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SOIL RESEARCH

Nitrogen dynamics in alpine soils of south-eastern Australia

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ABSTRACT

Context. The Australian Alps are recognised by UNESCO as a globally significant mountain range. Soils underpin all of these ecosystem services. However, sparse data exists on alpine soils. **Aims and methods.** We explored nitrogen dynamics of soils from four high mountain sites, using a combination of new and established field and laboratory techniques. **Key results.** Organic and inorganic N were of the same order of magnitude, with around twice as much inorganic N as organic N. Forty three small (<250 Da) organic N compounds were detected, with concentrations 30 times greater in microbial and salt-extractable pools than free in the soil solution. The net N mineralisation rate decreased four-fold over the growing season. The organic matter decomposition rate was close to the global mean ($k = 0.017$), while the stabilisation factor was high (0.28) in comparison with other ecosystems globally. **Conclusions.** These results begin to illuminate the complexity of the belowground processes that have formed the high C soils of the Australian Alps. The combination of moderate turnover times and high stabilization of organic matter support Costin's theory that these mountain soils formed in place as a result of biological activity, rather than reflecting their geological substrata. The pools of organic N adsorbed to mineral soil surfaces and bound up within microbes lend support to a theory of tight N cycling, with little organic or inorganic N free in the soil solution. **Implications.** This new knowledge of soil N dynamics can support land managers to design successful restoration works to preserve alpine soil ecosystem services impacted by climate change, feral animal disturbance, weed invasion and the increase in summer tourism infrastructure.

Keywords: Alps, capillary electrophoresis-mass spectrometry, decomposition, ion exchange resins, mountain soils, organic N, soil organic matter, TeaBag Index.

Introduction

Soils of the Australian Alps are already being impacted by climate change (Worboys *et al.* 2011). As ambient temperatures increase, snowpack depth and duration decrease, and the timing of spring snowmelt is becoming highly variable (Steger *et al.* 2013; McGowan *et al.* 2021). These abiotic drivers are likely to affect soil temperature and water content, and subsequently impact soil carbon and nitrogen cycling (Brooks *et al.* 1998; Glanville *et al.* 2012). Australian alpine soils are unusually well developed in comparison with alpine soils globally, due to their old age, relatively warm temperatures and the strong influence of biological activity in their formation (Costin 1955). As such, the soils of the Australian Alps provide a suite of nationally important ecosystem services. Water provisioning has long been recognised as a key service provided by alpine soils (Costin 1955); indeed, water catchment protection underpinned the establishment of national parks across the region (Costin 1952). The biodiversity that soils of the Australian Alps contribute to, both directly and as the life support system for terrestrial flora and fauna, has been internationally recognised (UNESCO 2019). More recently, the ecosystem service of carbon storage has been recognised as a potentially important function that soils of the Australian Alps provide (Wilson *et al.* 2022).

Management of the Australian Alps to preserve and retain these ecosystem services as the climate changes faces a myriad of challenges. In addition to the direct impact of warmer temperatures and less snow, increased impacts from feral animals, invasive plants and summer tourism (McDougall and Broome 2007) threaten the water provisioning,

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biodiversity and carbon storage services that the soils of the Australian Alps provide. Despite their national and international value, a recent review of the scientific understanding of the properties and functioning of Australian Alpine soils found scant research and no in-depth studies of C and N cycling (Wilson *et al.* 2022). Early work focused on soil genesis *in situ* (Brewer and Haldane 1973), followed by recognition of the importance of aeolian dust inputs (Johnston 2001) and more recently, differences in the forms of organic phosphorous in comparison with Australian soils from hotter, drier areas (Doolette *et al.* 2017). The most comprehensive alpine soil study to date surveyed soil from 219 locations across the mainland and Tasmanian Alps and documented the total C and N content, as well as inorganic N content, from 0 to 5 cm depth (Kirkpatrick *et al.* 2014). While the results of Kirkpatrick *et al.* (2014) confirm the long-held view that alpine soils are some of the nation's highest in carbon, understanding organic matter decomposition and fluxes of N is required for scientifically-grounded management of alpine areas. Organic N represents a key knowledge gap because it was not considered in past studies in the Australian Alps, yet is likely of special importance in these alpine soils, based on predictions organic N dominates in low productivity systems (Schimel and Bennett 2004) such that organic N pools are larger than inorganic N at infertile, low productivity sites (Nordin *et al.* 2001; Farrell *et al.* 2011).

Plant nutrition in the context of restoration works to preserve alpine soils' ecosystem services could benefit from a detailed understanding of the nitrogen and carbon dynamics of mountain soils (Jiang *et al.* 2017). Restoration practices are an evolving field, adaptive management of complex systems in flux. Current understanding of the nutrient requirements to support alpine plant and soil restoration is based on conventional agricultural and horticultural soil chemistry approaches. New techniques have demonstrated that, in subalpine soils, a multitude of hitherto unknown organic N compounds occur (Warren 2014*a*). Furthermore, it is now possible to distinguish between N in three biologically relevant pools within the soil; N that exists free in the soil solution (free N), N that exists bound to mineral surfaces (the majority of which is extractable with a weak salt solution, salt-extractable N) and N that exists within the bodies of soil microbes (microbial N) (Warren 2015). We combined new and more established field and laboratory techniques to explore organic and inorganic nitrogen in these three pools within high mountain soils from the Australian Alps. The specific aims of this study were to: (1) describe the organic N compounds present; (2) quantify the amount and seasonal availability of inorganic N; and (3) ascertain a globally comparable organic matter decomposition rate and stabilisation factor. This new knowledge of the dynamics of nitrogen in pools that are more and less available to plants, and more and less impacted by increased temperatures and decreased water availability, will add to the toolbox of mental models that land managers and alpine restoration practitioners use to inform their work to preserve the nation's alpine ecosystem services.

Materials and methods

Site description

The study was undertaken on the Bogong High Plains in the Alpine National Park at four low-relief mountain summits or exposed sites: Mt Jim (36.913°S, 147.211°E; 1797 m asl); Ruined Castle (36.877°S, 147.253°E; 1776 m asl); Knoll (36.905°S, 147.214°E; 1818 m asl); and Marum Point (36.870°S, 147.342°E; 1796 m asl). The vegetation at all sites is grassy open heathland dominated by patches of the shrubs *Orites lancifolius* F.Muell., *Grevillea australis* R.BR. (Proteaceae) and *Hovea montana* (Hook.f.) J.H.Ross (Fabaceae), with *Poa hiemata* Vickery (Poaceae) and *Craspedia* sp. G.Forst. (Asteraceae) and other forbs present in and around the patches of shrubs. The region has a subpolar oceanic climate (Cfc) with cool summers and cold, snowy winters in accordance with the Köppen Climate Classification (Beck *et al.* 2018). Mean annual minimum and maximum temperatures for the Bogong High Plains are in the range 2.7–9.5°C, with frequent frosts (>100 per annum, occurring at any time of year) and high mean annual precipitation of around 2417 mm (Bureau of Meteorology), much of which falls as snow between June and September. Acidic silty loam soils occurred at all sites, with low bulk density and high organic carbon content (see Supplementary Table S1), consistent Costin's (1954, 1955) description of Alpine Humus Soils.

Sample collection

Soil was sampled from each of the four mountain ridge top sites. A hand trowel was used to sample surface soil (0–10 cm) from three locations on each high mountain site: three subsamples were combined to create a composite sample and this was done in duplicate. The 0–10 cm depth was selected for this study because enzyme activity was reasoned to be highest in surface soils due to inputs of leaf litter onto the soil surface coupled with most roots being in the upper 10 cm. The 24 resultant soil samples were processed within 12 h of collection to minimise nitrogen transformations.

In situ quantification of net nitrogen mineralisation and organic matter decomposition

The net nitrogen mineralisation rate was measured *in situ* with ion exchange membranes (IEMs: Membranes International), a widespread approach to quantifying net nitrogen mineralisation in mineral soils (Hovenden *et al.* 2008; White-Monsant *et al.* 2015). Nitrate was not measured as previous studies

suggest that exchangeable ammonium is the dominant form of inorganic N in these soils, where low pH inhibits nitrification (White-Monsant *et al.* 2015, 2017). Ion exchange membranes were loaded with H^+ by shaking for 90 min in 0.5 M HCl. Primed membranes were rinsed thoroughly in deionised water, attached to plastic nursery tags and stored moist in sealed plastic bags prior to deployment in the field. At each high mountain site, 18 ion exchange membranes were carefully installed into slots cut into the soil (0–10 cm) in the same design as described above for soil sample collection. Ion exchange membranes were retrieved after 1 month, in December, January and February, synchronised with the teaBag study below. The inorganic NH_4^+ that had exchanged onto the resin membranes was extracted by shaking for 60 min in 0.5 M HCl. This extract was analysed colorimetrically as described below.

Organic matter decomposition

Organic matter decomposition was quantified using the TeaBag Index, as described in Keuskamp *et al.* (2013). Rooibos and green tea bags were incubated in the soil at 5 cm depth for each mountain ridgetop site. Six replicate green tea bags were incubated at each site for three 30-day periods spanning the growing season ($n = 72$). Ten replicates of both green and rooibos tea bags were incubated at each site for the entire 90 days ($n = 120$). Bags were weighed to three decimal places before and after incubation. Moisture was accounted for by oven drying at 70°C before (control bags only) and after (all bags) field incubation. Decomposition rate (k) and the stabilisation factor (S) were calculated from the mass loss of the green tea and the rooibos tea following the two pool decomposition model equations described in Keuskamp *et al.* (2013).

Ex situ quantification of organic nitrogen compounds and ammonium

Soil extractions for inorganic and organic nitrogen

Nitrogen was extracted from three different pools within the soil: (1) N that exists free in the soil solution (free N); (2) N that exists bound to mineral surfaces (salt-extractable N); and (3) N that exists within the bodies of soil microbes (microbial N), following (Warren 2014*b*), with adaptation of the chloroform fumigation method of extracting microbial biomass N (Brookes *et al.* 1985) to add chloroform directly to the extraction solution, as described in (Warren 2015). An 8.0-g subsample of 2-mm sieved field moist soil was weighed into 50 mL Falcon tubes. Nitrogen in the soil solution (free N) was extracted with 40.0 mL milliQ water. Labile N on soil surfaces plus N in the soil solution (salt-extractable + free N) was extracted with 40.0 mL 0.5M K_2SO_4. Microbial biomass N plus labile N plus soil solution N (microbial + salt-extractable + free N) was extracted with 40.0 mL 0.5M K_2SO_4 and 1.0 mL chloroform. Falcon tubes were shaken at 100 rpm for 15 min (free) or 60 min (salt-extractable + free and microbial + salt-extractable + free) and the extractant was filtered through N-free Whatman #1 cellulose filter paper. Extracts were frozen at −80°C until analysis. Results are presented as free, salt-extractable and microbial N, with the later two calculated by difference.

Capillary electrophoresis-mass spectrometry profiling of small organic N compounds

Capillary electrophoresis-mass spectrometry (CE-MS) was used for profiling of small organic N in the free and microbial + salt-extractable + free extracts, as described previously (Warren 2013*a*). To pre-concentrate samples prior to analysis, soil extracts were concentrated 20-fold by evaporating under reduced pressure (Vacufuge, Eppendorf, Hamburg, Germany), then taken up in a solution of 100 mM ammonium formate in 25% (v/v) acetonitrile that contained internal standards (0.4 μg mL^{-1} of methionine sulfone and homospermidine-d_4). Samples were analysed with a capillary electrophoresis system (P/ACE MDQ, Beckman-Coulter, Fullerton, CA, USA) and bare fused silica capillary (50 μm i.d. × 100 cm long) interfaced to an ion trap mass spectrometer (AmaZon SL, Bruker Daltonics, Bremen, Germany). Sheath liquid of 50% (v/v) methanol with 0.1% (v/v) formic acid was infused at 4 μL min^{-1} into a co-axial sheath-flow sprayer (G1607A, Agilent, Waldbronn, Germany). Samples were injected at 3 psi for 30 s and separated with an electrolyte of 2 M formic acid with 20% (v/v) methanol under 30 kV positive polarity. The mass spectrometer detected compounds in positive mode from m/z 50 to 255. For compound identification, composite samples were analysed under the same electrophoretic conditions but with the mass spectrometer obtaining data-dependent MS^2 spectra (Warren 2013*a*, 2013*b*).

Inorganic N: total ammonium

The amount of inorganic N in extracts from the ion-exchange resins (net N mineralisation rate) and each of the three N pools was measured colorimetrically, as described in Willis *et al.* (1996). Briefly, 200 μL of extract solution was shaken with 2.7 mL of the colouring reagent (32 g L^{-1} sodium salicylate, 40 g L^{-1} trisodium phosphate and 0.5 g L^{-1} sodium nitroprusside) and 0.75 mL of hypochlorite solution (50 mL L^{-1}) in a 10 mL Falcon tube. Absorbance at 685 nm was measured with a dual wavelength UV-Vis spectrometer 528 (Cintra 10e, GBC scientific, Melbourne, Australia) and the concentration of NH_4^+ was determined using a calibration curve.

Results

CE-MS detected 43 small (<250 Da) organic N compounds, of which 42 could be positively identified (Figs 1 and 2). The total concentration of measured small organic N compounds was around 30 times as large in microbial + salt-extractable N pools as in the free N pool. All soil extracts contained all protein amino acids except cysteine. Protein amino acids were the single most abundant compound class and comprised 78% of the free N pool and 59% of microbial + salt-extractable N pools. Four non-protein amino acids (i.e. amino acids other than the standard 20 that are genetically encoded, subsequently abbreviated as non-protein AA) were identified (Orn, γ-aminobutyric acid, citrulline, theanine) and they together accounted for 6–9% of the measured organic N compounds. Quaternary ammonium compounds (betaine, carnitine, acetyl carnitine, choline, hercynine, proline betaine, trigonelline, subsequently abbreviated as QAC) accounted for 12–13% of measured organic N compounds. Alkylamines (aliphatic (poly)amines) were at or below detection limits in the free N pool, but accounted for 19% of microbial + salt-extractable N pools. The remainder of the small organic N compounds detected comprised a modest pool of nucleobases + nucleosides (0.6–1.8% of the measured small organic N compounds), while a further <2% was accounted for by the peptide Pro-Xle or Xle-Pro, and an unknown.

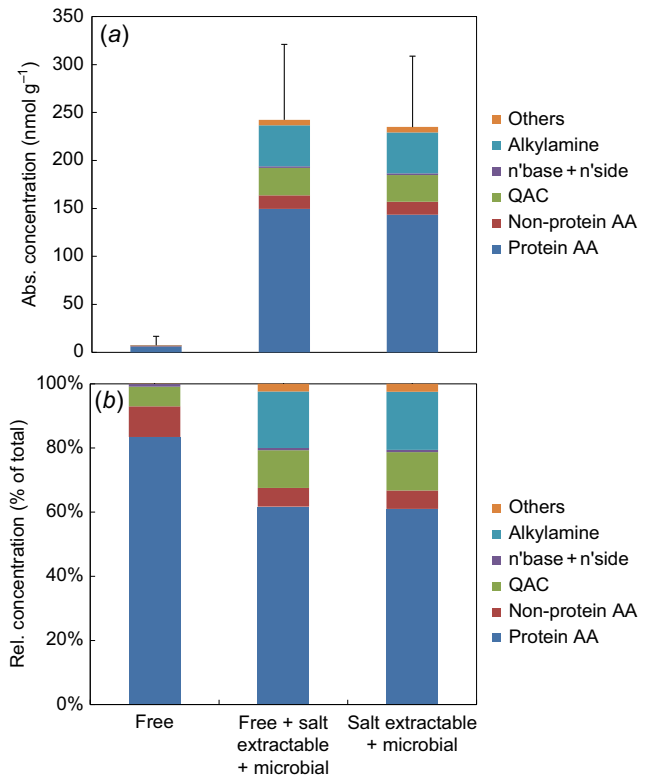

Fig. 1. Absolute (*a*) and relative (*b*) concentrations of major classes of monomeric organic N compounds in the free N pool (H_2O extracts); the microbial + salt-extractable + free N pools (K_2SO_4 with $CHCl_3$ extracts); and the microbial + salt-extractable pools (K_2SO_4 with $CHCl_3$ extract minus H_2O extract). Abbreviations are: protein AA, protein amino acids; non-protein AA, non-protein amino acids, alkylamines (aliphatic amines); n'base + n'side, nucelobases + nucleosides; QAC, quaternary ammonium compounds; others, ectoine + 1 peptide + 1 unknown. Data are means of the four sites and three replicates per site (i.e. $n = 24$), error bars are one s.e.

In addition to the large difference in concentrations between the free N pool and the microbial + salt-extractable N pools, there were large differences in relative compound concentrations. The general trend was for compounds and classes that are more basic to be relatively more abundant in microbial + salt-extractable N pools than in free N pool. For example, the five most abundant protein amino acids in the free N pool were Glu 12.0% of total, Ala 10.8%, Gly 9.1%, Asp 5.8%, Val 5.7%, whereas in the microbial + salt-extractable N pools arginine was the most abundant protein amino acid accounting for 14.9% of the measured organic N compounds. Moreover, alkylamines (aliphatic (poly)amines) were at or below detection limits in the free N pool, but accounted for 19% of microbial + salt-extractable N pools.

Among nucleobases + nucleosides, guanine was more abundant in the free N pool (1.0%) than in the microbial + salt-extractable N pools (0.1%), whereas cytidine was not detected in the free pool but accounted for 0.23% of the total in the microbial + salt-extractable N pools.

Among NPAA, Orn was more abundant in the free N pool (5.9% of total) than in the microbial + salt-extractable N pools (0.5%), while GABA was less abundant in the free N pool (2.3%) than in the microbial + salt-extractable N pools (4.7%).

Among QACs, choline and carnitine were relatively more abundant in the free N pool (4% of total vs 2–3% of total for the microbial + salt-extractable N pools) while betaine was more abundant in the microbial + salt-extractable N pools (7% of total vs 3% of total for the free N pool).

Inorganic nitrogen was present in all three pools within the soil; with more than twice as much bound to the mineral component of the soil (salt-extractable) compared with either the soil solution (free N) or the microbial N pool (Table 1). Inorganic N was readily exchangeable throughout the growing season, despite an almost five-fold decrease in the net N mineralisation rate from November to February (Table 2). Organic matter decomposition exhibited a different pattern, with a peak in decomposition in mid summer (Table 3). The rate of decomposition (k) and the stabilisation factor (S) were quantified over the whole study period from November to February, with values of 0.017 and 0.28, respectively (Table 3).

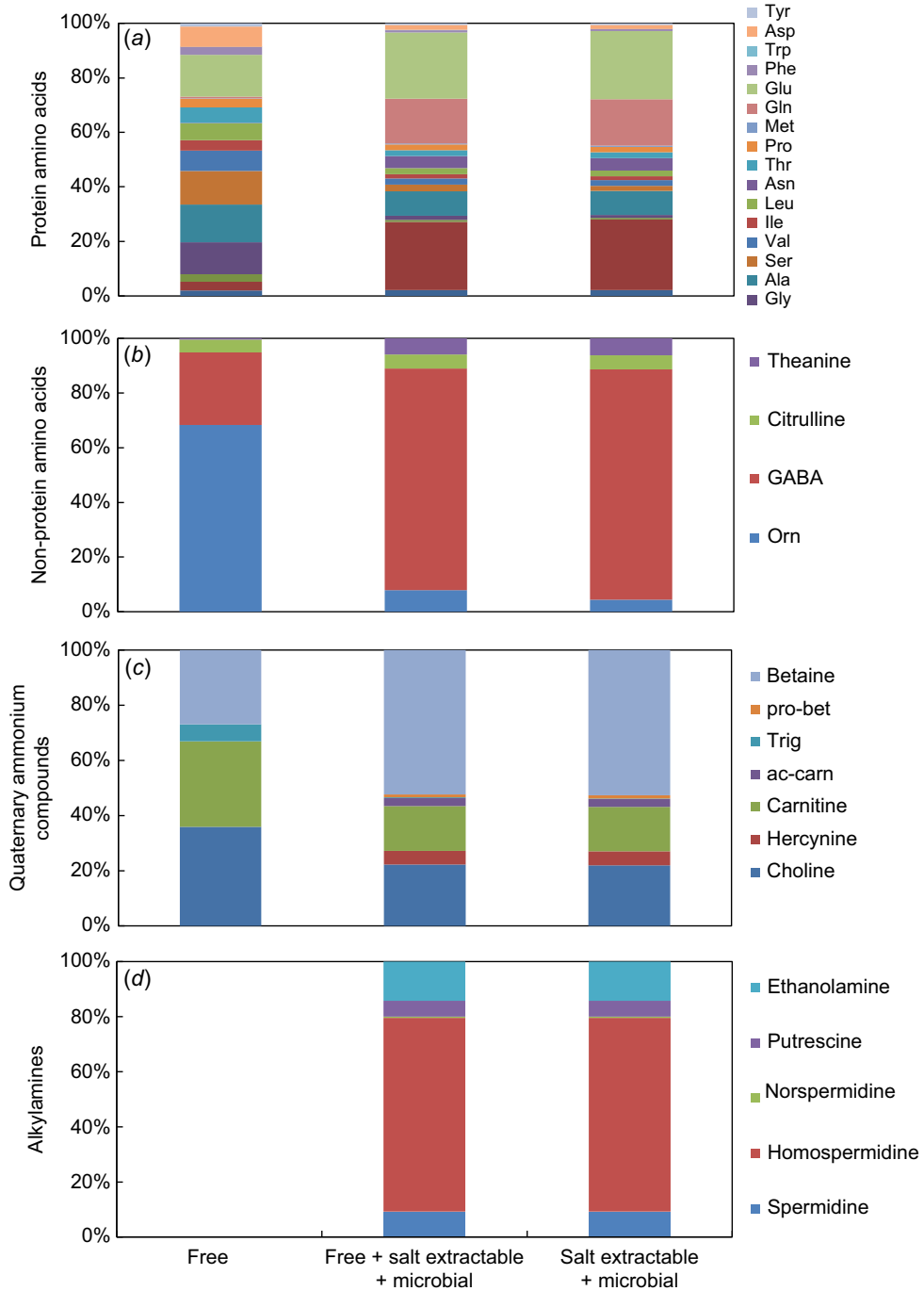

Fig. 2. Contribution of individual compounds to classes of protein amino acids (*a*), non-protein amino acids (*b*), quaternary ammonium compounds (*c*) and alkylamines (*d*) in the free N pool (H_2O extracts); the microbial + salt-extractable + free N pools (K_2SO_4 with $CHCl_3$ extracts); and the microbial + salt-extractable pools (K_2SO_4 with $CHCl_3$ extract minus H_2O extract). Data are means of the four sites and three replicates per site, duplicate samples from each replicate (i.e. $n = 24$). Abbreviations are; standard three-letter abbreviations for protein amino acids; GABA, γ-aminobutyric acid; pro-bet, proline-betaine; ac-carn, acetyl-carnitine.

Table 1. Ammonium concentrations in three pools within the soil; note the first three columns are directly measured and the last two columns are calculated by difference, $n = 96$.

	NH_4^+ nmol g^{-1}				
	Free	Free + salt-extractable	Free + salt-extractable + microbial	Salt-extractable	Microbial
Average	142.7	500.8	590.2	358.2	89.3
s.d.	55.2	317.4	341.5		

Table 2. Net N mineralisation rate (N min) in the soil solution over three 30-day periods during the Australian Alpine summer growing season. 10 cm^2 resin extraction membranes were buried at 0–10 cm for each period, $n = 72$.

	N min (nmol cm^{-2} day^{-1})		
	November–December	December–January	January–February
Average	12.9	7.8	3.0
s.d.	43.3	17.3	6.0

Table 3. Organic matter decomposition (mass loss) over three 30-day periods during the Australian Alpine summer growing season ($n = 72$), decomposition rate (k) and stabilisation factor (S) over the whole 90-day period ($n = 120$), following (Keuskamp *et al.* 2013).

	Decomposition mass loss (% day^{-1})			Decomposition rate (k)	Stabilisation factor (S)
	November–December	December–January	January–February	November–February	
Average	1.3	2.6	1.8	0.017	0.28
s.d.	0.3	0.2	0.5	0.0007	0.09

Discussion

Organic and inorganic nitrogen in high mountain soils

This is the first study to quantify organic and inorganic N from the three biologically relevant pools within the soil in high mountain soils. We described 43 small organic N compounds across the free N pool and the microbial + salt-extractable pools (Fig. 1). Previous studies on organic N have generally focused on the soil solution (the free pool) and even in that simpler framework, knowledge of organic N molecules beyond amino acids and hexosamines is poor (Warren 2014*a*). Small organic N and inorganic N were our focus for two reasons. First, small N compounds occupy a central (and often rate-limiting) step in N cycling because high molecular weight organic N has to depolymerise to small organic N and mineralise to ammonium before it becomes available for microbial and plant nutrition (e.g. Schimel and Bennett 2004). Second, some small organic N compound classes are not products of organic matter breakdown but instead products of microbial synthesis (e.g. Welsh 2000; Fujihara 2009) and thus can serve as indicators of microbial populations and physiology.

Small organic N compounds and inorganic N are potentially bio-available, thus by measuring pools of both we obtain a clearer picture of N availability. The total sum of small organic N compounds measured in the salt-extractable + microbial pools was of the same order of magnitude as inorganic N (250 and 590 nmol g^{-1}, respectively, Fig. 1 and Table 3). Previous studies have only measured inorganic N (Kirkpatrick *et al.* 2014; White-Monsant *et al.* 2015, 2017). Our results demonstrate the importance of considering both organic and inorganic N in attempting to better understand nutrient cycling in mountain soils.

The suite of small organic N compounds detected in these alpine soils (Figs 1, 2) was consistent with previous studies for a range of ecosystems including subalpine grassland soils from New South Wales (Warren 2013*a*, 2013*c*, 2014*c*). Protein amino acids were the single most abundant compound class (>80% free pool, >60% salt-extractable + microbial pools, see Fig. 1), and the composition of the amino acid pool was broadly similar to other studies. This is consistent with suggestions the mix of protein amino acids differs little among soils (Bremner 1966; Sowden *et al.* 1977) because the cycling of small organic compounds derived from depolymerisation (e.g. protein amino acids) is conservative and unaffected by community composition (van Hees *et al.* 2008).

A significant fraction of small organic N was comprised of compounds that are products of microbial synthesis (Figs 1, 2), and thus could provide clues to microbial populations or physiology. Notable among these other compound classes were: (a) quaternary ammonium compounds (QAC), which are often associated with abiotic stress tolerance (Warren 2014*c*) and accounted for 12–13% of measured organic N compounds in the free pool and the salt-extractable + microbial pools; and (b) non-protein amino acids, which comprised 6–9% of small organic N and tend to be species specific in microbes (Miller 1961) and differ among soils (Warren 2017). Alkylamines (aliphatic (poly)amines) were below detection limits in the free pool; however, this compound class accounted for a substantial 19% of organic N compounds in salt-extractable + microbial pools. Reports of alkylamine composition of soil are rare, but there is emerging evidence the pool can be large and its chemical composition may differ among soils (Warren 2014*b*). For example, a previous study on sub-alpine grassland soil reported a similarly large pool of alkylamines, but in contrast to the soils here ethanolamine was abundant and the free pool contained large amounts of aminobutylhomospermidine and putrescine (Warren 2014*b*). Thus, even among broadly similar alpine vs sub-alpine soils there are substantial differences in chemical composition of the alkylamine pool that probably reflect underlying differences in microbial populations.

Seasonal availability of inorganic nitrogen

The seasonal availability of inorganic N, quantified via the net N mineralisation rate, decreased over the course of the growing season (Table 2), consistent with strong N uptake associated with plant growth. This pattern was out of alignment with the seasonal mass loss quantified using the TeaBag Index. The seasonal mass loss results (Table 3) indicated that organic matter decomposition increased early in the growing season and then decreased again later in the season. This pattern can be explained by microbial activity inhibition due to low temperatures early in the season and due to lack of soil water late in the season. This out-of-phase pattern of nitrogen availability and organic matter decomposition suggests that, while both plant growth and organic matter decomposition can be expected to increase as temperatures increase, interactions with soil water content may result in a lack of nutrient availability in the Alps as snow cover and duration decrease. Soil water content can be driven by snow cover well beyond the snow season (Williams *et al.* 2009; Bilish *et al.* 2019).

Organic matter decomposition and stabilisation

This study was able to ascertain a globally comparable rate of organic matter decomposition (Table 3). The organic matter decomposition rate of mountain-top soils in the Australian Alps, as quantified using the TeaBag Index, is mid-range, in comparison with ecosystems globally (Keuskamp *et al.* 2013). The decomposition rates measured in this study are almost twice as high as those recorded with the same technique in a similar Australian alpine soil (Venn and Thomas 2021), however that study was conducted in a very different, sheltered, lee-side snowbed environment where snow cover can last up to 6 months and persist well into summer, insulating soils at a constant 0–1°C. Our rates are comparable with those measured at similar altitude in another southern hemisphere mountain TeaBag Index study (Becker and Kuzyakov 2018). However, at a latitude of 3°S, these similar altitude sites are forested. The rate of organic matter decomposition is central to nutrient cycling, as the microbial decomposition of plant litter and soil organic matter releases nutrients that growing plants can access (see fig. 1 in Venn and Thomas 2021). As such, the rate of organic matter decomposition quantified in this study (Table 3), in combination with the large number of small organic N compounds described (Figs 1, 2), suggests that nutrient cycling is active in the continent's highest soils. Organic matter decomposition rates are well known to be sensitive to temperature (Hartley *et al.* 2021) and thus land managers can anticipate that as temperatures rise, the rate of nutrient cycling in alpine soils may increase, with potential implications for vegetation composition and ecosystem function.

Organic matter stabilisation, as well as the decomposition rate, is important to understand in considering the future of the ecosystem services that alpine soils provide. While the decomposition rate that we quantified for Australian high mountain soils was mid-range, the stabilisation factor is high (Keuskamp *et al.* 2013). This global comparison, enabled by the use of the standardised TeaBag Index technique, helps us to understand the mechanisms behind the long held view that the soils of the Australian Alps are high in carbon, both on a national scale and on a global mountain scale (Costin 1955). Our results suggest that organic matter decomposition proceeds at a moderate rate but much of it is stabilised, which is consistent with Costin's theory of the genesis of Alpine Humus Soils – that they are largely independent of the underlying geology and these deep high C soils are a result of slow accumulation of organic matter from alpine grasslands combined with earthworm redistribution of underlying mineral material (Costin 1952, 1954). Deep high carbon soils have been able to build up in the Australian Alps because carbon is stabilised in these environments. The sensitivity of the stabilisation factor to climate change remains to be explored: this will be key to whether or not alpine soils are able to continue providing a carbon storage ecosystem service. The TeaBag Index has been proposed as an indicator of restoration success (MacDonald *et al.* 2018); the results from this study and the snowpatch work (Venn and Thomas 2021) could form the beginning of a baseline dataset against which land managers could reference the progress of restoration works aiming to preserve the mountain's water provisioning, biodiversity and carbon storage ecosystem services.

Conclusion

In conclusion, this study has demonstrated that organic N is abundant in high mountain soils of the Australian Alps. Both organic and inorganic forms of N are predominantly present in the microbial and salt-extractable pools, with less free N available in the soil solution. Nitrogen is available to plants and soil microbes throughout the growing season, which can be attributed to the ongoing breakdown of litter and soil organic matter measured with the TeaBag Index rate of organic matter decomposition. In comparison with other ecosystems around the globe, the organic matter decomposition rate was mid-range. Organic matter stabilisation, in contrast, was found to be high, using this globally comparable technique. Land managers tasked with preserving the ecosystem services provided by alpine soils now have a more nuanced understanding of their N dynamics. This new knowledge can lay the foundations for scientifically-based restoration works to retain water provisioning, biodiversity and carbon sequestration ecosystem services. However, the composition and functionality of alpine soil microbial

communities, key mediators of the cycling of C, N, P and hence plant nutrition, remains unknown and a multidisciplinary approach to soil health will be critical to monitoring, managing and preserving alpine ecosystems as the climate changes.

Supplementary material

Supplementary material is available online.

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