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# Nitrogen partitioning between plant species and soil microbes in alpine heath

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ABSTRACT

Nitrogen is rapidly taken up by plants and microbes, but questions remain as to which forms are preferred. Using *in situ* stable isotope labelling ($^{13}$C and $^{15}$N), we show that co-existing plant species of alpine heath mainly take up ammonium and nitrate, passing $^{15}$N from root to shoot over time, leading to accumulated nitrogen in the shoots (over 10-fold increase compared with roots), with more complex organic nitrogen forms such as amino acids taken up to a lesser extent. Conversely, soil microbes preferred amino acids, potentially as a side-effect of satisfying their carbon requirements to build cellular structures. We show that competition for nitrogen can be alleviated by differing growth rates in plants and varying microbial preference of nitrogen forms.

Despite the prevailing idea that vascular plants prefer inorganic nitrogen (N), there is mounting evidence that they take up a range of N molecules, including amino acids (Näsholm et al., 1998; Ma et al., 2021; Liu et al., 2025). Past work shows that fast-growing (often dominant) plant species generally prefer inorganic N (Weigelt et al., 2005; Harrison et al., 2007), given that more complex organic forms may be energetically expensive to take up (Raab et al., 1999; McKane et al., 2002; Bardgett et al., 2003). Evidence also points to slower growing dwarf shrubs showing a stronger preference for more complex molecular forms, particularly in ecosystems at higher latitudes, likely due to their mycorrhizal associations, which are stronger at lower temperatures (Näsholm et al., 1998; Hu et al., 2024). Soil microbes likely also use more complex N forms than plants due to their capacity to produce enzymes capable of degrading complex compounds. Here, the presence of N in the molecule could be incidental. Microbial requirements for carbon mean the N is taken up as well, and often excreted as ammonium through mineralisation-immobilisation turnover (Barraclough, 1997; Geisseler et al., 2009; Wilkinson et al., 2015). Therefore, inorganic N forms such as ammonium and nitrate may only be taken up by soil microbes when substrate C:N ratios are high (Hill and Jones, 2019). There is some evidence that microbes least prefer nitrate, with other N forms taken up first (Barraclough, 1997). However, in arctic and alpine ecosystems, low temperatures limit microbial activity in the soil, resulting in accumulation of organic matter and relatively high concentrations of dissolved organic N (Bardgett et al., 2007; Persson and Näsholm, 2001). Further, while microorganisms are highly competitive for N in the short-term, plants may be more competitive in the longer-term, but this is likely to be confounded by the enzymatic breakdown of complex amino acids into inorganic N (Harrison et al., 2007). Therefore, niche partitioning of N based on chemical form and temporal dynamics may facilitate plant-microbe coexistence (McKane et al., 2002), but substantial knowledge gaps remain as to how such processes operate *in situ*.

Here, we exposed co-existing alpine heath plant species, covering a range of growth rates and functional groups (dwarf-shrubs, graminoids and a forb), to mixtures of $^{15}$N-labelled inorganic and dual labelled ($^{13}$C and $^{15}$N) amino acids of varying molecular weights (MW, Table 1). We hypothesised that 1) N uptake is partitioned between plants and microbes, where microbes take up amino acids but can break these down and make N available to plants over time; 2) soil microbes take up more carbon-rich, complex N forms than inorganic forms; and 3) plants generally prefer inorganic N forms over amino acids, but faster growing, more dominant species take up higher amounts of inorganic N, while

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**Table 1**
Chemical properties of the six N forms.

| | Formula | C:N | Molecular weight |
|---|---|---|---|
| Ammonium | $NH_4$ | -[a] | 18 |
| Nitrate | $NO_3$ | -[a] | 62 |
| Glycine | $C_2H_5NO_2$ | 2 | 75 |
| Asparagine | $C_4H_8N_2O_3$ | 2 | 132 |
| Aspartic acid | $C_4H_7NO_4$ | 4 | 133 |
| Glutamic acid | $C_5H_9NO_4$ | 5 | 147 |

[a] Does not contain C.

slower growing dwarf shrubs may show a preference for amino acids.

The study was conducted in alpine heath on Glas Maol, Scotland (56°53′N, 3°22′W; 1000 m elevation; January/July average minimum/maximum temperatures: 5/-1 °C, 5/10 °C, respectively) in a plant community composed of, in increasing order of average dominance: *Galium saxatile* (forb), *Vaccinium vitis-idaea*, *V. myrtillus* (dwarf shrubs), *Carex bigelowii* (sedge) and *Festuca vivipara* (grass). In early spring, seventy plots (20 × 20 cm) were established across five blocks (14 plots per block) in a randomized block design (Fig. S1). Each plot contained all the aforementioned vascular plant species, which accounted for ~99% of total aboveground plant biomass within each plot. We created six solutions of 80 mg N $L^{-1}$ made up of a mixture of six equally weighted N forms (inorganic: ammonium [molecular weight 18], nitrate [62]; amino acids: glycine [75], asparagine [132], aspartic acid [133], glutamic acid [147]). The two inorganic N forms were labelled with 98% $^{15}N$, whereas the four amino acids were dual labelled with 98% $^{15}N$ and $^{13}C$. A seventh, control solution was made using only unlabelled compounds. Direct uptake of the amino acids by plants would be indicated by plant tissue enrichment of both $^{13}C$ and $^{15}N$ (Näsholm et al., 1998). In June, one of the labelled solutions was added to two randomly selected plots in each block. Each plot received 75 ml of labelled solution, via 25 × 3 ml injections in a 5 x 5 grid pattern across each plot, adding a total of 6 mg N to each plot. Using a soil bulk density of 0.35 g $cm^{-3}$ (Ayres et al., 2006) and a plot size of 20 × 20 × 5 cm, this additional N is equivalent to 1.4 μg $g^{-1}$ soil. A preliminary analysis of soil N pools revealed 5.2, 8.0 and 12.0 μg $g^{-1}$ soil of nitrate, ammonium and dissolved organic N, respectively. Therefore, the amount of added N was unlikely to markedly influence plant or microbial growth (Ravn et al., 2017).

To assess the temporal fate of $^{15}N$ and $^{13}C$, we collected turfs from the field experiment 2 and 45 days after labelling. At both sampling dates, seven turfs were taken from each block (one turf per labelled compound and the control). A 5 cm deep turf was removed from the central 15 × 15 cm of each plot and all vascular plant aboveground biomass was sorted by species within 24 h of turf collection, dried (60 °C, 48 h) and weighed to determine aboveground plant biomass. The soil was sieved (4 mm mesh) to collect the roots, and roots were dried (60 °C, 48 h) to determine community root biomass. Subsamples of shoot material from the five target species, as well as community root material, were ground for stable isotope analysis (Carlo-erba EA–DLT IRMS). The $^{15}N$ and $^{13}C$ in plant tissues were calculated according to standard methods, and correlations between $^{13}C$ and $^{15}N$ in each plant were assessed using Pearson's correlation coefficient to determine whether the molecule was taken up intact (Wanek and Arndt, 2002). Soil microbial biomass C and N were measured using fumigation-extraction (Brookes et al., 1985; Vance et al., 1987), and microbial biomass $^{15}N$ concentrations were determined by diffusion of extracted N onto acidified paper discs (MacKown et al., 1987). Microbial uptake of $^{15}N$ was calculated by dividing the excess $^{15}N$ by the microbial biomass N. We calculated rate-based metrics for N uptake into plants by dividing the total excess $^{15}N$ measured in each pool by the number of days from injection. $^{15}N$ budgets were calculated by multiplying the concentration of excess $^{15}N$

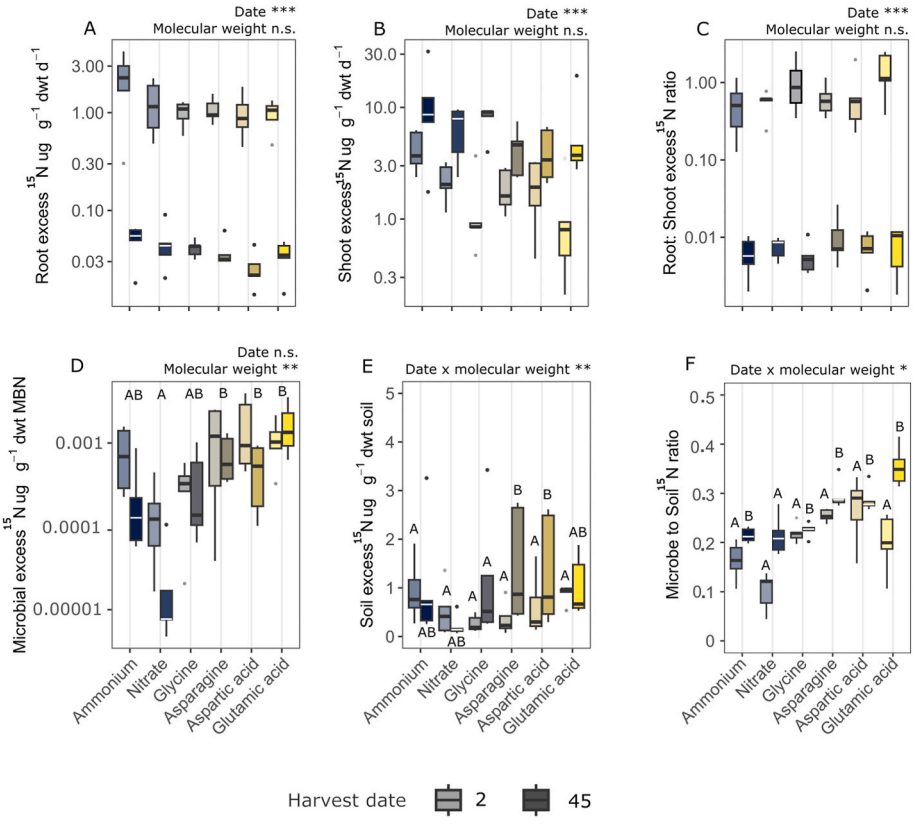


**Fig. 1.** Rate of uptake of different molecules with excess labelled $^{15}N$ across harvest dates for A) root uptake over time (Harvest date: $F_{1,44} = 384.02$, $p < 0.001$), B) shoot uptake over time (Harvest date: $F_{1,44} = 234.26$, $p < 0.001$; Molecular weight: $F_{5,44} = 6.83$, $p < 0.001$), C) Root to shoot $^{15}N$ ratio (Harvest date: $F_{1,44} = 58.95$, $p < 0.001$), D) microbial biomass $^{15}N$ content (Molecular weight: $F_{5,44} = 4.34$, $p = 0.003$), E) bulk soil $^{15}N$ content (Harvest date x Molecular weight: $F_{5,44} = 3.78$, $p = 0.006$), F) Microbial:Soil $^{15}N$ (Harvest date x Molecular weight: $F_{5,44} = 3.39$, $p = 0.011$). Significance stars refer to: *p < 0.05, **p < 0.01, ***p < 0.001.

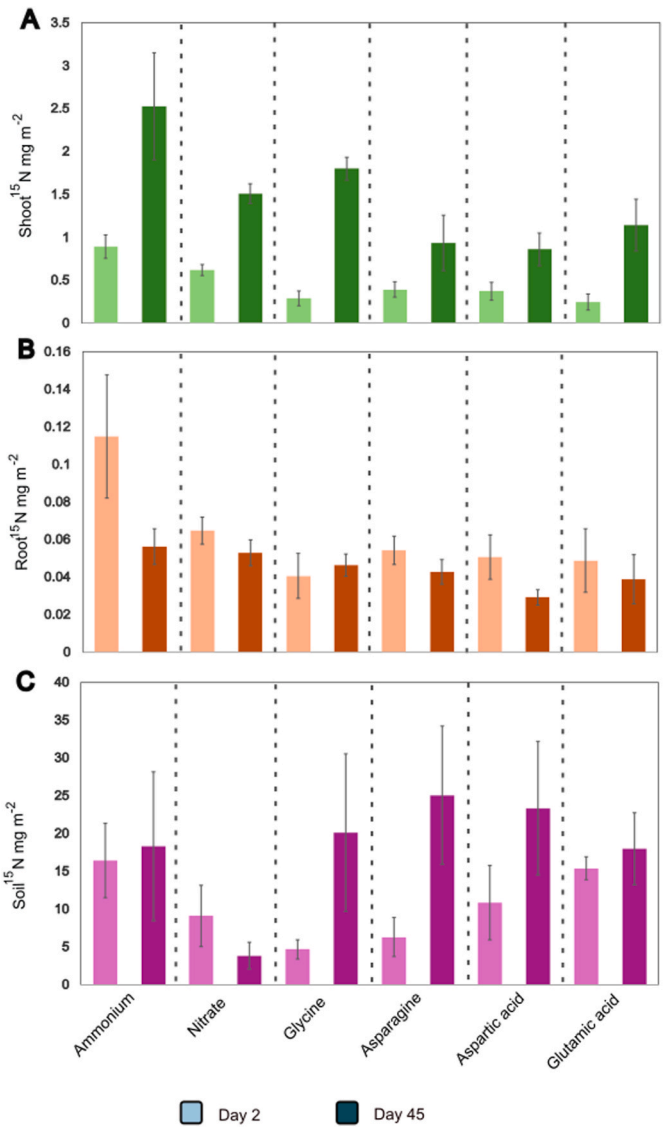


**Fig. 2.** Nitrogen budgets of the realised amounts of excess $^{15}$N in shoots, roots and soil on days 2 and 45. The initial amount of $^{15}$N added was 150 mg m$^{-2}$. Budgets were calculated by multiplying total biomass of each fraction, per turf, by the concentration of excess $^{15}$N and scaling by m$^2$. Soil mass is calculated to 5 cm deep at a bulk density of 0.35.

by the total turf level biomass of shoots, roots and microbes, or by the total weight of soil and scaling by area. Standard statistical analyses were then carried out (Text S1).

$^{13}$C uptake by plants was minimal, with some treatments losing $^{13}$C relative to the background (range: 5 - 11 μg g$^{-1}$ shoot dry weight per day). $^{15}$N uptake by roots slowed between days 2 and 45, as $^{15}$N accumulated in the shoots (Fig. 1).

Rate of uptake of excess $^{15}$N into the roots was significantly higher on Day 2 than 45 (Fig. 1A), but, while labelled amino acids appeared taken up at lower rates than labelled ammonium and nitrate, this was not statistically significant. The $^{15}$N budget for roots shows that the total amount of labelled ammonium and nitrate decreased between days 2 and 45, and labelled glycine and asparagine increased (Fig. 2). Shoots accumulated excess $^{15}$N at more rapid rates over the 45 days compared with the initial two days (Fig. 1B). In shoots there were also no effects of molecular weight, although again a slight downward trend with increasing molecular weight. The $^{15}$N budget confirmed the increase in $^{15}$N between days 2 and 45 in the shoots for all molecular forms (Fig. 2). Root to shoot ratios indicated greater (weight-corrected) retention by roots relative to shoots at day 2 than day 45 ($F_{1,44} = 88.22$, $p < 0.001$, Fig. 1C). This suggests that roots were pushing $^{15}$N rapidly through the plant regardless of initial labelled molecular type.

The correlation between $^{13}$C and $^{15}$N in shoot material could indicate direct uptake of the entire amino acid. However, we did not find strong evidence to suggest that large molecules were taken up intact by plants, and were more likely to have been mineralised by microbes and subsequently taken up by plants in inorganic forms (negative correlation; Table S1).

Excess $^{15}$N in the microbial biomass was not affected by harvest date, potentially indicating low turnover of the $^{15}$N through microbes (Fig. 1D). Retention of labelled nitrate by microbes was significantly lower than the three largest amino acids (Fig. 1D and 2). Further, there was a decline in nitrate, and to some extent ammonium, in microbial biomass between days 2 and 45. Nitrate must be reduced to ammonium through nitrate reductase before it can be used by microbes (Pan et al., 2023). Not all microbial taxa synthesise microbial reductase and for those that do, the energetic cost is high (Hiis et al., 2024). Therefore, nitrate uptake is often associated with low concentrations of ammonium in the soil (González et al., 2006). While ammonium is thought to be the preferred N form for microbial uptake, this tends to be the case when carbon rich molecules are abundant and was not the case in our study, as evidenced by the comparative rate of uptake of amino acids (Farrell et al., 2014). Additionally, ammonium can only be used by microbes if there are many carbon sources available to maintain cellular processes (Wilkinson et al., 2014). Taken together, it seems that in our study carbohydrates were low in the soil, meaning that nitrate and ammonium could not be effectively used by the microbes and were therefore discarded by day 45.

Soil excess $^{15}$N showed an interaction between date and molecular weight. The data in Fig. 1E shows that labelled N from both asparagine and aspartic acid accumulated in the soil on day 45 and were significantly higher than at day 2 and also accumulated in higher amounts than all the other molecular forms (Fig. 1E). The $^{15}$N budget shows that much labelled N was returned to the soil by day 45, which could indicate the microbial community had broken down the amino acids and retained the C, discarding excess N. The ratio of $^{15}$N uptake in microbes to soils also showed an interaction between date and molecular weight (Fig. 1F). On day 2 all ratios were the same between molecules, while on day 45 labelled ammonium, glycine, asparagine, aspartic acid and glutamic acid were significantly higher in microbes than the soil compared with nitrate. This trend indicated a clear preference by microbes for amino acids. Soil microbes are often C-limited, rather than N–limited due to generally low concentrations of available organic matter in soil and its physical and chemical protection (Lehmann and Kleber, 2015; Soong et al., 2020) and microbes synthesise enzymes capable of breaking down more complex C- and N-containing compounds (Daly et al., 2021). Our finding that microbes take up amino acids and retain them in their biomass, while nitrate uptake is extremely low, could be indicative of preference for amino acids. The fate of labelled nitrate that was lost from microbes between days 2 and 45, also seen in the $^{15}$N budget, is not explained by uptake into plant tissues or released to bulk soil (Fig. 2). Therefore, it is possible nitrate was denitrified to nitrogen oxide or leached to deeper soil layers so the N is not retained within microbial biomass. Nitrate leaching is one of the first signs of saturation of N in an ecosystem and is commonly observed in heathland (Phoenix et al., 2012). The $^{15}$N budget supports the likelihood of leaching and possibly denitrification, as it shows very low levels of labelled nitrate in all compartments on both days 2 and 45 (Fig. 2).

There are likely several factors contributing to the low recovery of all $^{15}$N forms observed in our study (150 mg m$^{-2}$ added compared with a maximum of 30 mg m$^{-2}$ total recovered on days 2 and 45), which is lower than reported in other labelling studies using similar approaches (Bardgett et al., 2003; Harrison et al., 2007). Potential reasons for this low recovery of $^{15}$N include the leaching or N to deeper soil layers and uptake by bryophytes, which wasn't accounted for in this study. Indeed,

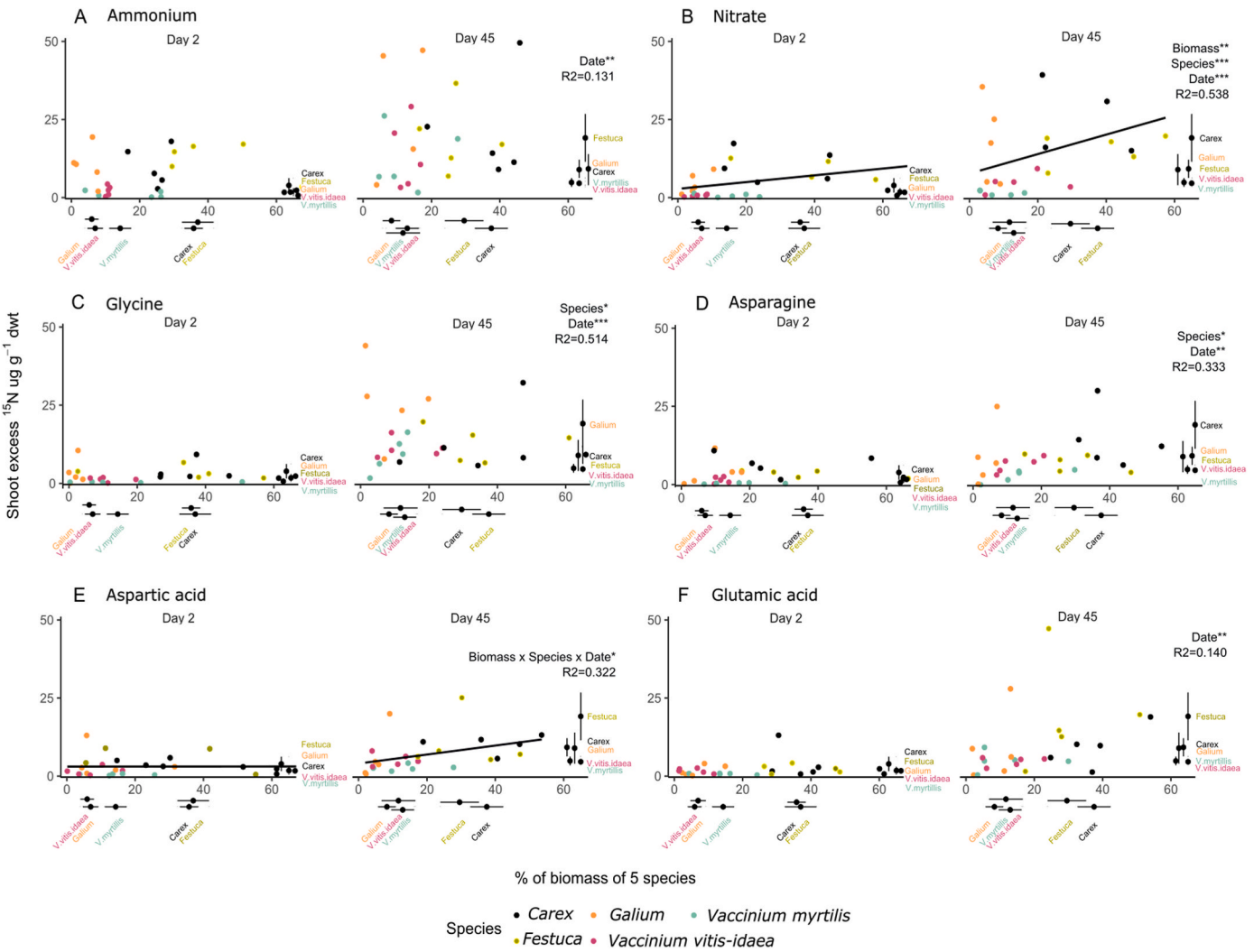


**Fig. 3.** Relationships between proportion of aboveground biomass of the five plant species and labelled $^{15}N$ uptake in the shoot biomass of each species on Day 2 and Day 45, presented by molecular weight of labelled N species. The black lines show the overall community trend where significant. The overarching model indicated highly significant interactions between harvest date and molecular weight: $F_{5,171} = 3.43$, $p = 0.006$; harvest date and biomass share: $F_{1,171} = 7.81$, $p = 0.006$; and molecular weight and species: $F_{20,171} = 2.08$, 0.006). See Table S3 for a simplified overview of $^{15}N$ uptake patterns and molecular weight-specific model output. The black points outside the graphs show the mean of the biomass share against the y axis and nitrogen uptake against the x axis for each species, with error bars representing standard error of the mean.

studies on fate of N indicate that N is commonly lost to deeper soil layers and that bryophytes can directly uptake $^{15}N$ from soil in these arctic (Ayres et al., 2006) and other heathlands (Ray, 2007; Phoenix et al., 2012). Albeit over longer timescales, other studies have also found comparably low retention of $^{15}N$ in the top 5 cm of soil (~20%) in the year after labelling (Andresen et al., 2023).

We observed a strong interactive effect between harvest date and the species' proportional share of community biomass on the concentration of shoot $^{15}N$, partially supporting our third hypothesis that fast growing, dominant plant species would take up N more rapidly than less dominant species (Fig. 3). On day 2, there was generally a neutral or weakly positive relationship between excess $^{15}N$ and increasing proportion of community biomass, while on day 45 the relationship tended towards positive or neutral except for glycine, which was slightly negative (Fig. 3). We did not find significant relationships between individual plant species abundance and shoot uptake of $^{15}N$, likely due to the small sample size. The two most dominant species in every turf were the sedge *Carex bigelowii* and the grass *Festuca vivipara*. In the case of ammonium, nitrate, glycine, aspartic acid and glutamic acid, where one species (e.g. *Carex*) was more dominant, the other, less dominant species (e.g. *Festuca*) took up more N, potentially indicating competition between the two species. Further, the forb *Galium saxatile* had very low relative abundance, often the lowest in the turf, but took up disproportionately high amounts of N for all forms, suggesting it is a highly acquisitive species. Our expectation in the third hypothesis was that the two *Vaccinium species*, as dwarf shrubs, would take up amino acids preferentially, but we found little evidence of that. Hill and Jones (2019) discussed the difficulty in identifying uptake of intact amino acids and suggested that a problem in definitively tracking $^{13}C$ could arise when background $^{13}C$ is high, which is potentially the case in alpine systems where decomposition is slow.

The partitioning of N forms by plants and soil microbes is a topic that has received relatively little attention, despite its potential importance for efficient N use in N limited ecosystems, such as alpine heath as studied here. Our findings indicate that over time $^{15}N$ from both inorganic forms and amino acids are retained in microbial and plant tissues. Fast-growing plants generally take up simpler forms of N and vascular plants and microbes have different preferences for chemical forms of N. We also found that plants that make up the highest proportion of community biomass tend to take up more $^{15}N$, but such biomass-N uptake relationships can differ at the community versus species level (Shen et al., 2024).

Here we showed that in alpine heath, partitioning of N based on chemical form occurs between plants and microbes. While we did not find evidence to determine whether amino acids were taken up by plants and microbes intact, we detected a clear preference for amino acids by microbes likely because of low availability of carbon. This is likely to arise through chemical or physical protection of soil organic matter from decomposition. Further, while higher plant biomass at a species level was associated with greater uptake for nitrate and aspartic acid, we showed that the two most dominant plant species did not follow the biomass-ratio hypothesis, which could indicate high plant-plant competition for N in these alpine heaths. The cold climate and low nutrient availability of these heathlands results in complex uptake patterns for plants and microbes as colimitation of nutrients, and competition for resources, result in constraints in effectively using nutrients when they become available.

## CRediT authorship contribution statement

**Ellen L. Fry:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Jonathan R. De Long:** Writing – original draft, Visualization, Investigation, Formal analysis. **Edward Ayres:** Methodology, Investigation, Data curation, Conceptualization. **René van der Wal:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Richard D. Bardgett:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Richard Bardgett, Rene Van der Wal reports financial support was provided by Lancaster University. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2026.110127.

## References

Andresen, L.C., Ambus, P., Beier, C., Michelsen, A., 2023. Moderate nitrogen retention in temeprate heath ecosystem after elevated $CO_2$, drought and warming through 7 years. European Journal of Soil Science 74, e13397.
Ayres, E., Van der Wal, R., Sommerkorn, M., Bardgett, R.D., 2006. Direct uptake of soil nitrogen by mosses. Biology Letters 2, 286–288.
Bardgett, R.D., Streeter, T.C., Bol, R., 2003. Soil microbes compete effectively with plants for organic-nitrogen inputs to temperate grasslands. Ecology 84, 1277–1287.
Bardgett, R.D., Van der Wal, R., Jónsdóttir, I.S., Quirk, H., Dutton, S., 2007. Temporal variability in plant and soil nitrogen pools in a high-Arctic ecosystem. Soil Biology and Biochemistry 39, 2129–2137.
Barraclough, D., 1997. The direct or MIT route for nitrogen immobilization: a $^{15}N$ mirror image study with leucine and glycine. Soil Biology and Biochemistry 29, 101–108.
Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil-nitrogen - a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biology and Biochemistry 17, 837–842.
Daly, A.B., Jilling, A., Bowles, T.M., Buchkowski, R.W., Frey, S.D., Kallenbach, C.M., Keiluweit, M., Mooshammer, M., Schimel, J.P., Grandy, A.S., 2021. A holistic framework integrating plant-microbe-mineral regulation of soil bioavailable nitrogen. Biogeochemistry 1–19.
Farrell, M., Prendergast-Miller, M., Jones, D.L., Hill, P.W., Condron, L.M., 2014. Soil microbial organic nitrogen uptake is regulated by carbon availability. Soil Biology and Biochemistry 77, 261–267.
Geisseler, D., Horwath, W.R., Doane, T.A., 2009. Significance of organic nitrogen uptake from plant residues by soil microorganisms as affected by carbon and nitrogen availability. Soil Biology and Biochemistry 1281–1288.
González, P.J., Correia, C., Moura, I., Brondino, C.D., Moura, J.J.G., 2006. Bacterial nitrate reductases: molecular and biological aspects of nitrate reduction. J. Inorg. Biochem. 100, 1015–1023.
Harrison, K.A., Bol, R., Bardgett, R.D., 2007. Preferences for different nitrogen forms by coexisting plant species and soil microbes. Ecology 88, 989–999.
Hiis, E.G., Vick, S.H.W., Molstad, L., Rosdal, K., Jonassen, K.R., Winiwarter, W., Bakken, L.R., 2024. UJnlocking the potential to reduce farmland $N_2O$ emissions. Nature 620, 421–428.
Hill, P.W., Jones, D.L., 2019. Plant-microbe competition: does injection of isotopes of C and N into the rhizosphere effectively characterise plant use of soil N? New Phytologist 221, 796–806.
Hu, C.-C., Liu, X.-Y., Driscoll, A.W., Kuang, Y.-W., Brookshire, E.N.J., Lü, X.-T., Chen, C.-J., Song, W., Mao, R., Liu, C.-Q., Houlton, B.Z., 2024. Global distribution and drivers of relative contributions among soil nitrogen sources to terrestrial plants. Nature Communications 15, 6407.
Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature 52, 60–68.
Liu, M., Xu, X., Wanek, W., Sun, J., Bardgett, R.D., Tian, Y., Cui, X., Jiang, L., Ma, Z., Kuzyakov, Y., Ouyang, H., Wang, Y., 2025. Nitrogen availability in soil controls uptake of different nitrogen forms by plants. New Phytologist 245, 1450–1467.
Ma, L.N., Xu, X., Zhang, C., Lv, Y., Liu, G., Zhang, Q., Feng, J., Wang, R., 2021. Strong non-growing season N uptake by deciduous trees in a temperate forest: a N-15 isotopic experiment. Journal of Ecology 109, 3752–3766.
MacKown, C.T., Brooks, P.D., Smith, M.S., 1987. Diffusion of N-15 Kjeldahl digests for isotope analysis. Soil Science Society of America Journal 51, 87–90.
McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B., Giblin, A.E., Kielland, K., Kwiatkowski, B.L., Laundre, J.A., Murray, G., 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415, 68–71.
Näsholm, T., Ekblad, A., Nordin, A., Giesler, R., Högberg, M., Högberg, P., 1998. Boreal forest plants take up organic nitrogen. Nature 392, 914–916.
Pan, W., Zhou, J., Tang, S., Wu, L., Ma, Q., Marsden, K.A., Chadwick, D.R., Jones, D.L., 2023. Utilisation and transformation of organic and inorganic nitrogen by soil microorganisms and its regulation by excessive carbon and nitrogen availability. Biology and Fertility of Soils 59, 379–389.
Persson, J., Näsholm, T., 2001. Amino acid uptake: a widespread ability among boreal forest plants. Ecology Letters 4, 434–438.
Phoenix, G.K., Emmett, B.A., Britton, A.J., Capron, S.J.M., Dise, N.B., Helliwell, R., Jones, L., Leake, J.R., Leith, I.D., et al., 2012. Impacts of atmospheric nitrogen deposition: responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. Global Change Biology 18, 1197–1215.
Raab, T.K., Lipson, D.A., Monson, R.K., 1999. Soil amino acid utilization among species of the Cyperaceae: plant and soil processes. Ecology 80, 2408–2419.
Ravn, N.M.R., Elberling, B., Michelsen, A., 2017. The fate of $^{13}C$ $^{15}N$ labelled glycine in permafrost and surface soil at simulated thaw in mesocosms from high arctic and subarctic ecosystems. Plant and Soil 419, 201–218.
Ray, N.D., 2007. Long Term Impacts of Nitrogen Deposition and Management on Heathland Soils and Vegetation. Manchester Metropolitan University, Manchester. PhD Thesis.
Shen, H., Dong, S., DiTommaso, A., Westbrook, A.S., Li, S., Zheng, H., Zhi, Y., Zuo, H., Wang, Q., Liu, J., 2024. Physiological factors contribute to increased competitiveness of grass relative to sedge, forb and legume species under different N application levels. Science of the Total Environment 906, 167466.
Soong, J.L., Fuchslueger, L., Marañon-Jimenez, S., Torn, M.S., Janssens, I.A., Penuelas, J., Richter, A., 2020. Microbial carbon limitation: the need for integrating microorganisms into our understanding of ecosystem carbon cycling. Global Change Biology 26, 1953–1961.
Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass-C. Soil Biology and Biochemistry 19, 703–707.
Wanek, W., Arndt, S.K., 2002. Difference in $\delta^{15}N$ signatures between nodulated roots and shoots of soybean is indicative of the contribution of symbiotic $N_2$ fixation to plant N. Journal of Experimental Botany 53, 1109–1118.
Weigelt, A., Bol, R., Bardgett, R.D., 2005. Preferential uptake of soil nitrogen forms by grassland plant species. Oecologia 142, 627–635.
Wilkinson, A., Hill, P.W., Farrar, J.F., Jones, D.L., Bardgett, R.D., 2014. Rapid microbial uptake and mineralization of amino acids and peptides along a grassland productivity gradient. Soil Biology and Biochemistry 72, 75–83.
Wilkinson, A., Hill, P.W., Vaieretti, M.V., Farrar, J.F., Jones, D.L., Bardgett, R.D., 2015. Challenging the paradigm of nitrogen cycling: no evidence of in situ resource partitioning by coexisting plant species in grasslands of contrasting fertility. Ecology and Evolution 5, 275–287.