



## Alleviation of P limitation makes tree roots competitive for N against microbes in a N-saturated conifer forest: A test through P fertilization and <sup>15</sup>N labelling

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### ABSTRACT

Chronic N deposition to forests may induce N saturation and stand decline, leading to reduced ecosystem N retention capacity, triggered by a shift from N limitation of trees to limitation by another nutrient. We conducted a <sup>15</sup>N soil labelling experiment in non-fertilized and P-fertilized plots at two elevations in an N-saturated Mediterranean-fir (*Abies pinsapo*) forest in southern Spain which shows P limitation symptoms. Root-exclusion was applied to identify the relative contributions of roots (plus mycorrhizal fungi) uptake, and heterotrophic immobilization by free-living microbes, to N retention. Overall <sup>15</sup>N recovery from the litter, 0–15-cm soil and root-uptake components was c.a. 35% higher in P-fertilized than in non-fertilized plots at both elevations. In non-fertilized plots, soil was the biggest sink for added <sup>15</sup>N. Phosphorus fertilization increased the competitive ability of tree roots for soil N resulting in equal importance of the autotrophic (roots plus associated mycorrhizal fungi) and heterotrophic (free-living microbes) components with respect to total <sup>15</sup>N recovery in P-fertilized plots. Phosphorus addition increased litter and soil N immobilization only if roots had been excluded. By combining *in situ* fertilization, root-exclusion and isotope labelling we have demonstrated that reduced N retention capacity and dominance of soil microbial over plant immobilization in a N-saturated forest results from a shift from N to P limitation of trees, while alleviation of P limitation makes tree roots and associated mycorrhizal fungi competitive for N against free soil microorganisms.

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### 1. Introduction

Atmospheric nitrogen (N) deposition is changing nutrient cycling of forest ecosystems in large parts of the industrialized world (e.g., Aber et al., 1998; Gruber and Galloway, 2008). Efficient N retention occurs in N-limited temperate forests, at least initially, when subjected to chronic N inputs. This has been attributed to the accumulation of N in the vegetation due to an increase in forest productivity and retention in soil compartments. Continued enhanced N inputs, combined with high mineralization and nitrification rates, can eventually lead N supply to exceed the combined biological demand for this nutrient and drive the ecosystem to N saturation stage. Throughout this process, tree demand for other nutrients could be enhanced. If this demand is in excess of nutrient supply, the ecosystem N retention capacity may decline (Magill et al., 1996) resulting in increased nitrate (NO<sub>3</sub><sup>-</sup>) leaching losses (Aber et al., 1995; Dise and Wright, 1995; Emmett, 2007; Vries et al.,

2007). This suggests that NO<sub>3</sub><sup>-</sup> leaching may be associated with deficiency in supply of another nutrient like P that then becomes the limiting one, in N-saturated stands.

Mechanisms contributing to the onset of P limitation may involve N-induced soil acidification and cation depletion which can result in reduced P availability (Carreira et al., 2000). More importantly, N may enhance the tree demand for P, unbalancing soil P supply with respect to biological demand, thus limiting plant growth and N uptake. This may explain why soil, rather than tree biomass, is often the main sink for N inputs added to the soils in temperate forests (Nadelhoffer et al., 1999, 2004). In this case, P fertilization might alleviate N saturation symptoms and increase the ecosystem NO<sub>3</sub><sup>-</sup> retention capacity. The hypothesis that N deposition may particularly induce P nutritional stress has previously been tested and found consistent with data in mensurative experiments along atmospheric deposition and N availability gradients (Mohren et al., 1986; Harrison et al., 1999; Naples and Fisk, 2010), in manipulative experiments artificially adding N (Carreira et al., 1997, 2000; Treseder and Vitousek, 2001; Pilkington et al., 2005; Prietzel and Stetter, 2010) and in studies combining both approaches (Gress et al., 2007; Braun et al., 2010);

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although this kind of response is not always observed (e.g., Finzi, 2009; Groffman and Fisk, 2011). Experimental P additions cause growth stimulation in forest ecosystems with high N availability (Tessier and Raynal, 2003; Gradowski and Thomas, 2008; Prietzel et al., 2008) and reduced  $\text{NO}_3^-$  concentration in soil water (Stevens et al., 1993; Nielsen et al., 2009). This suggests the weakening of N retention capacity in some N-saturated forests might be triggered by a shift from N limitation to P limitation. However, to our knowledge, no previous study has attempted to determine the underlying mechanisms to such a response to P fertilization in N-saturated forests. We explicitly quantified how the availability of N to plants plus associated mycorrhizal fungi and to heterotrophic microbial N immobilization changed following the alleviation of tree P limitation.

To date, most studies of the impact of nitrogen deposition have focussed in temperate forest ecosystems (Emmett et al., 1998; Tietema et al., 1998; Nadelhoffer et al., 2004), but some studies in Mediterranean-type forests (e.g., Fenn et al., 1996; see also the review by Ochoa-Hueso et al., 2011) suggest distinctive responses due to seasonal uncoupling between peaks of biological demand for N and hydrological fluxes. With the increase in average annual temperature (1.2–4.5 °C) and summer drought intensity (around 20% decrease in precipitation) predicted for Europe in the period 2070–2100, according to current climate change models (Houghton, 2004), competition for nutrients between plants and microbes, and thus N retention, will be affected (Rennenberg et al., 2009). Interactive effects of climatic change and P availability on competitive patterns of N partitioning between plants and free-living microorganisms in N-saturated forests have rarely been studied. In the present study, we test the hypothesis that the onset of tree P deficiency in a N-saturated, Mediterranean-fir (*Abies pinsapo* Boiss.) forest makes roots poorly competitive for N against soil microbes, thus triggering a loss of the ecosystem N retention capacity. *A. pinsapo* is a relic, temperate-like fir currently restricted to microclimatic refuges within the Mediterranean-type climate region of Southern Spain and Northwest Africa.

We report on the fate of  $^{15}\text{N}$  added to soils with or without root-exclusion treatments, both in non-fertilized and P-fertilized plots, in an *A. pinsapo* forest receiving high N deposition inputs. We used a stable isotope ( $^{15}\text{N}$ ) approach as it is a useful approach in determining the fate of N inputs in forest ecosystems where flows of N are small relative to stocks in both trees and soil (Emmett and Quarmby, 1991; Buchmann et al., 1996; Tietema et al., 1998; Nadelhoffer et al., 1995; Curtis et al., 2005). The experiment was conducted at two sites with different elevations to account for differences in climatic conditions and N saturation status within this forest locality. The main objective of this study was to determine if P fertilization influences N uptake by trees and N immobilization by free-living soil microorganisms in N-saturated stands of *A. pinsapo*. Likewise, we determined if an increase in P availability can modify foliar nutrients concentration, soil N mineralization and nitrification rates and N availability. We hypothesised that:

1. N retention would be higher in P-fertilized than in non-fertilized plots, especially at higher elevation where climate is colder, because a lower temperature could reduce net N mineralization rates and nitrification rates, reducing N availability (Ulrich, 1983). However, a warmer temperature could increase forest growth and N uptake (Fenn et al., 1998). Likewise differences in organic matter, C/N ratio and N deposition rates could be related to changes in elevation affecting N retention (Knoepp and Swank, 1998; Bonito et al., 2003).
2. In N-saturated forests, P deficiency will have a stronger reducing effect on N uptake by plant roots and associated mycorrhizal fungi than on N immobilization by free-living soil

microorganisms. It is known that, regulation of N/P ratios in plants is weaker than in bacteria (Güsewell, 2004). In addition, activity of soil bacteria is mainly carbon limited (Aber et al., 1998), while plant growth is most frequently limited by N or P availability (Vitousek and Howarth, 1991). In P-deficient plants, the rate of P uptake would setup a limit to their capacity to absorb other non-limiting nutrients (Aerts and Chapin, 2000). Consequently, N immobilization by soil microbes would be higher than N uptake by plants in N-saturated ecosystems if they are P limited. Thus, increasing P availability would enhance  $^{15}\text{N}$  uptake by tree roots and tree roots would be more responsive than soils to the P fertilization treatment.

## 2. Materials and methods

### 2.1. Study sites

The study was conducted at the upper and lower limits of the altitudinal range of *A. pinsapo* in the protected natural area Los Reales de Sierra Bermeja, in Southern Spain (Table 1). These two positions are hereafter called the SB-HE (Sierra Bermeja-higher elevation, 1400 m above sea level) and the SB-LE (Sierra Bermeja-lower elevation, 1200 m asl) sites. They are occupied by *A. pinsapo* stands growing in NE-facing, 30–40% slopes. Soils are Oxiacuc Hapludolls (USDA-Soil Taxonomy; Soil Survey Staff, 1999) developed on serpentines and peridotites. There is evidence that these stands have been well preserved since the nineteenth century (Arenas, 2011). Canopy structure generally corresponds to that of stands in reinitiation phase and most of the trees are from 20 to 100 years old. Climatic, stand canopy and soil properties at the two sites are summarized in Table 1. Mean annual precipitation ranges from 1200 to 1600 mm along the altitudinal gradient, which is high for a Mediterranean context and fits within the usual range

**Table 1**

Physiographic and climatic traits, N deposition rates, stand canopy attributes and soil physico-chemical properties at the two study sites in the *Abies pinsapo* forest of Sierra Bermeja (Málaga, southern Spain). SB-LE: Sierra Bermeja, lower elevation; SB-HE: Sierra Bermeja, higher elevation. Values in parentheses are standard deviations.

Site Reference:	SB-LE	SB-HE
Physiographic and climatic traits:		
Longitude	5° 12' 07"	5° 12' 26"
Latitude	36° 29' 26"	36° 29' 09"
Altitude (m above sea level)	1200	1400
Aspect	NE	NE
Mean Annual Precipitation (mm)	1266	1520
Mean Annual Temperature (°C)	11.8	10.3
Bulk N deposition (kg inorganic N ha <sup>-1</sup> yr <sup>-1</sup> ) <sup>a</sup>	7.8	10.4
Stand properties:		
Alive tree basal area (m <sup>2</sup> ha <sup>-1</sup> ) <sup>b</sup>	31.7 (15.3)	18.1 (13.1)
Tree density (individuals ha <sup>-1</sup> ) <sup>b</sup>	998.5 (286.3)	300.0 (124.4)
Mean tree diam. at breast height (cm) <sup>b</sup>	19.3 (3.4)	28.2 (8.4)
Litter mass (g m <sup>-2</sup> )	1128 (581)	2166 (79)
Soil characteristics:		
Bulk density (0–5 cm) (g cm <sup>-3</sup> )	0.90 (0.11)	1.12 (0.3)
Bulk density (5–15 cm) (g cm <sup>-3</sup> )	1.07 (0.10)	1.27 (0.13)
Sand (0–5 cm) (%)	56.9 (3.0)	59.1 (9.8)
Silt (0–5 cm) (%)	30.6 (0.7)	29.7 (8.3)
Clay (0–5 cm) (%)	12.5 (3.2)	11.2 (2.0)
pH (0–5 cm) (CaCl <sub>2</sub> )	6.10 (0.03)	5.80 (0.06)
CEC (0–5 cm) (meq/100 g)	34.5 (4.1)	27.3 (5.1)
O.M. (0–5 cm) (%)	16.0 (3.9)	11.4(4.6)
C/N (0–5 cm)	21.6 (2.8)	19.4 (2.5)
C/N (5–15 cm)	21.3 (3.2)	15.7 (1.6)

<sup>a</sup> Estimates from measurements in several periods between February 2000 and May 2006 (910 days of total sampling interval for SB-HE; 665 days for SB-LE) (Liétor, 2002; Salido, 2007; Torres-Cañabate et al., 2008).

<sup>b</sup> Linares et al. (2011).

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