

Rapid uptake of ^{15}N -ammonium and glycine- ^{13}C , ^{15}N by arbuscular and ericoid mycorrhizal plants native to a Northern California coastal pygmy forest

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Abstract

While it is well established that plants are able to acquire nitrogen in inorganic form, there is less information on their ability to ‘short circuit’ the N cycle, compete with microbes, and acquire nitrogen in organic form. Mycorrhizal fungi, known to enhance nutrient uptake by plants, may play a role in organic N uptake, particularly ericoid mycorrhizas. We asked the question—Can mycorrhizal fungi increase the ability of plants to take up organic N, compared to inorganic N? Here, we report on the abilities of three plant species, ericoid mycorrhizal *Rhododendron macrophyllum* and *Vaccinium ovatum* and arbuscular mycorrhizal *Cupressus goveniana* ssp. *pigmaea*, to acquire C and/or N from an organic and an inorganic N source. All three species are native to a California coastal pygmy forest growing in acidic, low-fertility, highly organic soils. In a pot study, glycine- $\alpha^{13}\text{C}$, ^{15}N and ^{15}N -ammonium were applied to pygmy forest soil for 17 or 44 h. Ericoid mycorrhizal species did not demonstrate a preference for either inorganic or organic sources of N while *Cupressus* acquired more $\text{NH}_4\text{-N}$ than glycine-N. For all species, glycine-N uptake did not increase after 17 h suggesting glycine uptake and glycine immobilization occurred rapidly. Both glycine-N and glycine-C were recovered in shoots and in roots suggesting that all species acquired some N in organic form. Regression analyses of glycine-N and glycine-C recovery in root tissue indicate that much of the glycine was taken up intact and that the minimum proportion of glycine-N recovered in organic form was 85% (*Cupressus*) and 70% (*Rhododendron*). Regressions were non-significant for *Vaccinium*. For all species, glycine-N remained predominantly in roots while glycine-C was transferred to shoots. In contrast, $\text{NH}_4\text{-N}$ remained in roots of ericoid plants but was transferred to shoots of arbuscular mycorrhizal *Cupressus*. Since net N mineralization rates in pygmy forest soils are low, our results suggest that organic N may be an important N source for plants in this temperate coniferous ecosystem regardless of mycorrhizal type. Acquisition of amino acid C by these species also may partially offset the carbon cost to plants of hosting mycorrhizal fungi.

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1. Introduction

Hydroponic studies have demonstrated that a wide array of plants have the physiological capacity to assimilate amino acids from soil solution (e.g., Virtanen and Linkola, 1946; Chapin et al., 1993). Since amino acids can comprise

more than 50% of the organic N pool in many soils (Stevenson, 1994), organic N uptake may have considerable ecological significance. However, there is still debate about the ability of plants to acquire amino acids in the presence of competing soil microbes and, therefore, the general importance of amino acid uptake to plant N budgets (Hodge et al., 2000; Owen and Jones, 2001; Miller and Cramer, 2004). Many studies have demonstrated that plants ultimately can access N originally supplied to soil as amino acids (e.g., McKane et al., 2002; Cheng and Bledsoe, 2004; Finzi and Berthrong, 2005). However, it is unclear

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how rapidly plants acquire organic N and whether plants acquire N as intact organic N (Hodge et al., 2000; Schimel and Bennett, 2004; Andresen and Michelsen, 2005). In soils, amino acids are dynamic; half-lives of free amino acids generally range from hours to days, depending on soil properties and temperature (Fokin et al., 1993; Jones, 1999; Henry and Jefferies, 2003; Finzi and Berthrong, 2005). If plants acquire a significant proportion of amino acid N prior to mineralization, then amino acids in soils represent an additional N pool for plants. However, if plant uptake of amino acids is restricted to mineralized N, then, while amino acids may be a particularly dynamic pool of organic N, they would not necessarily represent a novel N pool directly accessible to plants. This differentiation has implications for models of soil N cycles (e.g., Schimel and Bennett, 2004) and for mechanistic interpretations of plant resource utilization studies (e.g., McKane et al., 2002).

Previous studies, conducted primarily in boreal and cold temperate ecosystems, have indicated that uptake rates for organic and inorganic forms of N may differ among plant species (Kielland, 1994; McKane et al., 2002; Miller and Bowman, 2003; Persson et al., 2003). If robust, these differences lend support to the hypothesis that co-existing plant species partition N resources under N-limited conditions. N acquisition by plants may occur through direct transport across root tissues, or through mycorrhizal fungal partners (Miller and Cramer, 2004). Ericaceous shrubs are commonly found on organic soils worldwide, from the arctic tundra to the tropical forest canopy (Luteyn, 2002; Cairney and Meharg, 2003). This success may be due, in part, to formation of the specialized ericoid mycorrhiza which can ameliorate harsh soil conditions typically associated with organic soils, and increase plant access to organic N (Cairney and Meharg, 2003; Read and Perez-Moreno, 2003). In contrast, the most common type of mycorrhiza, arbuscular mycorrhiza, may not confer these additional attributes to their plant hosts (Read and Perez-Moreno, 2003; Reynolds et al., 2005).

In this study, we addressed three questions: (1) Does the ability to acquire organic N from soil solution differ among plant species colonized by either arbuscular mycorrhizal or ericoid mycorrhizal fungi? (2) After uptake, do C and/or N accumulate in belowground tissues (fine or coarse roots) or aboveground tissues (stems/branches or leaves)? (3) Does the form of N (organic vs. inorganic) applied to soil affect total N recovery by these species? To address these questions, we measured uptake of glycine- $\alpha^{13}\text{C}$, ^{15}N and $^{15}\text{NH}_4\text{Cl}$ by three species potted in field soil, ericoid mycorrhizal California rose-bay (*Rhododendron macrophyllum* D. Don) and California huckleberry (*Vaccinium ovatum* Pursh), and arbuscular mycorrhizal pygmy cypress (*Cupressus goveniana* ssp. *pigmaea* (Lemmon) J. Bartel). The three species co-exist in a temperate coniferous pygmy forest in coastal California; however, both *V. ovatum* and *R. macrophyllum* are widespread in Pacific coastal forests from southern Canada into California (Hitchcock et al., 1959). In contrast to adjacent ecosystems, the pygmy forest

plant community has low species diversity and very limited aboveground productivity (Westman and Whittaker, 1975). We expected that, if acquisition of intact organic N evident in boreal ecosystems extends to mild temperate coniferous forests, this ability should be well-developed in plants growing in the pygmy forest, where organic N dominates soil N pools (Yu et al., 2002).

2. Methods

2.1. Experimental design

The experimental design included two N sources (glycine- $\alpha^{13}\text{C}$, ^{15}N and $^{15}\text{NH}_4\text{Cl}$) and two harvest times (17 or 44 h) with three plant species and either three (*Rhododendron*, *Vaccinium*) or four (*Cupressus*) replications for a total of 40 pots. Six-month-old seedlings, germinated on peat:perlite:vermiculite (1:2:1), were transplanted into pots (Rootrainer, 350 cm³, Spencer-Lemaire Industries) containing pygmy forest soil and coarse sand (3:1). Pygmy forest soil was collected from the O and A horizons (Typic Albaquilt) below *Cupressus*, *Rhododendron*, and *Vaccinium* plants in the Jug Handle State Reserve, Mendocino County (Mendocino pygmy forest), about 200 km north of San Francisco, California, and homogenized prior to use in pots. The Mendocino pygmy forest occurs on the oldest and most highly weathered soils of the Mendocino Ecological Staircase (Gardner and Bradshaw, 1954; Jenny et al., 1969). In this ecosystem, plant roots are restricted primarily to the shallow O/A horizon where they grow in a dense mat (Gardner and Bradshaw, 1954). The O/A horizon is acidic (pH 4.0), highly organic (C/N: 64.5), and infertile (mineral N: 2.5 mg kg⁻¹ dry wt soil) (Yu et al., 2003). Over 99% of the dissolved N in this horizon is organic and comprised primarily of amino compounds (Yu et al., 2002). The majority of the standing phytomass N is contained in *C. goveniana* ssp. *pigmaea* followed by ericoid mycorrhizal *V. ovatum* (Westman, 1978). The understory is dominated by ericoid mycorrhizal shrubs, including *R. macrophyllum* (Westman, 1978).

Plants were grown for 2 years in a growth chamber (conditions reflective of Mendocino, California: summer: 26 °C/17 °C; winter: 15 °C/8 °C), fertilized bimonthly with $\frac{1}{4}$ strength Miracid fertilizer (Scotts Company, Ohio, USA, NPK 30:10:10), and watered as needed with distilled water.

2.2. Treatment, harvest, and assessment of mycorrhizal status

We added 100 ml of 1 mM N solution (1.5 mg N pot⁻¹) to each pot as either $^{15}\text{NH}_4\text{Cl}$ (98 at% ^{15}N) or glycine- $\alpha^{13}\text{C}$, ^{15}N (99 at% ^{13}C ; 98 at% ^{15}N) (Isotec Sigma-Aldrich Co, USA). We utilized glycine- $\alpha^{13}\text{C}$ rather than glycine- $\beta^{13}\text{C}$ because the β -C is more susceptible to decarboxylation in plants and soil (Näsholm et al., 1998). ^{15}N solutions were applied by inserting a syringe into the soil (3 locations per pot) and slowly depressing the plunger as the syringe was

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