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Experimental warming and fire alter fluxes of soil nutrients in sub-alpine open heathland

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ABSTRACT: Climatic changes in the Australian Alps are likely to raise mean ambient temperatures, decrease precipitation and increase the frequency of fires, which together are likely to affect soil nutrients. Changes in the availability of soil nutrients are in turn expected to influence plant growth and community composition. In alpine soils of the southern hemisphere, it is unknown how the interaction between warming and fire will affect nutrient availability and to what extent changes will resemble global trends. We used open-top chambers and ion-exchange membranes to examine the effects of warming and fire on the cumulative flux of available nutrients and toxic elements in soil of a sub-alpine heathland during the final 2 yr of a 9 yr passive warming and post-fire experiment at sites on the Bogong High Plains, Victoria, Australia. Compared to unwarmed plots, experimental warming increased NH_4^+, $H_2PO_4^-$, Na^+ and K^+, and decreased Mg^{2+}, Ca^{2+}, Al^{3+} and soil moisture. Increased N and P are consistent with changes in alpine soils of the northern hemisphere, but the effect of warming on other elements has not been reported. A consistent decrease in Al^{3+} availability with warming has implications for carbon turnover and invasion by exotic species. Fire increased Al^{3+} availability and decreased Mn^{2+} availability, indicating a change in potentially toxic elements in burnt areas. Warming and drying changed the availability of all measured nutrients and resembled trends in the northern hemisphere, indicating that changes in the alpine and sub-alpine ecosystems of the Australian Alps, and globally, are probably inevitable.

KEY WORDS: Alpine soil · Climate change · Ion-exchange membrane · IEM · Nitrogen · Open-top chamber · OTC · Soil moisture · Soil temperature

1. INTRODUCTION

In the alpine regions of Australia, research suggests that over the coming decades ambient temperatures, evapotranspiration and frequency of fire will increase, while precipitation, soil moisture, persistence and depth of snow, and biodiversity will decrease (Pickering et al. 2004, 2008, Hennessy et al. 2007, Slatyer 2010, Cai & Cowan 2013). These changes have been detected worldwide (Barnett et al. 2005, Calanca 2007) and have already affected the biota of the Australian Alps: the treeline has expanded into treeless areas (Wearne & Morgan 2001); the extent of some plant communities, such as snow patch vegetation, has contracted (Green & Pickering 2009); and the population of the mountain pygmy-possum *Burramys parvus* has declined (Broome et al. 2012).

Australia's alpine and sub-alpine ecosystems occupy only about 0.15 % of the mainland, yet this

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region contains many rare and endemic plants and animals (Brereton et al. 1995, Worboys & Good 2011, Williams et al. 2014). It is scientifically and culturally significant, a popular destination for both summer and winter recreation and an important water catchment that supplies over 40% of river base-flows in south-eastern Australia (Costin et al. 1952, 2000, Costin 1989, Worboys & Good 2011). Therefore, changes to the climate can have a significant impact on these ecosystems and their services.

Temperature affects soil processes such as C decomposition and N mineralization (Nadelhoffer et al. 1991, Davidson & Janssens 2006). Thus, climate change is likely to influence nutrient cycling and alter the availability of soil nutrients, which can directly affect plant growth, and hence affect the structure and composition of plant communities (Bassirirad 2000, Onipchenko et al. 2001, Wardle et al. 2004). Studies in alpine and sub-alpine regions of the northern hemisphere have shown that experimental warming increases N and P availability (Chapin et al. 1995, Rustad et al. 2001). These increases are particularly important for plant growth in alpine systems where N inputs are relatively small (Shaver et al. 1992). For example, in some species an increased availability of N and P resulted in increased root and shoot growth (Chapin & Shaver 1996).

Warming influences nutrient availability in several ways. It can increase soil nutrients by increasing decomposition of organic matter (Grogan & Chapin 2000, Natali et al. 2012), N mineralization (Chapin et al. 1995, Rustad et al. 2001, Koch et al. 2007, Borner et al. 2008), nutrient diffusion, nutrient dissolution and nutrient sorption (Essington 2004). Warming can also decrease soil nutrient availability by increasing uptake by plants (Schmidt et al. 2002, Welker et al. 2005). Thus warming affects plant communities through a feedback loop that involves plant growth, plant–plant interactions, soil processes and litter quality (Sundqvist et al. 2011, Camac et al. 2015). Fire can affect these processes and hence the availability of nutrients because fire typically causes some nutrients to increase (e.g. Ca, Mg, K, total N and P; Khanna & Raison 1986, Khanna et al. 1996, Durán et al. 2008) and others to decrease (e.g. total N, Kirkpatrick & Dickinson 1984). For instance, a large-scale fire on the Bogong High Plains in 2003 burnt substantial areas of sub-alpine heathland (Esplin 2003). A study set up in grassland, heathland and woodland prior to the fire documented increases in NH_4^+ and NO_3^- immediately after the fire (Huber et al. 2013). Two years after the fire, NH_4^+ had returned to pre-fire levels, but NO_3^- remained significantly lower than pre-fire levels (Huber et al. 2013). Other studies in the Australian Alps have found similar changes in the nutrient status of soil after fire (Khanna & Raison 1986, Shrestha 2009), but none of these studies examined long-term nutrient availability or examined the seasonal fluctuations of nutrients. Also, to our knowledge, no studies have examined the combined effects of fire and experimental warming on soil nutrient dynamics in a sub-alpine heathland. Understanding how warming and fire affects soil nutrient availability can help to explain measured vegetation changes and to improve predictions about how plants and plant communities are likely to change. Such knowledge is invaluable for the effective management of alpine and sub-alpine regions in an era of higher temperatures and increased fire frequency.

The primary aim of this study was to assess the effect of experimental warming and fire on the cumulative availability of plant nutrients in a sub-alpine open heathland of the Victorian Alps. We predicted that experimental warming would increase the availability of soil nutrients and that these changes would differ with fire. We examined the final 2 yr of a 9 yr experiment, which meant that we examined the long-term effects but did not assess the initial effects.

We passively warmed plots using open-top chambers (OTCs), a method that has been widely used in warming experiments worldwide (Henry & Molau 1997, Marion et al. 1997, Elmendorf et al. 2012). In our study, OTCs also decreased soil moisture, making the experiment one of combined warming and drying, which simulated the predicted climatic changes for the Australian Alps (Hennessy et al. 2007).

2. MATERIALS AND METHODS

2.1. Site description

The sites were located in sub-alpine open heathland on the Bogong High Plains, Victoria, Australia (36° 53′ 50″ S, 147° 16′ 30″ E; 1750 m above sea level). The characteristic soil is a deep, well-drained Humic Umbrosol (IUSS Working Group WRB 2006), also known as Alpine Humus soil or Chernic Tenosol (Australian Soil Classification; Isbell 2002) with a sandy-loam A-horizon of high (>8%) organic matter content and a weakly developed or absent B-horizon overlying rock that has weathered *in situ* (McKenzie et al. 2004, Rowe & Anderson 2006). The soil is acidic, with a pH of 4.3 to 5.2 (Gibbons et al. 2002, McKenzie et al. 2004, Rowe & Anderson 2006). The bedrock is Ordovician metasediment of the Omeo Metamorphic Complex with occasional outcrop (Rosengren & White 1997). The Cobungra Granite is regional metamorphic and is described as gneissic rock with thin layers and patches of leucogranite and pegmatite in dark biotite–sillimanite–cordierite gneiss and schist (Taylor et al. 2004). The plant community is a common open heathland that occupies about 25% of the treeless vegetation of the Bogong High Plains. Typical species include the shrubs *Grevillea australis* and *Asterolasia trymalioides*, several tussock-forming grasses of *Poa* spp., especially *P. hiemata*, and a diverse range of forbs in genera such as *Craspedia, Celmisia, Erigeron, Plantago, Oreomyrrhis* and *Ranunculus* (McDougall & Walsh 2007, Wahren et al. 2013).

During the 9 yr experiment, the mean annual maximum temperature was 9.6°C, the mean annual minimum temperature was 2.8°C, and mean monthly rainfall was 107 mm (Falls Creek, Australian Bureau of Meteorology, December 2012). During our 2 yr sampling period, conditions were cooler and wetter than the mean for the 9 yr period: the mean annual maximum temperature was 8.3°C, mean annual minimum temperature was 2.1°C, and mean monthly rainfall was 142 mm.

2.2. Experimental design

In November 2003, 4 sites of gentle slope (<3%) with similar elevation, underlying geology and vegetation were selected and set up according to the standard protocol of the International Tundra Experiment (ITEX) network (Molau & Mølgaard 1996). Sites 1 and 2 were unburnt, and each comprised 13 OTC and 13 control plots. Sites 3 and 4 were burnt in the 2003 fires, and each comprised 7 OTC and 7 control plots. Further details are given in Jarrad et al. (2008) and Wahren et al. (2013).

2.3. Soil nutrient sampling: ion-exchange membranes

We used 12 × 2 cm ion-exchange membranes (IEMs; Membranes International) that were initially washed 3 times with water. Exchange sites on these membrane strips were then loaded with H^+ or HCO_3^- by shaking for 12 h; cation-exchange membranes (CEMs) were shaken in 2 M HCl, and anion-exchange membranes (AEMs) were shaken in 1 M $NaHCO_3$. The membranes were then rinsed 3 times with water, shaken in water for 2 h, and then soaked in water for 12 h. The CEMs were soaked in water for another 12 h. The IEMs were kept moist, separately packed into sealed plastic bags, and briefly stored at 4°C prior to use. Ultrapure water (18.2 MΩ·cm at 25°C) was used throughout the study.

Five membrane pairs were used per plot, with each pair consisting of a CEM and an AEM strip placed 2.5 cm apart and inserted vertically into the soil to a depth of 10 cm. After the period of embedment, replacement strips were placed in new locations. To minimize root disturbance that might affect vegetation studies, the IEMs were placed along the outer edge of each plot (Fig. 1). The IEMs were embedded during the colder and wetter autumn to spring period (April to November) and the warmer and drier summer to early autumn period (November to April). They were first inserted in April 2010 and then collected and replaced in October and November 2010 at Sites 1 and 3, and then in April and November 2011 and April and November 2012 at all 4 sites. The low availability of nutrients in the alpine soils contributed to low adsorption to the membranes, supporting a longer period of embedment than other studies (Lisuzzo et al. 2008). The collected membranes were washed with water to remove all soil particles. To desorb the nutrient ions for analysis, the CEM strips were shaken for 2 h with 100 ml of 0.5 M HCl and the AEM strips with 100 ml of 1 M NaCl.

We also incubated IEMs for 32 d to assess how soil temperature, moisture and drying–rewetting cycles affected measurements of available elements. The methods and results are included in the Supplement ('Methodological test for bias by ion-exchange membranes', Fig. S1; www.int-res.com/articles/suppl/c064p159_supp.pdf). The results show no effects of warming, drying or drying–rewetting cycles on the measurements of NH_4^+, NO_3^- or Al^{3+}, indicating that our field results adequately represent these nutrient levels in the soil. The results also show that Mn^{2+} availability in the field was overestimated by dry-ing –rewetting cycles, and that Ca^{2+} and Mg^{2+} were underestimated by warming and overestimated by drying. Therefore, the IEMs are likely to accurately represent Ca^{2+} and Mg^{2+} availability in the field because warming and drying cycles occurred together, hence counteracting the underestimated and overestimated IEM biases.

2.4. Nutrient analyses

We used a flow injection analyser series-2 Quikchem 8500 (Lachat Instruments) to determine con-

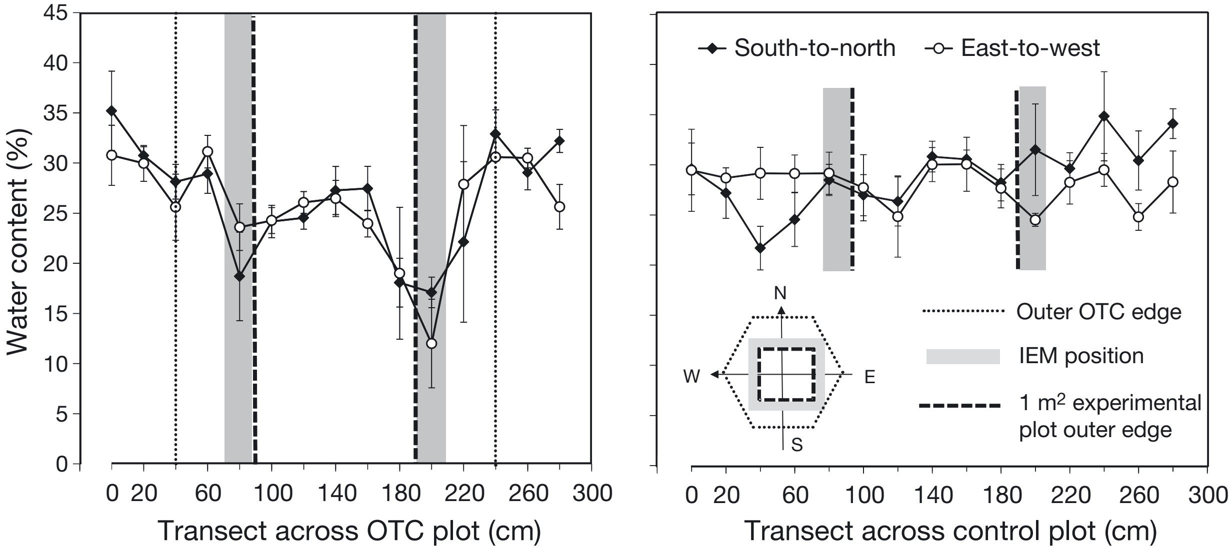

Fig. 1. Volumetric soil water content (%) at 20 cm intervals in south-to-north and east-to-west transects across open-top chambers (OTCs) and control plots at Site 1 in November 2011. Error bars: ± SE (n = 3). Ion-exchange membranes (IEMs) were embedded on the edge of the 1 m^2 experimental plot area, and within the OTC. The hexagonal OTCs had a maximum and minimum diameter on the ground of 203 and 168 cm, respectively

centrations of NH_4^+ and NO_3^-, a flame photometer model 420 (Sherwood Scientific) for K and Na, and an inductively coupled plasma optical emission spectrometer (Perkin Elmer Optima 8000) for Ca, Mg, Mn and Al. Inorganic P was analysed using the malachite green method (Motomizu et al. 1983).

2.5. Soil moisture and temperature

We used a Theta probe (Delta-T Devices) to measure soil moisture to 6 cm depth adjacent to each pair of membranes, in April 2010, April 2011 and November 2011. We sampled 4 times around each of the 5 pairs of membranes, and the mean provided a representative value per plot (n = 20).

Studies using OTCs have not previously assessed how soil moisture varies across the centres and edges of plots. Thus in November 2011, we randomly selected 3 OTC and 3 control plots at Site 1, and measured the soil moisture at 20 cm intervals along 2 perpendicular transects across each plot. The moisture data were compared between the treatments and between the centres and edges of plots using Tukey's post hoc analysis. These data were necessary to relate moisture values from loggers within the central plot area to the moisture around the IEMs on the edges of plots, and to validate correlations between vegetation studies and our soil studies (authors' unpubl. data).

Onset Micro Stations (Onset Computer) were installed in 4 OTC and 4 control plots at Site 1. These loggers recorded hourly measurements of ambient temperature (5 cm above ground), soil temperature (5 cm below ground) and volumetric water content (3–10 cm below ground using 2 soil moisture sensors at 3 and 10 cm below the soil surface) from November 2010 until completion of the experiment.

2.6. Statistical analyses

The experimental design was hierarchical: IEMs within plots within treatment within site. Consequently, a multi-level generalized linear model with random effects for plot, site and duration of IEM embedment was used to examine how experimental warming and burning interacted to affect the availability of each element in the soil. The IEMs within each plot were pooled for each nutrient measurement, thereby eliminating a random effect for their placement.

We used SPSS (IBM SPSS Statistics Version 19) to analyse element concentration, moisture and temperature. The number of samples used to calculate the mean values of each available element varied between sites, and were 132, 52, 70 and 28 for Sites 1, 2, 3 and 4, respectively (see Fig. 2). A correlation analysis between the number of samples and the standard error showed that sample number did not influence the data, indicating that heterogeneity was sufficiently captured. All data were assessed using the Shapiro–Wilk test of normality, Levene's test of homogeneity and ANOVA. Main effects for data that did not have a normal distribution were analysed using the non-parametric Mann-Whitney *U*-test for 2 samples or Kruskal-Wallis 1-way ANOVA for more than 2 samples. Bivariate linear correlations were calculated on nutrient data from all treatments, all sites and all IEM periods using Pearson's correlation coefficient and a 2-tailed test of significance at $p = 0.05$ ($n = 282$).

We also used a multi-level linear model (R software, Bates et al. 2013) to examine how daily maximum ambient temperature and daily minimum soil moisture affected available elements for the period April 2011 to November 2012 at Site 1. Maximum air temperature and minimum soil moisture were chosen for the model, as these abiotic factors have a strong effect on biological processes and are strongly affected by experimental warming. In this model, treatment, ambient temperature and soil moisture were treated as fixed effects, and the duration of IEM embedment (days) and the IEM extraction date were treated as random effects. Thus the main effect of climate was based on the temperature and soil moisture (as recorded by the microstations in the plots); we then used the means of these values for the sampling periods.

3. RESULTS

3.1. Effect of experimental warming and fire on nutrient availability

Experimental warming increased NH_4^+, K^+ and Na^+ in the soil ($p < 0.05$; Table 1; Tables S1 & S3 in the Supplement at www.int-res.com/articles/suppl/c064p159_supp.pdf). Warming marginally increased $H_2PO_4^-$. In contrast, warming decreased Ca^{2+}, Mg^{2+} and Al^{3+}. Fire decreased Mn^{2+} and increased Al^{3+} (Tables 1, S2 & S4). No significant interactions occurred between warming and fire. At all sites, the availability of NH_4^+ was consistently greater than NO_3^- ($p < 0.001$; Fig. 2). All sites, IEM periods and treatments were pooled to reveal that the strongest positive correlation ($r = 0.94$) was between Mg^{2+} and Ca^{2+}, and these ions positively correlated with K^+ ($r = 0.75$ and 0.65) and Al^{3+} ($r = 0.75$ and 0.74), respectively ($p < 0.05$; Table S5). Mn^{2+} correlated positively with K^+ ($r = 0.70$), Mg^{2+} ($r = 0.56$) and Ca^{2+} ($r = 0.53$) ($p < 0.05$), and with Al^{3+} ($r = 0.29$; $p < 0.001$). Ammonium correlated positively with NO_3^- ($r = 0.55$) and Na^+ ($r = 0.55$) ($p < 0.05$).

3.2. Soil moisture distribution in plots

The soil moisture was similar in the region of IEM embedment at the edge of the plots to the central plot area ($p > 0.05$; Fig. 1) and there was no significant difference in soil moisture across the south-to-north or east-to-west transects for the control plots. The mean soil moisture across the central plot area was lower in the OTC than the control plots ($p < 0.05$; Fig. 1). Furthermore, the OTC plots were consistently drier than control plots ($p < 0.05$) at all sites and all measurement dates (Fig. 3a,b).

3.3. Soil temperature

During the experimental period, the OTCs increased mean ambient temperatures by 1.1°C and maximum temperatures by up to 2.5°C (Fig. 4). This is consistent with other climate data published for this site (Camac et al. 2015). Minimum temperatures

Table 1. Parameter estimates for a multi-level mixed model of available elements (log [μg d^{-1} cm^{-2}]) extracted from sub-alpine soil using ion-exchange membranes. All results for NO_3^- were non-significant ($p > 0.10$). #$p < 0.10$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

	NH_4^+	$H_2PO_4^-$	K^+	Ca^{2+}	Mg^{2+}	Mn^{2+}	Al^{3+}	Na^+
Fixed effects								
Intercept	0.163	0.889	4.104***	4.666***	4.221***	3.010***	4.232***	2.060*
Warming treatment	0.790***	0.150#	0.528***	–0.160***	–0.081*	–0.022	–0.295***	0.771***
Fire treatment	–0.187	0.135	0.071	0.009	–0.030	–0.345*	0.315***	0.137
Warming × fire	–0.088	0.208	0.130	0.068	0.074	0.108	0.087	0.012
Variance of random component								
Plot	0.001	0.031	0.000	0.001	0.000	0.006	0.000	0.000
Days	0.058	0.081	1.057	0.102	0.102	0.119	0.098	7.323
Site	0.110	0.000	0.085	0.015	0.019	0.016	0.003	0.004

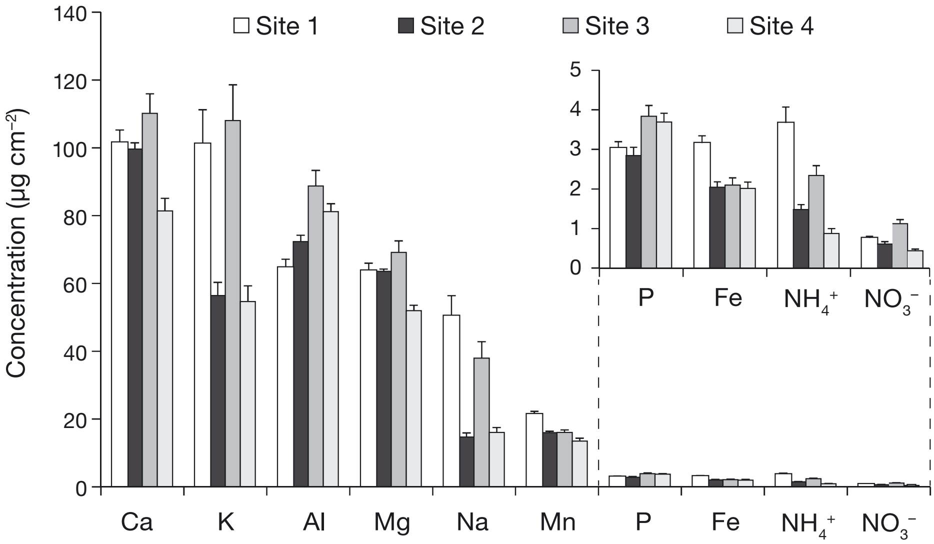

Fig. 2. Mean concentration (µg cm^{-2}) of elements and ions extracted from ion-exchange membranes (IEMs) for all sites, all IEM periods and pooled warming and control treatments. Sites 1 and 2 were unburnt, and Sites 3 and 4 were burnt in the 2003 fire. The inset shows a subset of the data at higher resolution. Error bars represent ± SE. n = 132, 52, 70 and 28 for Sites 1, 2, 3 and 4, respectively

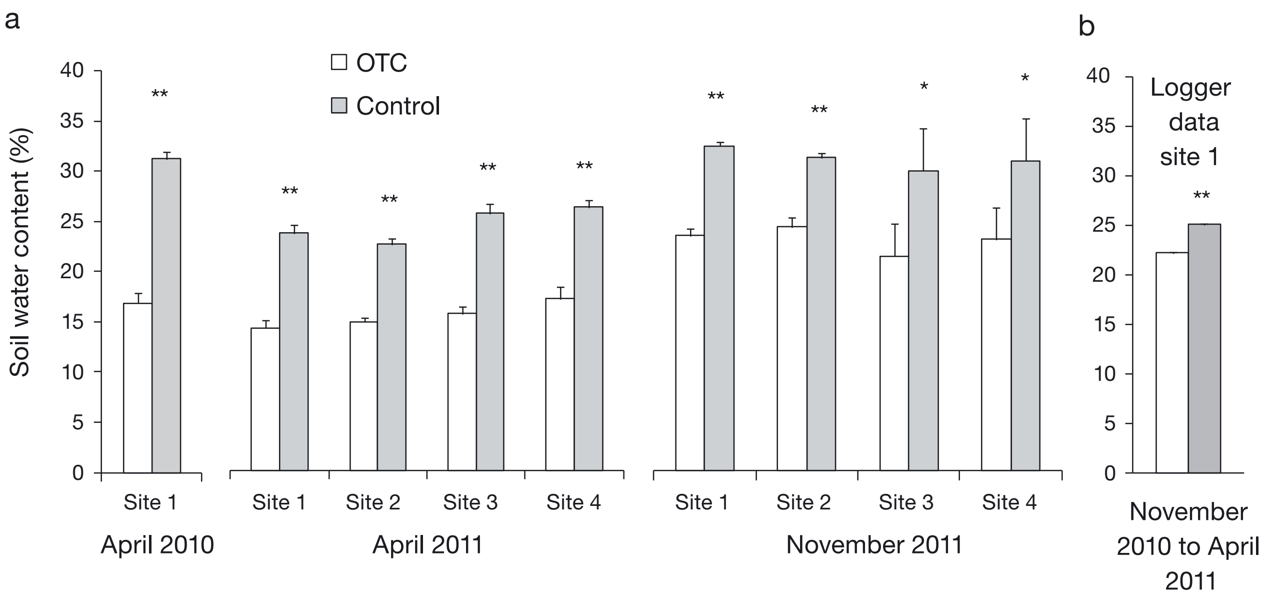

Fig. 3. Volumetric soil water content (%): (a) measured using 4 Theta probe measurements to 6 cm depth adjacent to each of 5 ion-exchange membrane pairs (n = 20) at each plot, at each site; (b) measured hourly using data loggers embedded at 3–10 cm depth from November 2010 to April 2011 at Site 1. *$p < 0.05$, **$p < 0.001$, OTC: open-top chamber

increased by around 0.9°C. Similarly, mean soil temperatures increased by 1.2°C, whereas the maximum increased by 1.8°C and the minimum increased by 0.9°C. The linear models showed that mean maximum temperatures at 5 cm above the surface significantly co-varied with NH_4^+, Ca^{2+} and Al^{3+}, but soil moisture did not (Table 2). This suggests that warming rather than drying increased NH_4^+ and decreased Ca^{2+} and Al^{3+} availability. Both temperature and moisture significantly co-varied with $H_2PO_4^-$, suggesting that warming and drying seasonally increased $H_2PO_4^-$ availability. The OTCs generally increased K availability, but with no detectable effect of climate variables.

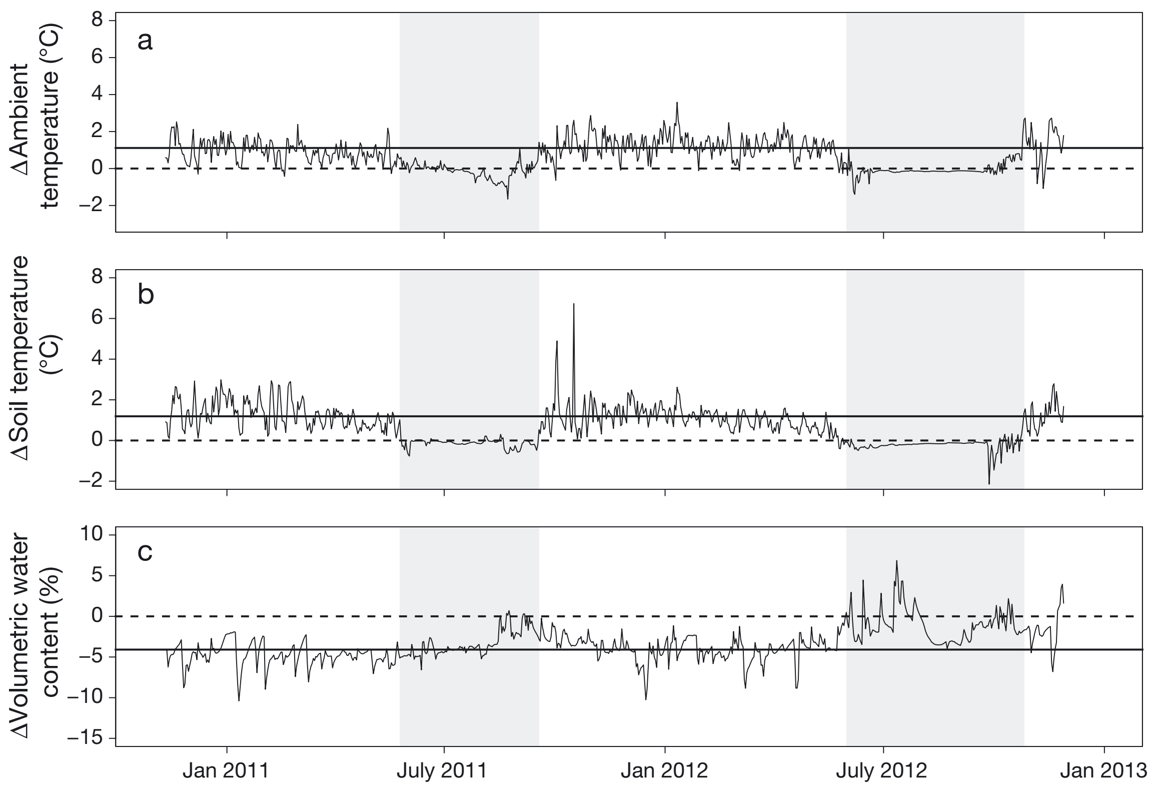

Fig. 4. Daily difference in microclimate between open-top chambers (OTCs) and control plots at Site 1 from November 2010 to December 2012: (a) ambient air temperature (5 cm above ground); (b) soil temperature (5 cm below ground); (c) volumetric soil water content at 3–10 cm depth. The mean difference in temperature and moisture was calculated from 4 OTC and 4 control plots. Dashed lines: 0 point where OTCs and controls did not differ; solid horizontal lines: mean growing season difference between OTC and control plots. Shaded areas: snow periods when the OTC chambers were removed

Table 2. Parameter estimates for a multi-level mixed model of warming and climatic factors on the available elements (log [μg d^{-1} cm^{-2}]) extracted from sub-alpine soil using ion-exchange membranes (IEMs). Elements absent from columns (NO_3^-, K^+, Mg^{2+} and Mn^{2+}) indicate non-significant results ($p > 0.05$). AT: ambient air temperature (5 cm above ground), SM: soil moisture (3–10 cm below ground), Days: number of days of IEM embedment in the soil. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

	NH_4^+	$H_2PO_4^-$	Ca^{2+}	Al^{3+}	Na^+
Fixed effects					
Intercept	0.655	–0.909**	–4.166	–0.655	–4.530
Treatment	0.015***	–0.005	–0.121*	–0.099**	0.152*
Log Mean Max AT	–0.058*	0.085**	0.409**	0.258*	–0.090
Log Mean Min SM	–0.334	0.508*	2.480	0.199	3.407
Variance of random component					
Plot	0.000	0.000	0.004	0.000	0.004
Days	0.000	0.000	0.000	0.000	0.012
IEM extraction date	0.000	0.000	0.000	0.000	0.011
R^2 of model					
R^2_M (fixed component)	0.52	0.29	0.39	0.54	0.16
R^2_C (fixed and random component)	0.64	0.93	0.69	0.64	0.88

4. DISCUSSION

4.1. Experimental warming changes nutrient availability

Nitrogen availability tends to be restricted in the acidic, well-drained soils of the Victorian Alps (Costin et al. 2000, McDougall 2001), and limited NH_4^+ availability tends to restrict plant growth in other alpine systems worldwide (Shaver & Chapin 1980, Marion et al. 1989, Hobbie et al. 2002, Körner 2003). Thus, a consistent increase in NH_4^+ availability with experimental warming is likely to have implications for open heathland ecosystems. For example, increased nutrient cycling may alter community structure because additional nutrients can initially favour the growth of graminoids, with little effect on shrubs (Michelsen et al. 1999). Furthermore, species diversity may also change as differential nutrient uptake and growth rates among distinct plant groups alter competitive interactions (Callaway et al. 2002) that may begin well before changes in soil nutrients can be detected (Bowman et al. 2006).

Warming increased NH_4^+ but had no detectable effect on NO_3^-. This was an expected result, as microbial processes, especially nitrification, tend to be restricted in these acidic soils (Bowman et al. 2006, Chu & Grogan 2010, Huber et al. 2011). This explains the higher ratio of NH_4^+ to NO_3^- present in the soil, which is similar to other alpine systems, both in Australia (Adams & Attiwill 1986, Kirkpatrick & Bridle 1999, Huber et al. 2011) and elsewhere (Haselwandter et al. 1983, Brooks et al. 1996, Freppaz et al. 2007).

Experimental warming marginally increased P availability. This accumulation of P in the soil occurred mainly during cold seasons, and may be due to continued P mobilization under cooler conditions by chemical (e.g. pH) and/or biochemical (e.g. root exudates) processes that are less affected by temperature than the microbial processes that immobilize P (Joner et al. 2000, Frey et al. 2013). Rui et al. (2012) also showed that warming increased P mineralization in an alpine meadow, but overall P availability decreased due to an increased uptake by plants and microbes. The increased P availability has the potential to alter microbial and plant dynamics. If P limitation favours greater species richness than N limitation (Venterink 2011), then increased P availability could decrease species richness (Marini et al. 2007).

In these sub-alpine soils, our results suggest that either the processes of P and N mobilization differ, or that P and N uptake differs between plants and microbes. This is because we found (1) no correlation between $H_2PO_4^-$ with either NH_4^+ or NO_3^-, and (2) that warming increased $H_2PO_4^-$ availability mainly in the cold seasons but increased NH_4^+ availability in both warm and cold seasons.

The effects of warming on the availability of plant nutrients other than N and P have rarely been studied in alpine soils. The decrease in Ca^{2+} availability with warming occurred mainly during the warmer periods (November to April; Tables 1, S1 & S3) and might be due to reduced adsorption to IEMs because of associated soil drying or increased demands by plants and rhizosphere microbes as they respond to warming. Alternatively, an increased frequency of drying–rewetting combined with warming might decrease cation solubility and mobility by increasing cation sorption, occlusion or precipitation in soil and thus reduce the availability of calcium.

Available K^+ and Na^+ increased with experimental warming. The main source of K^+ in soils is likely to be the exchangeable fraction from clay minerals and organic matter (Sparks & Huang 1985). In OTCs, the higher temperatures above the soil surface may have increased plant transpiration and root processes, thus increasing the diffusion and mass flow of K^+ in the soil solution. Warming also enhances K release through organic matter decomposition (Barber 1985). Sodium is not a plant nutrient and is found in very low concentrations in the leaves of many plants on the Bogong High Plains (van Rees & Beard 1984, Subbarao et al. 2003). Therefore, the increased Na^+ availability indicates an increase in mobile Na^+ from soil mineral surfaces and organic matter rather than a reduction in plant uptake. Increased Na^+ availability can be caused by mineral weathering (e.g. drying–rewetting cycles) and reduced leaching (e.g. drier soil).

Mn availability decreased in burnt plots, and because it is among the main toxic elements in acidic soils (Marschner 2011, Ryan & Delhaize 2012), any decrease has the potential to increase the growth and abundance of Mn-sensitive plants. This study did not determine the critical toxic levels of Mn^{2+} and Al^{3+}, so we cannot say how lower Mn might have affected plant responses over the past decade, such as the increase in cover of shrubs and some of the taller forbs (Wahren et al. 2013). Although small changes in soil pH can affect Mn availability, preliminary soil analyses indicated that experimental warming did not significantly affect soil pH (authors' unpubl. data).

Al availability significantly decreased with warming. The increased ambient air temperature, increased soil temperature and decreased soil moisture with experimental warming could have decreased Al^{3+} availability in 3 ways: (1) by reducing dissolution from silicate minerals (Mulder et al. 1989), (2) by reducing mobility due to drying or increased chemical precipitation and (3) by complexation with dissolved organic matter (Dalal 2001, Scheel et al. 2007). The formation of Al–organic matter complexes increases organic matter stability, which has implications for C turnover rates (Dalal 2001, Schrumpf et al. 2013). Similar to Mn^{2+}, a small increase in soil pH can decrease Al^{3+} availability in these acidic soils. Interestingly, we found a positive correlation between Al^{3+} and Mn^{2+} ($r = 0.29$, $p < 0.001$; Table S5). Soils in the Australian Alps and litter of the tussock-forming *Poa* spp. have high concentrations of Al^{3+} (Costin et al. 1952, McKenzie et al. 2004), suggesting that plants can develop ways to exclude or detoxify Al. Thus with the warmer and drier conditions predicted for the Australian Alps (Hennessy et al. 2007), lower Al^{3+} availability, together with increased availability of N, may favour the growth and abundance of exotic plants that were previously restricted by their Al-sensitivity.

The availabilities of Ca^{2+}, K^+, Al^{3+} and Mg^{2+} were greater than all other nutrients measured in these soils. This measure of availability represents the fluxes resulting from a combination of plant and microbial uptake and soil sorption, and does not predict the absolute availability to plants. However, plants generally take up greater quantities of N and K; therefore, it is likely that Ca^{2+}, K^+ and Mg^{2+} were sufficient to meet plant requirements (Marschner 2011). The availability of Al^{3+} was generally higher than all elements except Ca^{2+} and K^+, which could result from IEMs having a greater affinity for trivalent ions. Fluxes of Ca^{2+}, Mg^{2+}, K^+, Mn^{2+} and Al^{3+} were positively correlated, suggesting a common driver of their increased availability.

4.2. Fire changes nutrient availability

Although NH_4^+ availability increased with warming, there was no effect 9 yr post-fire. This is reasonable because available N has been shown to recover 1 yr after fire (Wan et al. 2001, Huber et al. 2013). Vegetation in the Australian Alps can recover quickly from fire, and some plants experience pyrogenic growth and/or flowering (Wahren et al. 2001, Walsh & McDougall 2004). In the 7 yr post fire and prior to the IEM measurements, any soil nutrient increases resulting from fire may have influenced the increased plant growth. Consequently, the increased nutrients may have been taken up from the soil and into the recovering plant biomass, which might explain why few soil nutrients were affected 9 yr post fire.

This current study found that Mn^{2+} was lower 9 yr post-fire. This decline indicates a depletion from burnt areas. Loss of Mn^{2+} is likely due to erosion of ash and topsoil during high-intensity rainfall or long-term leaching from the cation-rich ash–soil layer (Raison et al. 1985, Strømgaard 1992). Warming decreased the availability of Al^{3+}, but fire increased it even 9 yr later (Tables 1 & S1–S4). An increase in extractable Al in surface and deeper ash layers (Smith 1970) and an increase in Al^{3+} released from the residual ash of *Poa* spp. (Costin et al. 1952) might account for this trend.

4.3. Temperature and moisture

Increased temperature in the OTCs was associated with decreased soil moisture, which is an effect noted by others (Klein et al. 2005, Dabros et al. 2010, Liancourt et al. 2012). In our study, experimental warming consistently decreased soil moisture and increased ambient temperatures and subsurface soil temperatures. Therefore, the changes in nutrient availability mainly resulted from warmer ambient temperatures, and warmer and drier soils. A drier soil will reduce nutrient mobility and mineralization, reduce plant uptake of nutrient ions, and has been predicted to alter plant productivity and phenology more than changes in nutrient availability (Ernakovich et al. 2014).

In addition to these effects of warming and drying, drying–rewetting cycles frequently occurred throughout our experiment, with moisture fluctuations of up to 10% volumetric water content (Fig. 4). Such cycles have been found to expose soil organic matter to leaching and microbial degradation, to alter plant nutrient availability (Gordon et al. 2008, Zheng et al. 2013) and to release N and P (Blackwell et al. 2010, 2013, Butterly et al. 2011). The increased NH_4^+ and $H_2PO_4^-$ availability in OTCs might partly result from these cycles of drying–rewetting.

At Site 1, the availability of individual nutrients co-varied with ambient temperature and soil moisture (Table 2). This indicated that the increased NH_4^+ and decreased Ca^{2+} and Al^{3+} with experimental warming were associated with warmer ambient temperatures rather than with drier soil. The marginal increase in $H_2PO_4^-$ with experimental warming was associated with both warmer ambient temperature and higher soil moisture. In summary, we expect further warming in the Australian Alps to influence the availability of N, P, Ca and Al.

5. CONCLUSION

The warmer and drier conditions in the OTCs reflect the warmer and drier climate predicted for the Australian Alps, and thus our results are directly relevant to sub-alpine heathlands in Australia and possibly to other sub-alpine regions worldwide. Warming and drying increased ambient and soil subsurface temperatures, and decreased soil moisture, which affected the cumulative fluxes of all measured nutrients. Warmer conditions increased the availability of NH_4^+, K^+, Na^+ and $H_2PO_4^-$, but decreased Al^{3+}, Ca^{2+} and Mg^{2+}. Nine years post-fire led to increased availability of Al^{3+}, but a depletion of Mn^{2+}. These results indicate that global warming will affect nutrient availability in sub-alpine soils.

Changes in available nutrients together with abiotic and biotic responses to warming and drying are likely to significantly affect vegetation structure and composition. Increased NH_4^+ can favour the growth of graminoids and change species diversity, and the varying nutrient uptake and growth rates among distinct plant groups can alter competitive interactions. The increased availability of P can alter microbial and plant dynamics, and potentially decrease species richness. Decreased Al^{3+} with warming, and Mn^{2+} with fire, can increase the growth and abundance of Al- and Mn-sensitive plants, which, together with increased N, might favour the growth and abundance of exotic plants in the alpine region.

Changing nutrient levels, differential growth rates, differential nutrient uptake and the direct effects of warming and drying on plants are likely to have influenced the increased shrub cover in these heathlands (Wahren et al. 2013) and in other alpine and tundra systems (Tape et al. 2006). Continued warming and drying in the Australian Alps will select against growth forms that are less tolerant of drought and favour drought-tolerant species (e.g. the shrub *Grevillea australis*), which is a current trend that is expected to increase. A likely long-term consequence of such change is the continued expansion of sub-alpine heathlands, a decrease in species diversity and more extensive and severe fires. These are serious threats to a landscape of such high conservation, scientific and cultural significance.

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