

## COMPLEMENTARITY IN MINERAL NITROGEN USE AMONG DOMINANT PLANT SPECIES IN A SUBALPINE COMMUNITY<sup>1</sup>

ANDRÉ PORNON,<sup>2,4</sup> NATHALIE ESCARAVAGE,<sup>2</sup> AND THIERRY LAMAZE<sup>3</sup>

<sup>2</sup>Laboratoire Evolution et Diversité Biologique, CNRS-UMR 5174, Université Paul Sabatier, 31062 Toulouse cedex 4, France; and <sup>3</sup>Centre d'Etudes Spatiales de la Biosphère, CNES-CNRS-IRD-UMR 5126, Université Paul Sabatier, 31401 Toulouse cedex 4, France

The underlying mechanisms that enable plant species to coexist are poorly understood. Complementarity in resource use is among the major mechanisms proposed that could favor species coexistence but is insufficiently documented. In alpine soil, low temperatures are a major constraint for the supply of plant nitrogen. We carried out <sup>15</sup>N labeling of soil mineral N to determine to what extent four major species of a subalpine community compete for N, or develop ionic (NH<sub>4</sub><sup>+</sup> vs. NO<sub>3</sub><sup>-</sup>) or temporal complementarity. The Poaceae took up much more <sup>15</sup>N per soil area unit than the ericaceous species, and all species displayed three major strategies in exploiting <sup>15</sup>N: (1) uptake mainly early in the growing season (*Vaccinium myrtillus*), (2) uptake at a slow and similar rate throughout the growing season (*Rhododendron ferrugineum*), and (3) uptake at high rates over the growing season (*Festuca eskia* and *Nardus stricta*). However, while *F. eskia* used <sup>15</sup>NH<sub>4</sub><sup>+</sup> mainly early and <sup>15</sup>NO<sub>3</sub><sup>-</sup> mainly late in the growing season, the reverse was observed for *N. stricta*. Taking into account <sup>15</sup>N dilution in soil NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> pools, we calculated that NH<sub>4</sub><sup>+</sup> provided more than 80% of the mineral N uptake in Ericaceae and about 60% in grasses. Together, such ionic and temporal complementarity would reduce competition between species and could be a major mechanism promoting species diversity.

**Key words:** ionic and temporal complementarity; mineral N; <sup>15</sup>N uptake; plant interaction; subalpine community.

The term biodiversity encompasses the total biotic variations from the levels of genes to that of ecosystems (Purvis and Hector, 2000), but the most commonly considered facet of this term is species richness, i.e., the number of species in a region or habitat. Our understanding of how species arrive on a site through evolutionary (speciation) and demographic processes (population dynamics) has been considerably improved these last decades (Watkinson, 1997; Freeman and Herron, 2004). However, how species coexist in a community is still poorly understood and intensively discussed in both theoretical and empirical studies (Silvertown et al., 1999). Because plants basically have similar fundamental requirements and satisfy them in a very limited number of ways (they use the same ions from the same superficial soil compartment; Connell, 1978; Silvertown et al., 1999; McKane et al., 2002), coexisting species must largely overlap in the use of resources and, according to “competitive exclusion theory,” their number would not exceed the number of limiting resources (which usually are less than five; Tilman, 1982) in any given plant community (Stewart and Levin, 1973; Tilman, 1997). Although periodic changes in resource availability may favor stable coexistence between two species competing for the same limiting resources (Stewart and Levin, 1973), the presence of high diversity spots seems theoretically unlikely. This situation has led to some alternative hypotheses suggesting that species-rich communities could represent nonequilibrium transitory states that progress toward low-diversity equilibrium communities (Connell, 1978).

Interspecific competition has, for several decades, been

considered to be the main proximal driving force organizing plant communities but, as suggested above, cannot alone be responsible for species coexistence in communities. More recently, studies have highlighted how either positive interactions (Callaway et al., 2002; Cardinale et al., 2002) or complementarity (Hooper, 1998; Caldeira et al., 2001; Fridley, 2001; van Ruijven and Berendse, 2003; Lambers et al., 2004) can reduce competition between neighbors of other species thus facilitating species coexistence (Fridley, 2003). Resource-based niche differentiation has often been evoked to explain complementarity between species or functional groups, and many studies refer to niche complementarity to explain positive relationships between species diversity and ecosystem functioning (Loreau and Hector, 2001) but fail to propose mechanisms by which this complementarity could occur (van Ruijven and Berendse, 2003).

Resource partitioning and complementarity between species can occur in different ways. First, different growth forms can allow plants to exploit variable levels of ambient light (Fridley, 2003) and/or to explore variable volumes of the soil because of different rooting depths (Casper and Jackson, 1997). Second, there can be variable affinities of plants for the chemical forms of N (Chapin et al., 1993; George et al., 1999; McKane et al., 2002). Lastly, plants may use spatially or temporally different resource pools (Greenlee and Callaway, 1996; Theodose et al., 1996; Hooper, 1998; McKane et al., 2002). Together, these different modes of temporal or spatial resource partitioning likely allow species coexistence in the community.

In this work we examined the use of different N pools (N available as NO<sub>3</sub><sup>-</sup> or NH<sub>4</sub><sup>+</sup>) by dominant plant species in a subalpine plant community of conservation importance in the French Pyrenees. The dominant species *Nardus stricta* L. (Poaceae), *Festuca eskia*, Ram., (Pyreneo-Cantabric endemic Poaceae), *Vaccinium myrtillus* L. (Ericaceae), and *Rhododendron ferrugineum* L. (Ericaceae) coexist for several decades and structure many subalpine species-rich communities of the

<sup>1</sup> Manuscript received 18 January 2007; revision accepted 23 August 2007.

The authors thank the Pyrenees National Park for financial support and A. Gojon and P. Tillard (INRA-ENSAM Montpellier) for <sup>15</sup>N analyses.

<sup>4</sup> Corresponding author (e-mail: pornon@cict.fr), fax: + 33 5 61 55 73 27

Pyrenees (Tosca, 1986). According to European Economic Community laws (92/43/EEC habitat directives, 1992), the vegetation dominated and structured by these species (except *V. myrtillus*) must be locally preserved because of its high ecological and patrimonial value.

Our objectives were to determine whether the species use the same N pool (competition) or complement each other by simultaneously using different ionic forms ( $\text{NH}_4^+$  vs.  $\text{NO}_3^-$ ; ionic complementarity) or the same ionic form but at different periods (temporal complementarity; Theodose et al., 1996; McKane et al., 1990, 2002; Nordin et al., 2001). Continuous nutrient supply through mineralization may reduce competition. However, low alpine soil temperature has repeatedly been cited as a major constraint for mineralization and the supply of plant available N (Körner, 1999), so this element is often considered most limiting to alpine plant productivity. We studied N absorption because mechanisms underlying N spatial and temporal sharing between species could relax interspecific competition and promote species coexistence (Fridley, 2001). In addition, ecological processes and biogeochemical cycles (especially the N cycle) are currently disturbed by human activities. In high-elevation mountain ecosystems, the plant response to increase in anthropogenic N deposition is particularly acute and results in changes in community diversity, with increases in the abundance of nitrophilous species (Bowman et al., 2006). Consequently, it has become necessary to improve the scientific knowledge concerning the characteristics of mineral N uptake by the major species of the alpine community.

We performed  $^{15}\text{N}$  labeling of the soil mineral N pools and traced the label through the plant (belowground and aboveground) at three key periods of the growing season. Previous studies have used  $^{15}\text{N}$ -tracers in the field, but they did not test how species differed in their use of soil N (Theodose et al., 1996; Bowman et al., 2006), how plants allocated N to their component parts (McKane et al., 1990; McKane et al., 2002), or how plant N uptake varied over time (Nordin et al., 2001).

## MATERIALS AND METHODS

**Study site and species studied**—The study was conducted in the eastern end of the Pyrenees National Park buffer zone in the central French Pyrenees in a high altitude vale (vale of Estaragne 42°48' N; 0°9' E) oriented north/south and extending over 2 km between 2100 and 2200 m a.s.l. The vegetation of the vale is characteristic of many sites in the subalpine Pyrenees belt and is composed of a mosaic of meadow and patchy trees and shrubs with long heathland and meadow ecotones.

The subalpine climate prevailing in the site is milder because of Ibero-Mediterranean influences. Snow cover usually persists from late October until June (Lavandier, 1979). The average annual precipitation is 1500 mm. The geological substrate is granitic, amphibolitic, and schistic. Soils are acidic ( $\text{pH} = 4.7 \pm 0.1$  SE; total N:  $0.5 \pm 0.044\%$ ; bulk density:  $0.65 \pm 0.099$   $\text{kg}\cdot\text{L}^{-1}$ ).

One hundred and sixty-two vascular species were identified in 61 quadrats (each 25 m<sup>2</sup>) sampled over a 4-ha area in the vale, but four species coexist, dominate, and structure the vegetation. These species are the evergreen shrub *R. ferrugineum* (70 cm tall), the dwarf deciduous shrub *V. myrtillus* (20–30 cm tall) of mountainous or subalpine forests as well as subalpine and alpine meadows, and the tussock-forming meadow grasses *N. stricta* and *F. eskia* (10–30 cm tall).

**Plant cover and biomass**—At the end of spring 2000, 30 plots, each 50 × 50 cm and supporting the four target species, were selected at random in a 300 m<sup>2</sup> area. This area is included in a 1 ha area that is homogeneous for slope (40%), exposure (NW), soil depth (72 cm ± 22), and community structure (mosaic of shrub patches in meadow). The experiment was conducted over

three time periods (10 plots/period). Period T1 (3–18 July; 20 d after snow melt) was chosen within the early growing season. During this period, the four species grew simultaneously and achieved a substantial part of their growth (the two grasses and *V. myrtillus* started to grow earlier than *R. ferrugineum*). Many alpine plants are supported during the early growing season by internal remobilization with only minimal nitrogen uptake (Jeager and Monson, 1992; Pasche et al., 2002). In period T2 (3–18 August), the shrubs had finished their vegetative and reproductive growth, while the grasses developed their reproductive organs. Period T3 (3–18 September) corresponded to the last part of the growing season.

Plant cover was estimated at each period in the 10 plots by point intercept (Magurran, 2004): a dowel 5 mm in diameter was inserted perpendicularly into the vegetation at the intersections of a 10 × 10 cm grid. At each intersection (36 points in overall), the presence or absence of the target species was noted. We chose 10-cm spacing because it corresponded to the average diameter of smaller grass tussocks. We then calculated the cover of each target species in the 10 plots.

The above- and belowground biomasses (mg dry mass·cm<sup>-2</sup>) of grasses and *V. myrtillus* were estimated by removing 20 blocks (each 1 dm<sup>2</sup>) of the upper 15 cm of soil from the plots at the end of each period. In the laboratory, the shoots were manually separated with their roots, and the roots were extracted from the soil under water. The shoot and root dry masses were then multiplied by the area covered by the species to evaluate above- and belowground biomass over each 0.25 m<sup>2</sup> plot. Cover of *R. ferrugineum* was estimated by projection onto the soil of the crown area of 30 individuals (10 per period). The individuals were then excavated to determine the aboveground and belowground biomass.

**Estimation of soil  $\text{N-NO}_3^-$  and  $\text{N-NH}_4^+$  pools**—At each period, soil  $\text{N-NO}_3^-$  and  $\text{N-NH}_4^+$  pools were determined before labeling and at the end of the  $^{15}\text{N}$  absorption period in order to calculate the  $^{15}\text{N}$  dilution in the soil mineral N pool (upper 15 cm of soil) and estimate N uptake ( $\text{NO}_3^-$  or  $\text{NH}_4^+$ ) from  $^{15}\text{N}$ . We used a 7-cm-diameter core to sample the upper 15 cm of soil (three cores per plot and per date, which were pooled, i.e., 20 different samples at each period). We took the cores close to the plots prior to labeling and within the plots at the end of the  $^{15}\text{N}$  absorption period. The soil samples were stored on ice and transported to the laboratory. The day following the harvest, 10 g of the 2 mm soil fraction were extracted with 2 M KCl (1 : 5 soil extractant), filtered through filter paper (HA membrane, 0.45  $\mu\text{m}$ , Millipore, Billerica, Massachusetts, USA), and analyzed with a flow-injection autoanalyzer (Lachat, Milwaukee, Wisconsin, USA) to determine  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations. The gravimetric water content and density of soil samples was estimated after oven drying (70°C) until constant mass. Soil  $\text{N-NO}_3^-$  and  $\text{N-NH}_4^+$  pools were estimated in the upper 15 cm.

**$^{15}\text{N}$  labeling**—For estimating  $^{15}\text{NO}_3^-$  vs.  $^{15}\text{NH}_4^+$  uptake by the plants, at each date (T1, T2, and T3) the soil  $\text{NO}_3^-$  pool of five plots was labeled with  $\text{K}^{15}\text{NO}_3$  and the soil  $\text{NH}_4^+$  pool of five other plots in the vicinity was labeled with  $^{15}\text{NH}_4\text{Cl}$  (plots were selected at random within the same group of plots).

The labeling solution (20 mL, 0.732 mM,  $^{15}\text{N}$  abundance of 99 atom per cent) was injected in the upper 15 cm of soil at each intersection of a 10 × 10 cm grid (36 injection points in the 0.25 m<sup>2</sup> plots) at each of the three dates. The solution was distributed evenly within the 15 cm by sequential injections during the extraction of the needle from the soil. The amounts of  $^{15}\text{N}$  supplied to the plots were calculated to be suitable to detect the label after its dilution in the plant/soil system and were sufficiently low (26.57 mg N·m<sup>-2</sup>, i.e., 265.72 g·ha<sup>-1</sup>) to avoid any meaningful modification of the total soil N (about 325 g·m<sup>-2</sup>). Plots were watered after  $^{15}\text{N}$  injection with 1 L of water to prevent direct labeling of vegetation and, as far as possible, to spatially homogenize  $^{15}\text{N}$  distribution in the soil. Observations of soil trenches formed downhill in five additional control plots showed that watering did not induce  $^{15}\text{N}$  loss through leaching.

Plants were harvested 15 d after labeling and placed in cold storage. In the laboratory, they were separated (as for biomass determination) into two compartments (above- and belowground), oven-dried at 50°C for 48 h, and ground to a fine powder (<1  $\mu\text{m}$ ) before analysis of  $^{15}\text{N}$  abundance using a continuous-flow isotope ratio mass spectrometer coupled with an elemental analyzer (model ANCA-MS, Europa Scientific, Crewe, UK; Clarkson et al., 1996).

**Data analysis**—The amount of  $^{15}\text{N}$  in excess in each plant compartment was calculated as  $MCE$  where  $M$  = dry mass of the compartment (g);  $C$  = total N

TABLE 1. Mean cover (%) and aboveground and belowground dry biomasses ( $\text{g}\cdot\text{m}^{-2}$ , means  $\pm$  SE,  $N = 10$ ) for the four species (*Rhododendron ferrugineum*, *Vaccinium myrtillus*, *Festuca eskia*, and *Nardus stricta*) at the three labeling periods. T1: 03–18 July, T2: 03–18 August, T3: 03–18 September.

Period	Species	Mean cover	Aboveground biomass	Belowground biomass
T1	<i>R. ferrugineum</i>	9.7 $\pm$ 3.5	540 $\pm$ 170	400 $\pm$ 120
	<i>V. myrtillus</i>	44.4 $\pm$ 13.6	230 $\pm$ 120	190 $\pm$ 60
	<i>N. stricta</i>	13.6 $\pm$ 4.2	1250 $\pm$ 415	2930 $\pm$ 1610
	<i>F. eskia</i>	63.1 $\pm$ 11.9	1130 $\pm$ 168	2990 $\pm$ 1210
T2	<i>R. ferrugineum</i>	9.20 $\pm$ 3.4	580 $\pm$ 160	420 $\pm$ 180
	<i>V. myrtillus</i>	30.0 $\pm$ 2.64	200 $\pm$ 110	200 $\pm$ 90
	<i>N. stricta</i>	17.2 $\pm$ 5.8	1540 $\pm$ 800	3060 $\pm$ 1690
	<i>F. eskia</i>	66.9 $\pm$ 14.5	1460 $\pm$ 502	3280 $\pm$ 1200
T3	<i>R. ferrugineum</i>	5.8 $\pm$ 3.0	900 $\pm$ 250	660 $\pm$ 100
	<i>V. myrtillus</i>	18.1 $\pm$ 10.3	260 $\pm$ 120	2100 $\pm$ 100
	<i>N. stricta</i>	26.4 $\pm$ 13.6	1760 $\pm$ 590	3090 $\pm$ 1880
	<i>F. eskia</i>	56.7 $\pm$ 19.1	1260 $\pm$ 315	3440 $\pm$ 1050

concentration (%) of the compartment;  $e = {}^{15}\text{N}$  in excess of natural abundance (atom percent) in the compartment.

Isotopic excess was calculated as the difference between  ${}^{15}\text{N}$  abundance in the compartments of labeled plants and "natural"  ${}^{15}\text{N}$  abundance. Natural  ${}^{15}\text{N}$  abundance was determined for two nonlabeled individuals for each of the four species and reached about 0.365%. There were small differences in natural abundance between species and compartments, which were negligible as compared to the enrichment of the plant tissues with soil  ${}^{15}\text{N}$ .

Soil  ${}^{15}\text{NH}_4^+$  or  ${}^{15}\text{NO}_3^-$  labeling allowed assessment for each species and date of  ${}^{15}\text{N}$  accumulation on a plant mass basis ( $\mu\text{g } {}^{15}\text{N}\cdot\text{g}^{-1}$  plant DW),  ${}^{15}\text{N}$  uptake on a soil area basis ( $\mu\text{g } {}^{15}\text{N}\cdot\text{cm}^{-2}$ ), and  ${}^{15}\text{N}$  partitioning (on a plant mass basis) between belowground and aboveground plant compartments. Lastly, we estimated N uptake assuming a full mixing of injected  ${}^{15}\text{N}$  with the soil  $\text{NO}_3^-$  or  $\text{NH}_4^+$  pool (upper 15 cm of soil), no purging effect of the injection, no loss of injected  ${}^{15}\text{N}$  due to leaching, and no microbial transformation. For calculating N uptake ( $\text{NO}_3^-$  or  $\text{NH}_4^+$ ) from  ${}^{15}\text{N}$  uptake, abundances of  ${}^{15}\text{NH}_4^+$  or  ${}^{15}\text{NO}_3^-$  in the soil should ideally be uniform, and only one of the chemical forms of N must be labeled for a given treatment (excluding microbial transformation, which can lead to labeling of the other mineral form and of organic nitrogen). In the present study, we took several measures to reduce sources of errors. First, we made regular (in the three dimensions) and relatively close injections as compared to the area covered by the species. Thus, although  ${}^{15}\text{N}$  dilution may vary over space, the scale of the spatially regular variation in  ${}^{15}\text{N}$  dilution was smaller than the size of the sampling frame. In addition, for each plot, the whole biomass of each target species (corresponding to several individuals) was harvested. Second, although nitrification is likely low in acidic soils, the nitrification inhibitor dicyandiamide ( $\text{C}_2\text{H}_4\text{N}_4$ ; Sigma, St. Louis, Missouri, USA) was added ( $90 \mu\text{mol}\cdot\text{L}^{-1}$ ) to the  ${}^{15}\text{NH}_4^+$  solution to prevent ammonium oxidation. Nitrification inhibitors are compounds that efficiently delay the bacterial oxidation of ammonia to nitrite in the soil (first step of the

nitrification) by reducing the activity of *Nitrosomas* bacteria in the soil without phytotoxicity on gramineous species (Macadam et al., 2003). Finally, we did not observe any flow out of the soil solution from the core samples (either after watering or at the end of the uptake period). We also determined soil nitrate and ammonium contents before labeling and after the uptake period.

The effects of species, N forms (treatments), periods, and interactive effects on  ${}^{15}\text{N}$  accumulation per unit of plant dry mass ( $\mu\text{g}\cdot\text{g}^{-1}$ ) and  ${}^{15}\text{N}$  uptake per unit soil area ( $\mu\text{g}\cdot\text{cm}^{-2}$ ) were tested by three-way ANOVA (SYSTAT, version 9, San Jose, California, USA) with the three factors acting as fixed effects. One-way ANOVA was performed to test the differences between species at each date and between dates for each given species for N accumulation and uptake. ANOVA was also used for between-date differences in soil  $\text{NO}_3^-$  and  $\text{NH}_4^+$  pools and between-date differences in allocation of  ${}^{15}\text{N}$  in the plants. When significant variation among means was detected in ANOVA, a Tukey honestly significant different (HSD) multiple range test was performed to determine its source. Because of the low number of data, varying responses of species induced by the source of nitrogen ( $\text{NH}_4^+$  vs.  $\text{NO}_3^-$ ) at each period were tested by a Mann–Whitney *U*-test.

## RESULTS

**Species cover and biomass**—The community was mainly dominated by *F. eskia* and *V. myrtillus*, while *N. stricta* and *R. ferrugineum* had lower cover (mean cover averaged over three periods: 60%, 30%, 18%, and 10%, respectively; Table 1). The cover of other co-occurring species (e.g., *Leontodon pyrenaeicus*, *Plantago alpina*, *Potentilla erecta*) was very low (on average below 5%). The two grasses had comparable aboveground and belowground biomasses but three to seven times more aboveground biomass and 8–18 times more belowground biomass than *R. ferrugineum* and *V. myrtillus*. The belowground compartment made up two-thirds of the total biomass in both grasses but only half of the total biomass in the ericaceous species (Table 1).

**Soil  $\text{N}\text{-NO}_3^-$  and  $\text{N}\text{-NH}_4^+$  pools**—Soil had higher  $\text{N}\text{-NH}_4^+$  than  $\text{N}\text{-NO}_3^-$  concentrations over the entire growing season (Fig. 1). The concentration of  $\text{N}\text{-NH}_4^+$  was more or less stable until August (12 to 18  $\text{mg N}\cdot\text{kg}^{-1}$  soil DW) but decreased significantly (one-way ANOVA;  $\text{df}$ : 5,  $F$ : 10.058,  $P < 0.05$ ) early in September until it reached half the concentration observed in August (8  $\text{mg N}\cdot\text{kg}^{-1}$  soil DW). The concentration of  $\text{N}\text{-NO}_3^-$  was particularly low early (T1, 2 to 5  $\text{mg N}\cdot\text{kg}^{-1}$  soil DW) and at the end of the growing season (T3) but

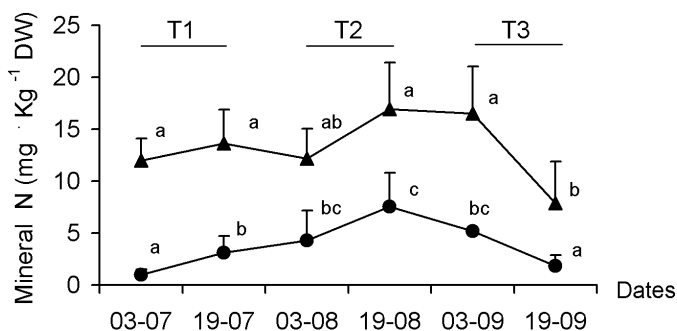


Fig. 1. Average mineral N concentrations in soil during the vegetation season. Values ( $\pm$ SE,  $N = 20$ ) sharing the same letter are not significantly different at  $P < 0.05$  (ANOVA followed by a Tukey HSD multiple-range test). DW = dry mass.

TABLE 2. Results of analysis of variance to detect effects of species, treatments ( $^{15}\text{NH}_4^+$  vs.  $^{15}\text{NO}_3^-$ ), time periods, and interactive effects on (A)  $^{15}\text{N}$  accumulation per unit of plant dry mass ( $\mu\text{g}\cdot\text{g}^{-1}$ ) and (B)  $^{15}\text{N}$  uptake per unit soil area ( $\mu\text{g}\cdot\text{cm}^{-2}$ ). \*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ , ns: nonsignificant.

Source	df	MS	F
A) $^{15}\text{N}$ accumulation ( $\mu\text{g}\cdot\text{g}^{-1}$ dry mass)			
Species	3	22.035	10.91***
Treatment	1	10.981	5.43*
Period	2	20.421	10.11***
Treatment $\times$ species	3	10.76	5.33**
Period $\times$ species	6	10.10	5***
Error	74	2.02	
B) $^{15}\text{N}$ uptake ( $\mu\text{g}\cdot\text{cm}^{-2}$ soil area)			
Species	3	4.59	18.45***
Treatment	1	0.67	2.69 ns
Period	2	0.95	3.84*
Treatment $\times$ species	3	0.94	3.71*
Period $\times$ species	6	0.53	2.12 ns
Error	74	0.25	

significantly higher (ANOVA; df: 5,  $F$ : 12.185,  $P < 0.05$ ) during summer.

**$^{15}\text{N}$  uptake and accumulation in plants**—Fifteen days after labeling, 12 to 30% of the  $^{15}\text{N}$  injected as  $\text{NO}_3^-$  or  $\text{NH}_4^+$  in the soil was recovered in total plant biomass. For  $^{15}\text{NO}_3^-$  labeling, the highest values were obtained at T1 (30.5%) and T3 (27.7%) as compared to T2 (18.2%). For  $^{15}\text{NH}_4^+$  labeling,  $^{15}\text{N}$  uptake

by the vegetation was lower (T1: 19.7%; T3: 12.7%) or similar (T2: 16.3%) to that for  $^{15}\text{NO}_3^-$  labeling.

Fifteen days after soil labeling, species, treatments, and periods (individually or in combination) significantly affected  $^{15}\text{N}$  accumulation in plant tissues ( $\mu\text{g}\ ^{15}\text{N}\cdot\text{g}^{-1}$  plant DW, Table 2). *Vaccinium myrtillus* accumulated  $^{15}\text{N}$  mainly at T1 and, at this period, the amount of  $^{15}\text{N}$  ( $^{15}\text{NO}_3^-$  plus  $^{15}\text{NH}_4^+$ ) in *V. myrtillus* tissues was about two- to five-fold larger than in the other species (Fig. 2). At T2 and T3, *V. myrtillus* had intermediate  $^{15}\text{N}$  concentrations. *Rhododendron ferrugineum* had low and similar values of  $^{15}\text{N}$  accumulation in the tissues for both treatments over the three dates. For  $\text{NH}_4^+$  labeling, *F. eskia* accumulated significantly higher amounts of  $^{15}\text{N}$  early in the growing season (T1 compared to T3), and for  $\text{NO}_3^-$  labeling, early and late in the growing season (T1 and T3 compared to T2). In addition, late in the growing period (T3), this species had a significantly higher concentration of  $^{15}\text{NO}_3^-$  than  $^{15}\text{NH}_4^+$  (Mann–Whitney  $U$ ,  $P = 0.054$ ). In *N. stricta*,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  labeling led to higher  $^{15}\text{N}$  accumulation late (T3 compared to T2) and early (T1 compared to T3) in the growing season, respectively. Finally, at early (T1, Mann–Whitney  $U$ ,  $P = 0.014$ ) and midseason (T2, Mann–Whitney  $U$ ,  $P = 0.05$ ), *N. stricta* accumulated greater amounts of  $^{15}\text{N}$  following  $^{15}\text{NO}_3^-$  rather than  $^{15}\text{NH}_4^+$  labeling.

Data on  $^{15}\text{N}$  uptake ( $\mu\text{g}\ ^{15}\text{N}\cdot\text{cm}^{-2}$ ) represent the amounts of  $^{15}\text{N}$  taken up by a species on a soil area basis ( $^{15}\text{N}$  recovered in monospecific biomass over 1  $\text{cm}^2$  area, Fig. 2). Periods and especially species significantly affected  $^{15}\text{N}$  uptake (Table 2). Treatments acted only in combination with species. Overall, the Poaceae absorbed more  $^{15}\text{N}$  ( $^{15}\text{NH}_4^+ + ^{15}\text{NO}_3^-$

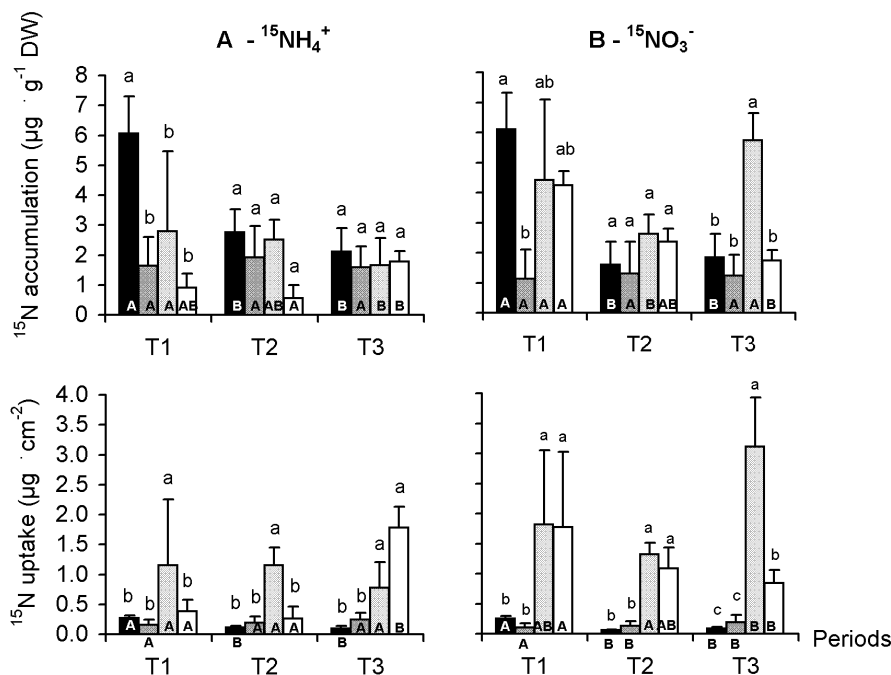


Fig. 2. Accumulation of  $^{15}\text{N}$  per unit of plant dry mass (+SE,  $N = 5$ ) and  $^{15}\text{N}$  uptake per unit soil area for  $^{15}\text{NH}_4^+$  or  $^{15}\text{NO}_3^-$  labeling. Vertical bars indicate standard error. Small letters indicate the between-species statistical differences at each period. Capital letters indicate the between-date statistical differences for each given species over the growing season. Values that share the same letter are not significantly different at 5% threshold (ANOVA followed by a Tukey HSD multiple-range test). T1: 3–18 July, T2: 3–18 August, T3: 3–18 September. Black: *Vaccinium myrtillus*; dark gray: *Rhododendron ferrugineum*; pale gray: *Festuca eskia*; white: *Nardus stricta*. Note the different scaling of the y-axes. DW = dry mass.

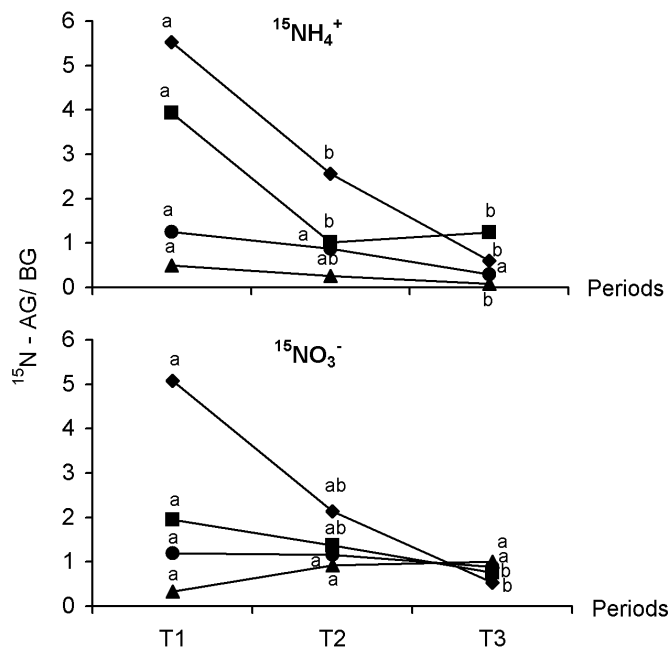


Fig. 3. Ratio of  $^{15}\text{N}$  amount in the aboveground (AG) and the belowground (BG) compartment of the plants. Values are the means of five plots. Values of a given curve that share the same letter are not significantly different at 5% threshold (ANOVA followed by a Tukey HDS multiple-range test). T1: 3–18 July, T2: 3–18 August, T3: 3–18 September.  $\blacklozenge$ : *Vaccinium myrtillus*;  $\blacksquare$ : *Rhododendron ferrugineum*;  $\bullet$ : *Nardus stricta*;  $\blacktriangle$ : *Festuca eskia*.

labeling) than the shrubs (Fig. 2). Except at T3 for  $^{15}\text{NO}_3^-$ ,  $^{15}\text{N}$  uptake of *F. eskia* did not vary significantly over the different periods. However, *F. eskia* took up three- to four-fold more  $^{15}\text{N}$  than *N. stricta* at T1 and T2 for  $^{15}\text{NH}_4^+$  labeling and at T3 for  $^{15}\text{NO}_3^-$  labeling. For the later period and labeling,  $^{15}\text{N}$  uptake was significantly greater for  $\text{NO}_3^-$  than for  $\text{NH}_4^+$  labeling (Mann–Whitney  $U$ ;  $P = 0.054$ ). *Nardus stricta* took up  $^{15}\text{NH}_4^+$  mainly late and  $^{15}\text{NO}_3^-$  mainly early in the growing season. Consequently, *N. stricta* took up greater amounts of  $^{15}\text{N}$  from  $\text{NO}_3^-$  labeling than from  $\text{NH}_4^+$  labeling at T1 (Mann–Whitney  $U$ ,  $P = 0.014$ ) and T2 (Mann–Whitney  $U$ ,  $P = 0.05$ ). The two ericaceous species had low and similar values of  $^{15}\text{N}$  absorption. However,  $^{15}\text{N}$  uptake by *R. ferrugineum* ( $^{15}\text{NH}_4^+$  and  $^{15}\text{NO}_3^-$ ) did not significantly differ for the three periods, whereas uptake by *V. myrtillus* decreased over the growing season.

**Allocation of  $^{15}\text{N}$  in the plants**—Early in the growing season (T1), whatever the ionic form used for labeling, the ericaceous plants allocated  $^{15}\text{N}$  mainly in aboveground biomass (Fig. 3). The ratio of aboveground to belowground allocation in ericaceous plants decreased steadily during the growing season, and at T3,  $^{15}\text{N}$  uptake was almost equitably partitioned between the above- and belowground compartments. In contrast, *F. eskia* mainly allocated  $^{15}\text{N}$  to belowground biomass, a trend that was amplified for  $^{15}\text{NH}_4^+$  labeling during the growing period.  $^{15}\text{N}$  was quite evenly distributed between the two compartments of *N. stricta* during the growing periods (except for  $^{15}\text{NH}_4^+$  labeling at

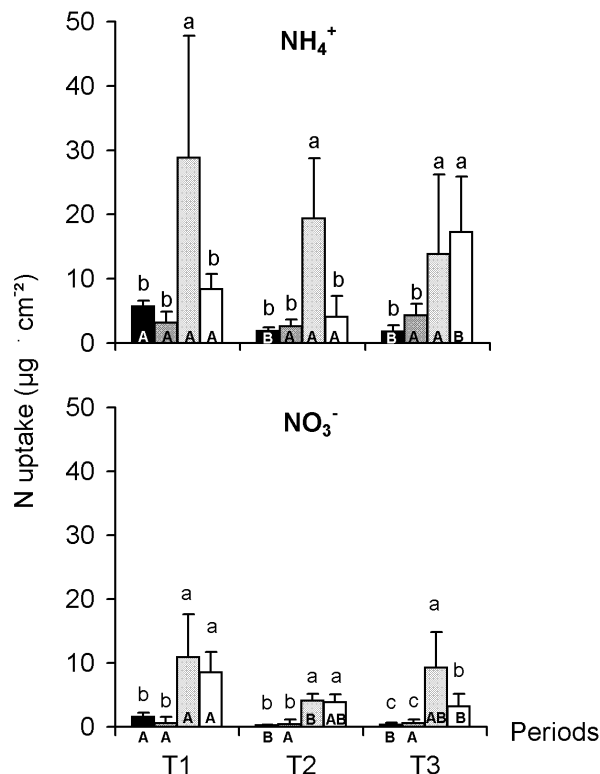


Fig. 4. Calculated N uptake ( $\pm$ SE,  $N = 5$ ) from  $\text{NH}_4^+$  and  $\text{NO}_3^-$ . Small letters indicate the between-species statistical differences at each period. Capital letters indicate the between-date statistical differences for each given species over the growing season. Values that share the same letter are not significantly different at 5% threshold (ANOVA followed by a Tukey HDS multiple-range test). T1: 3–18 July, T2: 3–18 August, T3: 3–18 September. Black: *Vaccinium myrtillus*; dark gray: *Rhododendron ferrugineum*; pale gray: *Festuca eskia*; white: *Nardus stricta*.

T3). Ionic forms did not affect the overall trend in the final distribution of  $^{15}\text{N}$  in the plant.

**N uptake**—Estimates of N- $\text{NH}_4^+$  and N- $\text{NO}_3^-$  uptake took into account the dilution factor of injected  $^{15}\text{N}$  in the soil  $\text{NO}_3^-$  and  $\text{NH}_4^+$  pools. Overall, the four species absorbed (per unit area of soil) much more  $\text{NH}_4^+$  than  $\text{NO}_3^-$ , and the Poaceae absorbed much more total N ( $\text{NH}_4^+ + \text{NO}_3^-$ ) than the shrubs (Fig. 4). The pattern of uptake over time was similar for N and  $^{15}\text{N}$ : at T1 and T2 for  $\text{NH}_4^+$  and T3 for  $\text{NO}_3^-$ , *F. eskia* took up three- to four-fold more N than *N. stricta*. *Nardus stricta* took up  $\text{NH}_4^+$  mainly late and  $\text{NO}_3^-$  mainly early in the growing season. The two ericaceous species had similar low nitrogen uptakes. Uptake of N ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) by *R. ferrugineum* was fairly constant over the three periods, whereas uptake of N by *V. myrtillus* decreased over the growing season. On average, soil  $\text{NH}_4^+$  provided more than 80% and about 60% of the exogenous N absorbed by ericaceous and gramineous species, respectively.

## DISCUSSION

The coexistence of species in plant assemblages is only partially understood and intensively discussed (Silvertown et

al., 1999). Indeed, because plants have similar fundamental requirements and satisfy them in a very limited number of ways (Connell, 1978; Silvertown et al., 1999; McKane et al., 2002) and because competition theoretically precludes species occupying the same niche (Stewart and Levin, 1973), opportunities for niche diversification have been thought to be low for plant species. This assertion implicitly assumes that the species are undifferentiated in the use of limiting resources and that those that can survive with the lowest concentration of resource should displace all others (Tilman, 1997). However, if co-occurring species acquire resources in different ways, competition could be sufficiently reduced to promote their coexistence in the community. Such niche complementarity has often been evoked to explain positive relationships between species diversity and ecosystem functioning (Loreau and Hector, 2001) but has been insufficiently documented (van Ruijven and Berendse, 2003).

**<sup>15</sup>N labeling methodology**—Fifteen days after labeling, a large proportion of the <sup>15</sup>N supplied to the soil was recovered in the vegetation, indicating that the tracer was relatively rapidly incorporated into the biomass as previously demonstrated in another study (Theodose et al., 1996). Although the amount of <sup>15</sup>N added was identical in the two treatments, the vegetation absorbed more <sup>15</sup>N from <sup>15</sup>NO<sub>3</sub><sup>-</sup> than from <sup>15</sup>NH<sub>4</sub><sup>+</sup>. This does not mean that NO<sub>3</sub><sup>-</sup> uptake was higher than that of NH<sub>4</sub><sup>+</sup>. Indeed, concentrations of soil NH<sub>4</sub><sup>+</sup> were 10 times greater than those of NO<sub>3</sub><sup>-</sup> at period T1 and four times greater at period T3, so <sup>15</sup>NH<sub>4</sub><sup>+</sup> was considerably more diluted than <sup>15</sup>NO<sub>3</sub><sup>-</sup> in the corresponding soil mineral N pools. Calculation of N uptake from <sup>15</sup>N uptake is difficult because of the potential instability of <sup>15</sup>NH<sub>4</sub><sup>+</sup> and <sup>15</sup>NO<sub>3</sub><sup>-</sup> (from microbial transformation and leaching) and nonuniform distribution of the <sup>15</sup>N in the soil mineral N pools. A proportion of the N tracer could have been transformed, taken up by microorganisms, lost before plant uptake, or unevenly distributed in the soil. However, we took several precautions (see Materials and Methods) to limit these sources of errors and ensure the validity of the data. In addition, any putative source of errors would have similarly affected all species studied and could not be responsible for different preferences in using the ionic forms of mineral soil N. Although microorganisms are likely to compete with plants for N, the competition between them would be low. According to the Schimel and Bennett's model (2004), detectable amounts of NO<sub>3</sub><sup>-</sup> occur only in soils where N availability is sufficient to supply both the microbial mineralizers and plants, thus reducing the competition between them for NH<sub>4</sub><sup>+</sup> access.

**Ionic and temporal species preferences**—Our findings indicated that plant species have various chemical preferences as has been observed in indoor experiments (Chapin et al., 1993) or in natural communities (McKane et al., 1990; McKane et al., 2002): (1) ericaceous plants used NH<sub>4</sub><sup>+</sup> (80% of the absorbed N) predominantly (De Graff et al., 1998) probably because they do not possess nitrate reductase activity in their leaves (A. Pornon et al., unpublished data; Smirnov and Stewart, 1985) and also perhaps because ericoid mycorrhizas may take up ammonium preferentially over nitrate as do ectomycorrhizas (Yoshida and Allen, 2001) and (2) Poaceae growing on acidic soils can use both NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> (Falkengren-Grerup, 1995) in more balanced proportions (40 and 60%, respectively). In fertilization experiments, the

abundance of certain functional groups (Bowman et al., 1993; Theodose and Bowman, 1997) and species (Bowman et al., 2006) changed according to the level and the type of nutrients supplied, suggesting variable species responses to fertilization.

Species in this study revealed three strategies with respect to their use of mineral soil N (actual <sup>15</sup>N uptake and accumulation, and calculated NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> uptake; Figs. 2 and 4). *Vaccinium myrtillus* took up N mainly early in the growing season and *R. ferrugineum* took up N at a slow and similar rate over the whole growing season. *Festuca eskia* and *N. stricta* took up N at high rates over the whole growing season. However, while *F. eskia* tended to use <sup>15</sup>NH<sub>4</sub><sup>+</sup> mainly early and <sup>15</sup>NO<sub>3</sub><sup>-</sup> mainly late in the growing season, the reverse was observed for *N. stricta* (Fig. 2). These varying nutritional strategies indicate that a temporal complementarity exists between the grasses and acts conjointly with the ionic complementarity. *Festuca eskia* always absorbed N mainly as NH<sub>4</sub><sup>+</sup> (high rate of ammonium uptake vs. medium rate of nitrate uptake over the growing season), while *N. stricta* used both NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> in early and midseasonal periods (medium rate of uptake for both ionic forms at T1 and T2; Fig. 4). Theodose et al. (1996), McKane et al. (1990), and McKane et al. (2002) found similar temporal patterns of nutrient use by the species of a community. Overall, the plants allocated greater amounts of exogenous N to the aboveground compartment early in the growing season rather than at the end (Fig. 3). This pattern agrees with the physiological roles and development of the compartments during the growing season. There is rapid leaf and inflorescence growth during the early season and storage of nutrients in the roots/rhizomes later (Jaeger and Monson, 1992).

Grasses are usually considered better competitors than dwarf shrubs for soil resources (Aerts et al., 1991) because of their dense mat of capillary roots (Caldwell and Richards, 1986). As shown by our results (Table 1), grasses have on average a higher root–shoot mass ratio (2.3) than shrubs (0.8). Accordingly, our results showed that grasses took up much greater amounts of N (actual <sup>15</sup>N and calculated mineral N) per unit soil area (Figs. 2 and 4). However, the absorbed <sup>15</sup>N was largely diluted in the plant tissues because grasses produced much more biomass per unit soil area than the shrubs did (see <sup>15</sup>N concentration in the tissues presented in Fig. 2). Our result partially agrees with those of McKane et al. (2002), who observed that the most productive species used the most abundant nitrogen forms and that the less productive species used the less abundant forms. Species with the highest cover (*F. eskia*) and biomass (*F. eskia* and *N. stricta*) used the largest proportion of the most available inorganic N form (NH<sub>4</sub><sup>+</sup>). Although shrub species have both low biomass and low N uptake, they did not preferentially use the less abundant N form (NO<sub>3</sub><sup>-</sup>).

**Complementarity between species**—The species studied here differ with respect to the amount, form, and the period of N uptake. Our results agree with other studies (Nordin et al., 2001; McKane et al., 2002; Miller and Bowman, 2003) in that co-occurring species used limiting resources in complementary ways. Our study highlights that the ways plants satisfy their fundamental requirements are much more diversified than usually considered in theoretical approaches. The resource partitioning and complementarity could even be enhanced if the plants used soil organic nitrogen like other species (Nordin

et al., 2001; McKane et al., 2002; Miller and Bowman, 2003). Ericaceous species (like *V. myrtillus* and *R. ferrugineum*) have been considered to be especially efficient in this respect because of their ericoid mycorrhizae (Read, 1996). The deeper rooting depth (60 cm) of *F. eskia* compared to *N. stricta* (20 cm) (Palmier et al., 1990) could allow this species to take up more leached nitrogen. This could explain why *F. eskia* took up about three-fold more  $^{15}\text{N}$  than *N. stricta* late in the growing season (T3) from  $^{15}\text{NO}_3^-$  rather than  $^{15}\text{NH}_4^+$ .  $\text{NO}_3^-$  leaching could occur at the end of summer because of drying–rewetting events (storms are frequent in the Pyrenees at the end of summer) killing soil microbes during this period (Schimel and Bennett, 2004).

It is quite clear that differing preferences of the species and temporal variations (as observed here) in soil resources support niche diversification and species coexistence. Moreover, the low needs in exogenous nitrogen associated with a strong ability of ericaceous species to uncouple growth and nutrient uptake (*R. ferrugineum*, Lamaze et al., 2003) or to take up nutrients possibly before other species (*V. myrtillus*, as suggested in the Fig. 2A) likely allow these species to relax the competition with grasses and to establish in meadows. In addition, plants such as *R. ferrugineum* that take up nutrients slowly retain those nutrients longer (in long-lived tissues, i.e., leaves and wood) than herbaceous species, deposit less litter than herbaceous species, and deposit low quality litter that decomposes slowly and thereby further decreases the resource supply (Grime, 2002; Pornon and Lamaze, 2007). This could create unfertile patches unfavorable for faster growing species such as grasses and favorable for species coexistence (Suding et al., 2004) and the maintenance of heathland patches in the vegetation mosaic. On the other hand, ericaceous species would be poor competitors in more fertile patches created by the grasses, which take up nutrients at a higher rate. Such fertile patches would limit the extension of heathlands in meadows and explain why meadow invasion by *R. ferrugineum* is a slow process that takes as long as 120–320 yr and mostly results in a more or less stable heathland/meadow vegetation mosaic (Pasche et al., 2004).

Complementarity between species is known to reduce competition through resource partitioning and to facilitate species coexistence (Fridley, 2003). Competition would otherwise be very strong in the communities studied here because of the more or less synchronous growth of all the species and the similar height and growth form of the two grasses. Although complementarity has been evoked in experimental biodiversity studies (Hooper, 1998; Tilman et al., 2001; Spehn et al., 2005), the mechanisms underlying it were not revealed. Because resource-based niche partitioning appears to be a prerequisite for complementarity between species (Fridley, 2001), our results provide a basis for a better understanding of how species complement each other and coexist in communities. Increases in the deposition of anthropogenic N alter ecosystem N cycling and soil N forms and availability (Bowman et al., 2006). Nitrogen should thus modify the relationship between species competition and complementarity. Our results, which show that ionic and temporal complementarity reduce competition and promote native species coexistence, help explain why ecological responses to increased N supply include changes in community diversity and why high elevation mountain ecosystems are potentially sensitive indicators of N deposition (Körner, 1999; Fenn et al., 2003).

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