steel rod with a circular cross-section 8 mm in diameter. For each depth measurement, the rod was pushed into the soil until it hit rock or a hard soil horizon. At each plot, three depth measurements were taken at the same points as the corresponding soil moisture measurements. To test the relationship between point soil depth and volumetric soil moisture, we performed a Kendall non-parametric rank correlation.

Three further measurements were then taken in other points in the plot with all six measurements used in calculations of the mean and standard deviation of soil depth. Linear regression (including a squared term for elevation) was performed for each mountainside to determine whether soil depth varied significantly with elevation.

Precipitation effects on soil moisture

Average θ was calculated for each mountain and each season. Each value was the average of all plots measured along each mountainside. The formula

$$\text{maximum rain held (mm)} = \text{soil depth (mm)} \times (\theta_{fc} - \theta_{wp})$$

was used to calculate the maximum water held in the soil following rainfall (Leeper and Uren 1993) assuming the soil was relatively uniform (Costin et al. 1964). This was repeated for each combination of mountain and elevation. The overall minimum (~10 mm) and maximum (~40 mm) values were extracted and considered to represent the minimum and maximum useful rainfall event, respectively, for the area studied. That is, falls <10 mm would fail to fully wet even the

shallowest soil and falls >40 mm would be in excess of the water-holding capacity of the deepest soil.

Climate records from the Falls Creek weather station were obtained for the period 2005–09 from the Bureau of Meteorology. Mean temperatures were calculated for the periods of 1, 2, 3 and 4 weeks prior to each field measurement. These were calculated by averaging the daily mean temperatures (themselves the average of the maximum and the minimum daily temperatures) over that period. Cumulative precipitation was summed for the periods of 1, 2, 3 and 4 weeks prior to each measurement. For each field measurement date, we then calculated the number of days since a minimum useful precipitation event. Where this precipitation fell over 24–48 h, the second day provided the day number. This was repeated to calculate the number of days since a maximum useful rainfall event.

The effect of each temperature and rainfall parameter on field soil moisture was first assessed graphically. Variables that showed clear effects were then investigated. Where correlations (>0.3) were detected between explanatory variables, a single appropriate representative variable was chosen to avoid collinearity. A simple polynomial model was fitted to the relationship between average volumetric soil moisture and days since a minimum useful rainfall event. The number of days to soil wilting point was calculated by fitting the mean wilting point (θ_{wp}) measured in the lab to the curve.

The number of days between minimum useful rainfall events in previous snow-free seasons (2005–09) and the amount of rainfall occurring, were then examined graphically, in order to detect differences between the 2006 and 2007 season, when plant death was observed, and other years.

Permanent grid

Field grass survival

The number of live and dead tussocks of each grass species was counted in each quadrat at the permanent grid in October 2007, January 2008 and April 2008 and then averaged to avoid variation due to ongoing mortality or small changes in quadrat placement.

Differences in the overall survival of each species were tested in two ways: the proportions of live tussocks per quadrat for *P. hothamensis* and *P. phillipsiana* were compared using a two-sided *t*-test, and logistic regression was performed with average number of surviving plants (rounded to the nearest integer) as the response variable weighted by the total number of plants and species as the explanatory variable.

We examined the effects of overall dry-season PAW (see below) on grass survival (as a proportion) using an appropriate linear model. This was chosen based on examination of the graphed data using the method described in the mountainside transect section. We also tested the effect of multiple environmental variables on grass survival at the permanent grid and mountainside sites in a series of logistic regression models, accounting for plant number as described above. Quasibinomial distributions were used for all models and modelling was repeated for each species. For the permanent grid site, average soil depth, soil depth vari-

ability and non-metric multidimensional scaling (NMDS) scores (representing the plant community structure: see below) were each used as centred explanatory variables.

PAW and soil depth

Volumetric soil water content (θ) was measured as described above for each of the 55 1 m^2 quadrats at the permanent grid site in October 2007 (spring), January 2008 (summer), April 2008 (autumn), October 2008 and January 2009. To test for a correlation between the dry-season measurements (January 2008 and April 2008), a linear regression was performed. The mean wilting point (θ_{wp}) calculated from the 15 bulk soil samples was subtracted from the θ values to convert these measurements to PAW, where PAW = 0 if $\theta < \theta_{wp}$. Dry-season PAW was then calculated from an average of the January 2008 and April 2008 θ values for each plot, since these values had shown a significant positive correlation.

Soil depth was measured as for the mountainside transects in April 2008 in each grid quadrat. Linear regressions were used to test for a relationship between average soil depth and θ in each month at the permanent grid site and to test for a correlation between soil depth and dry-season PAW.

Plant community composition

At the permanent grid site, the percentage cover of all species in each plot was estimated to the nearest 10% using a 1 m^2 quadrat each measurement period. Percentage cover was arcsin-square root transformed and species present in two or fewer quadrats (out of 55) excluded from the data set. Grass cover (*P. hothamensis*, *P. hiemata* and *P. phillipsiana*) was also excluded from the data set because this ordination was being used to test the relationship between non-grass community change and grass survival. NMDS was performed using the 'metaMDS' command in the 'vegan' package version 1.15-4 (Oksanen *et al.* 2009) in R. This is an iterative search technique that compresses multivariate data into a smaller number of artificial dimensions (Legendre and Legendre 1998). The resulting axes explain a certain amount of the total community variance, and each plot or species can be described in terms of its position on these axes (or NMDS score), with more similar plots/species close in position. Three dimensions were specified to produce a low stress level in the analysis and the run was extended for a maximum of 50 random starts.

Glasshouse grass survival

To compare species for drought resistance, *P. hothamensis* (*n* = 60) and *P. phillipsiana* (*n* = 38) plants were collected from the permanent grid site in April 2007. Plants were re-potted into 200 mm-diameter plastic pots in the following potting medium: one part coarse mined sand to four parts ground medium grade pinebark with Debco Green Jacket® No. 2 (N:P:K of 16.5:14.1:9.6, 4 000 g/m³), Saturaid® water retention crystals (1 500 g/m³) and dolomite (1 000 g/m³). Plants were grown outdoors and provided with 500 ml water per

day until October 2008, when water was withheld for 10 days as a drought-hardening treatment. The plants were then watered as before for 14 days, after which they were moved to a shadehouse. A randomly chosen control group was watered with 500 ml water per day, and water was withheld completely from the treatment group. Once a week, plants were scored as dead (no remaining green foliage) or alive. When all plants had died, they were rewatered for 6 weeks and checked for signs of re-sprouting.

A Kaplan–Meier test was used to detect species differences in survival over time, performed in the 'survival' package in R (Therneau 2009).

RESULTS

Grass survival

Mountainside transects

Grass mortality was first noticed in April 2007. No dead tussocks were observed to re-sprout over the 15-month period of this study between October 2007 and January 2009, whereas some seedling recruitment was observed. Seedlings remained small throughout this experiment and so were excluded from measurements.

Poa phillipsiana was uncommon along the mountainsides, so we only considered *P. hothamensis* and *P. hiemata*. Survival in a quadrat ranged from 0 to 100% for each species, though *P. hothamensis* experienced more mortality overall and showed a strong elevational pattern (Fig. 2A and B). *Poa hothamensis* survival had a significant positive curvilinear relationship to elevation at two out of three mountains also, with higher survival at both low and high elevations (Table 1, Fig. 2A). This
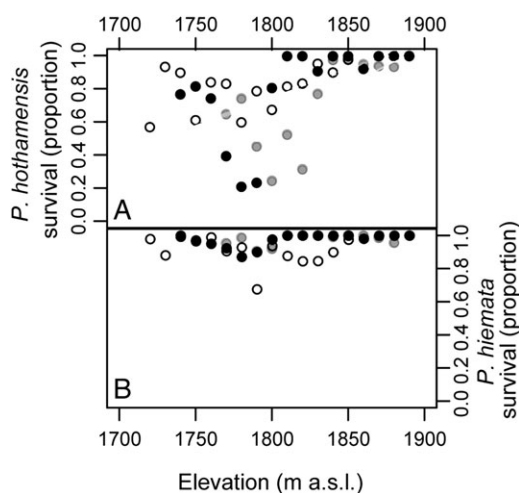
relationship varied in significance between January 2008 and April 2008 (Table 1), probably due to differences in quadrat placement, but the overall direction of the relationship remained consistent. *Poa hiemata* survival showed a similar curvilinear relationship to elevation at NCS, and a significant negative relationship with elevation but a positive relationship with elevation[2] at Mount Cope in April 2008 (Table 1, Fig. 2B).

After correcting for elevation, soil depth was negatively associated with *P. hothamensis* survival at two out of the three mountains (Mount Nelse Central and Mount Cope) but showed no significant association with *P. hiemata* survival (Table 1).

On the large spatial scale of the three mountainsides, *P. hothamensis* survival was not significantly predicted by PAW ($P > 0.05$), regardless of whether elevation was included in the model (Fig. 3A). PAW did predict *P. hiemata* survival, showing a strong fit to the data ($R^2 = 0.78$, $P < 0.001$; Fig. 3B). This was largely driven by one point (with the lowest PAW value) but

Figure 2: grass survival versus elevation. (**A**) *Poa hothamensis* survival versus elevation class for each mountainside (filled black circles: NCS; filled grey circles: MNC; empty circles: Mount Cope). Measurements were pooled into 10 m elevation classes for ease of plotting and each point shown represents the mean proportion survival plotted at the upper elevation limit of that distance class. (**B**) *Poa hiemata* versus elevation class for each mountainside.

Table 1: effects of elevation and average soil depth on grass survival at the mountainside transects

| | Mountain | | | | | |
| | Cope | | MNC | | NCS | |
	Estimate	SE	Estimate	SE	Estimate	SE
Poa hothamensis						
All measurement periods						
Elevation	3.2	2.9	24	4.1***	60	105
Elevation[2]	8	2.9**	6.3	3.0*	23	46
April 2008						
Soil depth	−0.20	0.060**	−0.015	0.10	−0.0058	0.047
April 2008						
Elevation	1.8	2.3	17	2.4***	48	15**
Elevation[2]	3	2.9	4.8	1.6**	19	6.1**
Soil depth	−0.17	0.064*	−0.42	0.10**	0.07	0.053
Poa hiemata						
All measurement periods						
Elevation	−2.0	2.3	11	5.1*	25	11*
Elevation[2]	3	2.3	4.8	5.4	0.75	5.1
April 2008						
Soil depth	−0.052	0.085	−0.14	0.22	−0.083	0.097
April 2008						
Elevation	−6.2	2.0**	53	95	78	40
Elevation[2]	3.7	1.8*	22	33	31	17*
Soil depth	0.072	0.076	−0.23	0.23	0.051	0.088*

Results from models both excluding and including elevation are shown. Mountainsides (Cope: Mount Cope) and measurement periods were modelled separately as described in the text. Estimates and standard errors (SE) from logistic regressions using quasibinomial distributions are presented. Significance levels are indicated as follows: *0.05 < $P < 0.1$, *0.01 < $P < 0.05$, **0.001 < $P < 0.01$, ***$P < 0.001$.

a significant positive linear relationship ($R^2 = 0.25$, $P < 0.05$) remained when this point was removed.

In summary, both *P. hothamensis* and *P. hiemata* survival exhibited elevational patterns and *P. hothamensis* survival was predicted by soil depth, whereas *P. hiemata* survival was predicted by dry-season PAW.

Permanent grid site

There were 37 species in the surveyed quadrats at the permanent grid site (Table S1, see online supplementary material). Other species were present at the site but did not occur in any of the quadrats measured. After excluding rare species and the grasses, the NMDS analysis was performed on a total of 26 species.

Grass survival ranged from 20 to 100% for *P. hothamensis* and 0 to 100% of tussocks in each quadrat for *P. phillipsiana*

(Fig. 3C and D). *Poa phillipsiana* had a higher mean survival (76% of all tussocks) than did *P. hothamensis* (65%) and this difference was significant, adjusted for the number of plants ($P < 0.05$). No significant effects were detected of soil depth (average or standard deviation), and there was no correlation with any of the NMDS axes representing community structure on survival of either species ($P > 0.1$ in all cases).

For *P. hothamensis* at the permanent grid site, dry-season PAW significantly predicted grass survival when all points were included ($R^2 = 0.29$, $P < 0.05$). Removing one outlier improved model fit ($R^2 = 0.57$, $P < 0.001$) (Fig. 3C). For *P. phillipsiana*, PAW did not significantly predict grass survival ($P > 0.05$) but low survival (<80%) always occurred with low PAW (<7 mm/10 cm) (Fig. 3D).

In summary, dry-season PAW predicted *P. hothamensis* survival at the permanent grid site but soil depth and plant
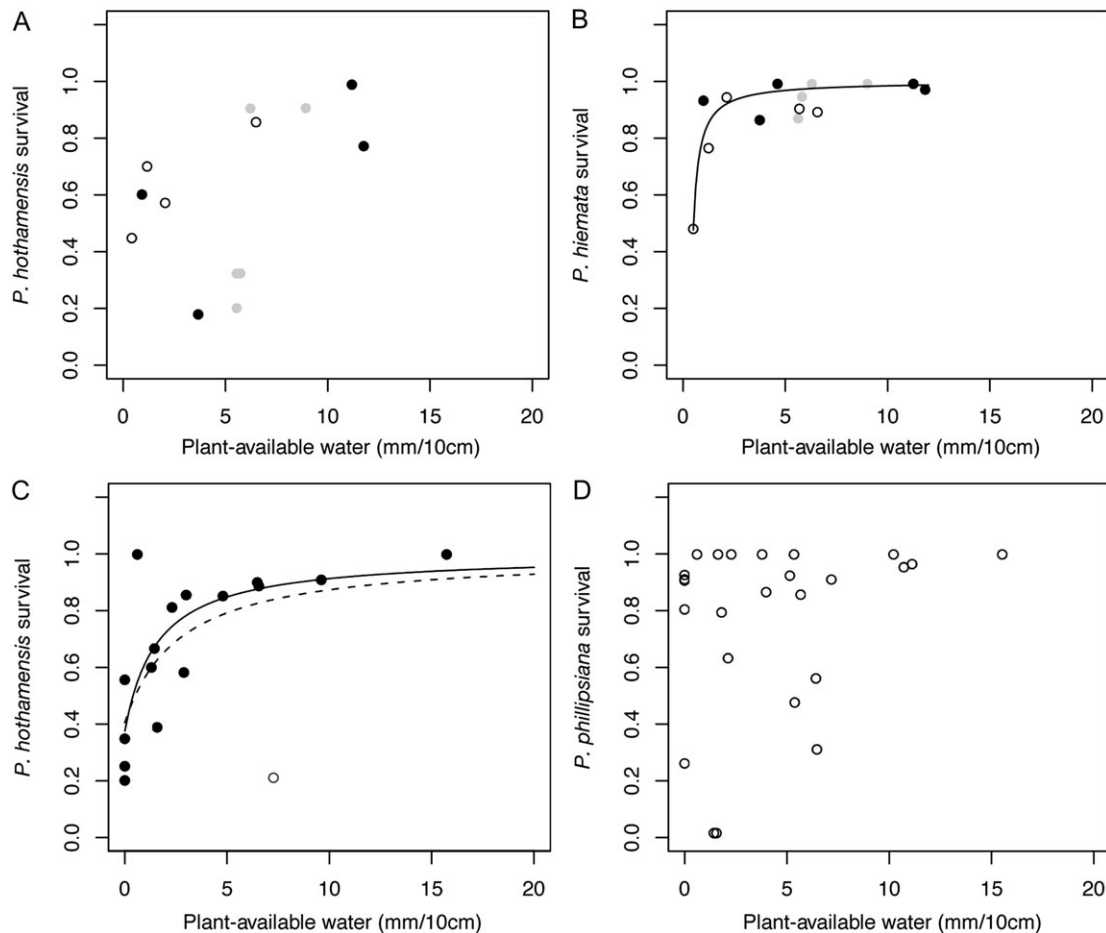

Figure 3: grass survival (proportion of tussocks) versus average dry-season PAW. (**A**) *Poa hothamensis* survival over the mountainside transects. No significant relationship was detected between survival and average dry-season PAW for this species. Labels indicate midpoint of each elevation category. Filled black circles: NCS; filled grey circles: MNC; empty circles: Mount Cope. (**B**) *Poa hiemata* survival over the mountainside transects. Line shows prediction from the non-linear model ($R^2 = 0.78$, $P < 0.001$) of the form: *P.hiemata* survival $= 1 - \frac{1}{6.600 \times \text{PAW} - 1.387}$. (**C**) *Poa hothamensis* survival at the permanent grid. Open circles show outliers. Lines show predictions from non-linear models including outlier (dashed line: $R^2 = 0.29$, $P < 0.05$) and excluding outlier (solid line: $R^2 = 0.57$, $P < 0.001$). The model excluding the outlier has the following parameters: *P. hothamensis* survival $= 1 - \frac{1}{1.01 \times \text{PAW} + 1.60}$. (**D**) *Poa phillipsiana* survival at the permanent grid. No significant relationship was detected between survival and average dry-season PAW for this species.

community did not. No variables tested significantly predicted *P. phillipsiana* survival.

Glasshouse grass survival

Poa phillipsiana survived significantly longer than did *P. hothamensis* under drought conditions in the common garden [asymptotic log-rank test, $\chi^2 = 9.2$ (1 d.f.), $P < 0.001$]. Despite rewatering for 6 weeks after all top growth had died, no plants re-sprouted.

Soil water-holding capacity

The bulk density of soil measured here ranged from 0.59 to 0.81 g/cm^3 (mean 0.684 g/cm^3). The water-holding capacity curve was similar for each of the 15 bulk samples (data not shown), but significant differences were detected between some pairs of samples measured at saturation, at field capacity (0.01 MPa) and at 0.5 MPa (Table S2, see online supplementary material). The two lowest-elevation MNC sites, the Cope site at 1 812 m a.s.l. and the NCS site at 1 787 m a.s.l. tended to have lower water-holding capacities at these pressures and the high-elevation (1 881 m a.s.l.) and the other Cope sites tended to have higher water-holding capacities (Table S2, see online supplementary material). No significant differences between sites were detected at 0.1 MPa.

Soil wilting point water content (θ_{wp}) ranged from 0.124 to 0.158 g/cm^3, but no significant differences were detected between the different bulk soil samples (Table S2, see online supplementary material). The overall wilting point of this alpine mountain soil was 0.138 ± 0.011 g/cm^3 (mean ± 1 SD).

Soil moisture and PAW

Volumetric soil moisture (θ) varied greatly along the mountainside transects over the observation period, from a minimum average below 0.1 g/cm^3 in January 2009 to a maximum of above 0.3 g/cm^3 at high elevation in January 2008, corresponding to zero PAW to 17 mm/10 cm PAW, respectively (Fig. 4A). When the squared term for elevation showed a significant association with average θ (9/15 cases), this was always positive. Where a significant ($P < 0.05$) linear relationship was detected between average soil moisture and elevation, it was positive at MNC and NCS in summer (January 2008) but negative at NCS in October 2007 and at NCS and Cope in January 2009. This meant that θ, and therefore PAW, were typically higher at high elevations in the dry-season months (Fig. 4A).

Volumetric soil moisture (θ) also varied substantially at the permanent grid site, with the coefficient of variation (for each 1 m^2 quadrat) averaging 23.9%. Taken across the whole grid, θ varied from a minimum of 0.075 g/cm^3 in January 2009 to a maximum of 0.29 g/cm^3 in October 2007 (Fig. 4B). 'Month' ($F_{4, 216} = 236.9$, $P < 0.001$) and 'quadrat' ($F_{54, 216} = 37.7$, $P < 0.001$) both had significant effects on average θ. Month explained 75.7% of the variance and quadrat explained a further 6.6%. Seasonal changes in θ were comparable to those measured on the mountainsides. The measured average θ was below wilting point in some quadrats in every season except October 2007. January 2009 was especially dry, with soil below wilting point in most quadrats, implying zero PAW (Fig. 4B). Summer and autumn (2008) θ were significantly positively correlated (Kendall's rank correlation tau = 0.31, $P <$
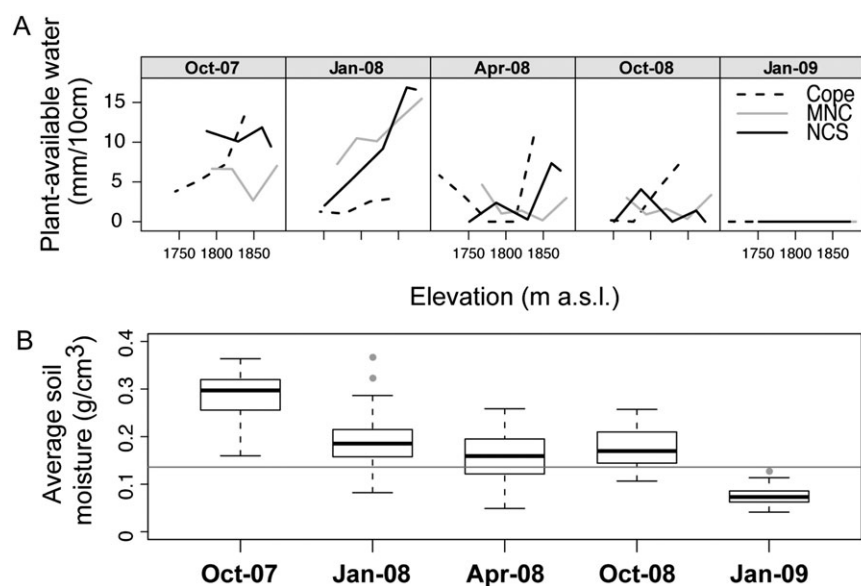

Figure 4: soil moisture and PAW measured at the study sites. (**A**) PAW versus elevation for the mountainside transects for each measurement period. PAW was calculated using the average volumetric soil water content measured for each elevation category (20 m vertical elevation plotted at the midpoint of each elevation category). Solid black lines: NCS; solid grey lines: MNC; dashed lines: Mount Cope. (**B**) Summary boxplots of average soil moisture measured over the entire permanent grid in each month. Thick solid line shows the median, points represent outliers. Horizontal line at 0.138 g/cm^3 soil moisture indicates the average wilting point of alpine humus soil measured in this study.

0.001), and hence were averaged to give an overall dry-season θ estimate.

Soil depth

Average soil depth along the mountainside transects ranged from 1.2 to 25.4 cm (mean 12.8 cm). Point soil depth did not predict point soil moisture (Kendall non-parametric rank correlation, $P > 0.05$). Soil depth showed a significant negative correlation with elevation at two mountains (linear regression: NCS estimate $\pm$ SE -15.8 ± 4.7, $P < 0.01$ for elevation, not significant for elevation^2; Cope not significant for elevation, -1.1 ± 0.044, $P < 0.05$ for elevation^2).

Average soil depth at the permanent grid site ranged from 2.8 to 22.8 cm (mean 13.3 cm). Soil depth did not significantly predict average soil moisture or PAW in any month (linear regression $P > 0.05$).

Precipitation effects on soil moisture

In estimating the minimum and maximum 'useful' rainfall events (the amount of rainfall necessary to fully wet the soil to field capacity), the average soil depth at each bulk soil collection site was considered, and it was assumed that the soil matric potential remained approximately constant across this entire soil profile. Using this method, most sites were calculated to require 25–40 mm of rainfall for complete soil wetting, but the mid- to high-elevation NCS sites required only 10–20 mm for complete wetting.

The number of days since $\geq$10 mm rain in a 48-h period, mean temperature and cumulative rainfall in the 1 or 2 weeks preceding measurement all showed apparent curvilinear relationships with field soil moisture when examined graphically. No effects of mean temperature or cumulative precipitation over the period of 3–4 weeks preceding the measurements were detected.

To avoid the strong correlations observed between temperature, cumulative rainfall and the number of days since $\geq$10 mm rain within 48 h, only the last of these variables was used in modelling soil moisture. The resulting model fit the data well ($R^2 = 0.83$, $P < 0.001$). It predicted soil wilting point would be reached after ~23 days without rainfall of $\geq$10 mm (Fig. 5). According to this prediction, soil wilting point was reached three to five times each snow-free season from 2005–06 to 2008–09 (Fig 6). Particularly long periods (>40 days) without a useful rainfall event occurred in autumn in 2005–06 and 2008–09 but in midsummer in 2006–07 (Fig. 6).

DISCUSSION

Precipitation is projected to decrease in the Australian Alps under climate change (95% confidence interval range: +2.3 to −24.0% change relative to 1990 average by 2050; Hennessy *et al.* 2003). This will likely produce more frequent and severe drought conditions in the snow-free season. Although drought has been considered a major disturbance in the Australian Alps
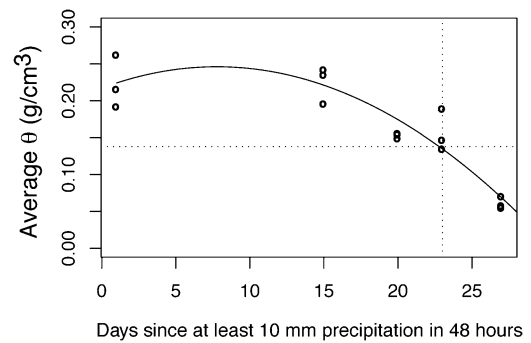

Figure 5: average volumetric soil moisture (θ, g/cm^3) measured in the field versus number of days since at least 10 mm precipitation fell within 48 h (t). Three 'replicate' averages from the three mountains NCS, Mount Nelse Central and Mount Cope are shown for each measurement point (details in text). The solid line shows a linear model of the form $\theta = -0.00048t^2 + 0.0075t + 0.217$ fitted to the data ($R^2 = 0.83$, $P < 0.001$). The dotted line shows the time (23 days) at which soil wilting point is reached according to this model.

(Costin *et al.* 2000; Scherrer and Pickering 2005), a lack of research on environmental factors influencing drought severity and species-specific responses has precluded wide-scale prediction of how future drought conditions will affect the alpine ecosystems. This study reveals environmental factors influencing the drought response of the dominant alpine tussock grasses.

We demonstrate for the first time that low water availability is associated with widespread death of the dominant alpine grasses in Australia. Dry-season PAW was a good predictor of *P. hothamensis* mortality at the local scale of the permanent grid but not at the larger scale of the mountainside transects (Fig. 3A and C). This suggests that the 2006–07 drought caused the observed *P. hothamensis* mortality but other factors influenced survival across different elevations. Soil moisture is important at the local scale because Australian alpine humus soils have high saturated permeability but low unsaturated permeability (Costin *et al.* 1964), meaning moisture tends to remain in localized patches once soil dries below field capacity. *Poa hiemata* showed a different pattern of mortality, with significantly reduced survival at very low dry-season PAW at the large spatial scale (Fig. 3B), while *P. phillipsiana* survival showed no relation to PAW at the small spatial scale (Fig. 3D). The lack of re-sprouting suggests these grasses do not utilize summer dormancy as a drought–response strategy, and that the moisture stress was sufficient to kill the plants completely.

Both *P. hiemata* (Fig. 2B) and *P. phillipsiana* showed lower mortality than did *P. hothamensis* in the field, and *P. phillipsiana* was indeed more drought tolerant in a glasshouse drought experiment. The two more-tolerant species could not be compared directly because they did not occur in sufficient abundance at the same field site. However, both have narrow, rolled, waxy leaves, and typically form smaller, shorter tussocks than does the wide- and soft-leaved *P. hothamensis*
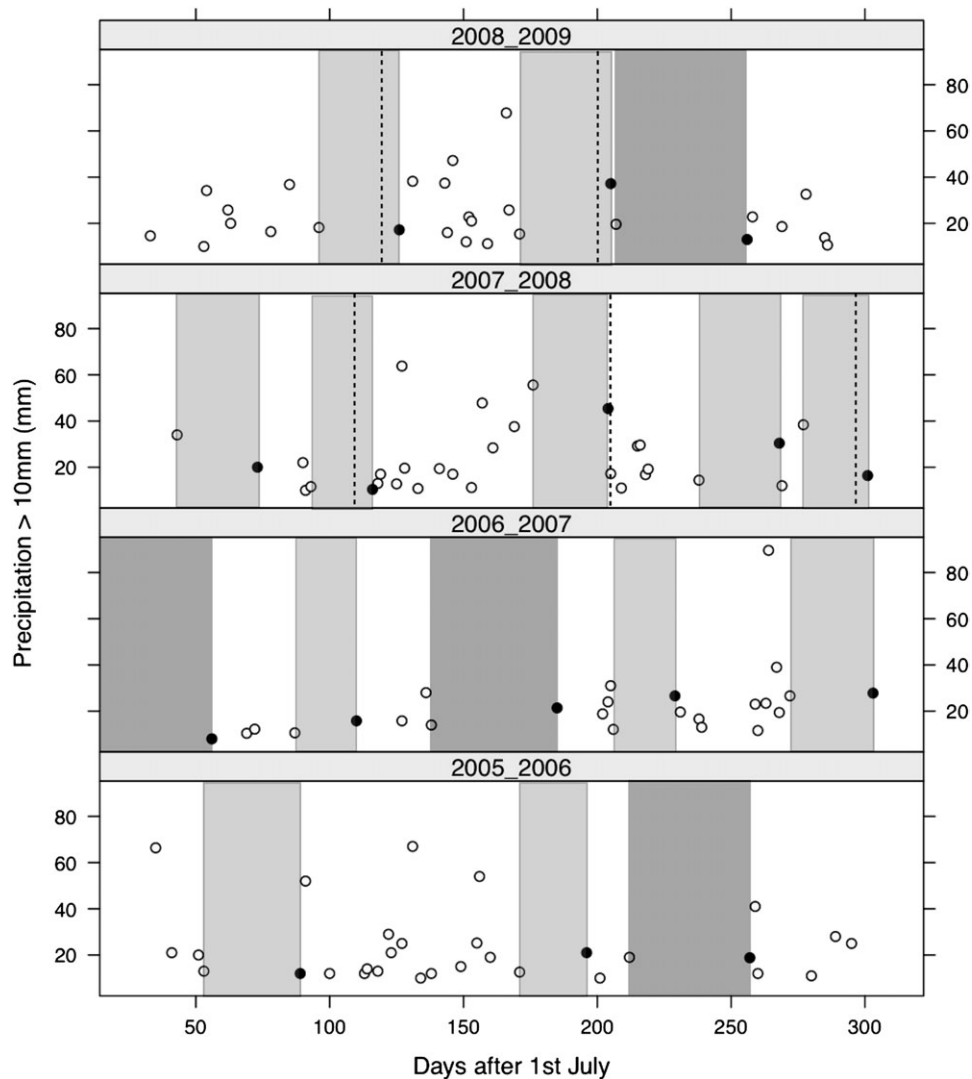
Figure 6: precipitation (only events >10 mm) versus time for Falls Creek, July–June for the four snow-free seasons 2005–06, 2006–07, 2007–08 and 2008–09. Precipitation events occurring 23 days or more after the previous one are shown as filled circles and the corresponding dry period shaded light grey; precipitation events occurring less than 23 days after the previous one are shown as open circles. Dark grey shading indicates periods of over 40 days without useful precipitation events. Dotted lines indicate timing of field soil moisture measurements.

(Walsh 1994), indicating possible morphological adaptations to drought. This finding is concordant with the extensive literature on drought tolerance differing between closely related taxon pairs (Brock and Galen 2005; Henry *et al.* 2009; Kolb and Sperry 1999) and between populations or ecotypes of a single species (Ladiges 1976; Li *et al.* 2000; Ober and Luterbacher 2002; Sangtarash *et al.* 2009).

The observed link between grass mortality and PAW was based on soil moisture measurements of the top 6 cm of soil. Although this may not represent the entire soil profile, these surface measurements appear ecologically relevant, probably because the majority of alpine plant root mass occurs in the top 10 cm of soil (Williams 1990). It was not feasible to take extensive measurements at greater soil depths at these sites because of rocks below the surface. Moisture is retained deeper in

alpine soil even when the top few centimetres reaches wilting point (Costin *et al.* 1964), so soil moisture holding capacity is below 6 cm; but the soil at the sites we considered was generally shallow (<25 cm) compared to meadow and alpine soils previously investigated (Costin *et al.* 1964). Measured soil moisture was not predicted by soil depth, and no effect of soil depth on survival was detected at the mountainside scale for *P. hiemata* or at the small-scale permanent grid site for *P. hothamensis* or *P. phillipsiana*. Surprisingly, *P. hothamensis* survived significantly better in shallower soils at two out of three mountains (correcting for elevation; Table 1). Perhaps rocky soils (which show lower average depth using this measurement method but may contain deep patches of soil between rocks) retain deep moisture during drying periods that is accessible to *P. hothamensis*.

At the broad scale, *P. hothamensis* mortality showed an elevational pattern at two out of three mountains, as did *P. hiemata* (Table 1). Soil depth decreased with elevation (Table 1), as seen in other mountain systems (Körner 1999). Precipitation, evapotranspiration, snow persistence, temperature and other ecological variables all vary along elevation gradients (Körner 1999). The elevation effects seen here that were not explained by soil moisture or depth may reflect some combination of these other variables that influenced grass survival. Alternatively, there may be genetic differences between plant populations at different elevations that explain the differential mortality observed: local adaptation and morphological variation that is both genetically and environmentally based has been demonstrated in *P. hiemata* (Byars *et al.* 2007; Byars *et al.* 2009).

Although soil nutrients can vary over small spatial scales in the Australian Alps (Huber *et al.* 2010; McDougall and Walsh 2007), we consider it unlikely that the observed grass mortality was due to resource depletion after the post-fire grass recolonisation. If this were the case, we would expect to see ongoing grass death in other areas after the initial observations (since all sites in this study were burnt in 2003); this was not seen. Microsite variation in soil nutrient levels may still be involved in the observed mortality, especially since mineralization rates typically decrease with drought (Adams and Attiwill 1986; Powers 1990; Sardans *et al.* 2008).

The bulk density of this alpine humus soil (mean 0.684 g/cm^3) is very low compared to most Australian agricultural soils (Leeper and Uren 1993) and about a third lower than alpine soils on the Tibetan Plateau (Genxu *et al.* 2002) and in Colorado, USA (Sherrod and Seastedt 2001). The soil water-holding capacity curve (data not shown) exhibits the typical shape for a soil with high macroporosity (Leeper and Uren 1993), indicating that air occupies much of the soil space. Mean soil wilting point (0.138 g/cm^3) is comparable to values of 0.127–0.236 g/cm^3 (recalculated from Costin *et al.* 1964) previously reported for alpine soils in New South Wales. Differences in θ_{fc} were likely due to localized differences in organic matter content, as no consistent patterns due to mountain or elevation were observed.

Soil moisture varied over time at both the large and the small spatial scales examined here (Fig. 4). The very low soil moisture observed in January 2009 can be explained by the timing of the measurement period: it occurred 27 days after the previous useful rainfall event (Figs 5 and 6). Previous research has reported seasonal variation in soil moisture on the Bogong High Plains, with soil at field capacity in spring and summer and approaching wilting point in autumn 2004 (estimated from Huber *et al.* 2010). Other researchers have detected soil well below wilting point (Good 1992; Venn 2007; Williams 1990), although early studies reported that alpine soil remains close to field capacity for the entire snow-free season (Costin *et al.* 1964). Clearly, intra- and inter-annual soil moisture variation is high in the Australian alpine zone: thus, extrapolations based on only one or two measurement periods should be avoided. This contrasts with soil moisture patterns in other drought-affected alpine areas, where available moisture is considered to vary predictably between ecological communities but not from year to year (Humphries *et al.* 1996). Soil moisture also varied spatially but, apart from the correlation observed between dry-season (January and April 2008) measurements, spatial patterns differed from season to season (Fig. 4A).

We present a simple polynomial relationship between rainfall and field soil moisture (Fig. 5), which predicts that the alpine soils in the Bogong High Plains dry to below wilting point several times each snow-free season (Fig. 6), once 23 days have elapsed without rainfall of ⩾10 mm within a 48-h period. This concurs with previous observations that vegetation drying and wilting is visible after 3 weeks without rain (Carr and Turner 1959). Much longer rain-free periods have occurred several times during the past few years, with the 2006–07 season characterized by a stretch over 40 days without useful precipitation (Fig. 6). We suggest the timing of such periods may be important, since this drought season rainfall gap occurred in midsummer but similarly long rain-free periods occurred in autumn in other years. Soil moisture has been linked to precipitation in some alpine regions (Penna *et al.* 2009), while topography (Oberbauer and Billings 1981) and snowmelt and runoff (Humphries *et al.* 1996; Isard 1986) are considered more important predictors of water availability in other regions. The relatively shallow alpine slopes and the long snow-free season in Australia (generally 7–9 months without permanent snow cover) may explain why precipitation is more important in this environment. Individual species may still be able to extract water from soil below wilting point, especiallybecause they encounter this condition several times a year.

CONCLUSIONS

We report direct evidence of drought mortality in two Australian alpine grass species, *P. hothamensis* and *P. hiemata*, with dry-season PAW influencing survival in both species. Glasshouse experiments support field observations that *P. hothamensis* is more drought-sensitive than its congeners *P. phillipsiana* and *P. hiemata*. The relatively drought-tolerant *P. phillipsiana* and *P. hiemata* may be resilient to the decreasing precipitation predicted for this region under anthropogenic climate change. In contrast, the relative abundance of *P. hothamensis* may decrease. A reduction in vegetation cover increases the risk of soil erosion in the Australian alpine zone (Durham 1956). Grass mortality will also affect overall plant community composition if drought conditions favour shrub over grass establishment, as previously reported (Williams 1990). Thus, the likely future increase in such drought conditions may lead to long-term ecosystem change, given average annual precipitation in the Australian Alps is projected to decrease rapidly under climate change (Hennessy *et al.* 2003).

SUPPLEMENTARY MATERIAL

Supplementary Tables S1 and S2 are available at *Journal of Plant Ecology* online.

FUNDING

ACKNOWLEDGEMENTS

REFERENCES

Adams M, Attiwill P (1986) Nutrient cycling and nitrogen mineralization in eucalypt forests of south-eastern Australia. *Plant Soil* **92**:341–62.

Aho K, Weaver T (2010) Alpine nodal and ecology and ecosystem evolution in the North-Central Rockies (Mount Washburn; Yellowstone National Park, Wyoming). *Arct Antarct Alp Res* **42**:139–51.

Balsamo R, Willigen C, Bauer A, *et al.* (2006) Drought tolerance of selected *Eragrostis* species correlates with leaf tensile properties. *Ann Bot* **97**:985–91.

Beck E, Fettig S, Knake C, *et al.* (2007) Specific and unspecific responses of plants to cold and drought stress. *J Biosci* **32**:501–10.

Block W (1996) Cold or drought—the lesser of two evils for terrestrial arthropods? *Eur J Entomol* **93**:325–39.

Brock M, Galen C (2005) Drought tolerance in the alpine dandelion, *Taraxacum ceratophorum* (Asteraceae), its exotic congener *T. officinale*, and interspecific hybrids under natural and experimental conditions. *Am J Bot* **92**:1311–21.

Byars S, Papst W, Hoffmann A (2007) Local adaptation and cogradient selection in the alpine plant, *Poa hiemata*, along a narrow altitudinal gradient. *Evolution* **61**:2925–41.

Byars S, Parsons Y, Hoffmann A (2009) Effect of altitude on the genetic structure of an Alpine grass, *Poa hiemata*. *Ann Bot* **103**:885–99.

Carr S, Turner J (1959) The ecology of the Bogong High Plains. I. The environmental factors and the grassland communities. *Aust J Bot* **7**:12–33.

Chaves M, Maroco J, Pereira J (2003) Understanding plant responses to drought—from genes to the whole plant. *Funct Plant Biol* **30**:239–64.

Costin A, Gray M, Totterdell C, *et al.* (2000) *Kosciuszko Alpine Flora*. Collingwood, Victoria, Australia: CSIRO.

Costin A, Wimbush D, Cromer R (1964) *Technical Paper No. 20. Studies in Catchment Hydrology in the Australian Alps. V. Soil Moisture Characteristics and Evapotranspiration*. Victoria, Australia: CSIRO, Division of Plant Industry.

CSIRO, Australian Bureau of Meteorology *Climate Change in Australia: Technical Report 2007*. Canberra, Australia: CSIRO.

Diaz H, Grosjean M, Graumlich L (2003) Climate variability and change in high elevation regions: past, present and future. *Clim Change* **59**:1–4.

Dona A, Galen C (2006) Sources of spatial and temporal heterogeneity in the colonization of an alpine krummholz environment by the weedy subalpine plant *Chamerion angustifolium* (fireweed). *Am J Bot* **84**:933–9.

Durham L (1956) Soil erosion problems in the Snowy Mountains area. *J Soil Conserv Serv N S W* **12**:121–31.

Eckhart V, Singh I, Louthan A, *et al.* (2010) Plant-soil water relations and species border of *Clarkia xantiana* ssp. *xantiana* (Onagraceae). *Int J Plant Sci* **171**:749–60.

Galen C (2000) High and dry: drought stress, sex-allocation trade-offs, and selection on flower size in the alpine wildflower *Polemonium viscosum* (Polemoniaceae). *Am Nat* **156**:72–83.

Genxu W, Ju Q, Guodong C, *et al.* (2002) Soil organic carbon pool of grassland soils on the Qinghai-Tibetan Plateau and its global implication. *Sci Total Environ* **291**:207–17.

Gilgen A, Buchmann N (2009) Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. *Biogeosciences* **6**:2525–39.

Giménez-Benavides L, Escudero A, Iriondo J (2007) Reproductive limits of a late-flowering high-mountain Mediterranean plant along an elevational climate gradient. *New Phytol* **173**:367–82.

Good R (1992) *Kosciuszko Heritage*. Hurstville, New South Wales, Australia: National Parks and Wildlife Service, NSW.

Green K, Osborne W (1994) *Wildlife of the Australian Snow-Country*. Chatswood, New South Wales, Australia: Reed Books.

Griffin P (2011) Phylogenetics and drought response of Australian alpine grasses (*Poa* spp.). *Ph.D. Thesis*. Melbourne, Australia: University of Melbourne.

Hadley J, Smith W (1989) Wind erosion of leaf surface wax in alpine timberline conifers. *Arct Alp Res* **21**:392–8.

Hennessy K, Whetton P, Smith I, *et al.* (2003) *The Impact of Climate Change on Snow Conditions in Mainland Australia*. Aspendale, Victoria, Australia: CSIRO Atmospheric Research.

Henry G, Yelverton F, Burton M (2009) Asymmetric responses of *Paspalum* species to a soil moisture gradient. *Crop Sci* **49**: 1473–80.

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical J* **50**:346–63.

Huber E, Bell T, Simpson R, *et al.* (2010) Relationships among microclimate, edaphic conditions, vegetation distribution and soil nitrogen dynamics on the Bogong High Plains, Australia. *Austral Ecol* doi:10.1111/j.1442-9993.2010.02128.x.

Humphries H, Coffin D, Lauenroth W (1996) An individual-based model of alpine plant distributions. *Ecol Model* **84**:99–126.

Isard S (1986) Factors influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, U.S.A. *Arct Alp Res* **18**:83–96.

Jones H (2007) Monitoring plant and soil water status: established and novel methods revisited and their relevance to studies of drought tolerance. *J Exp Bot* **58**:119–30.

Kirkpatrick J, Bridle K, Wild A (2002) Succession after fire in alpine vegetation on Mount Wellington, Tasmania. *Aust J Bot* **50**:145–54.

Kolb K, Sperry J (1999) Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). *Ecology* **80**:2373–84.

Körner C (1999) *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Berlin, Germany: Springer.

Ladiges P (1976) Variation in drought resistance in adjacent edaphic populations of *Eucalyptus viminalis* Labill. *Aust J Ecol* **1**:67–76.

Leeper G, Uren N (1993) *Soil Science: An Introduction*. Carlton, Victoria, Australia: Melbourne University Press.

Legendre P, Legendre L (1998) *Numerical Ecology*. New York: Elsevier.

Li C, Berninger F, Koskela J, et al. (2000) Drought responses of *Eucalyptus microtheca* provenances depend on seasonality of rainfall in their place of origin. *Aust J Plant Physiol* **27**:231–8.

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

McDowell N, Pockman W, Allen C, et al. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* **178**:719–39.

Morgan J (2004) Drought-related dieback in four subalpine shrub species, Bogong High Plains, Victoria. *Cunninghamia* **8**:326–30.

Norton M, Volaire F, Lelièvre F, et al. (2009) Identification and measurement of summer dormancy in temperate perennial grasses. *Crop Sci* **49**:2347–52.

Ober E, Luterbacher M (2002) Genotypic variation for drought tolerance in *Beta vulgaris*. *Ann Bot* **89**:917–24.

Oberbauer S, Billings W (1981) Drought tolerance and water use by plants along an alpine topographic gradient. *Oecologia* **50**:325–31.

Oksanen J, Kindt R, Legendre P, et al. (2009) *vegan: Community Ecology Package*.

Penna D, Borga M, Norbiato D, et al. (2009) Hillslope scale soil moisture variability in a steep alpine terrain. *J Hydrol* **364**:311–27.

Powers R (1990) Nitrogen mineralization along an altitudinal gradient: interactions of soil temperature, moisture, and substrate quality. *For Ecol Manag* **30**:19–29.

R Development Core Team *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reynolds W, Topp G (2008) Soil water desorption and imbibition: tension and pressure techniques. In Carter M, Gregorich E (eds). *Soil Sampling and Methods of Analysis*. Boca Raton, FL: CRC Press.

Rundel P (1994) Tropical alpine climates. In Rundel P, Smith A, Meinzer F (eds). *Tropical Alpine Environments: Plant Form and Function*. New York: Cambridge University Press 21–44.

Sangtarash M, Qaderi M, Chinnappa C, et al. (2009) Differential responses of two *Stellaria longipes* ecotypes to ultraviolet-B radiation and drought stress. *Flora* **204**:593–603.

Sanz-Elorza M, Dana E, González A, et al. (2003) Changes in the high-mountain vegetation of the Central Iberian Peninsula as a probable sign of global warming. *Ann Bot* **92**:273–80.

Sardans J, Peñuelas J, Prieto P, et al. (2008) Drought and warming induced changes in P and K concentration and accumulation in plant biomass and soil in a Mediterranean shrubland. *Plant Soil* **306**:261–71.

Scherrer P, Pickering C (2005) Recovery of alpine vegetation from grazing and drought: data from long-term photoquadrats in Kosciuszko National Park, Australia. *Arct Antarct Alp Res* **37**:574–84.

Sherrod S, Seastedt T (2001) Effects of the Northern Pocket Gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. *Biogeochemistry* **55**:195–218.

Smith A, Young T (1987) Tropical alpine plant ecology. *Annu Rev Ecol Syst* **18**:137–58.

Steffen W, Burbidge A, Hughes L, et al. (2009) *Australia's Biodiversity and Climate Change: A Strategic Assessment of the Vulnerability of Australia's Biodiversity to Climate Change*. A report to the Natural Resource Management Ministerial Council commissioned by the Australian Government. Canberra, Australia: CSIRO Publishing.

Taylor R, Seastedt T (1994) Short- and long-term patterns of soil moisture in alpine tundra. *Arct Alp Res* **26**:14–20.

Therneau T (2009) *survival: Survival Analysis, Including Penalised Likelihood*.

Venn S (2007) Plant recruitment across alpine summits in south-eastern Australia. *Ph.D. Thesis*. Bundoora, Victoria, Australia: La Trobe University.

Verslues P, Agarwal M, Katiyar-Agarwal S, et al. (2006) Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. *Plant J* **45**:523–39.

Vickery J (1970) A taxonomic study of the genus *Poa* L. in Australia. *Contrib N S W Natl Herb* **4**:145–243.

Walsh N (1994) Poaceae. In Walsh N, Entwisle T (eds). *Flora of Victoria*, Vol. 2. Melbourne, Australia: Inkata Press, 356–625.

Williams R (1990) Growth of subalpine shrubs and snowgrass following a rare occurrence of frost and drought in southeastern Australia. *Arct Alp Res* **22**:412–22.

Wimbush D, Costin A (1979a) Trends in vegetation at Kosciusko. II. Subalpine Range Transects, 1959–1978. *Aust J Bot* **27**:789–831.

Wimbush D, Costin A (1979b) Trends in vegetation at Kosciusko. III. Alpine range transects, 1959–1978. *Aust J Bot* **27**:833–71.