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Original article

N, P and K limitation of fine root growth along an elevation transect in tropical mountain forests

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A B S T R A C T

It is generally assumed that tree growth in tropical low-elevation forests is primarily limited by phosphorus while nitrogen limitation is more prominent in tropical montane forests where temperature is lower and the soils are poorly developed. We tested this hypothesis in mountain rainforests of South Ecuador by investigating the growth response of tree fine roots to N, P and K fertilization in ingrowth cores exposed at 1050 m (pre-montane) and 3060 m (upper montane) elevation. Root growth into unfertilized ingrowth cores (control treatment) was about 10 times slower at 3060 m than at 1050 m. At 1050 m, root growth was stimulated not only by P, but also by N and K. In contrast, N was the only element to promote root growth at 3060 m. The N concentration in fine root biomass dropped to nearly a third between 1050 and 3060 m, those of P, K, Ca and Mg decreased as well, but to a lesser degree. According to a $^{15}NO_3^{15}NH_4$ tracer study along the slope, tree fine roots accumulated nitrate and ammonium in root biomass at similar rates between 1050 and 3060 m, despite lower temperatures higher upslope. We conclude that the nature of nutrient limitation of tree fine root growth changes with elevation from an apparent co-limitation by P together with N and K at 1050 m to predominant N limitation at 3060 m, which is also reflected by low foliar N concentrations. Increasing N limitation may have caused the high fine root biomass and root/shoot ratio in the high elevation forest, while the capability of the roots to acquire mineral N apparently was not affected by lower temperatures at high elevations.

1. Introduction

The nature of nutrient limitation of tree growth is likely to change with elevation and may thus be different in tropical lowland and montane forests. The classical concept of nutrient limitation of plant growth attempts to identify a single limiting nutrient species for a given environmental constellation. Theory predicts that plant growth limitation by P is a key constraint in the tropical lowlands (Vitousek and Sanford, 1986; Tanner and Kapos, 1992; Tanner et al., 1998; Paoli et al., 2005; Benner et al., in press) because many lowland soils are highly weathered, and P, which is almost entirely supplied by the parent material and subsequently immobilized to a large extent, is rather short in supply (Walker and Syers, 1976). In accordance with this prediction, tropical forests growing on highly weathered lowland soils typically produce litter low in P (Tanner et al., 1998). Plant-available N, on the other hand, is often abundant since N mineralization rates are typically high in moist and hot climates. The situation is different in tropical montane forests which mostly grow on slopes exposed to soil erosion. Consequently, the soils may be richer in P while the lower temperature slows down N cycling (Marrs et al., 1988). Therefore, it has been hypothesized that the importance of N limitation should increase with elevation (Vitousek and Sanford, 1986; Vitousek, 2004).

More recently, the assumption of tree growth being limited by a single nutrient species was challenged by the 'non-Liebig' concept of nutrient limitation postulating that different growth processes should be limited by the shortage of different nutrients resulting in a simultaneous multi-element limitation of plant growth (Kaspari et al., 2008). In fact, there is evidence that K, Mg, Ca or other elements may also limit the growth of tropical trees under certain circumstances, but it is unclear how important these factors are in tropical mountain forests (e.g. Wilcke et al., 2008).

Independent of the specific nature of nutrient limitation, the nutrient availability to trees in tropical mountain forests generally seems to decrease with elevation as indicated by decreasing foliar nutrient concentrations, reduced specific leaf areas, and increasing root/shoot ratios with elevation (Tanner et al., 1998; Leuschner et al., 2007; Moser et al., 2008). These changes could be caused by the altitudinal temperature decrease reducing soil biological activity and slowing down nutrient cycling, or may result from increasingly adverse soil conditions or more frequent soil water

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logging at higher elevations (see reviews in Bruijnzeel and Veneklaas, 1998 and Roman and Scatena, in press). A putative temperature-dependent reduction in the specific nutrient uptake capacity of roots with increasing elevation might also lead to an upslope decrease in foliar nutrient concentrations.

Studies explicitly testing the prediction of the changing roles of P and N limitation along tropical mountain slopes are scarce. Similarly, the postulated change in root activity with elevation has not been tested experimentally. This study in the Andes of southern Ecuador used an experimental approach to test two hypotheses related to the frequently observed altitudinal decrease in tree foliar nutrient concentrations. We focused on the growth response and activity of tree fine roots (i.e. roots with a maximum diameter of 2 mm, but typically with less than 1 mm) because they are likely to respond more rapidly and are easier to be examined than above-ground parts of mature trees. Nutrient addition has been found to stimulate fine root growth in a similar manner as it promotes shoot or leaf growth if nutrients are short in supply; however, roots often respond more directly. With a replicated N, P, and K fertilization trial at different elevations and a ^{15}N tracer experiment, we tested the following hypotheses (1) that fine root growth in pre-montane rainforest (1000 m asl) is limited primarily by low P availability, whereas low N supply restricts root growth in upper montane rainforest (3000 m asl), and (2) that the N uptake capacity of fine roots decreases with increasing elevation due to decreased soil temperatures.

2. Materials and methods

2.1. Study sites

The experiments were conducted in three tropical mountain forest stands at 1050, 1890 and 3060 m asl (Table 1) located in the eastern cordillera of the South Ecuadorian Andes in the provinces of Loja and Zamora–Chinchipe. The stand at 1050 m was located close to the village of Bombuscaro inside Podocarpus National Park representing a pre-montane tropical moist forest with the most abundant tree species belonging to the families Annonaceae, Mimosaceae, Moraceae, Myrtaceae and Sapotaceae. Relatively abundant genera are *Ficus* (Moraceae) and *Inga* (Mimosaceae). The stand at 1890 m was a mid-montane tropical moist forest situated in the forest reserve of the Estación Cientifica San Francisco (ECSF). The most important tree species in terms of abundance in this stand belong to the Euphorbiaceae, Lauraceae, Melastomataceae and Rubiaceae. The most frequent (but not dominant) species is *Graffenrieda emarginata* (Melastomataceae). The uppermost stand represented an elfin forest in the upper montane Cajanuma region of Podocarpus National Park at 3060 m with the more frequent tree species belonging to Cunoniaceae, Rubiaceae, Clusiaceae, Aquifoliaceae, and Ericaceae (Homeier et al., 2008). Relatively abundant genera are *Weinmannia* (Cunoniaceae), *Clusia* (Clusiaceae) and *Cinchona* (Rubiaceae).

The vast majority of tree species in the stands at 1050 and 1890 m were found to possess arbuscular mycorrhizas; notable exceptions were *G. emarginata* (Melastomataceae) and three species in the family Nyctaginaceae at 1890 m with their roots forming ectomycorrhizas. In the upper montane stand, species with arbuscular mycorrhizas and species in the family Ericaceae with ericoid mycorrhizas were relatively abundant (Kottke et al., 2008).

Mean tree height decreased from 15.6 m in the lowermost stand to 5.2 m at the uppermost site (Moser et al., 2008). All sites were situated on moderately steep slopes (Table 1).

The climate of the region can be classified as humid to perhumid (Richter, 2003). Rainfall at 1050 and 1890 m averaged at about 2000 mm yr^{-1}, whereas precipitation was ca. 4500 mm yr^{-1} at 3060 m (Emck and Richter, unpublished data, Moser et al., 2008). Annual mean air temperature measured at 1.5 m above the forest floor in the stands decreased from 19.4 °C at 1050 m to 9.4 °C at 3060 m. Seasonal temperature variation was negligible. The volumetric water content of the organic layer increased from 30 to 49 vol % (annual means) along the elevation transect (Moser et al., 2007).

The soils of the study sites developed on granodiorits at 1050 m and metamorphous shale and quartzite bedrock at 890 and 3060 m. All soils are relatively rich in clay. The bedrock surface is found 48–62 cm underneath the mineral soil surface (Schrumpf et al., 2001). At all three sites, the soils are acidic and nutrient-poor. The pH ($CaCl_2$) value in the upper mineral soil (0–30 cm) ranged from 3.9 at 1050 m to 2.9 at 3060 m (Iost, unpublished data). A strong upslope increase (from 22 to 63 g g^{-1}) in the C/N ratio of the organic layers on top of the mineral soil and in organic layer thickness (from 48 to 435 mm) was a characteristic of the transect (Iost, unpublished data). The organic layers consist of undecomposed litter (L horizon), partly decomposed organic material (F horizon) and amorphic humus material (H horizon).

Table 1
Location and characteristics of the study sites. Temperature and air humidity were measured continuously from May 2003–April 2004 at 1.5 m height inside the stands, soil moisture measurements were done in the organic layer (means ± 1 SE). Rainfall data are extrapolated from measurements in the open field at ca. 1050 m (measuring period May 2003–May 2004, Moser et al., 2008), and from measurements at 1950 and 3170 m (three-year means, Emck and Richter, unpublished data). Data on tree and canopy height from Moser et al. (2008); data on organic layer thickness, pH and C/N ratio from Iost and Makeschin (unpublished data). Soil type description according to FAO taxonomy.

	Elevation (m asl)		
	1050	1890	3060
Coordinates	04°06′54″ S 78°58′02″ W	03°58′35″ S 79°04′65″ W	04°06′71″ S 79°10′58″ W
Slope (°)	26	31	27
Annual mean air temperature (°C)	19.4	15.7	9.4
Mean air humidity (%)	89	91	94
Rainfall (mm yr^{-1})	2230	1950	4500
Canopy height (m)	31.8	18.9	9.0
Mean tree height (m)	15.6 ± 0.7	10.1 ± 0.4	5.2 ± 0.3
Soil type	Alumic Acrisol	Gleyic Cambisol	Podzol
Depth of organic LFH layers (mm)	48	305	435
Organic layer temperature (°C)	20.0	16.0	9.7
Mineral soil temperature (°C)	19.4	16.4	9.8
Organic layer moisture (vol%)	10	12	45
Mineral soil moisture (vol%)	30	35	49
pH-$CaCl_2$ (organic layer)	3.9	3.5	2.9
C/N (organic layer)	22	28	63

2.2. Analysis of element concentrations in fine roots

For the analysis of element concentrations in fine root tissue, ten soil cores (diameter 5.2 cm, 15 cm long) were randomly taken in 100 m^2 plots from the organic layers of the stands at 1050, 1890 and 3060 m. Living fine roots (diameter < 2 mm) were sorted under the microscope using criteria such as root color and elasticity (see Persson, 1978; Leuschner et al., 2007). The roots were washed, dried at 70 °C for 48 h and ground. The concentrations of C and N were determined with a C/N-elemental analyzer (Vario EL 3, Fa. Elementar, Hanau, Germany). Phosphorus concentrations were analyzed through yellow-dyeing with NH_4VO_3 and $(NH_4)_6Mo_7O_{24}$ and subsequent photometric measurement after digestion with 65% HNO_3 at 195 °C. Potassium, Mg and Ca concentrations were determined by atomic absorption spectroscopy (AAS vario 6, analytik jena, Jena, Germany) after HNO_3 digestion.