Plant Soil (2008) 304:199–208
DOI 10.1007/s11104-008-9540-5

OpenAccess

REGULAR ARTICLE

Amino acid uptake among wide-ranging moss species may contribute to their strong position in higher-latitude ecosystems

Eveline J. Krab · Johannes H. C. Cornelissen · Simone I. Lang · Richard S. P. van Logtestijn

Received: 4 October 2007 / Accepted: 26 December 2007 / Published online: 29 January 2008

Abstract Plants that can take up amino acids directly from the soil solution may have a competitive advantage in ecosystems where inorganic nitrogen sources are scarce. We hypothesized that diverse mosses in cold, N-stressed ecosystems share this ability. We experimentally tested 11 sub-arctic Swedish moss species of wide-ranging taxa and growth form for their ability to take up double labelled (^{15}N and ^{13}C) glycine and aspartic acid in a laboratory setup as well as in a realistic field setting. All species were able to take up amino acids injected into the soil solution to some extent, although field uptake was marginal to absent for the endohydric *Polytrichum commune*. The 11 moss species on average took up 36±5% of the injected glycine and 18±2% of the aspartic acid in the lab experiment. Field uptake of both glycine (24±5%) and aspartic acid (10±2%) was lower than in the lab. Overall differences in uptake amongst species appeared to be positively associated with habitat wetness and/or turf density among different *Sphagnum* species and among non-*Sphagnum* species, respectively. Species from habitats of lower inorganic N availability, as indicated tentatively by lower tissue N concentrations, showed relatively strong amino acid uptake, but this was only significant for the field uptake among non-*Sphagnum* mosses. Further experiments are needed to test for consistent differences in amino acid uptake capacity among species and functional groups as determined by their functional traits, and to test how the affinity of cold-biome mosses for amino acids compares to that for ammonium or nitrate. Still, our results support the view that widespread moss species in cold, N-stressed ecosystems may derive a significant proportion of their nitrogen demand from free amino acids. This might give them a competitive advantage over plants that depend strongly on inorganic N sources.

Keywords Aspartic acid · Bryophyte · Glycine · Isotope labeling · Nitrogen availability · Sub-arctic

Responsible Editor: Herbert Johannes Kronzucker.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-008-9540-5) contains supplementary material, which is available to authorized users.

E. J. Krab · J. H. C. Cornelissen (✉) · S. I. Lang · R. S. P. van Logtestijn
Department of Systems Ecology,
Institute of Ecological Science,
Faculty of Earth and Life Sciences,
VU University Amsterdam,
De Boelelaan 1085,
1081 HV Amsterdam, The Netherlands
e-mail: hans.cornelissen@ecology.falw.vu.nl

Introduction

Recent studies on the comparative ecology of vascular plants have shown that interspecific variation in functional traits can help us to understand ecosystem

functioning and to predict ecosystem responses to environmental change (Walker et al. 1999; Grime et al. 2000; Lavorel and Garnier 2002; Westoby and Wright 2006). This contrasts sharply with our poor knowledge of the comparative ecology of non-vascular cryptogams, especially when it comes to their traits related to biogeochemistry (Cornelissen et al. 2007). Mosses are particularly abundant, and often dominant, in cold and cool biomes, especially in peatlands, boreal forest and high-latitude tundra (Gorham 1991; Woodin and Marquiss 1997; Forsum et al. 2006). In such ecosystems they control biogeochemical processes (Clymo and Hayward 1982; Bates and Farmer 1992; Cornelissen et al. 2007), either directly or indirectly via their impact on soil temperature and moisture regimes (Longton 1997; Woodin and Marquiss 1997; Van der Wal and Brooker 2004). The often cold and wet soils in these ecosystems have low nutrient mineralization rates and, consequently, generally low availability of inorganic nutrients. Nitrogen is usually the principal nutrient that limits plant assimilation and growth here, in some cases together with phosphorus limitation (Shaver and Chapin 1991; Chapin et al. 1995). However, in arctic tundra soil concentrations of organically bound nitrogen in the form of free amino acids may be an order of magnitude higher than those of inorganic nitrogen (Kielland 1995). Several predominant higher-latitude vascular plant species seem to have adapted to this naturally high amino acid availability in that they have a high capacity for the uptake of amino acids, whether or not with the aid of mycorrhizal fungi (Kielland 1994; Näsholm et al. 1998; Schimel and Chapin 1996; Näsholm and Lipson 2001). By this mechanism such plants short-circuit the N cycle by by-passing the phase of N mineralisation by soil microorganisms (Chapin 1995). Can arctic cryptogams do this as well? Indirect evidence from seven sub-arctic/arctic moss species and two lichens, based on natural abundance signatures of the isotope ^{15}N in their tissues, raised the suspicion that these cryptogams might derive significant amounts of N from organic matter relative to inorganic sources (Michelsen et al. 1998). Labeling studies have shown that several lichen species (Dahlman et al. 2004) and two bryophyte species have the ability to take up amino acids directly from their environment. Based on a laboratory assay, the peat moss *Sphagnum rubellum* can probably take up the small amino acid glycine directly from the soil solution (Kielland 1997). Forsum et al. (2006) used dual labelling with ^{13}C and ^{15}N to show that the moss *Hylocomium splendens* took up glycine under real field conditions. If the ability to take up and process both smaller and larger amino acids is shared among many of the predominant higher-latitude mosses, it could be an important factor contributing to their strong position there. Our study is, to our knowledge, the first to test this experimentally.

Specifically, we tested the following hypotheses: (1) the amino acids aspartic acid and glycine can be taken up by a range of different moss species and types, both in the lab and in the field; (2) there are differences in the relative uptake of the amino acids between the moss species, as related to their growth forms or their adaptations to habitat moisture and/or N availability. To answer our hypotheses we tested 11 sub-arctic moss species (four peat mosses *Sphagnum* sp., seven other mosses) for their potential uptake of dual ^{13}C and ^{15}N labelled glycine and aspartic acid, two amino acids known to be abundant in high-latitude organic soils (Kielland 1994, 1995; Weintraub and Schimel 2005). Thereto we injected these amino acids into tundra soil both in a standardized lab experiment and *in situ*.

Methods

Lab experiment: sampling

We selected 11 moss species of abundant and widespread, often circum-arctic, occurrence in tundra. Several of these species also occur in cool-temperate peatlands. We collected fresh turfs of these species within a 2 km radius around the Abisko Research Station, Abisko, Northern Sweden (68°21′ N, 18°49′ E, alt. c. 340–370 m), in mid July 2006. These species were tentatively classified into four groups based on (a) widely recognised overall differences in morphology and functioning between the phylogenetically distant *Sphagnum versus* non-*Sphagnum* mosses (Chapin et al. 1996); and (b) differences in typical habitat wetness and turf density within each of these higher taxa. Thus, we distinguished between: (1) 'wet' *Sphagnum* species (*S. riparium* Aongstr., *S. lindbergii* Schp.) which have a rather loose turf structure and grow in or just above standing water

in mires; (2)'drier' *Sphagnum* species (*S. fuscum* (Schimp.) Klingg., *S. cf. warnstorfii* Russ.), which grow in denser turfs above the water table in bogs and mires; (3) non-*Sphagnum* mosses that grow in rather dense turfs and are in relatively close contact with the water table in mires like the species in group 2 (*Aulacomnium palustre* (Hedw.) Schwaeg., *Paludella squarrosa* (Hedw.) Brid., *Tomentypnum nitens* (Hedw.) Loeske, *Drepanocladus revolvens* (Swartz) Warnst. *s.l.*); and (4) non-*Sphagnum* mosses that are more loosely packed on relatively dry substrata (*Hylocomium splendens* (Hedw.) Schimp., *Polytrichum commune* Hedw., *Pleurozium schreberi* (Brid.) Mitt.). Within group (4), *P. commune* stood out by the fact that it is endohydric (with water conducting tissues), which may help it to take up inorganic nutrients efficiently from the soil.

For each species 15 samples were collected from five blocks with mutual distances of at least 3 m. A PVC tube (15 cm deep, 5 cm diameter) was drilled into a moss turf in nearly complete monoculture, including both its green and brown parts. The tubes with the mosses were taken back to a greenhouse in day light (see below), where each moss sample was gently rinsed from its soil solution for 5–10 min in a 0.05 M KCl solution. Then they were placed back into the tube in the same density, put onto water-saturated foam blocks for 2 h in order to acclimate.

Lab experiment: amino acid uptake

The standardized tubes filled with the mosses were subjected to three treatments of five replicates each (blocks). In the control treatment, 5 ml demineralised water was injected. In the amino acid treatments 5 ml of 1 mM double labelled glycine (^{15}N, ^{13}C-2 glycine; one C atom labelled) or 5 ml of 1 mM double labelled aspartic acid (^{15}N,$^{13}C_4$ aspartic acid; all four C atoms labelled) was injected at five points halfway down the tube, around the transition of the green and brown moss parts. We considered this the relevant point in the profile with respect to amino acids in natural soil solutions, which are predominantly break-down products of organic matter (Kielland 1995), although we can not exclude the possibility that sub-arctic mosses might presently also intercept very small amounts of amino acid from anthropogenic N deposition in precipitation (*cf.* Forsum et al. 2006 and Discussion). We assumed that virtually all ^{15}N that was accompanied by corresponding amounts of ^{13}C (1:1 ratio for glycine, 1:4 ratio for aspartic acid) retrieved from a moss could be attributed to the uptake of whole, non-mineralised amino acids. Any refixation of respired $^{13}CO_2$ was probably negligible (see Discussion). After injection of the solutions the mosses were allowed to take up the amino acids for 24 h in the greenhouse (temperature close to 15°C, slightly lower than under ambient light regime). After 24 h the pH of the remaining water in the tubes was measured. Then the mosses were harvested and washed in 0.05 KCl solution for 10 minutes to make sure no labelled amino acids were left on the surface of the moss shoots. Subsequently the samples were dried at 70°C, weighed and ground.

Field experiment

There had been sufficient precipitation in the weeks and days before the start of the field experiment, so that we could assume none of the moss species to be desiccated during the experiment (authors' observations). The field experiment was carried out following the same methods and the same blocked design as for the lab experiment, with the difference that the tubes with the mosses were placed back into their own holes in the moss cushions in the field directly. The solutions were injected with demineralised water, glycine or aspartic acid in the same way as in the lab experiment and uptake was allowed again for 24 h. After harvesting the tubes were taken back to the lab, rinsed, dried, weighed and ground as above. Subsequent analysis was the same for both lab and field experiment.

Rinsing control experiment

To make sure only the amino acids taken up by the plant and not the amino acids on the surface of the moss were measured, an additional experiment was carried out to check whether 10 min of washing was sufficient. In that case, additional rinsing would not result in different (lower) concentrations of labelled isotopes. The methods used in this experiment were the same as in the lab experiment. For this experiment two species of contrasting morphology and habitat were used: *Hylocomium splendens* and *Sphagnum fuscum*. Each of these species was injected with either glycine or aspartic acid, and, upon harvesting after

24 h, rinsed either once for 10 min or three times for 10 min at a time. Replication was 3. Subsequent analysis was the same as for all the samples in the lab and field experiments (see below).

Stable isotope analysis

Nitrogen and carbon concentrations and atom percentages of ^{15}N and ^{13}C of the dried, ground samples were determined in separate runs for N and C using an elemental analyzer (NC2500, ThermoQuest Italia, Rodana, Italia), coupled with a continuous-flow isotope ratio mass spectrometer (Delta Plus, ThermoQuest Finnigan, Bremen, Germany). The IRMS also measured the total mass percentage of C and N in the samples, therefore together with the atom percentages of ^{15}N and ^{13}C, the fraction of amino acids taken up could be calculated using the formula:

$$\text{Fraction uptake} = \left(C_{\text{sample}}\right) * \left(\text{F}^{13}C_{\text{sample}} - \text{F}^{13}C_{\text{nat}}\right) \Big/ {}^{13}C_{\text{added}}$$

where C_{sample} is the total amount of C in the sample (g); $\text{F}^{13}C_{\text{sample}}$ is the fraction (^{13}C/total C) found after amino acid treatment; $\text{F}^{13}C_{\text{nat}}$, is the natural abundance of ^{13}C in the species, here represented by the average fraction of ^{13}C in the control treatment; and $^{13}C_{\text{added}}$ is the amount (g) of ^{13}C added. Since all moss species were placed in tubes with a surface area of 19.63 cm^2 at their field density, the total amino acid uptake represents their uptake per unit surface area. We did not carry out a correction for plant mass, because at unlimited supply a given moss species will presumably take up an amount of amino acid proportional to its own mass. The mass of the plants is already represented by C_{sample} in the calculation of the fraction uptake.

Statistics

Data analysis was performed using SPSS 10.1. We carried out a three-way ANOVA on atom percentages of ^{13}C, with species, amino acid type and rinsing treatment (rinsing once *versus* three times) as fixed factors. We used untransformed ^{13}C data, since their variances did not differ significantly (Levene's test, P=0.17).

Differences between the amino acid addition treatments (control *versus* glycine and control *versus* aspartic acid) were tested using two-way Analysis of Variance (ANOVA) on untransformed atom percentages of ^{13}C, with species and amino acid treatment as independent variables. Although in one of the groups the frequency distributions were not normally distributed, we proceeded with the analyses. Analyses of variance are known to be robust to deviations from normality as long as the sample sizes are nearly equal (Zar 1999). To test whether there were species-specific differences in the relative rate of amino acid uptake, a one-way ANOVA with a post hoc Tukey's test was carried out on the fraction of injected ^{13}C taken up. This test was carried out on untransformed data. We used linear regression to compare interspecific rankings for ^{15}N *versus* ^{13}C.

Results

Rinsing controls

There was no significant effect of rinsing the mosses once *versus* three times on ^{13}C % in the 3-way ANOVA (rinsing treatment, F=0.35, P=0.56), as contrasting with a significant difference between the two species (F=45.6, P<0.001) and between glycine *versus* aspartic acid added (F=24.4, P<0.001). There were no significant first or second order interactions. See Supplementary figure 1 for further details. These results indicate that any ^{13}C adhering to the outer surfaces of the mosses had been removed already with the first rinsing treatment. We therefore assume that ^{13}C enrichment in the lab and field experiments (see below) would be due to uptake.

Amino acid uptake

All species tested had the capacity to take up amino acids. In all species and all treatments the atom percentages of ^{13}C in the plants were higher than in the controls after addition of either of the amino acids, both in the lab and the field experiment (see Supplementary figure 2), The only exception was *Polytrichum commune*, which showed clear ^{13}C uptake in the lab experiment but not in the field. The ANOVA on percent ^{13}C confirmed that amino acid uptake was highly significant across the species set both for glycine and aspartic acid, both in the lab and in the field (Table 1). Also, in each of the treatments, both in the lab and in the field, there was

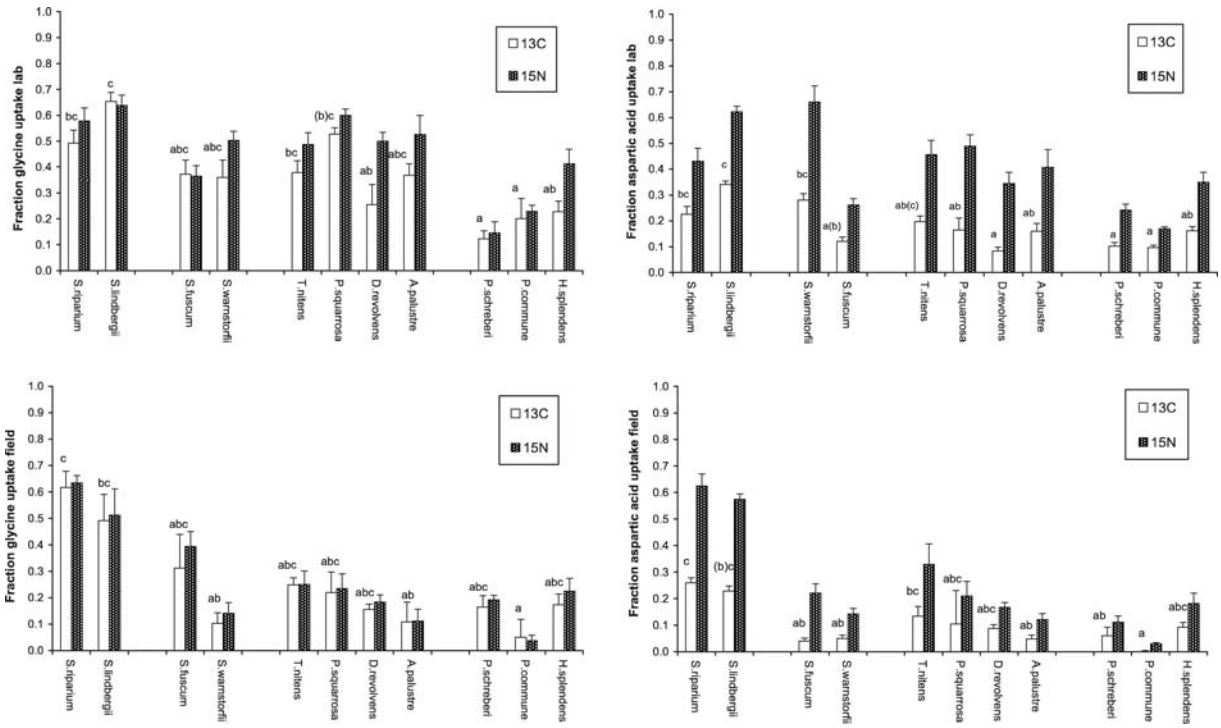

Fig. 1 The fraction of added amino acid retrieved in the plant after uptake for 24 h for **a** glycine in the lab; **b** aspartic acid in the lab; **c** glycine in the field; **d** aspartic acid in the field. *White bars* show the uptake of ^{13}C, *dark bars* that of ^{15}N. *Standard errors* are shown one-sided ($n=5$). The species are grouped as follows, from *left to right*: (1) wetter *Sphagnum* spp.; (2) drier *Sphagnum* spp.; (3) denser, wetter non-*Sphagnum* mosses; (4) loose, drier non-*Sphagnum* mosses. For ^{13}C, *bars that have no letters in common* are significantly different in Tukey's *post hoc* tests. The fraction of field uptake of ^{13}C in aspartic acid by *P. commune* was actually -0.020 ± 0.024

significant overall variation in the uptake of amino acids among species, as indicated by the interaction term. While both the lab and the field experiments showed an enrichment of ^{13}C and thus amino acid uptake in the treated samples, the fraction of the added amino acid that was taken up by the plants was in most cases lower in the field experiments than in the lab experiments (Fig. 1). A general pattern in all treatments was that ^{13}C was taken up in lower amounts than ^{15}N, and that the relative difference was greater for aspartic acid (mean $^{13}C/^{15}N=0.41$) than for glycine (mean $^{13}C/^{15}N=0.86$); see Figs. 1 and 2.

Table 1 Results of the 2-way ANOVAs on percent ^{13}C data with the independent variables amino acid addition treatment (2 levels) and species (11 levels), for glycine and aspartic acid in laboratory and field experiments, respectively ($n=5$)

Experiment	Independent variables	*F*	*P*
Glycine addition, lab	Treatment	292	<0.001
	Species × Treatment	3.02	0.003
Aspartic acid addition, lab	Treatment	584	<0.001
	Species × Treatment	10.8	<0.001
Glycine addition, field	Treatment	82.9	<0.001
	Species × Treatment	5.09	<0.001
Aspartic acid addition, field	Treatment	54.4	<0.001
	Species × Treatment	8.43	<0.001

Tests were carried out on untransformed data.

Whilst the numbers of species for each *a priori* functional group were not sufficient for formal statistical analysis, some trends can be derived from Fig. 1, as indicated partly by the Tukey's post hoc test results for the component species involved. The looser, 'wetter' *Sphagnum* species (group 1) tended to take up more ^{13}C than the denser, 'drier' *Sphagnum* species (group 2), especially in the field. Within the non-*Sphagnum* mosses, the denser, 'moister' species (group 3) appeared to generally take up more than the looser, 'drier' ones (group 4), particularly so for glycine in the lab, but for the field uptake of both amino acids this tendency was explained mostly by the lack of uptake by *Polytrichum commune*. Groups

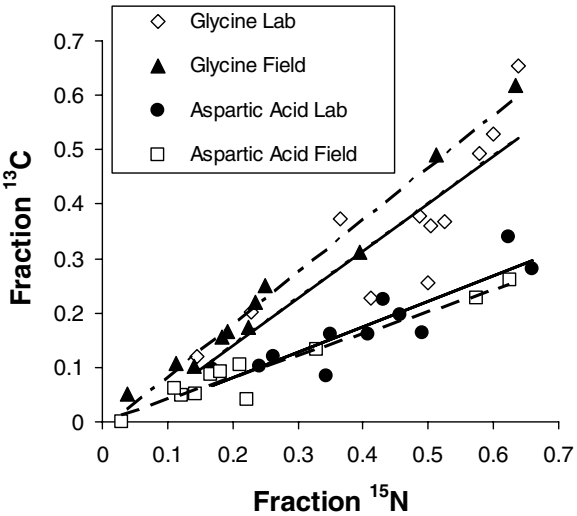

Fig. 2 Regression of uptake of ^{13}C *versus* ^{15}N for **a** glycine in the lab experiment (*dotted line*, slope 0.87, R^2=0.73), **b** glycine in the field (*irregularly dashed line*, slope 0.96, R^2=0.98), **c** aspartic acid in the lab (*dashed line*, slope 0.47, R^2=0.79), **d** aspartic acid in the field (*solid line*, slope 0.41, R^2=0.94). Each data point represents a species mean value. All 11 species are included

2 and 3 showed broadly similar uptake patterns, with substantial interspecific differences within each group.

We also tested for each of the amino acids in lab or field whether uptake, as indicated by fraction of ^{13}C taken up, was negatively related to total percent tissue N across the 11 species. Although all regression slopes showed a negative trend, none was significantly different from zero ($0.084 \leq R^2 \leq 0.18$). Since we thought that underlying relationship might be obscured by overall differences between *Sphagnum* and non-*Sphagnum* mosses, we also tested the same relationships for the subset of seven non-*Sphagnum* species. We found significantly negative slopes for both glycine (R^2=0.72, P<0.05) and aspartic acid (R^2=0.62, P<0.05) in the field, but not in the lab experiment (glycine, R^2=0.022; aspartic acid, R^2=0.12).

We also report consistent positive interspecific relationships between the natural abundance of ^{13}C in control plants and the fraction ^{13}C uptake in the amino acid addition experiments. The accompanying linear regression slopes were significantly greater than zero for glycine uptake in the lab as a function of natural ^{13}C abundance (R^2=0.64, df=9, P<0.01) and for glycine uptake in the field (R^2=0.46, df=9, P<0.05). However, for aspartic acid uptake such positive regression trends were not significant in the lab (R^2=0.18, df=9) or in the field (R^2=0.34, df=9). This would imply that amino acid carbon taken up from tundra soil has a higher ^{13}C percentage than plant carbon after fractionation of atmospheric carbon through photosynthesis processes. However, since we could only speculate about the underlying mechanisms at this stage, we shall not discuss these results below.

Discussion

In support of our first hypothesis, we have demonstrated that a wide range of sub-arctic moss species possess a high capacity for uptake of amino acids from their direct environment. This also confirms our suspicion based on earlier investigations on ^{15}N natural abundance signatures of seven sub-arctic/arctic mosses (three of which in common with our study), which implied possible long-term incorporation of N derived from organic rather than inorganic sources in soil or precipitation (Michelsen et al. 1998). Thus, many of the abundant higher-latitude mosses have the ability to short-cut the nitrogen cycle by being relatively independent of ammonium or nitrate for their N nutrition, which would give them a great ecological advantage in tundra soils with low availability of inorganic N forms. However, in order to interpret and refine our findings, several methodological and ecological factors need to be addressed first.

Methodological issues

Rinsing moss samples three times *versus* once as in the main experiments, had no effect on the fraction of ^{13}C taken up. Although ideally we should have tested this for all 11 species, the lack of a 'rinsing' effect in two contrasting species in terms of phylogeny, morphology and habitat choice, may justify our assumption that the elevated ^{13}C in the plants resulted predominantly from real uptake of the amino acids by the mosses, rather than adherence to their surface.

For the calculation of the fraction of amino acids taken up, we had to subtract the natural 'background' ^{13}C content of the mosses by averaging the ^{13}C content of control samples, since cutting off parts of moss samples to be injected with labelled amino acid

would have damaged the mosses and interfered with uptake. However, the background ^{13}C may differ between samples of the same species as well, making such subtractions doubtful for individual injected samples. To tackle this problem, the two-way ANOVAs, testing the control *versus* the amino acid treatment, were carried out on raw, uncorrected percentage ^{13}C data. We assumed the species by treatment interactions from these ANOVAs to best represent any interspecific differences in uptake.

Amino acid uptake: fact or artefact?

This study has shown that all 11 mosses tested here could take up two representative amino acids of contrasting molecular size, *viz*. glycine (small) and aspartic acid (larger). With the notable exception of *Polytrichum commune* (20 and 10% uptake for glycine and aspartic acid respectively in the lab, but negligible or no uptake in the field), this uptake was generally substantial and occurred both in a standardized albeit rather artificial lab environment and in a realistic but heterogeneous field setting. The fractions of amino acid taken up by the other 10 mosses ranged from 12–65% (average 36±5%) and 5–61% (average 24±5%) for glycine in lab and field, respectively, and from 5–34 (average 18±2%) and 0–26% (average 10±2%) for aspartic acid in lab and field. Thus, uptake was on average lower in the field than in the lab. This may be explained by a range of factors, including exchange of the added amino acid solution with water in the surrounding environment (via the open tube bottoms), differences in hydrology or microbial activity between the field and lab experiment, pH differences, and/or competition with vascular plants or other mosses for amino acids or other sources of nitrogen in the field (Näsholm et al. 2000).

Our main analyses were carried out on the ^{13}C data. For the ^{13}C measured in the plant after the injection of the amino acid, we assume the whole amino acid, or at least the part of the amino acid that is still in an organic form, to have been taken up. A general pattern in all treatments was that ^{15}N was taken up in greater amounts than ^{13}C, especially for aspartic acid, which could indicate the breakdown of the amino acids before uptake by for instance the microorganisms in the soil environment (Jones 1999; Lipson and Monson 1998, 1999). Theoretically shoot ^{13}C enrichment could also result from re-fixation of respired $^{13}CO_2$ upon such amino acid mineralization. However, this is unlikely to have caused any significant ^{13}C enrichment of moss shoots in our experiment since, similar to Näsholm et al. (2000), we did not measure any ^{13}C enrichment of adjacent moss shoots in our control treatment.

The isotopes ^{13}C and ^{15}N were in general taken up in more equal amounts in the glycine addition treatment than in the aspartic acid treatment. This seems to agree with a study by Lipson et al. (1999), who showed that microorganisms have low affinity for glycine compared to other, larger amino acids like for instance glutamate, which is more similar to aspartic acid.

Some ^{13}C may also have been lost initially inside the mosses, because inside plants both glycine and aspartic acid can be converted into glycolysis- or TCA-cycle intermediates and thus some of the ^{13}C could be respired relatively easily. Aspartic acid can be converted into oxalo-acetate (Mazelis 1980) while glycine can be transformed into pyruvate via serine respiring the carboxylic-C in the process (Oliver 1994). To avoid losing the ^{13}C via respiration after it entered the plant we used ^{15}N, ^{13}C-2 glycine, which is labelled on the non-carboxylic C atom. The aspartic acid (^{15}N, $^{13}C_4$ aspartic acid) was labelled on all C atoms, including a carboxylic part, so here loss via internal respiration could be a factor determining the low $^{13}C/^{15}N$ ratio after uptake. However, the loss of the carboxylic C atom could also be due to breakdown by microorganisms, as discussed above. Differences in respiration rates between mosses may not only be species dependent but may depend also on abiotic factors such as water availability (Dilks and Proctor 1979). However, any such differences in respiration rate are unlikely to explain the variation in ^{13}C and ^{15}N content among mosses. The breakdown of the amino acids in the soil by microorganisms is probably the main contributor to the differences in $^{13}C/^{15}N$ ratio found (Jones 1999).

Interspecific differences in amino acid uptake

For comparing species belonging to different functional groups for amino acid potential (hypothesis 2), the lab experiments are probably the most revealing, since the water availability was standardised across all species here. Owing to small numbers of species within functional groups as defined here *a priori*, we

could not test differences in amino acid uptake among groups statistically. However, some trends can be observed. Both within *Sphagnum* and within the non-*Sphagnum* mosses, the species from relatively wet habitats appeared to take up greater amounts of amino acids, although more clearly so for glycine than for aspartic acid. These patterns were also somewhat apparent in the field experiment. We might tentatively explain these observations from the growth circumstances of the species. The species adapted to wetter environments might hold more water in their cushions in order to maintain, and compete in, their wet environment. This way, they may have had more intense contact with the injected amino acid solution, which could have explained their higher amino acid uptake. For species from drier environments the water availability in the lab experiment may have been much higher than in the field, even though the weather before the experiment had not been dry. This might explain why they tended to show much greater uptake in the lab than in the field in relatively terms, compared to the small relative differences in uptake for the wetter *Sphagnum* species, for instance. However, we need data for the actual traits underpinning such apparent differences among species groups. One trait that showed some interesting pattern was total tissue N concentration, which among the non-*Sphagnum* mosses in the field experiments was negatively correlated with amino acid uptake capacity. We speculate that species more dependent on amino acids would be found in the more N-stressed environments, as tentatively indicated by low tissue N concentrations. In such environments a conservative N economy as supported by amino acid uptake would be beneficial. The low amino acid uptake of *Polytrichum commune* in the lab, and the virtual absence of uptake by this moss in our field experiment, is of particular interest, since this is the only endohydric species among the 11 studied here. Since *P. commune* has internal conducting tissues which may also transport inorganic nutrients from the soil relatively efficiently (Ligrone et al. 2000), it may rely mostly on inorganic N sources in the soil rather than on amino acids. However, injecting amino acids broadly at the boundary of brown and green parts means that potential uptake through rhizoids could have been partly missed in our experiment. Several other morphological features on the leaf surface could play a positive or role in amino acid uptake too, for instance protective waxes in certain species (e.g. *P. commune*) from less wet habitats might be expected to interfere with the permeability of the cell wall (Claytongreene et al. 1985). If lower photosynthetic rates are also associated with conservative N economy and amino acid uptake in mosses, this would be somewhat supported by the reported maximum photosynthetic rates (P_{max}) of some of the mosses. Skre and Oechel (1981) found that *P. commune* (low amino acid uptake) had high P_{max} compared to intermediate *H. splendens* and *P. schreberi* (rather low amino acid uptake), while two *Sphagnum* species (although different spp. from the ones in our study, which had relatively high amino acid uptake) had low P_{max}. It is clear that, in order to develop a framework for predicting amino acid uptake among wide-ranging moss species, we need to not only test for the uptake potential of more species, but also screen them for the morphological, chemical and/or physiological traits determining and predicting it.

Conclusions

In support of our first hypothesis, at least 10 out of 11 abundant and widespread subarctic moss species studied here show a substantial ability to take up nitrogen from free amino acids in the soil, represented here by glycine and aspartic acid. The next step in this research could be to study the relative preference for different N sources in different moss species, by supplying inorganic and organic N forms in different combinations in the same experiment (cf. Schimel and Chapin 1996, Forsum et al. 2006). Anthropogenic nitrogen deposition plays a relatively small but perhaps not negligible role in high-latitude regions (Woodin and Marquiss 1997) and a relative increase in ammonium compared to amino acids in tundra soils could potentially reduce the advantage of amino acid uptake as reported here. There is recent evidence that anthropogenic N deposition in lower-latitude regions also contains an organic fraction, including amino acids (Cornell *et al*. 2003, Forsum *et al*. 2006), and it would be interesting to investigate whether this could be of any consequence to the nitrogen nutrition of higher-latitude bryophytes.

There was a significant difference in the uptake of the two amino acids among the species tested. Thus, it would be useful to know whether the species that had

low amino acid uptake, have a preference for NH_4^+ or NO_3– and *vice versa* (Schimel and Chapin 1996; Forsum *et al.* 2006), and whether that would relate to their site preference. We also need to do more empirical work to be able to link the amino acid capacities of different species to the morphological, chemical and/or physiological traits determining them. Even so, by linking our results to the high concentrations of amino acids and the low concentrations of inorganic N in widespread higher latitude soils (Shaver and Chapin 1991; Kielland 1995), it is likely that the uptake of free amino acids in N-stressed arctic ecosystems generally provides a significant proportion of the nitrogen demand of a wide range of mosses. This might be a key factor explaining how they can maintain their strong position in extensive N-stressed areas in cool and cold northern biomes.

Acknowledgements We thank Abisko Research Station, Sweden, and several of its staff, for providing research facilities and hospitality, and Nadia Soudzilovskaia and Peter van Bodegom for advice. We thank Staatsbosbeheer, particularly Erik Gerrevink and Wouter Maatje at the Guisveld, for allowing us to take some moss samples for a pilot experiment. This study benefited greatly from funding by NWO (Netherlands Organisation for Scientific Research) to JHCC through grants 047.017.010 and 852.00.070.

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