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Plant limiting nutrients in Andean-Patagonian woody species: Effects of interannual rainfall variation, soil fertility and mycorrhizal infection

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Abstract

Andean-Patagonian forests are especially interesting for the study of N and P limitation because they receive minimal atmospheric pollution, have little influence of vascular N-fixing species, and grow on volcanic soils that retain P. In a previous study of 10 woody species (four broad-leaved deciduous species, three broad-leaved evergreens and three conifers) conducted during an exceptionally dry year in NW Patagonia, and on the basis of nutrient resorption efficiency and proficiency, we suggested that N was the most limiting nutrient except for the broad-leaved evergreen *Lomatia hirsuta*. In the present work, we compared patterns of nutrient limitation during a dry and a wet year, quantified the percentage of mycorrhizal infection, and related mycorrhizal behavior and nutrient limitation to soil fertility. We used N and P concentrations in green leaves as indicators of nutrient requirements, and N and P concentrations in senescent leaves (resorption proficiency) and the N/P ratio in green leaves as indicators of nutrient limitation. We also determined leaf mass area (LMA) and lignin concentration as indicators of structural and chemical defences. From previous works, the following soil fertility indicators were included: pH, organic C, total N, exchangeable cations, Olsen-P, potential N mineralization (pNmin) and N retained in microbial biomass (N-MB). Nitrogen, P and lignin concentrations in green and senescent leaves did not differ significantly between the dry and the wet year either by species or by functional groups. Most species behaved as N-proficient and P-non-proficient; this together with values of foliar N/P ratios lower than 14–16 confirmed N limitation in these forests. The only species limited by P but not by N was *L. hirsuta* (1.0–1.1% N in senescent leaves, N/P ratio = 21–23), a non-mycorrhizal species with cluster roots. The lack of P limitation in the other species was probably related to the high percentages of infection with arbuscular mycorrhizae (80–90% in *Maytenus boaria* and the conifers *Araucaria araucana*, *Austrocedrus chilensis* and *Fitzroya cupressoides*), and ectomycorrhizae (73–79% in five *Nothofagus* species). Nitrogen and P requirements were positively correlated among themselves and negatively with lignin and LMA. Soil fertility was positively correlated with nutrient requirements and negatively with lignin and LMA. Conifers had lower N and P requirements, higher LMA, lower foliar N/P ratio and grew on soils of lower soil N dynamics (lower pNmin and N-MB) than ectomycorrhizae-associated species.

Keywords: Nutrient proficiency; Foliar N/P ratio; Ectomycorrhizae; Arbuscular mycorrhizae; Volcanic soils

1. Introduction

In most boreal and temperate forests N is considered more limiting than P for plant growth, although atmospheric N deposition is reducing N limitation in several areas of the Northern Hemisphere (Lambers et al., 1998; Aerts and Chapin, 2000; Fisher and Binkley, 2000). Phosphorus can be limiting in calcareous, old acid or volcanic soils, where it is retained by precipitation with Ca, Fe and Al, or specific anion sorption in amorphous soil colloids (Shoji et al., 1993; Parfitt et al., 2005).

As an indicator of N and P limitation, resorption proficiency has been recommended by Killingbeck (1996) for woody species, and is currently worldwide applied (Aerts and Chapin, 2000; Pérez et al., 2003; Diehl et al., 2003; McGroddy et al., 2004; Carrera et al., 2005). It is defined as the ability of a species to reduce N and P concentrations below established benchmark levels in senescent leaves: <0.7% N for all species, and <0.04% P in evergreens and <0.05% P in deciduous species (Killingbeck, 1996). Resorption proficiency is mainly the result of two contrasting strategies, high nutrient resorption before senescence (high resorption efficiency) usually related to high nutrient requirements, or low nutrient requirements

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coupled to long-lived tissues (Aerts and Chapin, 2000). Long-lived leaves tend to be associated with high dry-mass investment per leaf area (structural tissues), chemical defences (lignin, polyphenols), and low N concentrations (Reich et al., 1999; Wright et al., 2004), resulting in slow litter decomposition and low nutrient availability (Wardle et al., 2004a). Lignin production seems to be especially associated with limited protein synthesis under low N availability (Lambers et al., 1998).

During the last years, the stoichiometry between leaf N and P has been increasingly proposed as a relevant indicator of nutrient limitation at species and community level. This index derived from the Redfield ratio for aquatic environments (the ratio above which P becomes limiting for biological processes relative to N), has been applied to terrestrial ecosystems since the early 1970s (Van den Driessche, 1974; Ingestad, 1979). Contrary to proficiency, there is not yet a unique benchmark level, since differences have been observed depending on functional groups, species, plant age, climate and fertilization. Koerselman and Meuleman (1996) have proposed for wetland plants foliar N/P values lower than 14 to indicate N limitation, higher than 16 to indicate P limitation, and between 14 and 16 as N and P co-limitation. These values have been further recommended by Aerts and Chapin (2000) as general limits for other natural ecosystems. In posterior reviews of grassland and forest data, lower values (N/P = 10–11) have been suggested by Tessier and Raynal (2003) and Knecht and Göransson (2004), while Güsewell (2004) proposed a broader range (<10 and >20). In New Zealand forests, an increase of N/P from 10 to 14 or from 8 to 15–18 has been interpreted as a shift from N to P limitation (Parfitt et al., 2005). The stoichiometry between N and P has been also applied to humus layer and litter (N/P = 16) in the study of long-term chronosequences (Wardle et al., 2004b).

Mycorrhizae acquire special interest in nutrient limited soils, because they contribute to nutrient uptake by enhancing root growth, spatial exploitation and the production of organic acids and hydrolytic enzymes (Pedersen and Sylvia, 1996; Aerts, 2002). It is considered that arbuscular mycorrhizae (AM), which represent the most abundant group, are particularly efficient in P solubilization and uptake (Fox et al., 1990; Aerts and Chapin, 2000; Cornelissen et al., 2001; Aerts, 2002; Smith et al., 2004; Karandashov and Bucher, 2005). However, they have limited ability to degrade organic matter, while ectomycorrhizae (Ecto) and ericoids can release organic bound nutrients, especially contributing to the acquisition of N (Fox et al., 1990; Aerts and Chapin, 2000; Cornelissen et al., 2001; Aerts, 2002; Treseder and Cross, 2006). This differential functioning has been suggested by Cornelissen et al. (2001) as a valuable tool to understand plant controls on nutrient cycling and to characterize plant functional groups.

Andean-Patagonian forests are especially interesting to study N limitation, because they represent ecosystems with minimal atmospheric pollution (Perakis and Hedin, 2002; Pérez et al., 1998). Besides, the influence of nodulating species in these forests is minimal, although epiphytic lichens could be contributing to N fixation (Godoy et al., 2001). Since regional soils are mainly Andisols which retain P, deficiency of this element could also be expected; however, in a previous work we found that it is not limiting for plant growth (Diehl et al., 2003). In that work, we studied some mechanisms of nutrient conservation in 10 dominant tree species belonging to three functional groups (broad-leaved deciduous species, broad-leaved evergreens and conifers) during an especially dry year. Based on nutrient resorption efficiency and proficiency, N appeared as the most limiting nutrient except for the broad-leaved evergreen *Lomatia hirsuta*. In broad-leaved deciduous species, the main mechanism of nutrient conservation was high N resorption efficiency, while conifers presented low N and P requirements, and high C/N and lignin/N ratios in senescent leaves. In other work (Satti et al., 2007), we reported that conifers were associated with lower chemical (organic C, organic P) and biological (potential N mineralization, phosphatase activity) fertility than deciduous species. Patterns of soil fertility and nutrient conservation in broad-leaved evergreens were closer to deciduous species or conifers depending on the species. All studied conifers (*Austrocedrus chilensis*, *Fitzroya cupressoides*, *Araucaria araucana*) and one broad-leaved evergreen (*Maytenus boaria*) were associated with AM. Broad-leaved deciduous species and one evergreen, all belonging to genus *Nothofagus*, were associated with Ecto, while one broad-leaved evergreen (*L. hirsuta*) was a non-mycorrhizal Proteaceae with cluster roots (Fontenla et al., 1998; Diehl et al., 2003).

The Andean-Patagonian region is characterized by precipitations concentrated mostly in autumn–winter with strong interannual variations due to the ENSO (El Niño-Southern Oscillation) phenomenon, which can affect also seasonal temperatures (Paruelo et al., 1998). Since water availability can markedly affect soil nutrient availability and plant nutrient resorption (Escudero et al., 1992; Pugnaire and Chapin, 1993), these interannual variations of precipitation should be taken into account to validate general trends of nutrient conservation.

In the present study, our objectives were to (i) compare the effect of a dry and a wet year on nutrient conservation patterns (N, P and lignin concentrations in green and senescent leaves) of species and functional groups; (ii) confirm N limitation using the foliar N/P ratio and leaf mass per area (LMA) in addition to resorption proficiency; (iii) study the relationship between nutrient limitation and the intensity of mycorrhizal infection; and (iv) relate both aspects mycorrhizal behavior and nutrient limitation to soil fertility.

2. Materials and methods

2.1. Study site

A detailed description of sites has been reported by Diehl et al. (2003) and Satti et al. (2003, 2007). All sites correspond to monospecific native forests located in NW Patagonia (ca. 39°36′–41°22′S, 71°02′–71°45′W). Historic mean annual temperatures range between 5 and 9 °C (decreasing from N to S and with altitude), and historic mean annual precipitations