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Plant and Microbial Uptake and Allocation of Organic and Inorganic Nitrogen Related to Plant Growth Forms and Soil Conditions at Two Subarctic Tundra Sites in Sweden

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Abstract

In order to follow the uptake and allocation of N in different plant functional types and microbes in two tundra ecosystems differing in nutrient availability, we performed a ^{15}N-labeling experiment with three N forms and followed the partitioning of ^{15}N label among plants, microorganisms and soil organic matter. At both sites the deciduous dwarf shrub *Betula nana* and the evergreen *Empetrum hermaphroditum* absorbed added ^{15}N at rates in the order: $NH_4^+ > NO_3^- >$ glycine, in contrast to the graminoid *Carex* species which took up added ^{15}N at rates in the order $NO_3^- > NH_4^+ >$ glycine. *Carex* transported a high proportion of ^{15}N to aboveground parts, whereas the dwarf shrubs allocated most ^{15}N to underground storage. Enhanced ^{13}C in *Betula nana* roots represents the first field evidence of uptake of intact glycine by this important circumpolar plant. Plant and microbial uptake of label was complementary as plants took up more inorganic than organic N, while microbes preferred organic N. Microbes initially took up a large part of the added label, but over the following four weeks microbial ^{15}N decreased by 50% and most ^{15}N was recovered in soil organic matter, while a smaller but slowly increasing proportion was retained in plant biomass.

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Introduction

In arctic ecosystems, low nitrogen (N) availability often limits plant production (Chapin and Shaver, 1996; Jonasson and Shaver, 1999; Jonasson et al., 1999) and microbial turnover of soil organic matter (SOM) (Weintraub and Schimel, 2003; Mack et al., 2004). Microbes take up both inorganic and organic N forms, while the common assumption had been that plants take up N only in inorganic form. The plants therefore are dependent on either release of N to the soil through microbial mineralization or on supply of N via mycorrhizal symbionts. However, for some years, it has been known that mycorrhizal as well as nonmycorrhizal plants also take up organic N (Chapin et al., 1993; Kielland, 1994; Näsholm et al., 1998; Nordin et al., 2004). Thus, plants are able to compete with free-living microorganisms for organic N without need for prior mineralization.

At relatively nutrient-rich tundra sites, deciduous shrubs, graminoids, and forbs dominate the vegetation, whereas at relatively nutrient-poor tundra sites, evergreen shrubs typically are more abundant (Monk, 1966; Miller, 1982). The availability of different N forms may vary among sites with different vegetation types. Some studies have shown that sites with one dominant N form in the soil are dominated by species with a high uptake capacity for this particular N form (McKane et al., 2002; Weigelt et al., 2005). Consequently, uptake of different chemical N forms among co-existing species has been suggested as an important factor determining plant competition and dominance patterns and vegetation dynamics (McKane et al., 2002; Weigelt et al., 2005). However, other studies have reported that uptake preferences for either NH_4^+, NO_3^- or glycine are unrelated to N-form prevalence in the soil N pool (Nordin et al., 2001; Bardgett et al., 2003; Miller and Bowman, 2003; Nordin et al., 2004).

Plants take up N in competition with microorganisms (Schimel and Chapin, 1996; Kaye and Hart, 1997; Hodge et al., 2000). Plants and microbes may take up different N forms with complementary preferences, and thus reduce the competitive pressure between plants and microorganisms (Lipson and Näsholm, 2001).

Short-term ^{15}N-labeling studies (hours to days) in arctic (Nordin et al., 2004; Grogan and Jonasson, 2005) and in temperate (McFarland et al., 2002; Bardgett et al., 2003) ecosystems show that the microorganisms absorb a large part of the added label, whereas the uptake rate by plants is much lower. However, only a few studies in arctic and alpine ecosystems have followed the partitioning of added label in plants and microorganisms during periods of weeks to years. The overall conclusion from these studies is that plant proportion of added N increases with time (Marion et al., 1982; McFarland et al., 2002), mainly because of plant sequestration of N that continuously is released from the microbes with much shorter turnover time (Kaye and Hart, 1997).

In this study, we used *in situ* injections of ^{15}N-labeled NH_4^+ and NO_3^- and ^{15}N-^{13}C-labeled glycine in mixed solutions to follow the uptake and allocation of the N forms in plants and microorganisms. The ^{13}C labeling of glycine was included to examine whether glycine was taken up as intact amino acid by plants in these ecosystems, as shown for a limited number of species in other field experiments (Näsholm et al., 1998; Henry and Jefferies, 2003b; Nordin et al., 2004).

The study had three objectives: The first was to test if the plant uptake of NH_4^+, NO_3^- and glycine varied among plant functional types and/or between two sites of different nutrient availability. Second, we wanted to follow the label in different plant compartments (fine roots, woody tissues and leaves) to test for effects of

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between-ecosystem differences in soil nutrient status and plant functional type on the allocation of N within the plants. The third objective was to follow the short-term (days) and longer-term (weeks) partitioning of label between plants and microorganisms.

Materials and Methods

SITE DESCRIPTION

The experiment was conducted near the Abisko Scientific Research Station in Northern Sweden (68°19′N, 18°51′E). The climate is subarctic with an average July temperature of 11°C, and an annual mean temperature of −0.5°C (Royal Swedish Academy of Sciences, Abisko Scientific Research Station, www.ans.kiruna.se/ans.htm). We worked at two communities with differences in vegetation height and species composition that indicated different levels of nutrient availability and plant productivity.

One community was a low-productive, dry heath dominated by prostrate-growing *Empetrum hermaphroditum*. *Empetrum hermaphroditum* grew together with the subdominant deciduous and low-growing *Betula nana* and *Vaccinium uliginosum*, the evergreen dwarf shrub *Andromeda polifolia* and the sedges *Carex vaginata* and *Carex distica*. The vegetation canopy was open, less than 15 cm high, and underlain by mosses. The organic horizon had a depth of about 10 cm and a well-defined transition to the underlying mineral soil.

The other community was a shrub tundra with a canopy height of 40 to 50 cm dominated by *Betula nana*. *Carex paralella* made up the understorey together with mosses. Other common species were *E. hermaphroditum*, *V. uliginosum*, *Equisetum arvense*, *A. polifolia,* and *Salix myrsinites*. The organic horizon was 15 to 50 cm deep, moist and more mixed with the underlying mineral soil than at the heath. Hereafter the two communities are designated the heath tundra and the shrub tundra, respectively.

EXPERIMENTAL DESIGN

In each community, 48 0.2 × 0.2 m plots were laid out in six replicate blocks, i.e. with eight plots per block. The plots were selected so that there were at least one rooted individual of *E. hermaphroditum* and *B. nana* plus either *C. vaginata* (heath) or *C. paralella* (shrub tundra) in each of them. The labeling took place on 18 July 2003 at the heath tundra and on 22 July at the shrub tundra. NH_4^+, NO_3^- and glycine were mixed so that the three N-forms made up equal proportions of N in the solution. In each solution, one N-form was labeled, either as ^{15}N-NH_4Cl, ^{15}N-KNO_3^- or, ^{15}N-2(^{13}C)-glycine (^{15}N 96–99 atom%, ^{13}C 98 atom%, Cambridge Isotope Laboratory). Within each community, we dispensed 100 mL of each solution evenly into the top 5 cm of two plots in each block, leaving two plots as untreated controls. The added amount corresponded to 136 mg ^{15}N m^{-2}.

SOIL CHEMICAL ANALYSIS

The content of NH_4^+-N, NO_3^--N, microbial extractable N, dissolved organic N (DON), total amino acid N, and glycine N was analyzed in soils of the control plots sampled at both sites on 18 July and at the heath and shrub tundra on 21 and 23 August, respectively. In the same samples, we determined the soil water content gravimetrically and the soil organic matter content (SOM) by combustion of dry soil at 660°C for 6 h.

Microbial extractable N was determined after $CHCl_3$ fumigation of 10 g of fresh soil per sample for 24 h followed by extraction for 1 h in 50 mL 0.1 M K_2SO_4 (Anderson and Domsch, 1977; Brookes et al., 1985; Hobbie, 1992; Cheng and Virginia, 1992; Greenfield, 1995). Another 10 g fresh soil was treated as above, but without fumigation to extract soil NH_4^+, NO_3^-, and DON. Amino acids were extracted with 50 mL demineralized water in an additional 10 g soil. The extracts were filtered through Whatman GF-D filters and frozen until analysis.

NO_3^--N and NH_4^+-N were analyzed in the extracts from the unfumigated soils using an auto analyzer (Fiastar 5000, Foss Tecator, SE). K_2SO_4-extracts of fumigated and unfumigated soils were digested with persulfate to oxidise the organic N fractions to inorganic N (Zhou et al., 2003) followed by analyses as above. DON was determined as the N content in digested, unfumigated extracts after subtraction of the inorganic N fraction, and the extractable microbial N was calculated by subtracting the N in the digested, unfumigated extracts from the content in the digested, fumigated extracts (Brookes et al., 1985).

The analyses of amino acids were done by HPLC using a gold amperometry cell and the analytical column AminoPac PA10, with separation of arginine, alanine, asparagine, glutamic acid, glutamine, glycine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, proline, serine, valine, tryptophan, and tyrosine. Their concentrations were summed to a measure of total soil amino acid N concentration.

^{15}N uptake by micro-organisms was determined using the acid-trap diffusion technique (Stark and Hart, 1996). Five milliliters of digested, fumigated extract and 10 ml of unfumigated extracts spiked with 70 μg N (as $NaNO_3$ with $\delta^{15}N = -0.38$ ‰) were placed in 60 ml HDPE flasks. The spiking of the unfumigated extracts was necessary to obtain enough N of 50 to 150 μg for optimal sensitivity of the isotope-ratio measurements. Devardas alloy was added to reduce any NO_3^-/NO_2 to NH_4^+, and KCl was added to increase the ionic strength of the solution. Immediately before sealing the flasks with lids, 1 mL 5 M NaOH was added in order to raise the pH to >13 and convert the NH_4^+ to NH_3. An acidified (15 μL 1.5 M H_2SO_4) Millipore quartz filter of 0.8 cm diameter was attached inside the lids to trap the NH_3 as $(NH_4)_2SO_4$. The flasks were gently shaken for four days on a shaking table at 50 rpm, after which the filters with the trapped N were removed, dried and analyzed for their ^{15}N/^{14}N isotope ratios. In order to calculate the microbial ^{15}N recovery, we used the microbial N pools measured with the auto analyzer, because the N spiking of the unfumigated samples decreased the precision of the total N analysis in diffused samples. Recovery of ^{15}N in dissolved total N (DTN) is reported as the total recovery of ^{15}N in digested unfumigated extracts, i.e. soluble organic ^{15}N plus inorganic ^{15}N.

SAMPLING AND PREPARATION OF PLANTS AND SOIL FOR ISOTOPE ANALYSIS

Two and 26 days after labeling, we harvested six plots from each treatment by excavating the whole labeled 20 × 20 cm soil column, including attached plants, to a depth of 10 cm on the heath and to 15 cm on the shrub tundra. The samples were brought to the Abisko Scientific Research Station, kept at 2°C and sorted in order to detect differences in uptake patterns among plants of different functional type. Three ''target species'' from each site were selected for analysis of isotope ratios viz. the deciduous *B. nana*, the evergreen *E. hermaphroditum,* and the sedges *C. vaginata* (heath tundra) or *C. paralella* (shrub tundra), while all other species were pooled into one fraction of ''mixed species.'' The target species were carefully separated from the soil with as much as possible of the root

TABLE 1

Biomass (means ± 1 SE, $n = 6$) of different growth forms at the heath and shrub tundra.

	Biomass (g dw m^{-2})	
Plant growth form	Heath tundra	Shrub tundra
Deciduous shrubs	738 ± 235	1565 ± 284
Evergreen shrubs	558 ± 111	340 ± 52.2
Graminoids	143 ± 42.7	123 ± 13.8
Forbs	212 ± 52.2	204 ± 52.0
Mosses	131 ± 60.1	170 ± 35.4
Lichens	23.8 ± 8.6	0 ± 0
Total biomass	1806 ± 222	2402 ± 270

system attached. The two sedges were subsequently separated into roots and leaves + rhizomes, while *Betula* and *Empetrum* were separated into leaves, fine roots (<0.5 mm diameter) and woody tissues (coarse roots + above- and belowground stems). The mixed species were separated into roots (i.e. all belowground) and leaves + stems (i.e. all aboveground). The soil was cut into cubes of about 2 × 2 × 2 cm and mixed, after which roots and rhizomes were sorted from randomly chosen cubes and processed further as for aboveground plant parts before drying, and the remaining soil was used for soil chemical analysis.

Samples for analyses of ^{15}N and ^{13}C natural abundance were collected from the control plots on 21 August (heath tundra) and on 23 August (shrub tundra) and fractionated as the labeled samples. The aboveground plant parts were sorted into the target species, and the mixed species were sorted into growth forms of deciduous shrubs, evergreen shrubs, graminoids, forbs, mosses, and lichens. The root biomass of each growth form was estimated by assuming the same proportions of root mass among growth forms as measured in the aboveground biomass.

All plant material was washed several times in 0.5 mM $CaCl_2$ to remove any label adhering to the surface. All plant and soil samples were dried at 70°C for 48 h, weighed and milled, and stored in darkness until further processing.

The $^{15}N/^{14}N$ and $^{13}C/^{12}C$ isotope ratios, total N and C contents of about 5 mg of the plant and soil samples were analyzed with a Eurovector CN analyzer coupled to an Isoprime isotope ratio mass spectrometer (IRMS) (Micromass-GV Instruments). Natural abundance of isotopes is expressed in the δ notation relative to international standards: δX_{sample} (‰) = $1000 \times [(R_{sample}/R_{standard}) - 1]$ where R is the molar ratio of $^{heavy}X/^{light}X$. The C standard Vienna Pee Dee Belemnite has a $^{13}C/^{12}C$ ratio of 0.011237 and the N standard atmospheric N_2 has a $^{15}N/^{14}N$ ratio of 0.003676. Atom-percentages of ^{15}N in samples from control plots (natural abundance) were subtracted from atom-percentages of the treated samples. The recovery of ^{15}N in bulk soil (soil + microorganisms) was determined as the average recoveries in the two separately processed samples from each plot, i.e. the dried subsample of sorted soil used in the extractions and the dried bulk soil sample remaining after sorting. The amount of ^{15}N in the extractable microbial biomass plus ^{15}N in the DTN pool was subtracted from the bulk soil to give the reported ^{15}N recovery in the SOM fraction.

STATISTICAL ANALYSIS

The statistical analyses were performed using SAS statistical package (SAS Institute v8.02, 2001). Soil variables were tested separately for the July and August harvests using one-factor ANOVAs with site as main factor. Three-factor ANOVAs were used to test for differences in ^{15}N recovery in the different plant compartments separately including site, treatment and harvest time as main factors and with biomass included as covariate. Since there were significant differences between sites in the ^{15}N recovery in many plant species and compartments, we increased the resolution of the test by analyzing the treatment and harvest effects by two-factor ANOVAs for each plant species and each site separately, followed by Tukey's test to compare means of each treatment. Total ^{15}N recoveries in microorganisms were tested with two-factor ANOVAs as above, but with the N pool included as covariate. Block was included in the models whenever the block effect was significant at $P < 0.10$. Prior to the ANOVA tests, all data were tested for homogeneity of variances with Levene's test and, if necessary, transformed.

Results

PLANT BIOMASS, SOIL WATER AND ECOSYSTEM NITROGEN POOLS

The total plant biomass (Table 1) was about 1800 g m^{-2} at the heath tundra, with deciduous and evergreen shrubs each making up about one-third of the biomass. *B. nana*, *E. hermaphroditum,* and *C. vaginata*, i.e. the "target species", made up 9, 14, and 2%, respectively, of the total plant biomass. At the shrub tundra, with an estimated biomass of about 2400 g m^{-2}, deciduous shrubs dominated and made up 63% of the plant biomass. *B. nana*, *E. hermaphroditum,* and *C. paralella* made up 31, 6, and 5%, respectively, of the biomass.

There were no differences in plant N pools among treatments or harvest dates. We therefore pooled the data over the different treatments and present the N distribution among plant groups and plant fractions at the July harvest where the biomass peaked (Fig. 1). The N pools of *Betula*, *Carex,* and the mixed species were larger at the shrub tundra than at the heath tundra (Fig. 1a, c, d), while the N pools of *Empetrum*, particularly in stems and roots, were largest at the heath tundra (Fig. 1b). Generally, the root biomass made up a higher proportion of the total biomass at the heath than at the shrub tundra. For instance, the pool in roots of *Carex* made up 37% of the total N pool at the heath but only 15% at the shrub tundra (Fig. 1a), and N in fine roots of *Empetrum* made up 12% at the heath and 8% at the shrub tundra. The pools in fine roots of *Betula*, however, made up an equal proportion of about 9% of the total *Betula* N pool at both sites.

In July, the soil water content and the concentrations of NH_4^+, DON, extractable microbial N, and amino acid N were significantly higher at the shrub tundra than at the heath tundra (Table 2), while in August only the soil water content and DON concentration were higher at the shrub tundra (Table 2). In contrast, the NO_3^- concentration was significantly higher at the heath tundra in July but nonsignificantly lower in August. At both sites, the NH_4^+ concentration increased significantly from July to August and the extractable microbial N concentration at the shrub tundra decreased.

Among the three N forms used in the labeling experiment, NH_4^+ dominated at both sites. At the heath tundra, the concentration was 30 (July) to 250 (August) times higher than the concentration of NO_3^- and about 3 to 4 times higher than the concentration of amino acid N (Table 2). At the shrub tundra, the NH_4^+ concentration was 150 to 230 times higher than the concentration of NO_3^- and 3.5 times higher than the amino acid N concentration. Amino acid N made up about 1% of the DON at both sites (Table 2).

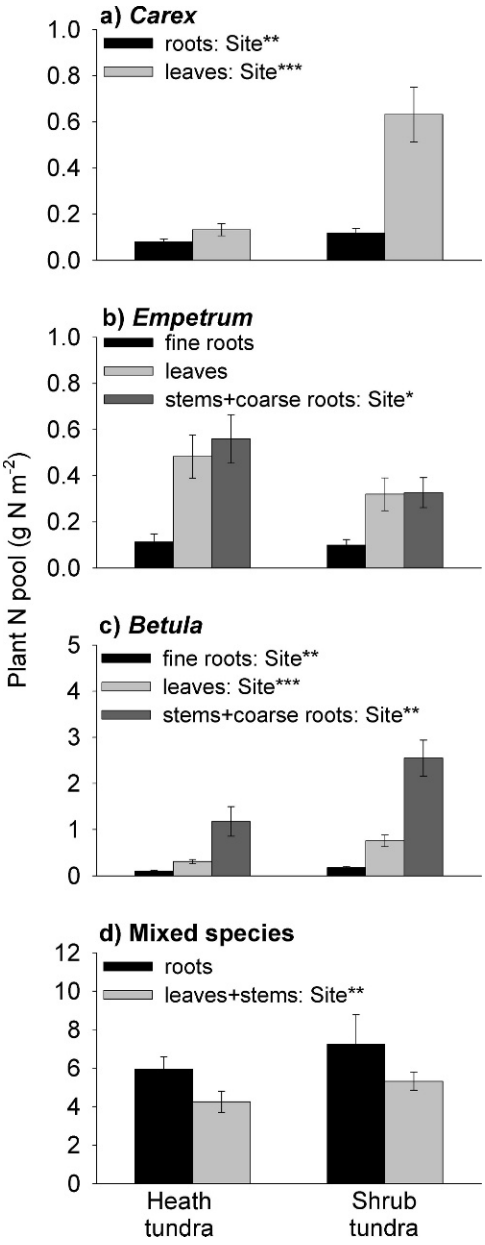

FIGURE 1. Pools of N in July at the heath and the shrub tundra in plant fractions of a) *Carex*, b) *Empetrum*, c) *Betula,* and d) Mixed species. Data are means ±1 SE, $n = 36$. The effects of site were analyzed with one-way ANOVAs for each fraction separately: ** $P < 0.01$, *** $P < 0.001$

The total N content of the soil at the heath was high, exceeding the plant N pool 7- to 10-fold, while the content was lower at the shrub tundra, but yet exceeded the plant N pool 2- to 4-fold. The N content in the extractable microbial biomass made up between 2 and 7% of the bulk soil N pool corresponding to about 1/5–1/8 of the plant N pool (Fig. 2).

^{15}N UPTAKE AND ALLOCATION IN PLANTS

Due to the low concentrations of inorganic and glycine N in the soil solution, the added ^{15}N-NH_4^+, ^{15}N-glycine, and ^{15}N-NO_3^- made up 92.3, 99.7, and 99.7% of the respective soil solution pools at the heath and 89.6, 99.6, and 99.9 % at the shrub tundra immediately after labeling. However, at both harvests, ^{15}N recovery in DTN was low (0.08–0.24% of the added label) at the heath tundra and slightly, but significantly ($P < 0.001$) higher (0.30–0.46%) at the shrub tundra, indicating that virtually all added ^{15}N was incorporated into either microbes, plants or the insoluble soil organic matter pool.

The plants took up ^{15}N label from all added N forms. The ^{15}N concentration in plants was generally higher in *Carex* than in *Betula* and *Empetrum*, and higher at the shrub than at the heath tundra except in *Carex*, which had significantly higher concentrations at the heath.

Across the sites, the ^{15}N recovery in plants generally increased from day 2 to day 26 (Table 3). Also, the ^{15}N plant recovery differed between sites and between the different ^{15}N treatments (Table 3). At the shrub tundra, the ^{15}N recovery in both roots and leaves of *Carex* were significantly higher in the $^{15}NO_3^-$ treatment than in the other treatments ($P < 0.001$ and $P < 0.0001$ for roots and leaves, respectively; one-way ANOVA), and at the heath tundra we found the same treatment effect in both *Carex* roots ($P < 0.001$) and leaves ($P < 0.0001$) separately, and also for total *Carex* recovery (Fig. 3a). In *Empetrum* at the shrub site after 2 d, the ^{15}N recovery was similar in the NH_4^+ and NO_3^- treatment and near significantly lower in the glycine treatment (Fig. 3b) ($P = 0.052$, total *Empetrum* recovery). *Betula* took up more $^{15}NH_4^+$ than $^{15}NO_3^-$ and ^{15}N-glycine at the heath tundra, and this preference pattern was also evident at the shrub tundra, but only after 26 d. At the shrub tundra there was a proportionally higher uptake of $^{15}NO_3^-$ than ^{15}N-glycine, compared to the heath site, although this was not significant (Fig. 3c). In the mixed species, tested across the harvest occasions, there were significant effects of treatments at both sites, with lower uptake of ^{15}N-glycine than of the inorganic N-forms and lower recovery of ^{15}N-glycine than of $^{15}NH_4^+$ at the shrub tundra (Table 3, Fig. 3d).

The different species and growth forms allocated ^{15}N into the various plant compartments in different manners. However, there were no significant differences in the relative ^{15}N allocation patterns of the three N types into plant compartments within species (two-way ANOVAs). Already 2 d after labeling, *Carex* had allocated a large part of the absorbed ^{15}N to the aboveground parts (Fig. 3a), and 26 d after labelling, the distribution of ^{15}N had approached that of the total *Carex* N pool (Fig. 1a). In *Empetrum* and *Betula*, the fine roots contained 30 to 70% of the total absorbed ^{15}N 2 d after labeling and this proportion decreased only slightly with time (Fig. 3b-c). At both sites, the fraction of ^{15}N allocated to *Betula* leaves had doubled after 26 d, although it made up only about 12% of the total ^{15}N uptake, while the N fraction in *Betula* leaves was about 25% of the total N pool (Fig. 1c). *Empetrum* shows a similar pattern with only about 20% of the absorbed ^{15}N allocated to the leaves (Fig. 3b), while 40% of the total *Empetrum* N pool was in the leaves (Fig. 1b).

Based on the data on ^{15}N-glycine uptake 2 d after labeling, we calculated the $\delta^{13}C$ values that the plant root theoretically would obtain if uptake of glycine was in intact form. These $\delta^{13}C$ values were compared with the natural $\delta^{13}C$ values from the control plots and the $\delta^{13}C$ values measured in the ^{15}N-2(^{13}C)-glycine treated plots (Table 4). Only in fine roots of *Betula* at the heath tundra we identified a significantly higher $\delta^{13}C$ value in the ^{15}N-2(^{13}C)-glycine treatment than in the control plots. Here we found a ^{13}C:^{15}N-ratio of 1.78 ± 0.38. However, there was a clear tendency for all plants to be more enriched with ^{13}C in treated than in control plots.

RECOVERY OF ^{15}N AMONG PLANTS, MICROBES AND SOM

At both the heath and the shrub tundra, there were significant effects of treatment on incorporation of label into plants (Fig. 4).

TABLE 2

Soil characteristics of heath and shrub tundra (means ± 1 SE, $n = 6$). Monthly means between sites that do not share the same letters are significantly different ($P \leq 0.05$; Tukey's test).

Soil variable	July		August	
	Heath	Shrub	Heath	Shrub
SOM (% of dry matter)	88.0 ± 1.0	91.2 ± 0.6	90.4 ± 1.2	91.4 ± 1.3
H_2O (% of dry matter)	241 ± 19[b]	503 ± 43[a]	194 ± 9 [b]	525 ± 37 [a]
NH_4^+-N (μg N g^{-1} SOM)	1.61 ± 0.32[b]	3.48 ± 0.31[a]	3.74 ± 0.49	4.89 ± 0.49
NO_3^--N (μg N g^{-1} SOM)	0.054 ± 0.014[a]	0.015 ± 0.007[b]	0.015 ± 0.015	0.033 ± 0.012
DON (μg N g^{-1} SOM)	59.8 ± 8.5[b]	99.8 ± 9.0[a]	56.0 ± 4.6[b]	92.9 ± 5.2[a]
Amino acid N (μg N g^{-1} SOM)	0.411 ± 0.125[b]	1.007 ± 0.185[a]	1.398 ± 0.351	1.505 ± 0.248
Glycine N (μg N g^{-1} SOM)	0.066 ± 0.036	0.105 ± 0.055	0.064 ± 0.032	0.132 ± 0.047
Microbial N (μg N g^{-1} SOM)	361 ± 118 [b]	551 ± 32 [a]	402 ± 53	446 ± 27

Two days after labeling, the plants had incorporated about 6% of the added $^{15}NO_3^-$ and $^{15}NH_4^+$ at the heath and about 10% at the shrub tundra but only about 3 and 4% of the ^{15}N-glycine at the two tundra types. After 26 d, the proportion recovered in the plants at the heath had increased significantly to 9, 7, and 4% in the $^{15}NH_4^+$, $^{15}NO_3^-$ and ^{15}N-glycine treated plots while there was no significant change at the shrub tundra.

Most of the recovered label was incorporated in the soil organic matter, with no significant change of the recovery between the early and late harvest. There was, however, a significant treatment effect at the shrub tundra of more recovered ^{15}N in SOM of $^{15}NH_4^+$ than $^{15}NO_3^-$ and ^{15}N-glycine treated plots 26 d after labeling. Two days after label addition, a large part of the ^{15}N was recovered in the extractable microbial biomass, but the proportion had decreased significantly by about 50% at day 26. While there was no significant treatment effect at the heath, less ^{15}N was recovered in the extractable microbial biomass in the $^{15}NO_3^-$ than in the $^{15}NH_4^+$ and ^{15}N-glycine treatments at the shrub tundra. Despite the reduced proportion recovered in the extractable microbial biomass between day 2 and 26, the ^{15}N recovery in microbes in $^{15}NH_4^+$ and ^{15}N-glycine treated plots exceeded the ^{15}N recovery in plants also at day 26, while the microbial recovery of ^{15}N in $^{15}NO_3^-$ treated plots did not exceed the ^{15}N recovery in plants.

Discussion

N UPTAKE, ALLOCATION, AND UPTAKE PREFERENCES RELATED TO PLANT SPECIES AND SITE CONDITIONS

Within 2 d after labeling, the plants had absorbed N from all added sources, i.e. also from the organic glycine source as direct glycine uptake and/or as mineralized N. The difficulties in detecting uptake of organic N is well known and is due to large dilution of an expected and proportionally small uptake in comparison with the large ^{13}C pool already present in the tissues (Näsholm and Persson, 2001), as also observed in the present experiment (Table 4). Despite the dilution, we yet detected a significant difference between δ^{13}C in *Betula* roots from controls and glycine treated plots at the heath tundra (Table 4), which is the first field evidence of uptake of intact glycine by the important circumpolar arctic dwarf shrub *Betula nana*. The ^{13}C:^{15}N-ratio of 1.78 ± 0.38 in *Betula* roots from the heath site 2 d after glycine addition is close to the ^{13}C:^{15}N-ratio of 2 in the added glycine, which points to a high degree of intact glycine uptake. In addition, the trend towards higher δ^{13}C-values in roots from glycine treated than from control plots for all species at both sites indicates uptake of intact glycine also among the other species. The uptake of glycine-derived ^{15}N 2 d after labeling, and the fast exhaustion of ^{15}N from the dissolved soil N pools in all treatments, also shows that the plants are able to take up glycine-N either directly in competition with free-living microorganisms or after fast microbial mineralization taking place within a short time after the glycine is supplied. However, at both sites the plants generally had lower initial recovery of ^{15}N in the glycine treatment than in the inorganic ^{15}N treatments (Fig. 3). In the only other field study of N form preferences after injections of mixed N forms to an arctic ecosystem that we are aware of, the uptake of amino acid-N sources also was lower than uptake of added inorganic N sources (Nordin et al., 2004)

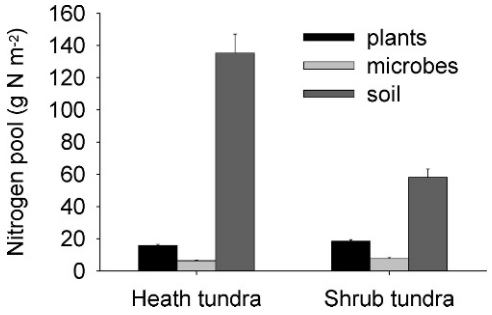

FIGURE 2. Total pools of N (g m^{-2}) in plants, microbes, and soil at the heath tundra and the shrub tundra. Data are pooled across treatments and harvests, means ±1 SE, $n = 36$.

There was a tendency for *Carex* to take up more NO_3^- than NH_4^+, while both *Betula* and the mixed species generally showed increased preference in the order $NH_4^+ \geq NO_3^- \geq$ glycine. Other labeling studies in northern ecosystems also have shown preference for uptake of NO_3^- over uptake of NH_4^+ and glycine among graminoids, e.g. *Carex bigelowii* in an Alaskan tussock tundra (McKane et al., 2002), *Eriophorum vaginatum* in an acidic tussock tundra (Nordin et al., 2004) and *Deschampsia flexuosa* in a boreal forest (Persson et al., 2003). One explanation to the observed high graminoid NO_3^- uptake could be that at our study sites as in the studies cited above, the biomass of graminoids was low compared to the biomass of dominant deciduous and evergreen shrubs. The graminoids may therefore have taken up NO_3^- because the dominant shrubs tend to acquire NO_3^- at slower rates resulting in a relative increase of the NO_3^- available for uptake (McKane et al., 2002). However, in our experiment, virtually all the added label was taken up within the first 2 d after labeling, and the availability of all N forms therefore should be equally high even shortly after labeling. Furthermore, graminoids are most often dominant in relatively nutrient-rich sites where availability of NO_3^- is high, and observations of high nitrate reductase activity in arctic graminoid species compared to other

TABLE 3

***P*-values from three-factor ANOVA of recovery of ^{15}N in different plant fractions sampled at the heath tundra and the shrub tundra 2 (July) and 26 (August) days after labeling. *P*-values are for main factor effects: Site (S), Treatment (T) and Harvest (H) and interactions between main effects. Only significant ($P \leq 0.05$) or near-significant ($P \leq 0.1$) values are included; n.s. not significant ($P > 0.1$).**

Fraction	Site	Treatment	Harvest	S × T	S × H	T × H
Carex, roots	n.s.	0.007	n.s.	n.s.	n.s.	n.s.
Carex, leaves	0.0011	<0.0001	0.0027	n.s.	0.0042	0.0267
Empetrum, fine roots	n.s.	0.0384	n.s.	n.s.	n.s.	n.s.
Empetrum, leaves	0.0185	n.s.	0.0083	n.s.	n.s.	n.s.
Empetrum, coarse roots+stems	0.0009	n.s.	0.0137	n.s	0.0526	n.s.
Betula, fine roots	<0.0001	0.0097	0.0051	n.s.	0.0058	n.s.
Betula, leaves	n.s.	0.0009	0.0827	n.s.	n.s.	n.s.
Betula, coarse roots+stems	n.s.	0.0017	<0.0001	n.s.	<0.0001	0.0177
Mixed species, roots	n.s.	0.0009	0.0827	n.s.	n.s.	n.s.
Mixed species, leaves+stems	0.0009	n.s.	0.0031	n.s.	n.s.	n.s.

plant growth forms (Michelsen et al., 1996) point to high uptake capacity for NO_3^-.

Compared to the initial uptake rate of label into the plant pool during the 2 d following the addition, the rate during the following 24 d declined (Figs. 3, 4). In Alaskan tussock tundra, Schimel and Chapin (1996) found the highest uptake rate within 5 d after labeling, followed by slight increases in the plant ^{15}N recovery during the following 25 d. Likewise, Grogan and Jonasson (2003) found some incorporation of label into evergreen plants 4 to 7 d after labeling in October, followed by no uptake during the winter, but a subsequent high uptake by all plant growth forms from May to July the following year. There can be at least two explanations for this pattern of uptake rates. First, the uptake rate in our study was high immediately after label addition because of the pulse of available N, but decreased rapidly as most of the added N was efficiently incorporated in the extractable microbial biomass and the SOM pool within a few days. Thus, the ^{15}N released from microbial biomass over the following 24 d was diluted by the N pool already contained in microbial biomass and by the native N pool processed by the microbes over this period. This would lead to a substantial pool dilution of the available soil ^{15}N pool and to underestimated plant N uptake based on ^{15}N uptake alone. Second, the plants take up N mainly in the beginning and middle of the growing season, and not late in the season (August). For instance, McKane et al. (2002) observed that most plant species took up more N after injection of label in June than after injection of label in August. However, *Betula nana* took up more label in August than in June (McKane et al., 2002), a pattern also found in our study, as the ^{15}N recovery in *Betula* at the shrub tundra, but not at the heath tundra, had doubled from the first to the second harvest.

Despite the differences in vegetation type and plant biomass, and therefore assumed differences in nutrient supply rates between the two sites, we did not find any differences between the relative availability of three N forms at the two sites (Table 2), contrary to reported differences along a nutrient gradient of a boreal forest (Nordin et al., 2001). However, reports on fast turnover of soil nutrients in arctic soils (hours to a few days) (Jackson et al., 1989; Jones and Kielland 2002) suggest that nutrient concentrations are poorly related to nutrient availability, which may depend more on nutrient fluxes. Because of the apparent lack of difference in relative supply of the different N forms between the two sites, we assumed that the uptake preferences would not differ between sites. However, we did find a tendency of higher preference for NO_3^- uptake in *Betula* at the shrub tundra than at the heath tundra. Also, at our sites, the leaf natural abundance of $\delta^{15}N$ in *Betula* was -6.24 ± 0.56 ‰ at the heath and higher, -4.10 ± 0.52 ‰, at the shrub tundra. Hobbie et al. (2000) found that plant foliar $\delta^{15}N$ was lower at sites with low N availability than at sites with high N availability over a range of sites at Glacier Bay, Alaska, mainly owing to higher dependency on N supply from mycorrhiza at sites with low N availability. Furthermore, ectomycorrhizal fungi seem to discriminate against uptake of NO_3^- (Finlay et al., 1992; Gessler et al., 2005). Therefore, the higher $\delta^{15}N$ values and higher *Betula* preference for NO_3^- at the shrub than at the heath tundra could be caused by a combination of higher inorganic nutrient availability and lower relative N supply via mycorrhiza at the wet shrub tundra than at the drier heath, as the nutrient availability was higher at this site.

The two *Carex* species translocated a much larger part of the acquired ^{15}N to the leaves than the dwarf shrubs already two days after label addition, and after 26 d, more than half of the ^{15}N in *Carex* was recovered in the leaves (Fig. 3a). Other field (Schimel and Chapin, 1996; Grogan and Jonasson, 2003) and mesocosm (Grogan et al., 2004) studies of ^{15}N uptake and allocation also showed high allocation of recently acquired ^{15}N to leaves in graminoids and low allocation to leaves of shrubs. High growth rates and thereby a demand for high photosynthetic rate in *Carex* may drive the fast allocation to leaves, while *Betula* and *Empetrum* give priority to long-term N storage.

^{15}N PARTITIONING AMONG MICROBES, PLANTS, AND SOIL ORGANIC MATTER

At the shrub tundra, the microbes showed a preference for glycine over the other N forms, opposed to the plants, which took up more of the inorganic N-forms. These results support the theory on complementary N-form preferences by microbes and plants (Lipson and Näsholm, 2001). The microbes probably take up glycine at higher rates than the inorganic N-forms as it acts as a source of C for the generally substrate-limited microbes (Jonasson et al., 1996; Schmidt et al., 1997).

The proportion of added ^{15}N taken up by plants was low compared with the microbial uptake, and of the same order of magnitude as in reports from other arctic ecosystems (Schimel and Chapin, 1996; McFarland et al., 2002; Grogan and Jonasson, 2003). In the extractable microbial biomass, we observed a high initial ^{15}N uptake (Fig. 4), which confirms that retention of nutrients in microbes play a crucial role in the control of N cycling in arctic ecosystems (Schimel and Chapin, 1996; McFarland et al., 2002; Grogan and Jonasson, 2003; Henry and Jefferies, 2003a;

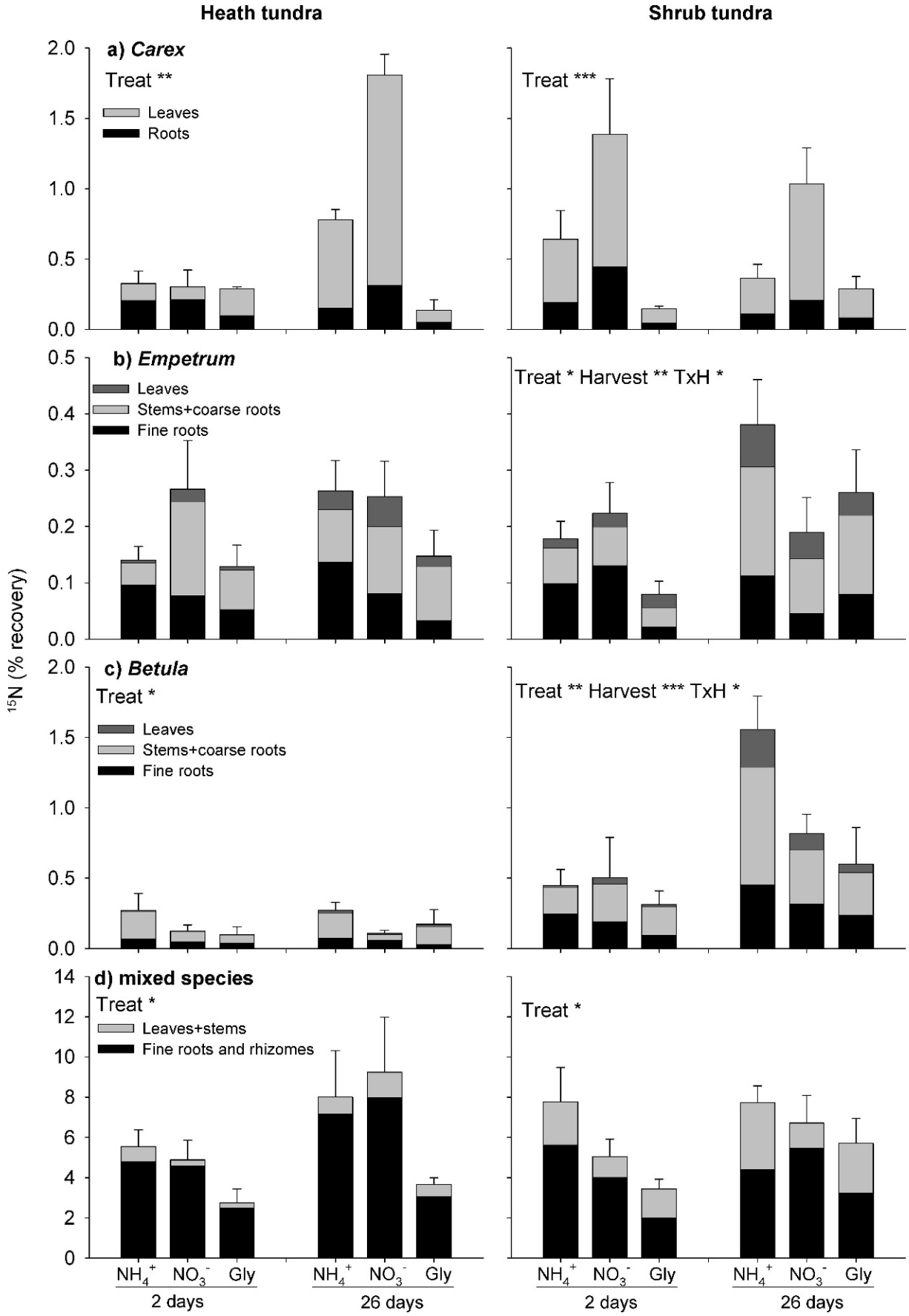

FIGURE 3. Distribution of ^{15}N enrichment in percent recovery of added ^{15}N, 2 and 26 d after labeling with $^{15}NH_4^+$, ^{15}N-glycine, or $^{15}NO_3^-$ at the heath and the shrub tundra in plant fractions of a) *Carex*, b) *Empetrum*, c) *Betula,* and d) Mixed species. The effects of treatment and time of harvest and their interactions were analyzed with two-factor ANOVAs for each fraction separately: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

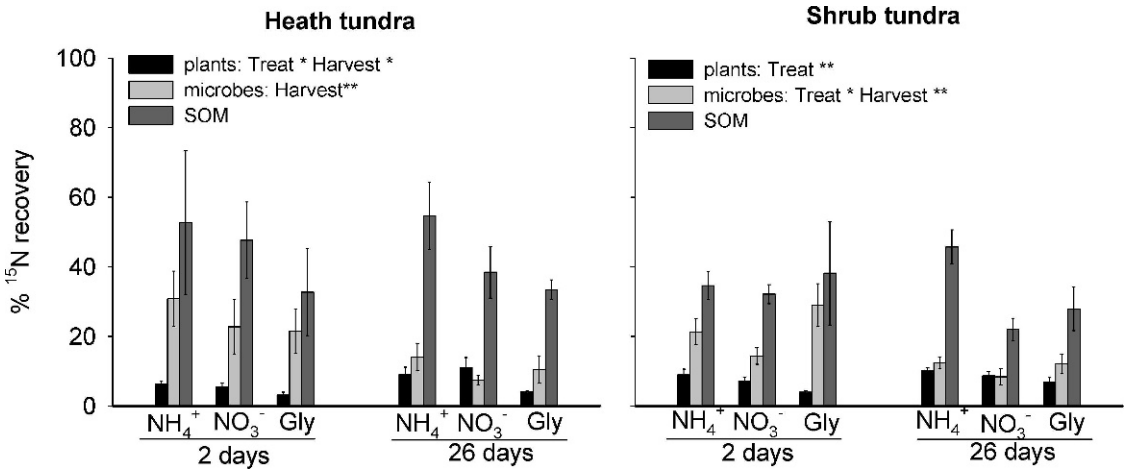

FIGURE 4. Distribution of ^{15}N enrichment in percent recovery of added ^{15}N in plants, extractable microbial biomass, and SOM, 2 and 26 d after labeling with $^{15}NH_4^+$, ^{15}N-glycine, or $^{15}NO_3^-$ at the heath and the shrub tundra. Data are means ±1SE, $n = 6$. The effects of treatment and time of harvest and their interactions were analyzed with two-factor ANOVAs for each fraction separately: * $P < 0.05$, ** $P < 0.01$.

Nordin et al., 2004). However, after 26 d, the extractable microbial ^{15}N pool was reduced to half the size it had after two days. Furthermore, the proportion of ^{15}N incorporated in the soil organic matter pool strongly increased (Fig. 4), a pattern that agrees with findings in other labelling studies (Marion et al., 1982; McFarland et al., 2002; Grogan et al., 2004). Some of the decline in the microbial ^{15}N pool could be a result of methodological overestimation of initial ^{15}N uptake in microbes, as the ^{15}N incorporated in the microorganisms after 2 d may be more chloroform labile and, hence, with higher extractability than the microbial ^{15}N 26 d after label addition. Also, a high proportion of fungal derived microbial biomass in the soil may lead to an underestimation of the microbial biomass, as fungi in some cases seem to be less extractable by the chloroform fumigation than bacteria (Ingham et al., 1991; Wallander et al., 2003). This could explain part of the high incorporation of ^{15}N into the SOM pool. However, most of the change in the microbial ^{15}N pool is probably a consequence of rapid microbial turnover of ^{15}N and subsequent incorporation into a more recalcitrant SOM pool, eventually approaching the same proportion of a few percent of the bulk soil N incorporated in the microbes (Fig. 2). Because we observed little plant ^{15}N uptake between day two and 26 after label addition, it appears that the label once it is incorporated in the bulk soil is only slowly released to plant available forms.

Conclusions

Our study has shown, first, that all co-existing plant species did take up all added N-forms but all species generally showed higher preference for the inorganic forms, either NH_4^+ or NO_3^-, than for N from the glycine source. The shrub species *Betula* preferentially absorbed NH_4^+ while *Carex* preferred NO_3^-. Second, we found a tendency for higher preference for NO_3^- than for NH_4^+ at the shrub tundra compared to the heath in *Betula*, probably caused by lower dependency of uptake via mycorrhiza than at the nutrient-poor heath tundra. Third, the *Carex* species translocated a higher proportion of the absorbed ^{15}N to the aboveground parts than the shrubs, supposedly for immediate photosynthetic use, while the shrubs gave priority to longer-term N storage. Fourth, the microbes showed a preference for the organic N form while the plants preferentially took up inorganic N, which could release the competition for resources between plants and microbes. Fifth, we found that microbial ^{15}N immobilization was high immediately after the label addition, whereas after 26 d, the ^{15}N recovered in the microbes was reduced to half of the amount found 2 d after label addition, and most of the label was recovered in the nonmicrobial part of the soil. During the same period, the plant ^{15}N uptake rate decreased strongly compared with the rate within the 2 d following label addition, and the ^{15}N recovery was, hence, similar (NO_3^-) or

TABLE 4

$\delta^{13}C$-values in roots of control plots, of glycine treated plots two days after labeling and the theoretically $\delta^{13}C$-values calculated under the assumption of 100% uptake of intact glycine. Species means that do not share the same letters are significantly different ($P \leq 0.05$; Tukey's test).

Site	Plant species	$\delta^{13}C$		
		Control	Glycine treated	Theoretical
Heath tundra	*Carex*	−27.10 ± 0.05	−26.69 ± 0.42	−24.85 ± 1.23
	Empetrum	−27.78 ± 0.22	−27.63 ± 0.26	−27.32 ± 0.10
	Betula	−29.59 ± 0.11^{b}	−28.69 ± 0.30^{a}	−28.70 ± 0.27^{ab}
	Mixed species	−28.03 ± 0.01 ^{b}	−27.47 ± 0.24 ^{ab}	−26.70 ± 0.32 ^{a}
Shrub tundra	*Carex*	−27.44 ± 0.31 ^{b}	−27.09 ± 0.25 ^{ab}	−26.20 ± 0.25 ^{a}
	Empetrum	−28.36 ± 0.23 ^{b}	−28.04 ± 0.26 ^{ab}	−27.29 ± 0.22 ^{a}
	Betula	−29.44 ± 0.24 ^{b}	−28.82 ± 0.17 ^{ab}	−28.40 ± 0.11 ^{a}
	Mixed species	−28.97 ± 0.17 ^{b}	−28.91 ± 0.16 ^{ab}	−28.33 ± 0.10 ^{a}

lower (NH_4^+ and glycine) in plants than in microbes 4 wk after N addition.

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