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Fine root dynamics and resource uptake in a South Ecuadorian mountain rainforest as dependent on elevation

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CHAPTER 1

General introduction

Tropical mountain rainforest, carbon cycles and climate change

Tropical mountain rainforests are diverse and unique ecosystems, which can be found at altitudes between 1000 and 3500 m asl in mountainous regions at lower latitudes. They occur within a wide range of rainfall regimes (up to 6000 mm yr^{-1}), and are characterized by a frequent presence of clouds and mist (Cavelier 1996; Bubb et al. 2004), which is an important factor for ecosystem functioning in these forests. This is underlined by the abundance of epiphytic plants, which play an important role for water storage and nutrient input from clouds (Veneklaas and van Eck 1990; Bruijnzeel and Proctor 1995; Benzing 1998; Bubb et al. 2004). Tropical mountain rainforests are characterised by steep elevational gradients, which result in strong temperature changes over short distances. Typically, forest stature and leaf size decrease with increasing elevation (Cavelier et al. 1996; Leuschner et al. 2007; Moser et al. 2007). Another characteristic of montane rainforests is the large accumulation of organic matter, and consequently a slow release of mineral nutrients (Edwards and Grubb 1977; Tanner et al. 1998; Benner et al. in press), which points to a possible nutrient limitation in these ecosystems.

Tropical rainforests are known to play a major role in the global carbon cycle (Soepadmo 1993; Clark et al. 2004). Forest ecosystems and forest soils are estimated to account for 46% of the world's living terrestrial carbon pool and about 12% of the world's soil carbon pool (Soepadmo 1993; Lal et al. 1995). Soil carbon sequestered in mineral surfaces can be hundreds of years old, whereas carbon resides for only a few decades in living tree biomass (Vieira et al. 2005). Malhi et al. (1999) estimated a mean carbon residence time in tropical lowland forests of approximately 29 years. Generally, C turnover is faster in those forest stands which are characterised by large, fast-growing trees (Vieira et al. 2005). Under natural conditions, the amount of carbon fixed annually by world biota through photosynthesis is balanced by the release of carbon by plant respiration and decomposition of organic residues (Lal et al. 1995). Trumbore et al. (2006) estimated that 80% of the CO_2, which is produced between 1 and 6 m depth in Amazonian lowland rainforests, originated from root and rhizosphere processes, and returns as CO_2 to the atmosphere within 1-2 years. It is estimated that tropical forests store 230 Mg ha^{-1} C belowground (of which 38 Mg ha^{-1} is contributed by fine roots, and 162 Mg ha^{-1} by soil organic matter), and 217 Mg ha^{-1} C in aboveground biomass (Malhi et al. 1999).

It is expected that global climate change will affect net primary production and carbon cycles of forests, however it is still speculative if rising temperatures and atmospheric CO_2 concentrations will enhance or decrease forest productivity (Clark et al. 2004, UNESCO-SCOPE 2006). Raich et al (2006) examined the influence of temperature on carbon fluxes and storage in tropical evergreen forests, and found NPP to increase by 0.2 – 0.7 Mg C ha^{-1}

yr^{-1} °C^{-1}. Soil organic matter accumulation on the other hand decreased by –8 Mg C ha^{-1} °C^{-1}, which was due to accelerated organic matter decomposition under higher temperatures. Hence, increasing temperature resulted in an obvious shift in ecosystems structure, but there was no effect on total carbon storage. However, there is also evidence from the work of Melillo et al. (1993), who predicted that NPP in tropical forests will decrease by 9-20% in regions where nitrogen availability is not limiting production, which they attributed to increased plant respiration at higher temperatures. Obviously, ecosystems will respond to a warmer climate by releasing more carbon to the atmosphere (UNESCO-SCOPE 2006). King et al. (2001) and Heath et al. (2005) found a reduced sequestration of root-derived soil carbon under elevated CO_2, as fine root production was enhanced, which resulted in a greater soil C efflux in form of soil respiration.

Not only temperature and atmospheric CO_2 changes, but also conversion of natural forests to agriculturally used land impacts carbon cycles, as an immediate removal of aboveground biomass and a gradual subsequent reduction in soil organic carbon leads to a reduction in ecosystem carbon storage (Raich 1983; Van Noordwijk et al. 1997). It is estimated that over the last five years deforestation in tropical regions released 1.5 Gt C per year, which is one fifth of total anthropogenic carbon emissions (UNESCO-SCOPE 2006).

The exceptional ecology and location of mountain slopes makes tropical mountain rainforests particularly susceptible to climate change and deforestation (Bubb et al. 2004). Evidence exists that forest with abundant epiphytes and clouds will respond most adversely to climate change, as the tolerance of the vegetation for growing conditions is very narrow in these ecosystems (Benzing 1998). Due to global warming and rainfall changes, it is expected that optimum climatic conditions of tropical mountains will increase in altitude, with the consequence that higher altitude forests will be displaced by lower altitude vegetation (Bubb et al. 2004). Another serious threat to tropical mountain rainforests is the conversion of old-growth forests to pastures (Bruijnzeel and Hamilton 2000). This is especially due for Ecuadorian mountain rainforests, as this country suffers the highest deforestation rate in South America (-1.7% yr^{-1}, Mosandl et al. 2008). Also regional land-use changes may influence cloud cover patterns in mountain forests, thus affecting water cycles and related ecosystems services (Bubb et al. 2004).

The role of fine roots for resource acquisition

The main function of tree roots is to link below-ground and above-ground ecosystem processes via organic and inorganic resource flows. Fine roots (generally defined as roots with a diameter < 2 mm) capture water and nutrients, supply C and nutrients to the below-ground ecosystem, and mobilize nutrients and C from soil reserves (van Noordwijk et al. 1998). Roots provide a path for the movement of carbon from plant canopies to soils, thus root production and turnover (i.e. the replacement of existing fine root biomass by new fine root biomass) directly impact biogeochemical cycles of carbon (Gill and Jackson 2000; Clark et al 2001; Matamala et al. 2003). The growth of roots is triggered by the import of carbohydrates from the shoot, as well as the subsequent metabolisation and associated respiration of those carbohydrates. However, the control of carbon fluxes is shared by many processes in all parts of the plant and is strongly affected by the capability of the canopy to assimilate C (Pregitzer et al. 2000; Farrar and Jones 2003). The ability of a root system to take up efficiently water and nutrients depends mainly on the production and loss of individual roots, as the physiological activity of roots diminishes with age (Eissenstat and Yanai 2002).

It is assumed that global warming and atmospheric CO_2 enrichment will influence the production and turnover of fine roots, and hence also carbon sequestration in soils (Vogt et al. 1993). The adaptation of ecosystems to climate change will depend on how trees allocate resources to their components. Tingey et al. (2000) found elevated CO_2 concentrations to increase fine root growth in conifers, but there was no evidence that the proportion of C allocation to fine root biomass was affected. Joslin et al. (2000) simulated increasing and decreasing water inputs within the scope of a throughfall displacement experiment in Tennessee, USA, and found highest fine root turnover to occur in the wet treatment, which they related to a positive relationship between fine root turnover and nutrient availability.

Root turnover rates are found to increase exponentially with mean annual temperature, hence fine root turnover is higher in tropical forests (0.76 yr^{-1}) than in temperate forests (0.64 yr^{-1}, Gill and Jackson 2000; Lauenroth and Gill 2003). Highest estimates for fine root turnover in tropical forests even exceed 1.0 yr^{-1} (Herbert and Fownes 1999; Priess et al. 1999). However, it is assumed that temperature is not the direct cause for differences in fine root turnover, but rather a covariate for other process-driving factors, such as root pathogens, maintenance respiration, solar radiation and nutrient mineralization, which tend to increase with increasing temperature (Lauenroth and Gill 2003). Apart of climatic variables also nutrient pools are important controlling factors in determining fine root biomass and turnover and hence carbon allocation to roots (Vogt et al. 1996).

In their global review, Hertel and Leuschner (in press) found fine root production in tropical forests to span a broad range from 100 to > 2000 g m^{-2} yr^{-1}. They further assumed that fine root production is higher on nutrient poor soils. Tropical montane forests are known to have higher amounts of fine root biomass than tropical lowland forests (Vogt et al. 1996; Cairns et al. 1997, Hertel and Leuschner in press). Studies along elevational gradients in montane rainforests revealed a significant increase of fine root biomass and necromass with increasing elevation (Roederstein et al. 2005; Leuschner et al. 2007; Moser et al. 2008). Due to the apparently positive effect of temperature on fine root turnover, it is assumed that the longevity of fine roots increases with increasing elevation. However, tropical mountain rainforests are still poorly understood regarding fine root dynamics and associated fluxes of C and nutrients. Apart of temperature also adverse soil conditions (i.e. low nutrient availability, high soil moisture contents) may affect fine root turnover in these ecosystems. Studies along altitudinal gradients in tropical mountain rainforests are therefore strongly needed, in order to contribute to the understanding how fine roots will respond to changing environmental conditions.

Objectives and approach

This thesis is part of the DFG funded Research Unit 402 “Functionality of a tropical mountain rainforest: diversity, dynamic processes and utilization potentials under ecosystem perspectives”. The study aimed at investigating turnover and resource acquisition of fine roots in a South Ecuadorian Mountain rainforest in five forest stands at altitudes ranging from 1050 to 3060 m asl (see next chapter for a detailed study sites description).

Major aims of the study were

(1) to analyse the effect of temperature and soil conditions on fine root turnover along the elevational transect by means of minirhizotrons (chapters 2 & 3).

(2) to assess the role of possible limiting factors for fine root growth and turnover (i.e. nutrient limitation and water-logging) by means of a fertilization experiment at 1050 and 3060 m, and a throughfall exclusion experiment at 3060 m, respectively. Additionally, nitrogen (nitrate and ammonium) uptake capacity was examined by ^{15}N tracer application in three forest stands (chapter 4).

(3) to investigate the dependence of root sap flow on environmental variables (i.e. VPD, temperature, soil moisture) in forest stands at 1050, 1890 and 3060 m by means of miniature heat balance sap flow gauges, and to analyse related anatomical characteristics of root cross sections (chapter 5).

Study area

The study area is located in the Eastern cordillera of the South Ecuadorian Andes in the provinces of Loja and Zamora-Chinchipe (Fig. 1). Experimental work was conducted in five forest stands at 1050, 1540, 1890, 2380 and 3060 m asl, representing an altitudinal gradient of 2000 m (Fig. 2, Fig. 3).

Fig. 1. Map of Ecuador with the study region in the provinces of Loja and Zamora-Chinchipe.

The forest stands at 1050 and 1540 m were located near Bombuscaro inside Podocarpus National Park (Fig. 2). The lowermost stand represents an upper pre-montane tropical moist forest with dominant tree species of the families *Annonaceae*, *Mimosaceae*, *Moraceae*, *Myrtaceae* and *Sapotaceae*. The stand at 1540 m is a lower montane tropical moist forest with *Arecaceae*, *Lauraceae*, *Melastomataceae* and *Rubiaceae* being the most widespread families present (Homeier et al. 2008).

The two mid-elevation stands at 1890 and 2380 m were situated in the forest reserve of the Estación Científica San Francisco (ECSF) (Fig. 2), and consist of mid-montane and upper-montane tropical moist forest, respectively (Fig. 3). The most important tree species in terms of abundance in the stand at 1890 m belong to the *Euphorbiaceae*, *Lauraceae*, *Melastomataceae* and *Rubiaceae*, and in the case of the stand at 2380 m to the *Aquifoliaceae*, *Clusiaceae*, *Cunoniaceae*, *Ericaceae* and *Rubiaceae* (Homeier et al. 2008).

The uppermost stand at 3060 m is located close to the treeline in the upper montane Cajanuma region of Podocarpus National Park (Fig. 2, Fig. 3), representing an elfin forest with dominant tree species belonging to *Cunoniaceae*, *Rubiaceae*, *Clusiaceae*, *Aquifoliaceae*, and *Ericaceae* (Homeier et al. 2008).

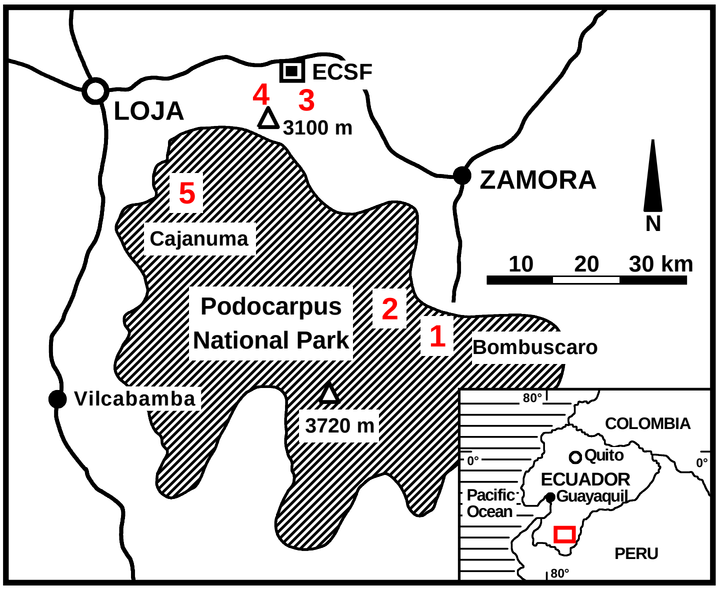

Fig. 2. Location of the five study sites (1 = 1050 m, 2 = 1540 m, 3 = 1890 m, 4 = 2380 m, 5 = 3060 m).

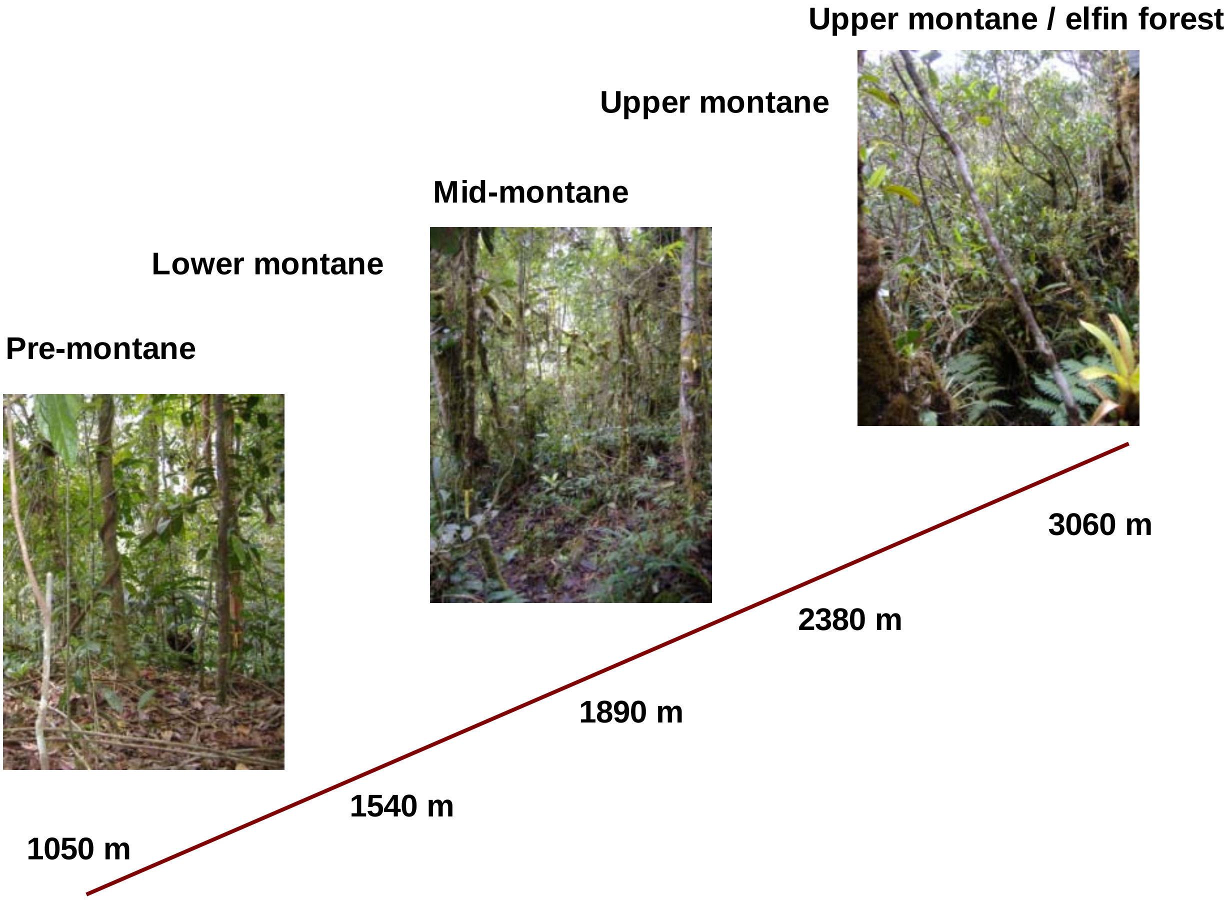

Fig. 3. Altitudinal transect of the five study sites.

Except for the stand at 1540 m, all sites were situated on moderately steep slopes (26 to 31°) facing northeast to northwest. The mean canopy height decreased from 32 m at the lowermost stand to 9 m at the uppermost stand, and mean tree height decreased accordingly from 15.6 m to 5.2 m. Fine root biomass was found to increase significantly from 2.7 t ha^{-1} at 1050 m to 10.8 t ha^{-1} at 3060 m (Moser et al. 2008, Table 1).

The study area is located on the weather divide between the humid Amazon and the dry Inter-Andean region, and the climate is characterized by easterly winds from the Amazonian lowlands, which transport humid air masses to the slopes. Rainfall at 1050, 1540 and 1890 m asl averages about 2000 mm yr^{-1}, whereas precipitation is ca. 5000 mm yr^{-1} at 2380 and 4500 mm yr^{-1} at 3060 m asl (P. Emck & M. Richter, unpublished data, Moser et al. 2008). There is no marked dry season in the region, but somewhat lower rainfall occurs during the months of October to January. The climate can be classified as humid to perhumid, with 11 to 12 humid months (Richter 2003). Another characteristic of the study area is a high cloudiness, and an increase in cloud frequency with increasing altitude (Bendix et al. 2006).

Rollenbeck et al. (2005) found rainfall to increase by 230 mm 100 m^{-1}, and fog by 240 mm 100 m^{-1}, along an altitudinal gradient between 1800 and 3200 m in the study region.

Relative air humidity inside the forest stands is high and increases slightly with elevation from 88.7 to 93.5%. Annual mean air temperature measured 1.5 m above the forest floor in the stands decreases from 19.4°C at 1050 m asl to 9.4°C at 3060 m asl, representing a temperature lapse rate of 5 K km^{-1} along the slope. The volumetric water content of the organic layer increased from 29.7 to 49.1 vol% along the elevational transect (Table 1).

The soils of the forest stands derived from granodiorits at the two lowermost sites and from metamorphous shale and quartzite bedrock at the higher altitudes. According to the FAO soil type description, soils at 1050 and 1540 m are classified as Alumic Acrisol, at 1890 and 2380 m as Gleyic Cambisol, and at 3060 m as Podzol, respectively (Iost 2008).

Table 1. Location and characteristics of the study sites. Temperature and air humidity were measured at 1.5 m height inside the stands, soil moisture was measured in the organic layer. Rainfall data are from Moser et al. (2008) and P. Emck and M. Richter, personal communication. Data on tree and canopy height and fine root biomass are from Moser et al. (2008) and on organic layer thickness, pH and C/N from Iost (2008).

Plot N°	1	2	3	4	5
Elevation (m asl)	1050	1540	1890	2380	3060
Coordinates	04°06’54’’ S 78°58’02’’ W	04°06’42’’ S 78°58’20’’ W	03°58’35’’ S 79°04’65’’ W	03°59’19’’ S 79°04’55’’ W	04°06’71’’ S 79°10’58’’ W
Slope (°)	26	10	31	28	27
Mean air temp (°C)	19.4	17.5	15.7	13.2	9.4
Mean air humidity (%)	88.7	88.9	90.8	93.2	93.5
Precipitation (mm yr^{-1})	2230	2300	1950	5000	4500
Organic layer (mm)	48	243	305	214	435
Soil moisture (vol%)	9.9	12.9	11.6	34.0	45.3
pH ($CaCl_2$)	3.9	3.9	3.5	3.3	2.9
C/N (L/Of_1)	22	29	28	46	63
Canopy height (m)	31.8	21.7	18.9	12.0	9.0
Mean tree height (m)	15.6	12.1	10.1	7.4	5.2
Basal area (m^2 ha^{-1})	33.6	27.5	36.9	27.2	42.2
Fine root biomass (t ha^{-1}) profile total	2.7	5.6	6.2	6.3	10.8

Soils at the higher elevations are less developed and show hydromorphic properties due to high precipitations and low temperatures. The bedrock surface is found at a depth of 48-62 cm below the mineral soil surface (Schrumpf et al. 2001). At all sites, the soils are acidic and nutrient-poor. The pH($CaCl_2$) values in the upper mineral soil (0-30 cm) range from 3.9 at 1050 m to 2.9 at 3060 m (Iost 2008), and all sites are poor in exchangeable nutrient cations. However, the proportion of exchangeable nutrient cations to total ECEC is higher in the upper montane and forest stands where soils are less weathered (Schrumpf et al. 2001). A strong increase in the C/N ratio of the organic layer (from 22 to 63 g g^{-1}) and of the organic layer thickness (from 48 to 435 mm) exists along the transect (Iost 2008, Table 1).

Wilcke et al. (2002) assumed that the turnover of organic matter and nutrients in the thick organic layers are limited by periodic waterlogging, which has the consequence that plant growth in these forests may be limited by several nutrients (e.g. S, Mn, Zn and Ca). They further found macro- (N, P, Ca) and micronutrient (Mn) concentrations in the organic layer and the mineral A horizon to be positively correlated to tree growth along a transect between 1900 and 2500 (Wilcke et al. 2008).

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CHAPTER 2

Estimating fine root turnover in tropical forests along an elevational transect using minirhizotrons

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Abstract

Growth and death of fine roots represent an important carbon sink in forests. Our understanding of the patterns of fine root turnover is limited, in particular in tropical forests, despite its acknowledged importance in the global carbon cycle. We used the minirhizotron technique for studying the changes in fine root longevity and turnover along a 2000 m-elevational transect in the tropical mountain forests of South Ecuador. Fine root growth and loss rates were monitored during a five-month period at intervals of four weeks with each 10 minirhizotron tubes in three stands at 1050, 1890 and 3060 m asl. Average root loss rate decreased from 1.07 to 0.72 g g^{-1} yr^{-1} from 1050 to 1890 m, indicating an increase in mean root longevity with increasing elevation. However average root loss rate increased again toward the uppermost stand at 3060 m (1.30 g g^{-1} yr^{-1}). Thus, root longevity increased from lower montane to mid-montane elevation as would be expected from an effect of low temperature on root turnover, but it decreased further upslope despite colder temperatures. We suggest that adverse soil conditions may reduce root longevity at high elevations in South Ecuador, and are thus additional factors besides temperature that control root dynamics in tropical mountain forests.

Keywords: altitudinal transect, Ecuador, fine root growth, fine root mortality, root longevity

Introduction

Root turnover is an important component of the ecosystem's carbon and nutrient cycles (Clark et al. 2001). Global climate change, in particular with respect to warming and CO_2 enrichment, as well as nitrogen input are expected to influence the rates of root production and death, and hence the carbon sequestration in soils (Vogt et al. 1993). Unlike leaves, whose initiation and abscission can readily be observed (Raich et al. 1997; Williams-Linera 2000), the timing and rate of root growth and root death are difficult to study and hence this part of the belowground carbon turnover continues to be one of the most challenging issues in terrestrial biogeochemistry (Vogt et al. 1993; Vogt et al. 1996). This is particularly true for tropical forests, which have been identified as major carbon sinks on the continents, but are poorly understood with respect to their root dynamics and the associated fluxes of C and nutrients (Lauenroth and Gill 2003). Only a few studies have been conducted on production and turnover of fine roots (roots < 2 mm in diameter) in tropical forests (Cuevas and Medina 1988; Herbert and Fownes 1999; Ostertag 2001).

The existing estimates of fine root production (FRP) in tropical moist forests span a broad range, from approximately 100 to >2000 g m^{-2} yr^{-1} (Hertel and Leuschner, in press). Deducing from the few existing data it is likely that FRP is higher in forests on nutrient-poor soils than on more fertile ones (Hertel and Leuschner, in press) and it appears that fine root turnover (FRT), i.e. the replacement of the existing fine root biomass (FRB) by new root biomass, is higher in tropical than in temperate or boreal forests (Gill & Jackson 2000, Lauenroth & Gill 2003). Gill & Jackson (2000) estimate FRT of temperate and boreal forests at 0.64 and 0.42 yr^{-1}, respectively, whereas FRT of tropical forest is around 0.76/yr. In fact, many of the existing estimates of FRT in tropical forests exceed 1.0 yr^{-1} (e.g. Herbert and Fownes 1999; Priess et al. 1999). The exogenous and endogenous controls of fine root longevity and turnover in tropical forests are not known. Therefore, we are not able to predict how root turnover and the associated belowground carbon dynamics will change with the expected rise in temperature, CO_2 concentration and N availability in the tropical zone in the coming decades.

Studies along steep temperature gradients in tropical mountains could well contribute to our understanding of how tree root dynamics of old-growth forests respond to altered temperatures and associated changes in nutrient supply. In contrast to temperate grasslands (e.g. Fitter et al. 1998), there are no studies investigating altitudinal changes in fine root longevity and turnover in tropical forests so far. Since a temperature decrease often coincides with a decrease in nutrient availability as one moves upslope in tropical mountains, the elevational change in tree fine root dynamics is difficult to predict from the existing knowledge on environmental controls of FRT.

In most studies comparing forests across latitudinal gradients, a higher FRP and a higher FRT, and thus a decrease in average root longevity, were found in warmer climates compared to colder ones, whereas fine root biomass remained more or less unchanged (Vogt et al. 1996; Gill and Jackson 2000). From this temperature effect we predict that fine root longevity increases with increasing elevation in tropical mountains resulting in a lower turnover in high-elevation forests. On the other hand, there are reports that fine root longevity decreases, and turnover increases, with decreasing nutrient (nitrogen) availability (Pregitzer et al. 1993; Godbold et al. 2003). Since nitrogen availability was found to decrease with elevation in several tropical mountains (Tanner et al. 1998; Benner et al. in press), we would expect a shorter longevity, but a higher turnover, of fine roots at high elevations. Therefore, temperature and nutrient effects (Cavelier 1996; Tanner et al. 1998) might have opposite consequences for average root longevity and turnover in tropical mountain forests and it is possible that both effects may compensate each other at high elevations.

In the context of a more comprehensive study on the carbon balance and nutrient regime of tropical mountain forests, we applied the minirhizotron technique in a lower montane (1050 m asl), a mid-montane (1890 m) and an upper montane forest (3060 m) with the aim to examine two partly contradicting hypotheses by field data from a 2000 m-altitudinal transect in South Ecuador. Our main hypothesis is that a large decrease in temperature (> 10 K) between 1050 and 3060 m leads to higher average fine root longevity and a lower fine root turnover at high elevation. We formulated the alternate hypothesis, that adverse soil conditions at high elevations result in a decreased average fine root longevity and hence a higher root turnover than at lower elevations.

Methods

Study sites

The study was conducted in the Eastern cordillera of the Ecuadorian Andes in the provinces of Loja and Zamora-Chinchipe. Three forest stands at 1050, 1890, and 3060 m asl were selected, representing an altitudinal gradient of 2000 m. Stand N$^{\underline{o}}$ 1 (1050 m) was located near Bombuscaro inside Podocarpus National Park and represents a lower montane tropical moist forest with tree species of the families *Sapotaceae*, *Annonaceae*, *Myrtaceae*, *Mimosaceae,* and *Moraceae* covering notable proportions of the stand (J. Homeier, unpublished data). Stand N$^{\underline{o}}$ 2 (1890 m) was situated in the forest reserve of the Estación Científica San Francisco (ECSF) which consists of a mid-montane tropical moist forest; the most important tree species belong to the *Melastomataceae*, *Lauraceae*, *Rubiaceae*, and *Euphorbiaceae* (J. Homeier, unpublished data). The uppermost stand N$^{\underline{o}}$ 3 (3060 m) represents an elfin forest in the upper montane Cajanuma region of Podocarpus National Park; dominant trees belong to the *Cunoniaceae*, *Rubiaceae*, *Clusiaceae*, *Aquifoliaceae*, and *Ericaceae*. All study sites were situated on moderately steep slopes (26 to 31°) facing northeast to northwest (Table 1). The mean canopy height decreased from 32 m at the lowermost site to 9 m at the uppermost one, and mean tree height from 15.6 m to 5.2 m (Moser et al., in press).

The region’s climate is characterized by easterly winds from the Amazonian lowlands which transport humid air masses to the slopes. Rainfall at 1050 and 1890 m asl averages about 2000 mm yr^{-1}, whereas precipitation is ca. 4500 mm yr^{-1} at 3060 m asl (P. Emck and M. Richter, unpublished data, G. Moser, unpublished data). There is no marked dry season in the region, but somewhat lower rainfall occurs during the months of October to January. The climate can be classified as humid to perhumid, with 11 to 12 humid months (Richter 2003). Relative air humidity inside the forest stands increases slightly with elevation from 88.7 to 93.5%. Annual mean air temperature measured 1.5 m above the forest floor in the stands decreases from 19.4°C at 1050 m asl to 9.4°C at 3060 m asl, representing a temperature lapse rate of 0.5 K 100 m^{-1} of altitudinal distance (Table 1). The volumetric water content of the organic layer was continuously recorded with TDR sensors and increased from 29.7 to 49.1 vol% along the elevational transect (Table 1). The site-specific coefficient of temporal variation of soil moisture was low during the study period (CV = 0.2).

The soils of the forest stands are derived from granodiorits at the lowest site and from metamorphous shale and quartzite bedrock at the higher altitudes. The bedrock surface is found at a depth of 48-62 cm below the mineral soil surface (Schrumpf et al. 2001). At all three sites, the soils are acidic and nutrient-poor: the pH($CaCl_2$) values in the upper mineral soil (0-30 cm) range from 3.9 at 1050 m to 2.9 at 3060 m (S. Iost, unpublished data) and all sites are poor in exchangeable nutrient cations (Schrumpf et al. 2001). A strong increase in the C/N ratio of the organic layer (from 22 to 63 g g^{-1}) and of organic layer thickness (from 48 to 435 mm) existed along the transect (S. Iost, unpublished data). Foliar and fine root N concentrations were found to decrease by about 50% from the lowermost to the uppermost stand (Table 1).

Table 1. Location and characteristics of the three study sites. Temperature and air humidity were measured 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 a gap at ca. 1050 m (measuring period May 2003 - May 2004, Moser et al., 2008), and from measurements in gaps at 1950 and 3170 m (three-year means, P. Emck & M. 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 S. Iost & F. Makeschin (unpublished), data on foliar and fine root N-concentrations are own measurements (means ± 1 SE, different letters indicate significant differences between the study sites). Soil type description according to FAO taxonomy.

Plot Nº	**1**	**2**	**3**
Elevation (m asl)	1050	1890	3060
Coordinates	04°06’54’’ S	03°58’35’’ S	04°06’71’’ S
	78°58’02’’ W	79°04’65’’ W	79°10’58’’ W
Slope (°)	26	31	27
Mean air temperature (°C)	19.4 ± 0.06	15.7 ± 0.05	9.4 ± 0.03
Mean air humidity (%)	88.7 ± 0.33	90.8 ± 0.23	93.5 ± 0.13
Rainfall (mm yr^{-1})	2230	1950	4500
Soil type	Alumic Acrisol	Gleyic Cambisol	Podzol
Organic layer thickness (mm)	48	305	435
Mean soil moisture (vol%)	9.9 ± 0.001	11.6 ± 0.001	45.3 ± 0.002
pH ($CaCl_2$)	3.9	3.5	2.9
C/N (L/Of_1)	22	28	63
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
Foliar N concentration (mmol g^{-1}), n=10	2.18 ± 0.13 *a*	1.82 ± 0.1 *b*	1.39 ± 0.09 *c*
Fine root N concentration (mmol g^{-1}), n=10	1.29 ± 0.04 *a*	1.07 ± 0.04 *b*	0.61 ± 0.03 *c*

Measurement of fine root growth and death

In each forest stand, a study plot of 20 m x 20 m was established in patches of representative, undisturbed forest with closed canopy. In each plot, ten transparent minirhizotron tubes with an external diameter of 70 mm were installed in June 2005. They were inserted at a 90° angle to the slope to a depth of 10 to 40 cm in the soil (depending on the firmness of the soil). Holes were made with a soil corer that had the same diameter as the tubes, which ensured a tight contact of the tubes to the surrounding soil. To prevent entrance of water into the tubes, the bottom was sealed and the top end was covered with a removable cap. Those parts of the tubes that extended above the soil surface were covered with black tape to avoid incidence of light that might influence root growth. A circular plastic foil with a diameter of 16 cm was placed around the tubes on the soil surface to prevent water runoff on the surface of the tubes which could attract root growth.

For monitoring root growth, a root scanner system (CI-600 Root Growth Monitoring System, Fa. CID, USA) was used in the tubes from September 2005 to March 2006 at monthly intervals. With each scanner image we recorded a soil compartment of 20 cm length and 345° of the tube's inner surface (i.e. a total soil surface area of 219.9 cm^2). Pictures were taken in grayscale and with 400 dpi. In this study, only the first 10 cm below soil surface were considered for analysis of fine root dynamics, as the very shallow soil at the lowermost site did not allow a deeper placement of the tubes. However, earlier studies on fine root distribution in the same stands had shown a strong exponential decrease in fine root density with soil depth with the consequence that more than 50 % of the fine root biomass of the profile total was located in the uppermost 10 cm of the soil (Roederstein et al. 2005; Moser et al. 2008).

The images were analyzed with the program WinRHIZO Tron (Règent, Canada). Root length and diameter were marked manually on the screen for each image. For analyzing subsequent images, the previous analysis was superposed over the current image. This allowed to mark root sections originating from recent root growth or sections that had disappeared due to root death and decomposition. Software-assisted data analysis gave the length and surface area of recently born and disappeared root sections. Only fine roots (diameter < 2 mm) were taken into account in the analysis. By comparing visible and disappeared fine root length of current and previous images, cumulative root length production and root length loss were calculated per month (unit cm mo^{-1}, Buckland et al. 1993; Majdi, 1996). Relative root length increase (RRLI) and root length loss (RRLL) were calculated by relating monthly root length increase or loss to the visible root length at the previous measuring date (cm cm^{-1} mo^{-1}). Relative annual root loss rate (RRLR) of the visible fine root population in the rhizotron tubes was calculated according to Nadelhoffer (2000) as

RRLR = (mean RRLL x 12) / 100

We equate annual root loss rate with “root turnover”. Root longevity (days) was calculated as the inverse value of annual root loss rate.

Statistical analysis

Based on 10 replicate measurements (tubes) per each stand, we calculated means and standard errors for all parameters. A non-parametric analysis of differences between groups (Kruskal-Wallis test) and a subsequent Mann-Whitney two-sample test (U-test) for pairwise comparisons were used to analyze significant differences in root length or root surface area of different imaging dates and between the three stands. All calculations were done with SAS/STAT software ($p < 0.05$).

Results

Standing fine root populations

Regular inspection of the minirhizotron tubes at four-week intervals after their installation in June 2005 showed that branch fine roots took less than 12 weeks to explore the direct vicinity of the tubes in the three stands. Five months after installation, we recognized that visible root length had reached a quasi steady-state in the lower and mid-elevation stand, and tended to do so in the uppermost stand (Fig. 1). Hence, only data from November 2005 onwards (i.e. ca. 150 days after tube installation) were considered for analysis to avoid artifacts due to disturbance during tube installation (Hendrick and Pregitzer 1996; Majdi 1996; Joslin and Wolfe 1999).

Despite considerable within-site variability in root length density, the three stands differed markedly in their mean root length that was visible in November 2005 and thereafter (Fig. 1). The smallest mean root length was recorded in the upper montane stand (3060 m: 40 cm per 220 cm^2 tube surface area), the highest in the mid-elevation stand (1890 m: 150 cm per 220 cm^2), while the lower montane stand (1050 m) showed an intermediate average root length (80 cm per 220 cm^2). These differences were significant at $p < 0.05$.

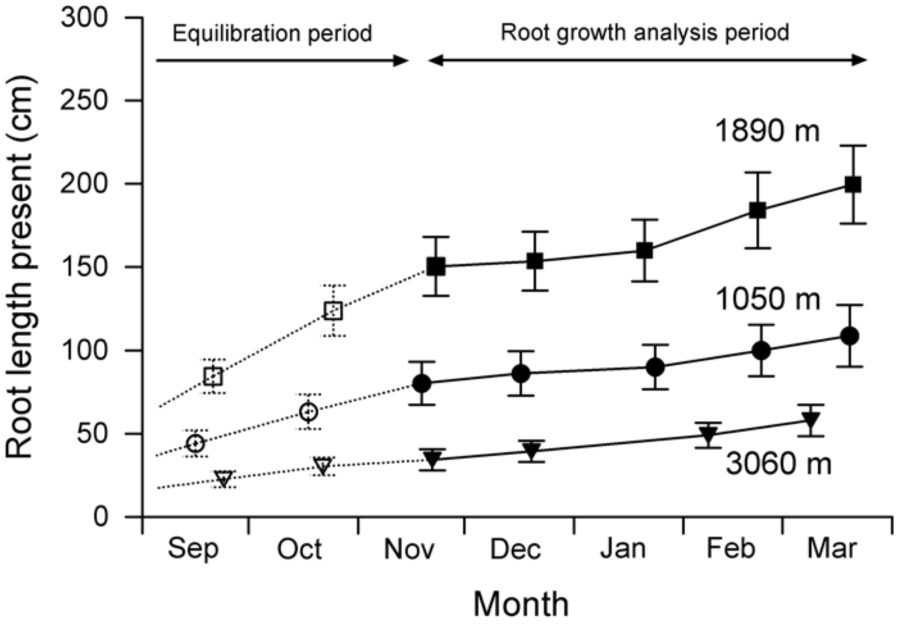

Fig. 1. Root length present per minirhizotron tube surface area (220 cm^2) in the study period from September 2005 to March 2006 (means ± 1 SE, n = 10).

Fine root growth and death

During the observation period of four months, we counted a root length production per tube that varied between 3 and 10 cm/mo in the lower montane stand (1050 m), between 3 and 23 cm mo^{-1} in the mid-montane stand (1890 m), and between 5 and 9 cm/mo in the upper montane stand (3060 m, Fig. 2A). Thus, absolute fine root growth rates were, on average, highest in the mid-elevation stand, lowest in the uppermost stand, and intermediate in the lowest stand. This sequence of root growth rates between the three stands was valid in three of the four months except for December 2006, when the lowermost stand had the highest and the intermediate stand the lowest absolute growth rate. In general, root growth rate did not differ between the four months more than twofold and the differences were not significant. An exception was a particularly high root length production in the mid-elevation forest in February and March 2006, which was three to four times higher than during the previous months.

The rate of root death reached values similar to those of root growth, indicating that the root populations were in a steady state during the period of observation. Root length loss varied between 4 and 8 cm mo^{-1} in the lower montane stand (1050 m), between 8 and 11 cm mo^{-1} in the mid-montane stand (1980 m), and between 3 and 5 cm mo^{-1} in the upper montane stand (3060 m, Fig. 2B). Similar to root growth rate, the highest death rate typically occurred in the mid-elevation stand and the lowest in the uppermost stand, but the differences between these stands were only significant in the months of February and March. A somewhat elevated root death rate was recorded in the lowermost stand in January and February 2006.

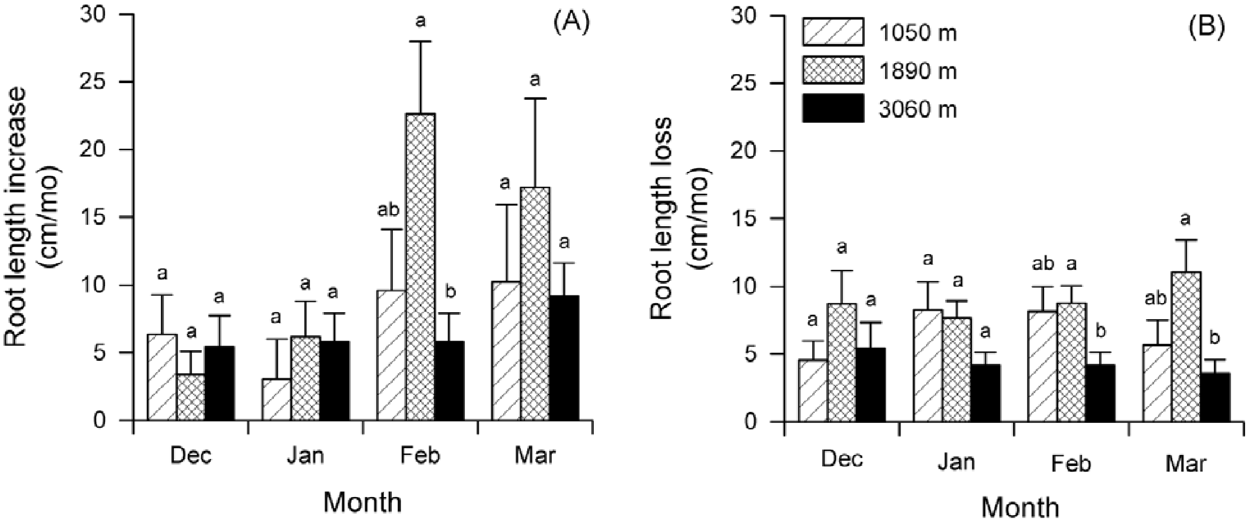

Fig. 2. Monthly production (A) and loss (B) in root length per minirhizotron tube (means ± 1 SE, $n = 10$). Different letters indicate significant differences between the three study sites ($p < 0.05$).

A different pattern of the elevational dependence of fine root dynamics was observed when root growth and root death were expressed in relation to standing root biomass, i.e. as relative root length increase or relative root loss (both in cm cm^{-1} mo^{-1}, Fig. 3A and B). Since the three stands had different absolute values in root length per tube, highest monthly relative root length increase rates were found in the upper montane stand (0.14-0.22 cm cm^{-1} mo^{-1}), lowest in the mid-montane stand (0.03-0.14 cm cm^{-1} mo^{-1}), and intermediate specific growth rates in the lower montane stand (0.05-0.15 cm cm^{-1} mo^{-1}). Significant differences existed only between the stands at 1890 m and 3060 m in the months of December 2005 and January 2006. Monthly rates of relative loss in root length (cm cm^{-1} mo^{-1}) were similar to relative root length increase, and thus reached highest values in the upper montane stand (0.08-0.18 cm cm^{-1} mo^{-1}), followed by moderate values in the lower montane stand (0.07-0.12 cm cm^{-1} mo^{-1}), while lowest values were found in the mid-elevation stand (0.05-0.07 cm cm^{-1} mo^{-1}). However, differences were only significant between the mid-elevation and the upper montane stand in December 2005.

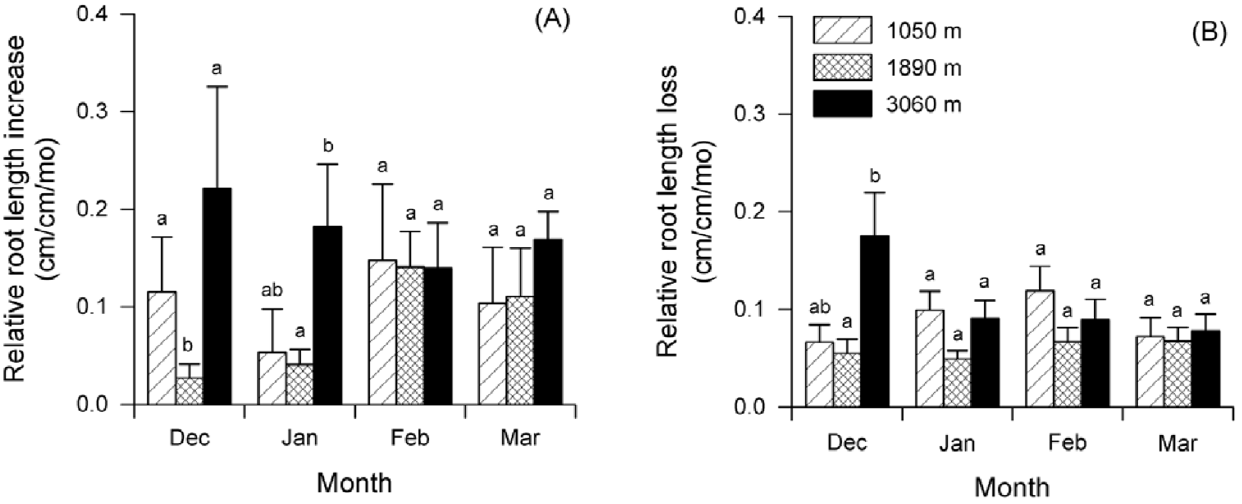

Fig. 3. Relative root length production (A) and relative root length loss (B) in the 4-month study period. The fine root length of the respective previous month was used as a calculation basis (means ± 1 SE, n = 10). Different letters indicate significant differences between the study sites ($p < 0.05$).

Fine root turnover and longevity

By extrapolating the fine root loss data from the five-month study period to a full year, we obtained an estimate of average fine root turnover and longevity for the fine root populations visible in the tubes. For the upper montane stand, we calculated fine root turnover rates of 1.30 yr^{-1}, for the mid-montane stand of 0.72 yr^{-1}, and for the lower montane stand of 1.07 yr^{-1} (Table 2). This corresponds to an average fine root longevity of 256 d in the upper montane stand, of 340 d in the lower montane stand and of 467 d in the mid-montane stand (Table 2).

Table 2. Average relative loss rate ($g\ g^{-1}\ yr^{-1}$) and estimated mean longevity (d) of the fine root populations visible in the minirhizotrons in the study period (means ± 1 SE). Different letters indicate significant differences between the three study sites ($p < 0.05$).

	1050 m	1890 m	3060 m
Relative root loss rate ($g\ g^{-1}\ yr^{-1}$)	1.07 ± 0.15 ab	0.72 ± 0.10 a	1.30 ± 0.21 b
Root longevity (days)	340 ± 45 αβ	467 ± 67 α	256 ± 39 β

Discussion

Estimating root turnover of tropical forests with minirhizotrons

The minirhizotron technique is a non-destructive method which allows to continuously record data of root length-specific growth and loss rates (change in root length per standing root length and time). A major strength of the method is the identification of the same roots on successive sampling dates, which enables to monitor roots for its lifetime. The minirhizotron images can be stored in a digital archive for processing. There is general agreement that in comparison with other methods minirhizotrons are yielding the most reliable root production and turnover estimates for forests (Crocker et al. 2003; Hendricks et al. 2006; Vogt et al. 1998). Minirhizotron data can also be combined with soil coring data on fine root biomass to provide reliable estimates of fine root production in absolute terms (root mass per soil volume or stand ground area) (Majdi 1996).

In this study, root dynamics were assumed to have equilibrated after 5-6 months based on the stabilization of fine root standing length visible in the tubes. This is shorter than the 8 months (e.g. Hendricks et al. 2006) or even 1-2 years (e.g. Joslin and Wolfe 1999) generally allowed for equilibration in temperate or boreal forests. We applied this rather short period because the minirhizotron images and the results from alternative methods (ingrowth cores, sequential coring) taken at short time intervals had shown that fine root turnover in these forests is rather high (G. Moser and M. Röderstein, unpublished data).

One problem with the minirhizotron technique is the definition of root death, in particular in species-rich stands where a mixture of roots with different structural and physiological properties appears at the tube surface. Following Tingey et al. (2000), we used root disappearance or loss as a criterion, but this may overestimate root longevity since initial stages of decomposition are included in the biomass fraction. The definition of root death is problematic under any circumstances since death occurs gradually (Comas et al. 2000). Moreover, tree species of different forest types may differ in the patterns of fine root mortality, hence introducing uncertain bias to our comparative data from the elevation transect.

The definition of root turnover has also created confusion (Norby and Jackson 2000). Certain authors define turnover as fine root production divided by fine root standing crop (either the maximum or the mean of the measuring period, e.g. Gill and Jackson 2000), others use root death per standing crop (e.g. Nadelhoffer 2000). In a system where root biomass is not strictly seasonal as in tropical forests, fine root growth and death are expected to reach similar rates if sufficiently long observation periods are considered. Since our study only covered a core observation period of five months, we reported both growth and loss rates. Nevertheless, the two parameters of root turnover were roughly similar in the three stands indicating that the fine root systems were more or less close to a steady-state. Root longevity was estimated from extrapolation of root death observed in the tubes.

Root turnover in tropical mountain forests as influenced by the environment

In their global review of fine root turnover, Lauenroth and Gill (2003) concluded that tropical forests have higher turnover rates than temperate forests which they explained with higher temperatures, the greater length of the growing season and also with a higher virulence of plant pathogens in tropical forests. A study conducted by Priess et al. (1999) reported high fine root turnover rates > 2.0 yr^{-1} for a tropical premontane forest in Venezuela. By comparing two sugar maple forests, Hendrick and Pregitzer (1993) found that root longevity was higher on the colder site, providing further support to the conclusions of Lauenroth and Gill (2003). Higher fine root longevity in colder environments was also reported for *Populus tremuloides* (King et al. 1999) due to reduced root productivity and mortality rates. If applied to our transect from lower montane (warm) to upper montane (cool) forests, one should expect a decrease in turnover, or a higher mean longevity, with increasing elevation, as stated in our main hypothesis. Our data show a decrease in turnover when moving from the lower montane (1050 m) to the mid-montane stand (1890 m), which is in line with this assumption. However, the uppermost stand showed a higher turnover rate than the lower montane stand despite mean temperature being approximately 10K lower.

Short longevity of fine roots at low mean temperatures could be the consequence of adverse soil physical or chemical conditions at the high-elevation site. Soil chemical analyses revealed very high C/N ratios and low pH values in the organic layer (Table 1) and mineral topsoil (data not shown) in this stand, indicating a restricted N supply to the trees. Even though N mineralisation data are missing, low foliar and fine root N concentrations support this assumption (Table 1). Due to very low pH values in this soil, there is also the possibility that the roots are exposed to elevated concentrations of free aluminium in the soil solution, which is known to reduce the longevity of fine roots in temperate forests (e.g. Raynal et al. 1990). Another possible stressor may be oxygen deficiency in the temporarily waterlogged soils, a factor that has also been found to increase root mortality in plant species lacking adaptation to anoxia in the soil (Jackson and Ricard 2003). Nitrogen deficiency typically increases fine root biomass of temperate and boreal forest ecosystems (Nadelhoffer 2000), but decreases root turnover (Eissenstat and Yanai 1997). However, opposite effects of nutrient availability on fine root longevity have been reported as well. For example, Pregitzer et al. (1993) found that fine roots in fertile microsites of a North American hardwood forest grew more rapidly but also lived longer than control roots on less fertile microsites. Similarly, Sitka spruce roots had increased longevity with increasing nitrogen fertilization (Alexander and Fairley 1983). In these latter two cases, root responses to increased nutrient availability were probably dependent on past effects of soil fertility and may differ from stands that either received short nutrient pulses (i.e. explored nutrient rich microsites) or were subjected to continuous nutrient addition (i.e. fertilizer treatment).

Our results of fine root turnover did not show a clear trend with altitude, which implies that principles developed for temperate or boreal regions (e.g. an increasing longevity with decreasing temperature) can not be simply transferred to tropical montane ecosystems. Further, the South Ecuadorian transect is characterized by a high tree species turnover, which includes the possibility that different root turnover rates at low and high elevations partly reflect adaptive mechanisms of the tree species to prevailing climatic and soil conditions. The results of our study indicate that a direct temperature effect on root turnover is only one of several factors influencing root dynamics in these tropical montane forests. We suggest that one or more stressors must be effective at high elevation possibly including free aluminium (Raynal et al. 1990; Godbold et al. 2003) and anoxia (Jackson and Ricard 2003), which counteract the negative effect of low temperature on root growth activity, resulting in a reduced root longevity and increased turnover. Temperature most likely has not only direct but also indirect effects on fine root growth and dynamics. Nitrogen mineralisation and root pathogen activity should be positively related to temperature (Gill and Jackson 2000), and thereby may increase fine root turnover. However, some of the temperature effects on root growth will be mediated indirectly through changes in shoot physiology because the turnover rates of tree root systems are also determined by the capacity of the tree to sustain belowground biomass. It is still a matter of discussion whether carbon sink strength (i.e. root growth and activity, Eissenstat and Yanai 1997) or the source (photosynthesising organs, Fitter et al. 1998) is more important in determining carbon allocation to roots in mature trees. In the case of the latter, any constraints on canopy activity at high elevations (i.e. low light or infertile soils) could possibly influence root activity through reduced carbon supply. Fitter et al. (1998) found a close link between canopy assimilation and root respiration along an elevational transect in grasslands. In contrast, the relatively high fine root production rate in the upper montane stand of our study indicates that root growth limitation due to restricted carbon supply was probably not an influential factor in this stand.

Finally, mycorrhizal infection, which has been found to enhance fine root longevity of trees (e.g. Eissenstat et al. 2000), could be different at lower and upper montane elevation in the Ecuador transect, thus influencing fine root longevity independently of temperature or nitrogen effects on root dynamics. However, quantitative data on mycorrhizal infection of the trees along the transect are not yet available.

Conclusions

Tree fine roots in the lower montane forest of the Ecuador transect have a relatively high turnover with a mean lifespan of about 1 yr, whereas root turnover in the mid-montane forest is considerably lower. This is supportive for our main hypothesis, which postulates that a decrease in temperature results in reduced root turnover rates. However, we did not observe a continuous decrease in root turnover towards the coolest high-elevation site. Instead, fine root lifespan was lowest at highest elevation (> 3000 m asl), which is evidence in favour of our alternate hypothesis. We propose that adverse soil chemical or physical conditions in the high-elevation forest imposed severe stress on the fine root system, thereby counteracting any decline in fine root turnover rate due to low temperature. More direct observational data on fine root dynamics in tropical mountain forests are needed, including experiments with altered soil chemical and physical conditions, in order to fully understand the consequences of temperature decrease and the soil environment along mountain slopes on fine root dynamics in tropical forests.

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CHAPTER 3

Fine root dynamics along a 2000-m elevation transect in South Ecuadorian mountain rainforests

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Abstract

Fine root turnover plays an important role in the cycling of carbon and nutrients in ecosystems. Not much is known about fine root dynamics in tropical montane rainforests, which are characterized by steep temperature gradients over short distances. We applied the minirhizotron technique in five forest stands along an elevational transect between 1050 and 3060 m asl in a South Ecuadorian montane rainforest, in order to test the influence of climate and soil parameters on fine root turnover. Turnover of roots with d < 2.0 mm was significantly higher in the lowermost and the uppermost stand (0.9 cm cm^{-1} yr^{-1}) than in the three mid-elevation stands (0.6 cm cm^{-1} yr^{-1}). Root turnover of finest roots (d < 0.5 mm) was higher compared to the root cohort with d < 2.0 mm, and exceeded 1.0 cm cm^{-1} yr^{-1} at the lower and upper elevations of the transect. We propose that the non linear altitudinal trend of fine root turnover originates from an overlapping of a temperature effect with other environmental gradients (e.g. adverse soil conditions) in the upper part of the transect and that the fast replacement of fine roots is used as an adaptive mechanism by trees to cope with limiting environmental conditions.

Keywords: altitude, minirhizotrons, montane rainforest, root morphology, root length production, root turnover

Introduction

Fine root turnover (i.e. the replacement of root mass within a year) represents one of the major carbon and nutrient sources in soils and thus plays an important role in ecosystem carbon cycling (Gill and Jackson 2000). Numerous studies on fine root dynamics in temperate forests are now available (e.g. Santantonio and Grace 1987; Aerts et al. 1989; Hendrick and Pregitzer 1992 Pregitzer et al. 1993; Hendrick and Pregitzer 1996; Joslin et al. 2000; Mainiero and Kazda 2006). In contrast, studies on fine root turnover in tropical forests are still scarce and were mostly conducted in lowland forests (e.g. Jordan and Escalante 1980; Cuevas and Medina 1988; Green et al. 2005; Silver et al. 2005; Trumbore et al. 2006). Even less is known about fine root dynamics in tropical montane forests despite their acknowledged importance in carbon cycling. Recent studies showed that high elevation tropical montane forests may possess a remarkably high fine root biomass due to a pronounced carbon allocation to the roots in the trees (Leuschner et al. 2007; Moser et al. 2008; Hertel and Leuschner in press).

A global meta-analysis indicates that root turnover increases from boreal to tropical regions as a consequence of increased root maintenance respiration, a more rapid nutrient mineralization and a higher pathogen activity at higher temperatures (Gill and Jackson 2000). The effects of soil resource availability on fine root longevity are less clear than those of climatic factors, but might also be important variables explaining patterns of fine root dynamics (Pregitzer et al. 1993; Vogt et al. 1996; Pregitzer et al. 2000). Along a natural fertility gradient in Hawaii, root dynamics were related to nutrient availability, but N availability had a smaller effect than P availability (Ostertag 2001). In a northern hardwood forest, Burton et al. (2000) found root lifespan to be longer where N availability was higher. However, there are data both supporting (Alexander and Fairley 1983; Vogt et al. 1986; Pregitzer et al. 1993) and refuting (Roy and Singh 1995; Eissenstat and Yanai 1997; Nadelhoffer 2000; Yavitt and Wright 2001; Powers et al. 2005) the assumption that roots live longer in more fertile soils.

Nutrient mineralization in tropical montane forest is slowed down due to low temperatures and sometimes high soil water content (Tanner 1981; Vitousek and Sanford 1986; Benner et al. in press). In their review, Benner et al. (in press) conclude that montane forests are usually nitrogen-limited and often also phosphorus-limited. Soethe et al. (2007) found decreasing fine root nutrient concentrations with increasing altitude, which is also evidence for nutrient limitation in tropical montane forests. Thus, not only low temperature but also nutrient limitation and, probably, other factors may affect fine root turnover in tropical forests at high altitudes.

We applied the minirhizotron technique in five south Ecuadorian montane rainforest stands along an altitudinal transect between 1050 and 3060 m asl in order to assess fine root dynamics by direct observation. Along this 2000-m altitudinal transect we tested for temperature and soil effects on fine root production, mortality and turnover. We hypothesized that fine root turnover decreases with decreasing temperature and increasing altitude along the transect. It was further assumed that in the upper part of the altitudinal transect a temperature effect on root turnover is suppressed by adverse soil conditions, resulting in enhanced root turnover rates at the highest elevation.

Materials and Methods

Study sites

The study was conducted on the Eastern slopes of the South Ecuadorian Andes in the provinces of Loja and Zamora-Chinchipe. Five forest stands at 1050, 1540, 1890, 2380, and 3060 m asl were selected, representing an altitudinal gradient of 2000 m. The two lowermost stands were located near the village of Bombuscaro in the area of the Podocarpus National Park. The stand at 1050 m represents an upper pre-montane tropical moist forest with dominant tree species of the families *Annonaceae*, *Mimosaceae*, *Moraceae*, *Myrtaceae* and *Sapotaceae*. The stand at 1540 m is a lower montane tropical moist forest with *Arecaceae*, *Lauraceae*, *Melastomataceae* and *Rubiaceae* being the most widespread families present (Homeier et al. 2008). The stands at 1890 m and 2380 m were situated in the forest reserve of the Estación Científica San Francisco (ECSF), and consist of mid-montane and upper-montane tropical moist forest, respectively. The most important tree species in terms of abundance in the stand at 1890 m belong to the *Euphorbiaceae*, *Lauraceae*, *Melastomataceae* and *Rubiaceae*, and in the case of the stand at 2380 m to the *Aquifoliaceae*, *Clusiaceae*, *Cunoniaceae*, *Ericaceae* and *Rubiaceae* (Homeier et al. 2008). The uppermost stand at 3060 m represents an elfin forest close to the tree line in the upper montane Cajanuma region of Podocarpus National Park; dominant trees belong to the *Aquifoliaceae*, *Clusiaceae*, *Cunoniaceae*, *Ericaceae* and *Rubiaceae*. Except for the stand at 1540 m, all sites were situated on moderately steep slopes (26 to 31°) facing northeast to northwest (Table 1). The mean canopy height decreased from 32 m at the lowermost stand to 9 m at the uppermost stand, and mean tree height decreased accordingly from 15.6 m to 5.2 m. Fine root biomass increased from 2.7 t ha^{-1} at 1050 m to 10.8 t ha^{-1} at 3060 m (Moser et al. 2008).

Table 1. Location and characteristics of the study sites. Temperature and air humidity were recorded at 1.5 m height inside the stands at hourly intervals, soil moisture was recorded every six hours in the organic layer (measuring period from June 2005 – January 2007). Rainfall data are extrapolated from measurements in a gap at ca. 1050 m (Moser et al., in press) and from measurements in gaps at 1950, 2680 and 3170 m (three-year means, P. Emck and M. Richter, unpublished data). Data on tree and canopy height, basal area and fine root biomass from Moser et al. (2008); data on organic layer thickness, pH and C/N ratio from S. Iost and F. Makeschin (unpublished data). Soil type description according to FAO taxonomy.

Plot Nº	1	2	3	4	5
Elevation (m a.s.l.)	1050	1540	1890	2380	3060
Coordinates	04°06’54’’ S 78°58’02’’ W	04°06’42’’ S 78°58’20’’ W	03˚58’35’’ S 79˚04’65’’ W	03°59’19’’ S 79°04’55’’ W	04˚06’71’’ S 79˚10’58’’ W
Slope (°)	26	10	31	28	27
Mean air temperature (°C)	19.4	17.5	15.7	13.2	9.4
Mean air humidity (%)	88.7	88.9	90.8	93.2	93.5
Mean VPD (hPa)	2.7	2.5	2.0	1.2	0.9
Monthly mean VPD (min-max) (hPa)	1.5-8.1	1.4-7.1	0.9-5.9	0.2-3.3	0.3-2.6
Precipitation (mm yr^{-1})	2230	2300	1950	5000	4500
Soil type	Alumic Acrisol	Alumic Acrisol	Gleyic Cambisol	Gleyic Cambisol	Podzol
Organic layer thickness (mm)	48	243	305	214	435
Mean soil moisture (vol%)	9.9	12.9	11.6	34.0	45.3
pH (CaCl2)	3.9	3.9	3.5	3.3	2.9
C/N (L/Of1)	22	29	28	46	63
Canopy height (m)	31.8	21.7	18.9	12.0	9.0
Mean tree height (m)	15.6	12.1	10.1	7.4	5.2
Basal area (m^2 ha^{-1})	33.6	27.5	36.9	27.2	42.2
Fine root biomass (t ha^{-1}) profile total, d < 2 mm	2.7	5.6	6.2	6.3	10.8

The climate of the region is influenced most of the year by easterly winds from the Amazonian lowlands transporting humid air masses to the slopes. Rainfall at 1050, 1540 and 1890 m asl averages to about 2000 mm yr^{-1}, whereas precipitation is ca. 5000 mm yr^{-1} at 2380 m asl and 4500 mm yr^{-1} at 3060 m asl (P. Emck and M. Richter, unpublished data; Moser et al. 2008). There is no marked dry season in the region, but lower rainfall during the months of October to January is common. The climate can be classified as humid to perhumid, with 11 to 12 humid months (Richter 2003). Air temperature and relative air humidity of the stands were measured 1.5 m above the forest floor with Hygroclip S temperature and humidity sensors (Rotronic AG, Switzerland). Annual mean air temperature decreased from 19.4°C at 1050 m asl to 9.4°C at 3060 m asl, representing an average temperature lapse rate of 5 K km^{-1} along the slope (Table 1). Relative air humidity was high and increased slightly from 89 to 94% along the transect. The volumetric water content of the organic layer was continuously recorded with TDR sensors, and increased from 29.7 vol% at the lowermost stand to 49.1 vol% at the uppermost stand (Table 1).

The soils of the forest stands derived from granodiorites at the two lowermost sites and from metamorphous shale and quartzite bedrock at the higher altitudes. Although the soils at all sites were acidic and relatively nutrient-poor (Schrumpf et al. 2001), the pH($CaCl_2$) values in the upper mineral soil (0-30 cm) decreased from 3.9 at 1050 m to 2.9 at 3060 m (S. Iost, unpublished data). A strong increase in the C/N ratio of the organic layer (from 22 to 63 g g^{-1}) and in the depth of the organic layer thickness (from 48 to 435 mm) was found with increasing altitude (S. Iost, unpublished data).

Measurement of fine root growth and death

In each forest stand, a study plot of 20 m x 20 m was selected in patches of undisturbed forest with a closed canopy that were representative for the forest community of the respective altitude. In each plot, ten transparent minirhizotron tubes with an external diameter of 70 mm were installed in June 2005 at randomly selected locations. They were placed at a 90° angle to the slope and inserted to a depth of ca. 40 cm. In the lowermost stand with a very shallow soil, most of the tubes could not be inserted to a soil depth greater than 10 cm. Holes were dug with a soil corer that had the same diameter as the tubes, which ensured a tight contact of the tubes to the surrounding soil. To prevent entrance of water into the tubes, the bottom was sealed and the top end was covered with a removable cap. Those parts of the tubes that extended above the soil surface were covered with black tape to avoid incidence of light that might influence root growth. A circular plastic foil with a diameter of 16 cm was placed around the tubes on the soil surface to prevent water runoff on the surface of the tubes which could attract root growth.

For monitoring root growth, a root scanner system (CI-600 Root Growth Monitoring System, Fa. CID, USA) was used in the tubes from September 2005 to January 2007 at monthly intervals. Due to shortage in personnel we were not able to monitor root growth between April and July 2006. Five months after installation of the tubes we recognized a steady-state of visible root length in most of the tubes in all stands except for the uppermost stand. Hence, only data from November 2005 onwards were considered for analysis to avoid artifacts due to disturbance during tube installation (Hendrick and Pregitzer 1996; Majdi 1996; Joslin and Wolfe 1999). In each scanning procedure, we recorded a 345° sector of a soil compartment of 20 cm length at the tube's inner surface (i.e. a total soil surface area of 219.9 cm^2 per image). In this study, only the uppermost 10 cm below the soil surface were considered for analysis of fine root dynamics, as the very shallow soil at the lowermost site did not allow a deeper placement of the tubes. Earlier studies on fine root distribution in the same stands had shown a strong exponential decrease in fine root mass density with soil depth with the consequence that more than 50 % of the fine root biomass of the profile total was located in the uppermost 10 cm of the soil (Roederstein et al. 2005; Moser et al. 2008). This justifies the focus on root growth analysis of the uppermost soil horizons. The images were analyzed with the program WinRHIZO Tron (Règent, Quebec, Canada). Root length and diameter were traced manually on the screen for each image. For analyzing alteration in root length over time, the respective previous image was superposed over the current image. This allowed the identification of root sections originating from recent root growth or sections that had disappeared due to root death and decomposition. Software-assisted data analysis gave the length and surface area of recently born and disappeared root sections. Only fine roots (diameter < 2 mm) were taken into account, which were grouped into two diameter classes (< 2 mm and < 0.5 mm) for further analysis.

By comparing visible and disappeared fine root length of current and previous images, cumulative root length production and root length loss were calculated per month (unit: cm mo^{-1}, Buckland et al. 1993; Majdi 1996). Relative root length production and relative root length loss were calculated by relating root length production or loss to the visible root length at the previous measuring date (cm cm^{-1} mo^{-1}). By extrapolating monthly relative root length loss to a full year (i.e. mean loss in a tube times 12), this data allowed for an estimation of average annual root loss rate of the visible fine root population in the rhizotron tubes (Nadelhoffer 2000). We equate annual root loss rate with “root turnover” by relating loss to the standing stock of fine root length in the image.

Statistical analysis

Based on 10 replicate measurements (tubes) per stand, we calculated means and standard errors for all parameters. After applying a Shapiro-Wilk test to test for normality, a non-parametric global analysis of significant effects (Kruskal-Wallis test) and a Mann-Whitney two-sample test (U-test) were used to analyse significant differences in root length production, loss and turnover between the five stands. As we observed a significant variation of mean vapor pressure deficit (VPD) in the study period as the most obvious change in environmental conditions, we examined the relationship between mean VPD and root dynamics by means of a linear regression analysis (i.e. mean VPD 30 days prior to image recording was related to relative root length production and loss of the respective month). Spearman’s rank correlation was used to detect significant influences of environmental factors on root production parameters. All calculations were done with SAS/STAT software ($p < 0.05$).

Results

Fine root populations present

The highest mean root length visible in the minirhizotron tubes was recorded at the two mid-elevation stands at 1540 m and 1890 m (320 and 220 cm per image surface area of 219.9 cm², respectively). The lowermost stand (1050 m) and the two uppermost stands (2380 and 3060 m) showed a considerably smaller root length (Fig. 1). It became evident that steady state conditions of root turnover were reached earlier at the lower elevations. Except for the stand at 3060 m root length did not increase significantly from December 2005 onwards. At the highest site root length was still increasing after 12 months of image recording (i.e. 18 months after tube installation). The average diameter of the fine root populations visible at the rhizotron tubes did not vary markedly among the stands: it varied between 0.55 and 0.68 mm and showed no significant elevational trend (Table 2). The percentage of fine roots with a diameter less than 0.5 mm ranged between 27 and 42%. While the percentage of these small roots was comparable in the two lowermost and the uppermost stand, the trees at 1890 and 2380 m tended to have a higher proportion of thicker roots.

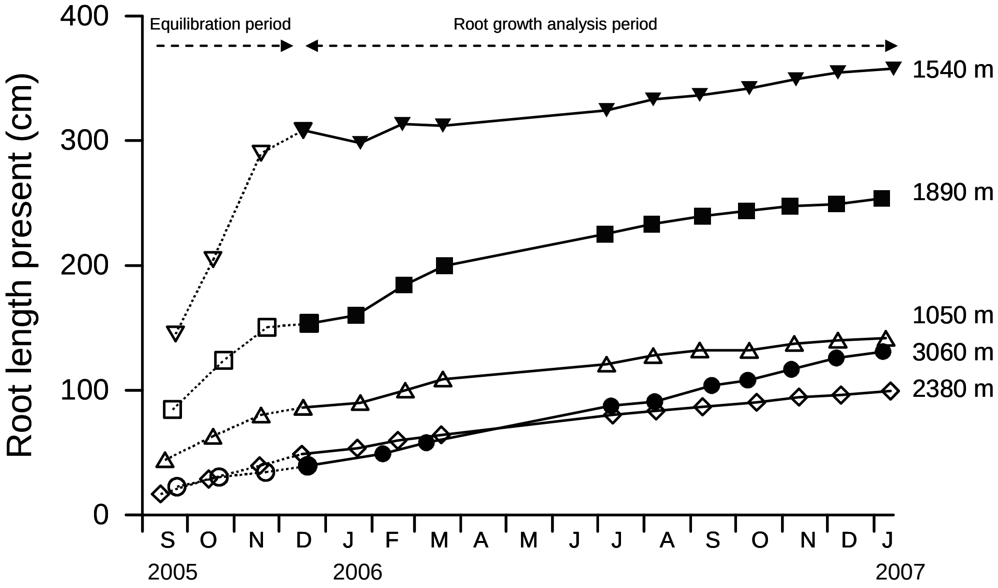

Fig. 1. Root length present per minirhizotron surface area (220 cm²) in the study period from September 2005 to January 2007 (n = 10). Change in marker color represents the transition from equilibration period to root growth analysis period.

Table 2. Average root diameter of fine roots with d < 2.0 mm (means ± 1 SE) and percentage of roots in diameter class < 0.5 mm at the five study sites. Different letters indicate significant differences between the study sites.

Altitude (m asl)	Average diameter (mm)	Percentage of roots with diam. < 0.5 mm
1050	0.55 ± 0.02 *a*	37.0
1540	0.62 ± 0.06 *a*	41.6
1890	0.68 ± 0.08 *a*	31.8
2380	0.59 ± 0.02 *a*	27.3
3060	0.66 ± 0.07 *a*	40.6

Fine root production and loss

Monthly fine root length production showed no clear elevational trend: highest root length productivity was found in the two mid-elevation stands at 1540 and 1890 m (Fig. 2a), while root length production was lowest at 2380 m. Both the lowermost and the uppermost stand showed medium root length production rates. Root length production of finest rootlets (d < 0.5 mm) was not significantly different among the five stands except for the stand at 2380 m. Finest roots contributed by 30-50% to the total fine root (d < 2.0 mm) production. Hence root length production of the smallest roots was disproportionably high related to the standing root length stock. The proportion of finest root production was especially high at the lowermost and the uppermost stand.

Monthly root length loss also showed no clear elevational trend (Fig. 2b). As for root length production, monthly loss in root length was highest in the stand at 1540 m. At 1050 and 1890 m monthly root length loss was much lower (about half). The lowest root length loss was recorded in the stand at 2380 m. The uppermost stand at 3060 m showed a significantly higher root length loss than the stand at 2380 m. Roots < 0.5 mm in diameter contributed to a large extent to length loss of roots < 2.0 mm. However, monthly loss of finest roots was highest at the two lowermost stands, and lower in the mid- and high-elevation stands.

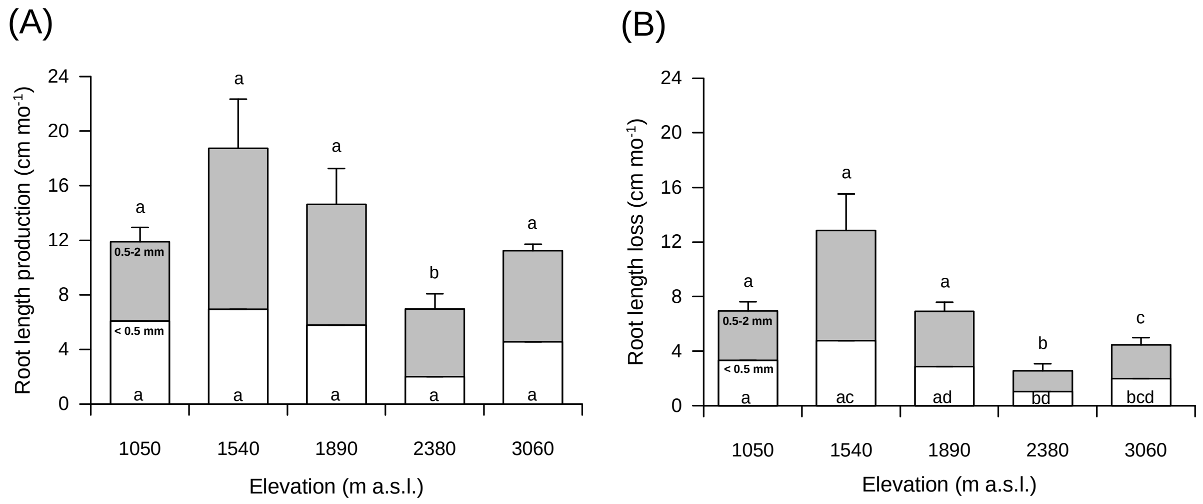

Fig. 2. Monthly means of root length production (A) and root length loss (B) (means ± 1 SE, n = 10). Different letters indicate significant differences between the study sites.

A different view arose when production and loss of fine roots were related to the root length present around the tubes at the beginning of a respective observation period. Except for the lowermost stand, relative root length production (RRLP) increased significantly with elevation (Fig. 3a). In the diameter class < 2.0 mm lowest RRLP was found at 1540 m (0.07 cm cm^{-1} mo^{-1}), while the uppermost stand showed highest RRLP (0.19 cm^{-1} mo^{-1}). The RRLP of fine roots in the lowermost stand was comparably high as in the stand at 2380 m. Roots of diameters < 0.5 mm showed higher RRLP than the root population with a diameter < 2.0 mm. This was especially evident for the lowermost site, were RRLP of the small diameter class was as twice as high than of the larger diameter class. However, the increase in RRLP from 1540 to 3060 m was even more pronounced in the finest roots than in the fine roots (< 2.0 mm).

Regarding monthly means of relative root length loss (RRLL, Fig. 3b) a similar elevational trend was observed as in relative root length production. In the diameter class < 2.0 mm, the three mid-elevations stands showed RRLL of about 0.05 cm cm^{-1} mo^{-1}, whereas the lowermost and the uppermost stand had RRLL values of 0.08 cm cm^{-1} mo^{-1}. Except for the stand at 1540 m, a higher RRLL was recorded in the small diameter class than in the larger diameter class, but the differences were less pronounced than with respect to RRLP. The highest relative root length loss with more than 0.1 cm cm^{-1} mo^{-1} was recorded at the lowermost site. However, RRLL at the uppermost stand was nearly as high and differed not significantly from the lowermost site.

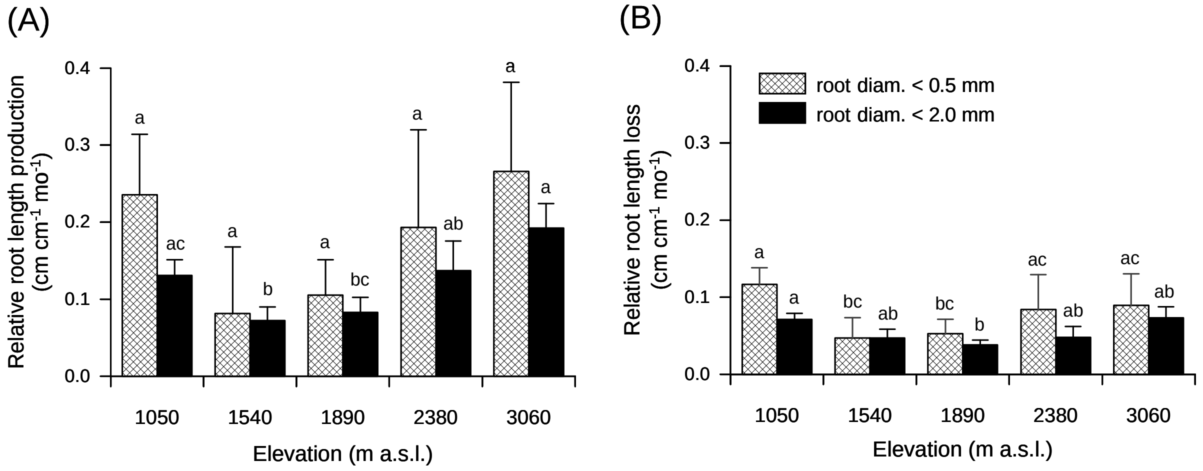

Fig. 3. Monthly means of relative root length production (A) and relative root length loss (B) (means ± 1 SE, n = 10). Different letters indicate significant differences between the study sites

Fine root turnover

Roots in the lowermost and the two uppermost stands had a higher annual root turnover (i.e. loss per root standing stock) than the roots in the mid-elevation stands (1540 and 1890 m) (Fig. 4). Roots of diameters < 0.5 mm had a considerably higher turnover than roots of < 2.0 mm (Fig. 4). However, this difference was only significant in the stands at 1050 and 2380 m. While highest turnover in the diameter class < 2.0 mm occurred in the uppermost stand, the highest turnover of roots with diameters < 0.5 mm was recorded in the lowermost stand (1.4 cm cm^{-1} yr^{-1}), followed by the two uppermost stands. Turnover of fine roots (< 2.0 mm) was significantly higher at the lowermost and the uppermost stands (about 0.9 cm cm^{-1} yr^{-1}) compared to the mid-altitudes, where turnover was < 0.6 cm cm^{-1} yr^{-1}. Annual root turnover of the < 0.5 mm diameter roots showed a continuous increase with elevation from the 1540 m to the 3060 m stand.

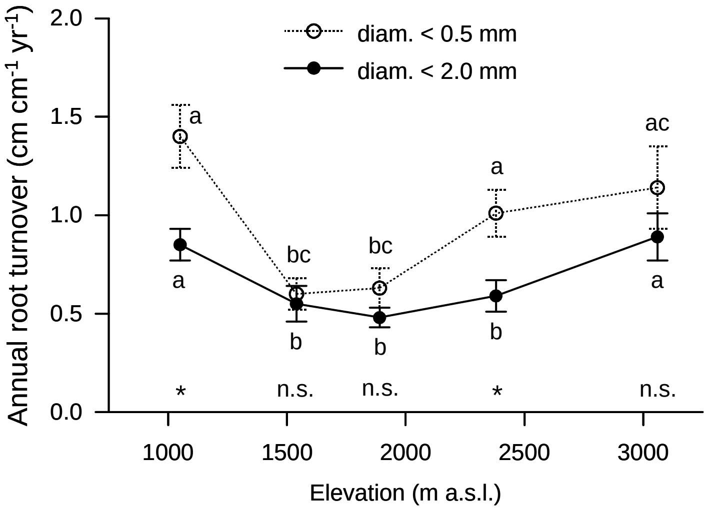

Fig. 4. Annual root turnover in the fine root populations visible in the minirhizotron tubes (means ± 1 SE, n = 10). Different letters indicate significant differences between the study sites, asterisk indicate significant differences between diameter classes.

Influence of environmental factors

A striking feature of the microclimate along the transect was that VPD inside the stands was much more variable over time at the lower elevations than higher upslope (Table 1). At the two lower-most stands a very high variability of mean VPD 30 days preceding the dates of images recording was found, which ranged between 1.5 and 8 hPa for the different observation periods. Variability in mean VPD at the higher altitudes was considerably smaller (Table 1). A significant influence of VPD on RRLP was detected in the stand at 1050 m, but not at the other altitudes (Table 3). In the lowermost stand RRLP showed a strong positive correlation to mean VPD. In contrast, RRLL was not significantly related to the VPD level at any of the five sites (Table 3).

Table 3. Linear regression analysis of relative root length production and root length loss (roots of < 0.5 mm in diameter) on mean VPD 30 days prior to image recording.

Altitude	Relative root length production (cm cm^{-1} mo^{-1})		Relative root length loss (cm cm^{-1} mo^{-1})	
(m asl)	r	p	r	p
1050	0.94	0.01	0.72	n.s.
1540	0.05	n.s.	0.05	n.s.
1890	0.09	n.s.	0.21	n.s.
2380	0.61	n.s.	0.45	n.s.
3060	0.08	n.s.	-0.02	n.s.

All investigated soil and climate parameters showed a significant influence on RRLP in the five stands (Table 4). A negative correlation existed with pH, air temperature and VPD, and a positive one to precipitation, soil moisture and C/N. When testing the influence of the parameters separately for the lower and upper transect sections (Table 5), it turned out that a given environmental factor typically influences fine root turnover at stands at lower and at higher elevations differently. In the stands between 1050 and 1890 m, turnover was positively affected by air temperature and VPD and negatively by soil moisture and soil C/N. At mid- and upper elevations (1890 - 3060 m) turnover was negatively related to air temperature, VPD and pH, while soil moisture and soil C/N showed positive effects.

Table 4. Results of a Spearman's correlation analysis of the relationship between soil and climate parameters and RRLP or RRLL in the entire dataset of the transect.

	Relative root length production (cm cm^{-1} mo^{-1})		Relative root length loss (cm cm^{-1} mo^{-1})	
	r_s	p	r_s	p
Air temperature (°C)	-0.41	< 0.01	0.04	n.s.
Precipitation (mm yr^{-1})	0.42	< 0.01	0.09	n.s.
VPD (hPa)	-0.41	< 0.01	0.04	n.s.
Soil moisture (vol%)	0.38	< 0.05	0.02	n.s.
pH ($CaCl_2$)	-0.50	< 0.001	-0.04	n.s.
Soil C/N (L/Of$_1$)	0.38	< 0.05	0.02	n.s.

Table 5. Results of a Spearman's correlation analysis of the relationship between soil and climate parameters and fine root turnover done separately for the lower and upper transect sections.

	1050, 1540, 1890 m asl		1890, 2380, 3060 m asl	
	r_s	p	r_s	p
Air temperature (°C)	0.58	< 0.001	-0.46	< 0.05
Precipitaion (mm yr^{-1})	0.09	n.s.	0.12	n.s.
VPD (hPa)	0.58	< 0.001	-0.46	< 0.05
Soil moisture (vol%)	-0.49	< 0.01	0.46	< 0.05
pH ($CaCl_2$)	0.38	< 0.05	-0.46	< 0.05
Soil C/N (L/Of$_1$)	-0.49	< 0.01	0.46	< 0.05

Discussion

Elevational changes in fine root dynamics

Gill and Jackson (2000) examined the influence of climate on root turnover on a global scale and identified temperature as the most important variable for explaining patterns of root turnover. Despite high variability in data, a positive relationship between root turnover and mean annual temperature emerged. They suggest that an increase in temperature is associated with an increase of maintenance respiration, higher rates of nutrient mineralization and an increased pathogen and herbivore activity, which should decrease root lifespan. Empirical evidence in grassland and forest ecosystems supports the assumption that root turnover is higher under higher temperatures (e.g. Forbes et al. 1997; King et al. 1999). In the Ecuadorian transect, a temperature decrease by 3.7 K between 1050 and 1890 m a.s.l. in the lower transect resulted in a 40% decrease of annual root loss rate, which is best explained by a temperature effect on root turnover. However, other factors could be responsible as well. In fact, we found an opposite trend in root turnover rate towards higher altitudes. The absence of a linear altitudinal trend in fine root dynamics seems to indicate that temperature is only one of several factors influencing fine root turnover. Fitter et al. (1998) suggest that root growth is determined more by resource availability and source-sink relationship within the plant than temperature. In a study of an altitudinal gradient in temperate grasslands, these authors found root respiration to be correlated with radiation totals but not with temperature. This indicates that carbon supply is a major control for root activity in grasses and that high altitude species are well acclimated to low temperatures. In the upper part of the Ecuador transect (1890 – 3060 m) relative root loss increased by about 50%, suggesting that temperature effects on root turnover are overlaid by other influential factors despite a decrease in mean annual temperature of 6.3 K.

The growth of tropical montane forests has widely been found to be limited by the availability of nitrogen (Tanner et al. 1998; Benner et al. in press). Several lines of evidence indicate that N availability decreases with elevation in South Ecuador, including topsoil C/N-ratios and foliar and root N concentrations (Roederstein 2006; G. Moser, unpublished data). N deficiency is usually expected to increase fine root biomass and root longevity, and to decrease root turnover (Roy and Singh 1995; Eissenstat and Yanai 1997; Nadelhoffer 2000; Yavitt and Wright 2001; Powers et al. 2005) and the respiration costs of root maintenance (Eissenstat et al. 2000). However, opposite effects of nutrient availability on fine root longevity have been reported as well (Vogt et al. 1986; Pregitzer et al. 1993; Burton et al. 2000). Whether N deficiency decreases or increases root longevity may depend on the cost of maintaining a root as compared to the costs of allowing a root to die and to produce a new root (Van Noordwijk et al. 1998; Eissenstat et al. 2000). Roots may be maintained as long as the nutrients they provide outweigh the C cost of keeping the roots alive (Burton et al. 2000). It appears that in the high-elevation stands of Ecuador the costs for a tree in terms of C supply to the roots for extended periods are too high when related to the nutrients the roots provide. In those nutrient-poor soils it may be advantageous to produce new roots which are more efficient in nutrient uptake than older roots.

Tryon and Chapin (1983) found a reduced root elongation in boreal trees with decreasing temperature, and a large reduction in root growth below 5°C. Their findings also suggest a shift in carbon allocation from large exploratory roots to fine absorbing roots at low temperatures. In the uppermost stand (3060 m) of the Ecuador transect, where night temperatures below 5°C may occur incidentally, the percentage of very fine roots with diameters < 0.5 mm was relatively high. Thus, a high root turnover in this stand is mostly a consequence of a rapid shedding and regrowth of the very fine roots.

Another factor that may reduce root longevity at the highest altitude could be the very low pH value of the soil. Elevated concentrations of free aluminum associated with low pH were found to reduce root longevity in temperate forests (Raynal et al. 1990; Godbold et al. 2003). Godbold et al. (2003) reported increased fine root turnover in Norway spruce stands subjected to soil acidification. Soethe et al. (2007) found decreasing Mg concentrations in the fine root biomass with increasing altitude in the South Ecuadorian transect, which may be a consequence of Al/Mg antagonism in root uptake when Al-concentrations are high. Finally, oxygen deficiency may be an additional stressor reducing fine root longevity (Jackson and Ricard 2003) in the high elevation stands, where soil moisture is typically high and water logging may persist for extended periods.

In the absence of continuous high-resolution radiation and soil moisture measurements, we used VPD as a proxy of sunny-dry and clouded-wet periods. By correlation analysis we detected a positive influence of precipitation and soil moisture, and a negative one of VPD on root length production when the data of the entire transect are analyzed (Table 4). This indicates that, as a whole, root growth of the mountain forest trees is stimulated by a higher water availability which seems to act as a second controlling factor besides temperature. This is in accordance with results from tropical lowland forests in Malaysia and Panama, where root growth was higher in moist than in dry seasons (Green et al. 2005; Yavitt and Wright 2001). An exception was the lowermost stand at 1050 m, which showed a positive effect of the VPD of the preceding month on fine root birth rate. We speculate that a higher VPD and thus a higher radiation input may have increased carbohydrate availability for root growth at this site, probably outweighing any drought-induced root losses.

Fine root turnover depending on root diameter

Studies on the morphological patterns of fine roots in tropical forests are very scarce, which is partly a consequence of the high species diversity of these forests which makes more general conclusions difficult. By analyzing fine root dynamics separately for the size classes < 2.0 mm and < 0.5 mm, a clear root size effect on root turnover and root longevity became evident, with thinner roots being more dynamic than thicker ones. Similarly, other authors also found this strong dependence of root survivorship on root diameter (Gill and Jackson 2000; Wells and Eissenstat 2001; King et al. 2002; Baddeley and Watson 2005). This may be explained by higher nutrient concentrations and respiration rates of small diameter roots, i.e. a generally higher metabolic activity (Pregitzer et al. 1997; Pregitzer et al. 1998; Withington et al. 2006). However, longevity also depends on branching order, as roots of high branching orders emerge later but die simultaneously with their carrier root (Majdi et al. 2001).

In our study it became obvious that at sites with highest fine root turnover (i.e. the sites at 1050, 2380, 3060 m) the proportion of finest roots (diameter < 0.5 mm) in overall fine root turnover was especially high. One may speculate that the fast replacement of finest roots is an adaptive mechanism under limiting environmental conditions, i.e. high temperatures at lower altitudes and nutrient limitation or adverse soil chemical conditions at higher altitudes. Manipulative studies have to reveal what type of exogenous or endogenous factors may be responsible for elevated root turnover rates at different sections of this elevation transect. In fact, root dynamics seem to be controlled by several factors along this 2000-m elevation transect, which play different roles at different altitudes.

Conclusions

This transect study allows the conclusion that relatively high temperatures increase root turnover in the lower, rather hot and moist section of the transect. In contrast, at higher altitudes with a perhumid, cool climate and unfavorable soil fertility and acidity conditions, root longevity was probably restricted by the adverse soil physical and chemical environment. Thus, the U-shaped curve of fine root turnover rate along the slope is explained by different overlaying environmental gradients along the transect.

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CHAPTER 4

Nutrient shortage and soil anoxia as possible limiting factors of fine root growth and nitrogen uptake capacity in tropical mountain forests at pre-montane to upper montane elevation

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Abstract

Theory predicts that phosphorus is a key nutrient limiting tree growth in tropical lowland forests while nitrogen is a primary limiting element in tropical montane forests where temperature is lower and soils are often younger. Because of their large carbon and nutrient demand, fine roots should respond particularly sensitively to nutrient limitation and also to nutrient addition. We investigated the nature of root growth limitation by N, P or K fertilization experiments conducted at 1050 m (pre-montane) and 3060 m (upper montane) elevation in two mountain forests of South Ecuador. In addition, we conducted a throughfall exclusion experiment at 3060 m to test the hypothesis that water-logging and partial anoxia represents an additional stressor for fine roots in high-elevation forests. Root growth stimulation was highest after P addition at 1050 m, but greatest after N addition at 3060 m, thus supporting the general theory of nutrient limitation in tropical forests. Rainfall exclusion and avoidance of soil anoxia, however, did not reduce fine root mortality in the 3060-m stand and, hence, seems not to be the primary stressor leading to high fine root turnover in high-elevation tropical forests. The concentration of N in fine root biomass dropped nearly threefold from 1050 to 3060 m, and also decreased in the case of P, K, Ca and Mg, but to a lesser degree. Despite lower temperatures and increasingly adverse soil chemical and physical conditions, tree fine roots maintained a constantly high nitrate and ammonium uptake capacity between 1050 and 3060 m elevation, as evidenced by a $^{15}NO_3{}^{15}NH_4$ uptake study along the slope. We conclude that increasing nitrogen limitation toward higher elevations is most likely the principal cause of a large increase in stand fine root biomass, while the relatively high root turnover in the upper montane forests is probably a consequence of adverse soil chemical conditions resulting from periodic water-logging.

Keywords: anoxia, Ecuador, fine roots, nitrogen, nutrient addition, nutrient limitation, nutrient uptake, phosphorus, tracer study

Introduction

Different factors are thought to control forest growth in tropical lowland and montane forests. Tropical montane forests are supposed to be mainly limited by nitrogen, whereas tropical lowland forests are primarily limited by phosphorus (Vitousek and Sanford 1986; Tanner et al. 1992; Tanner et al. 1998; Paoli et al. 2005; Benner et al. 2008). In tropical lowland forests, plant available N is often abundant since N mineralization rates are typically high (Tanner et al. 1998). Tropical montane forests, on the other hand, which mostly grow on rather young soils, appear to be low in nitrogen. In fact, it was found that upper montane forests cycle less nitrogen than lower montane forests (Vitousek and Sanford 1986; Marrs et al. 1988). A characteristic of tropical lowland soils is that they are mostly highly weathered, and phosphorus, 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). It was shown that forests growing on highly weathered soils produce litter low in phosphorus (Tanner et al. 1998).

There is evidence for tree nutrient status to become less favourable with increasing altitude in tropical montane forests (Tanner et al. 1998), which is thought to be a consequence of decreasing soil temperatures and unfavourable soil water conditions (Bruijnzeel and Veneklaas 1998). Hertel and Leuschner (2008) found a negative relation of fine root biomass and necromass to temperature in a tropical transect, which implies an increasing investment of carbon to the root system with increasing altitude. The authors conclude that this is most likely a result of low nutrient availability at high elevations.

Despite high levels of standing fine root biomass at high altitudes in a South Ecuadorian mountain rainforest (Moser et al. 2008), fine root turnover (i.e. the replacement of root mass per time) displayed a U-shaped-curve along an elevational transect between 1000 and 3000 m asl. Low turnover rates were observed in a mid-elevation forest stand (~2000 m asl), whereas high turnover rates were recorded at the lower and upper ends of the transect (Graefe et al. 2008). The causes of the remarkably high fine root turnover at high altitudes are not yet fully understood.

The aim of this study was to assess the role of putative limiting factors for root growth, i.e. nutrient limitation and water-logging, by N, P or K fertilization trials and a throughfall exclusion experiment along a 2000 m-elevational transect in mountain rainforests of South Ecuador. In addition, the nitrate and ammonium uptake capacity of the roots was investigated by ^{15}N tracer experiments at pre-montane, montane and upper montane elevation. We tested the following three hypotheses: (I) fine root growth of pre-montane rainforest (~1000 m asl) is limited primarily by phosphorus supply, whereas fine root growth of upper montane rainforest (~3000 m asl) is limited by nitrogen availability; (II) nitrogen uptake capacity of fine roots decreases with increasing elevation due to decreasing soil temperatures; and (III) the high mortality of fine roots as observed in the upper montane forest is caused by periodic water-logging and associated anoxia of the soil.

Materials and methods

Study sites

The experiments were conducted in three tropical mountain forest stands at 1050, 1890 and 3060 m asl (Table 1), which were located in the Eastern cordillera of the South Ecuadorian Andes in the provinces of Loja and Zamora-Chinchipe. Stand Nº 1 (1050 m) was located close to the village of Bombuscaro inside Podocarpus National Park representing a pre-montane tropical moist forest. Stand Nº 2 (1890 m) was situated in the forest reserve of the Estación Científica San Francisco (ECSF) which consisted of a mid-montane tropical moist forest. The uppermost stand Nº 3 represented an elfin forest in the upper montane Cajanuma region of Podocarpus National Park at 3060 m. Data on tree species composition are given in Homeier 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 about 2000 mm yr^{-1}, whereas precipitation was ca. 4500 mm yr^{-1} at 3060 m (P. Emck and M. 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. The volumetric water content of the organic layer increased from 29.7 to 49.1 vol% along the elevational transect (Table 1).

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 (S. Iost, unpublished data). A strong upslope increase in the C/N ratio of the organic layer (from 22 to 63 g g^{-1}) and in organic layer thickness (from 48 to 435 mm) characterized the transect (S. Iost, unpublished data).

Table 1. Location and characteristics of the study sites. Temperature and air humidity were measured 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, P. Emck and M. 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 S. Iost and F. Makeschin (unpublished data). Soil type description according to FAO taxonomy.

Plot Nº	1	2	3
Elevation (m asl)	1050	1890	3060
Slope (°)	26	31	27
Annual mean air temperature (°C)	19.4 ± 0.06	15.7 ± 0.05	9.4 ± 0.03
Mean air humidity (%)	88.7 ± 0.33	90.8 ± 0.23	93.5 ± 0.13
Rainfall (mm yr^{-1})	2230	1950	4500
Soil type	Alumic Acrisol	Gleyic Cambisol	Podzol
Organic layer thickness (mm)	48	305	435
Mean soil moisture (vol%)	9.9 ± 0.001	11.6 ± 0.001	45.3 ± 0.002
pH-$CaCl_2$ (organic layer)	3.9	3.5	2.9
C/N (organic layer)	22	28	63
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

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 deep) were randomly taken from the organic layer in the forest stands at 1050, 1890 and 3060 m. Living fine roots were sorted out under the microscope using criteria such as root colour and elasticity. Roots were washed, dried at 70°C for 48 h and ground. The concentrations of C and N were determined with a C/N-Analyser (Vario EL 3, Fa. Elementar, Hanau, Germany). Phosphorus concentrations were analyzed by yellow-dyeing and photometric measurement after digestion with 65% HNO_3 at 195°C. K, Mg and Ca concentrations were determined by atomic absorption spectroscopy (AAS vario 6, analytik jena, Jena, Germany) after HNO_3 digestion.

Fertilization experiment

In both the lowermost (1050 m) and the uppermost stand (3060 m), a fertilization experiment with application of nitrogen (N), phosphorus (P) and potassium (K) to root ingrowth cores was conducted. The experiments were set up in August 2005. Ingrowth cores were established with a soil corer (diameter 5.2 cm, 15 cm long) and filled either with fertilized vermiculite or root-free soil material from the uppermost 15 cm of the soil. Following the protocol given by Cuevas and Medina (1988) and Raich et al. (1994), the vermiculite was soaked for 24 hours in 0.1 M NH_4Cl (N fertilization), $NaHPO_4$ (P fertilization), KCl (K fertilization), or pure water (control treatment, termed $\text{control}_{\text{verm}}$). A second control was established with local soil material from the respective stands, of which all roots had been removed ($\text{control}_{\text{soil}}$). At both elevations, three sub-plots of approximately 4 m² size were established. Five replicate ingrowth cores per treatment were randomly placed in each sub-plot, resulting in a total of 15 replicate ingrowth cores per treatment and 75 cores per stand. At 1050 m, first root ingrowth was observed by the end of February 2006, at 3060 m fine root ingrowth did not show up before mid-May 2006. Therefore, it was decided to re-collect the ingrowth cores by the end of July 2006 in the low-elevation stand and in mid October 2006 in the high-elevation stand, resulting in root ingrowth periods of five months at both altitudes. Roots present in the ingrowth cores were precisely sorted out and washed. The root material was dried at 70°C for 48 h to determine dry weight.

^{15}N-tracer study

In all three stands (1050, 1890 and 3060 m), a ^{15}N-tracer study was established in December 2006. In each stand, three sub-plots of 0.75 m² were demarcated, in which the leaf litter was removed from the soil surface. Each litter-free sub-plot was watered with a solution of 1 l pure water containing 0.4 g double-labelled $^{15}NH_4{}^{15}NO_3$ (95 atom% ^{15}N). This corresponded to 1.77 kg ^{15}N ha^{-1} or 1.86 kg total N ha^{-1}. After tracer application, the litter material was redistributed in the sub-plots. At intervals of 2 h, 2 d and 5 d after ^{15}N-application, soil samples were taken with a soil corer (diameter 5.2 cm, depth 15 cm) at nine replicates in each stand (three replicates per sub-plot). In each stand, nine soil samples were additionally taken before tracer application as a reference for natural ^{15}N abundance in fine root mass.

Processing of the samples took place within 24 h after sampling. Living fine roots were sorted out under the microscope, carefully washed and dried at 70°C for 48 h. The dried samples were ground and the ^{15}N signature in the fine root material was analysed with an isotope ratio mass spectrometer (Delta plus, Finnigan MAT, Bremen, Germany) coupled to an elemental analyser (EuroVektor, HEKAtech, Wegberg, Germany). ^{15}N enrichment is expressed as δ^{15}N, which was calculated as

$$\delta^{15}\text{N}\ (‰) = [(\text{atom\%}_{\text{sample}} / \text{atom\%}_{\text{standard}}) - 1] \times 1000$$

where $\text{atom\%}_{\text{standard}}$ is 0.3662%.

Desiccation experiment

In order to analyse the effect of different soil water contents on root growth in the upper montane forest stand, a desiccation experiment in conjunction with minirhizotron observation tubes was set up at 3060 m asl (Cajanuma site) in June 2005. To exclude rainfall and hence to reduce soil moisture, four roofs of transparent polyvinyl (2m x 2m) were constructed above each two minirhizotron tubes (a total of eight tubes under the roofs). Further, ten minirhizotron tubes, which were placed nearby outside the roofs (Graefe et al. 2008), served as a reference (control treatment). The volumetric water content of the soil under the roofs and at the control sites was determined at monthly intervals with a portable TDR probe (Time Domain Reflectrometry, Trime-HD, IMKO, Germany).

The minirhizotron tubes had an external diameter of 70 mm and were inserted at a 90° angle to the slope. Monitoring of fine root dynamics was done with a root scanner system (CI-600 Root Growth Monitoring System, Fa. CID, USA) at monthly intervals, but only images from November 2006 onwards (5 months after minirhizotron installation) were considered for analysis, in order to avoid artefacts due to disturbance during tube installation (Hendrick and Pregitzer 1996; Majdi 1996; Joslin and Wolfe 1999). Due to shortage in personnel we were not able to monitor root growth between April and July 2006. With each scanner image, a soil compartment of 20 cm length and 345° of the tube’s inner surface was recorded, representing a soil surface of 219.9 cm². In this study, only the first 10 cm below the soil surface were considered for analysis, since more than 50 % of the fine root biomass of the profile total was located in the uppermost 10 cm of the soil (Roederstein et al. 2005; Moser et al. 2008). Furthermore, roots of this soil depth were assumed to respond more rapidly to the desiccation treatment.

The rhizotron images were further analyzed with the program WinRHIZO Tron (Régent, Canada). Root length and diameter were determined by manually tracing the roots on the screen of each image. For analyzing subsequent images, the previous analysis was superposed over the current image. This allowed extending root sections originating from recent root growth or to delete sections that had disappeared due to root death and decomposition. To estimate annual fine root turnover we extrapolated monthly relative root length loss to a full year (Nadelhoffer 2000; Graefe et al. 2008).

Statistical analysis

All data sets were analyzed for normal distribution using a Shapiro and Wilk test. Normally distributed data were tested using an ANOVA procedure followed by pair-wise comparison after Scheffé. Data sets deviating from normal distribution were analyzed with a non-parametric global analysis of significant effects (Kruskal-Wallis test) and a Mann-Whitney two-sample test (U-test). All calculations were done with SAS/STAT software ($p < 0.05$).

Results

Element concentrations in fine roots

As expected, carbon concentrations in fine root dry matter did not differ significantly between the three stands (Table 2). For nitrogen concentration, a decrease with increasing altitude was observed, with values being significantly lower at 3060 m than at 1050 m. This resulted in a strong increase upslope of the C/N ratio from 33 to 102 g g^{-1}. Phosphorus and potassium concentrations decreased significantly with increasing altitude as well. The N/P ratio was significantly lower at 3060 m than at 1050 and 1890 m. The calcium and magnesium concentrations in the roots showed no linear elevational trend: the Ca concentration was markedly higher at 1050, but did not differ between the stands at 1890 and 3060 m. The Mg concentration was significantly lower at 3060 m but did not differ between the two lowermost stands.

Table 2. Element concentrations in fine root biomass of the organic layer. Given are means ± 1 SE, n = 10. Different letters indicate significant differences between the study sites ($p < 0.05$).

	Elevation (m asl)		
Element	1050	1890	3060
C (mmol g^{-1})	122.4 ± 4.6 a	134.4 ± 6.9 a	134.9 ± 9.2 a
N (mmol g^{-1})	3.4 ± 0.3 a	2.7 ± 0.4 a	1.2 ± 0.1 b
P (µmol g^{-1})	33.7 ± 2.7 a	23.6 ± 1.9 b	16.4 ± 0.8 c
K (µmol g^{-1})	111.5 ± 8.6 a	97.6 ± 12.1 ab	77.6 ± 9.3 b
Ca (µmol g^{-1})	112.7 ± 27.6 a	46.7 ± 14.0 b	49.0 ± 7.3 b
Mg (µmol g^{-1})	91.7 ± 11.2 a	91.7 ± 12.2 a	53.1 ± 5.5 b
C/N	33.1 ± 4.2 a	46.5 ± 4.9 b	102.1 ± 8.8 c
N/P	103.1 ± 7.6 ab	114.8 ± 11.6 a	72.3 ± 6.0 b

Fertilizer effects on fine root growth

At 1050 m, the strongest growth of roots into the ingrowth cores was observed in the phosphorus treatment, while the nitrogen and potassium treatments led to a ca. 25% lower root ingrowth (Fig. 1A); however, P, N or K fertilization differed not significantly from each other. Fine root ingrowth into both controls (control$_{\mathrm{verm}}$ and control$_{\mathrm{soil}}$), on the other hand, was significantly lower than in the fertilizer (N, P, K) treatments. At 3060 m, root ingrowth was 8 to 10 times slower than at 1050 m and the absolute differences between the treatments were much smaller. Highest ingrowth of fine roots was observed in the control cores filled with unfertilized soil substrate, which significantly exceeded growth in fertilizer treatments and also in the control with vermiculite as a substrate (Fig. 1B). Highest ingrowth among the three fertilizer treatments occurred with N addition, which contrasts with the results obtained at 1050 m.

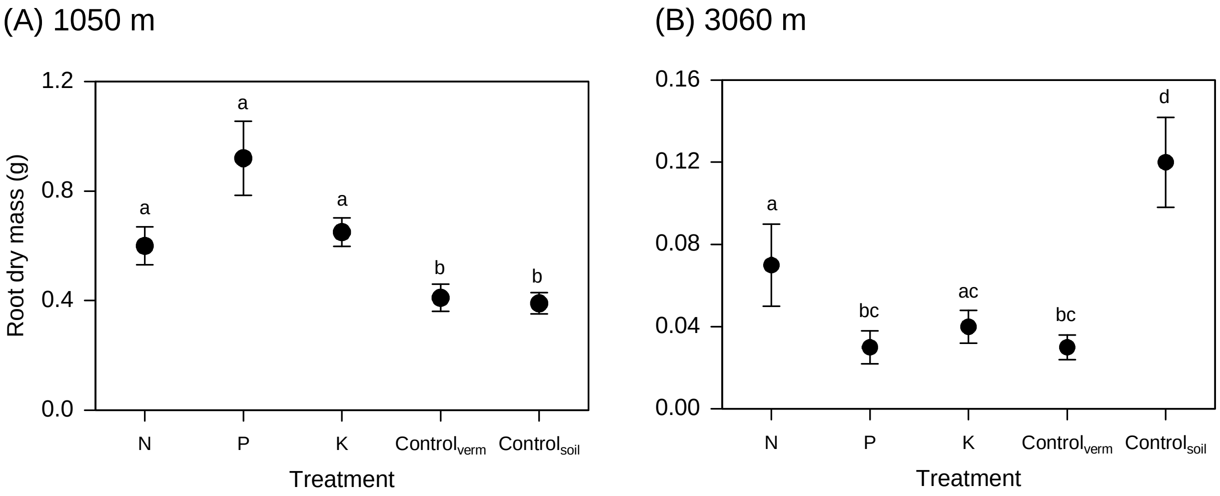

Fig. 1. Growth of fine roots in ingrowth cores fertilized by N, P, or K and in control cores for 5 months at 1050 m (A) and 3060 m elevation (B). Different letters indicate significant differences between the treatments ($p < 0.05$). Given are means ± 1 SE for 15 cores per treatment. Control$_{\mathrm{verm}}$ and control$_{\mathrm{soil}}$ refer to ingrowth cores filled with vermiculite or natural soil without fertilization. Note different scale of y-axes.

Relating fertilizer effects to the direct control, i.e. the unfertilized vermiculite cores (control$_{\mathrm{verm}}$), reveals that the largest stimulation of fine root growth occurred at 1050 m after adding P, and at 3060 m after adding N (both effects significant at $p < 0.05$). Table 3 compares the extent of root growth stimulation by N, P or K at the two elevations by expressing growth relative to the vermiculite control. For N, the relative growth stimulation was higher at 3060 m than at 1050 m; however this difference was not significant ($p < 0.05$). Phosphorus addition led to a twice as high ingrowth stimulation in the pre-montane forest stand compared to the upper-montane forest. For K, moderate root growth stimulation was observed which was not different between the two stands.

Table 3. Increase of root dry mass relative to control (growth in vermiculite = control$_{verm}$) after fertilization with N, P, or K at 1050 m and 3060 m. Different letters indicate significant differences between the study sites ($p < 0.05$). Given are means ± 1 SE for 15 cores per treatment.

Elevation (m asl)	Treatment N	 P	 K
1050	1.49 ± 0.17 a	2.27 ± 0.33 a	1.61 ± 0.13 a
3060	2.35 ± 0.65 a	1.09 ± 0.26 b	1.38 ± 0.25 a

^{15}N tracer study on nitrogen uptake capacity

Two hours after the application of ^{15}N-labeled NH_4NO_3 solution, a clear increase of δ^{15}N values in the fine root dry matter was observed in all three stands (Fig. 2). The strongest increase took place in the mid-elevation stand (reaching up to 1500‰), and the weakest increase was found in the lowermost stand (640‰), with the difference between the stands being significant at $p < 0.05$. After 2 days, the δ^{15}N values had further increased in the lowermost and the mid-elevation stands, but no marked change had occurred in the uppermost stand. Five days after the onset of the experiment, similar δ^{15}N values in the root biomass were reached in all stands (between 1500 and 1900‰) independently of the temporal uptake dynamics.

In the stands at 1890 and 3060 m, 50% of the maximum δ^{15}N value in fine root tissue was reached in less than 2 hours after tracer application. In the stand at 1050 m, on the other hand, 50% of the maximum δ^{15}N value was approached only after ca. 32 hours.

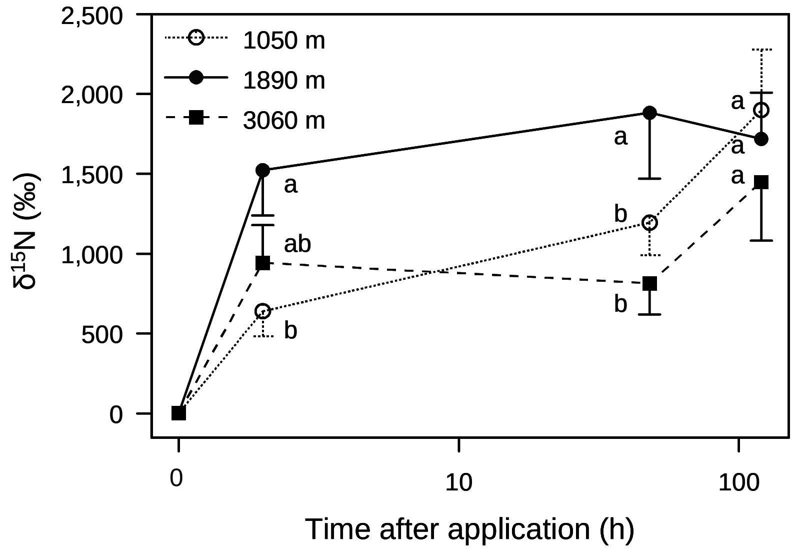

Fig. 2. δ^{15}N values of fine root dry matter after application of $^{15}NH_4{}^{15}NO_3$ (means ± 1SE). Different letters indicate significant differences between the study sites per date ($p < 0.05$). Mean soil temperature of the organic layer was 20.4°C at 1050 m, 14.4°C at 1890 and 10.3°C at 3060 m, respectively, during the study period.

Desiccation experiment in the upper montane forest

The installation of the roofs in the stand at 3060 m reduced soil moisture in the organic layer within one month after roof closure by more than 50%. While soil moisture in the control plots varied between ca. 25 and 60 vol% (mean: 39.0 vol%) with a strong dependence on rainfall events (data not shown), soil water content under the roofs ranged between 9 and 18 vol% (mean: 14.6 vol%) during the study period from August 2005 to January 2007 (Fig. 3A).

The root length visible in the minirhizotron tubes was equal in both treatments during the first seven months of the observation period (Fig. 3B). During the second half of the study (from April 2006 onwards), root length further increased in the control treatment, while it remained constant in the desiccation treatment until July to increase thereafter at a lower rate than in the control. At the end of the observation period after 17 months, root length in the desiccation treatment averaged at about 80 cm per minirhizotron tube, while it reached a mean of 130 cm in the control.

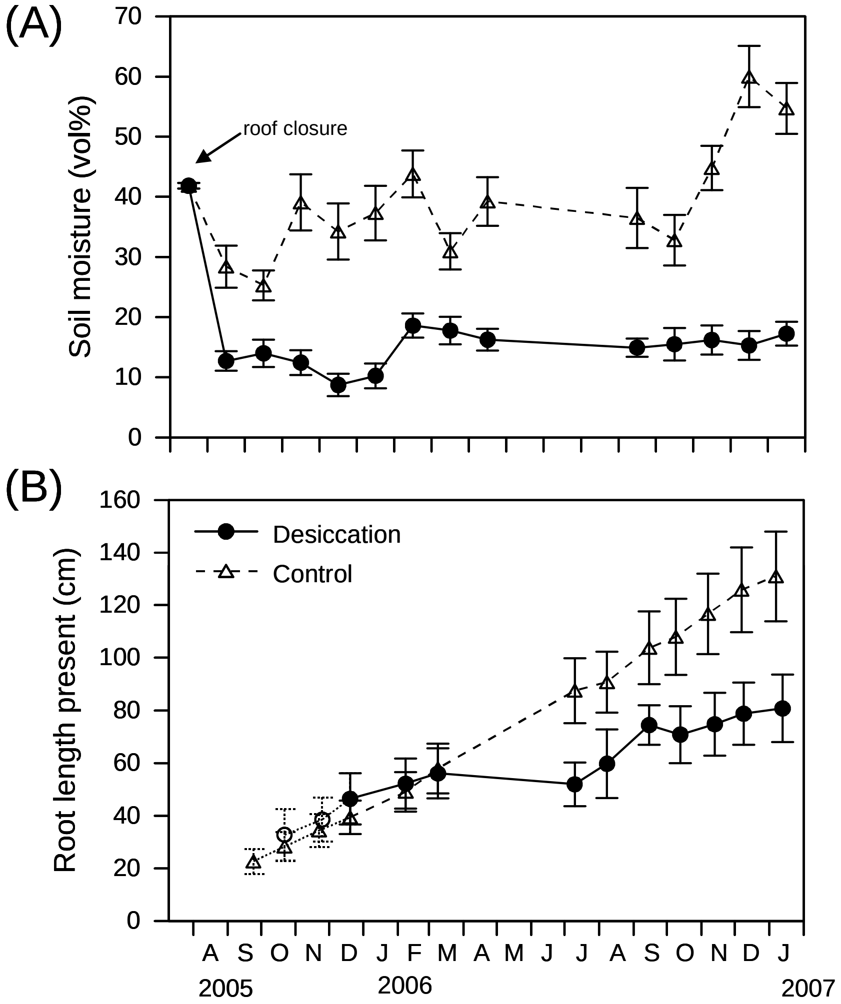

Fig. 3. Soil moisture of the organic layer (A) and root length present in minirhizotrons (B) in the desiccation and the control treatment during the study period from August 2005 to January 2007 (means ± SE).

Mean monthly root length production was significantly higher in the control (11.2 cm mo^{-1}) than in the desiccation treatment (8.5 cm mo^{-1}) during the whole study period (Fig. 4A). In contrast, no significant differences could be observed in monthly root length loss between the desiccation and control plots (3.5 and 4.4 cm mo^{-1}, respectively). Fine root turnover tended to be somewhat higher under desiccation (1.2 g g^{-1} yr^{-1}) than in the control plots (0.9 g g^{-1} yr^{-1}), but this difference was not significant (Fig. 4B).

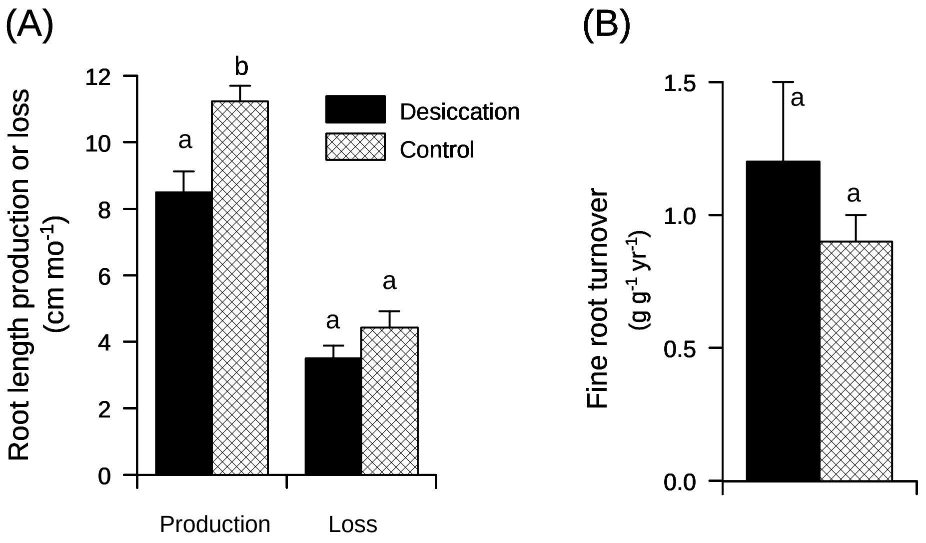

Fig. 4. Monthly means of root length production and loss (A) and annual fine root turnover (B) in the stand at 3060 m in the desiccation and the control treatment calculated from monthly minirhizotron data during the study period from August 2005 to January 2007 (means ± SE). Different letters indicate significant differences between the treatments ($p < 0.05$).

Discussion

Evidence for phosphorus and nitrogen limitation in tropical mountain forests and consequences for fine root activity

Conventionally, the limitation of a specific nutrient is shown if the rate of an ecosystem process is increased by addition of that nutrient (Tanner et al. 1998). There exists general agreement that P is the main limiting element of plant growth in tropical lowland and pre-montane forests on strongly weathered soils (Vitousek and Sanford 1986; Vitousek 2004; Paoli et al. 2005), as P becomes less available during pedogenesis (Walker and Syers 1976). However, Cuevas and Medina (1988) found fine root growth in two Amazonian lowland forests to react differently to the addition of N, P and Ca, which indicates different limiting nutrients in these ecosystems. In montane forests, on the other hand, which mostly grow on rather young soils, N is often short in supply, mainly because of slow decomposition and mineralization of organic matter (Tanner et al. 1998; Benner et al. 2008).

N limitation in tropical montane forests was documented by several nutrient addition experiments which examined either the response of above ground plant parts to fertilization, such as diameter increment and leaf flushing (e.g. Tanner et al. 1992; Raich et al. 1996; Nomura and Kikuzawa 2003), or of root growth (e.g. Raich et al. 1994; Stewart 2000; Nomura and Kikuzawa; 2003). Because of their large carbon and nutrient demand, fine roots should be particularly sensitive to nutrient limitation and should respond rapidly to nutrient addition. For assessing the below ground response of trees, ingrowth cores proved to be a reliable method for detecting nutrient limitation (Denslow et al. 1987; Cuevas and Medina 1988; Raich et al. 1994, Stewart 2000).

The results of our fertilization experiments indicate that P is indeed the primary limiting nutrient at pre-montane elevation (1050 m), while N plays this role in the upper montane forest (3060 m), if fine root growth stimulation is used as a criterion. In the upper montane stand, N addition led to a 2.4 fold increase of root ingrowth compared to the control, whereas in the pre-montane stand, root ingrowth was only stimulated by a factor of 1.5. P addition, on the other hand, yielded a 2.3 fold increase at 1050 m, whereas at 3060 m, no response in root growth could be observed to P fertilization. K does not seem to be a main limiting nutrient at either elevation.

Due to the very low root mass that had grown into the cores at 3060 m, some caution is required when interpreting the results from this stand. In fact, the absolute differences between the treatments were quite small. The amount of root ingrowth at this site is not unrealistic, because it compares well with results obtained by Stewart (2000), who conducted a similar nutrient addition experiment in a montane forest in Jamaica with an ingrowth period of one year. Nevertheless, root growth into an artificial medium such as vermiculite may yield different results than growth in natural soil, which would explain the high ingrowth in the control treatment with local soil material in the 3060-m stand. Vermiculite is much more coarse grained and contains lower amounts of organic matter. Even though the absolute root growth rates in the experiment in the upper montane stand may be biased by the experimental conditions, N limitation of fine root growth at 3060 m elevation is not only supported by this fertilization experiment, but also by very low N concentrations in living fine roots of this stand. In fact, tissue nitrogen concentration showed the steepest decrease upslope between 1050 m and 3060 m of all investigated elements. This observation is in agreement with results from other tropical gradient studies (e.g. Tanner et al. 1998). In their review on nutrient limitation of tropical montane rainforests, Tanner et al. (1998) reported decreasing foliar N, P and K concentrations with increasing altitude, while no consistent trend could be found for Ca and Mg. Litterfall mass decreased considerably above 1500 m and went along with lower N mineralization rates and lower extractable and total soil P contents. Marrs et al. (1988) provided evidence of reduced N mineralization and nitrification rates at higher altitudes along an altitudinal transect in Costa Rica, which they mainly attributed to the high moisture content of the montane soils. Decreased nutrient concentrations in plant tissue at higher altitudes might also be caused by increased nutrient immobilization, as large amounts of soil organic matter are built up at high elevation due to slow decomposition (Tanner et al. 1998).

Tanner et al. (1998) suggest that the amount of nutrients in litterfall may be taken as an approximation of net nutrient uptake into aboveground plant parts. This is in line with results of Paoli et al. (2005), who found extractable soil P to be positively related to litter production in a lowland rainforest of Borneo. Nutrient (most likely nitrogen) shortage is also implied by root studies along elevation transects. Hertel and Leuschner (2008) found an increase of fine root biomass with elevation, and also a higher fine root production in upper montane compared to lower montane forests. These authors assumed that a large fine root system at higher altitudes is a consequence of nutrient limitation and perhaps adverse soil chemical or physical conditions.

N-uptake activity of tropical trees at different altitudes

An increased viscosity of water at low temperatures reduces the rate of nutrient transport to roots in mass flow and thereby decreases uptake by roots. Furthermore, low temperatures reduce the diffusivity of nutrient ions in the soil solution and also may decrease active nutrient transport across root membranes (Chapin 1980). This would imply that nutrient uptake capacity of roots is strongly linked to soil temperature (Pregitzer and King 2005). We therefore expected a decreasing ^{15}N uptake with increasing altitude in the South Ecuadorian transect study. However, the rate of nutrient uptake of a plant also depends on the size of the total root surface area and on the surface-specific uptake capacity of the roots. Plants may be able to compensate for low nutrient supply rates from the soil by increasing the specific nutrient uptake capacity when acclimatizing or adapting to cold soils (Lambers et al. 1998).

Contrary to our initial hypothesis we observed a relatively high ^{15}N uptake in the uppermost stand at 3060 m even shortly after nitrate and ammonium application, suggesting that the inhibition of uptake through low temperatures might have been compensated by adaptive mechanisms. However, the experiment only yielded information on how much ^{15}N had been accumulated in fine roots, but not on the translocation of ^{15}N from root to stem during the course of the experiment, which also could have influenced the rate of accumulation in fine root tissue (Lazof et al. 1992). It remains a speculation that a rapid shift of ^{15}N-labelled nitrate or ammonium to the shoot has occurred at 1050 m, where the tracer accumulated initially more slowly than in the other two stands.

Eissenstat and Volder (2005) suggest that the proportion of young roots can strongly affect overall plant nutrient uptake and that plants with higher fine root turnover would maintain a higher nutrient uptake capacity. Due to a high fine root turnover in the upper montane stand (Graefe et al. 2008); finest roots are relatively young at this site, which could be the reason for the relatively high ^{15}N absorption capacity at this altitude. Chapin et al. (1986) found nutrient uptake to be rather insensitive to temperature in slow-growing taiga tree species, which may reflect an effective adaptation to low soil temperatures. Such a low-temperature adaptation could also exist in our stand at 3060 m, which is characterized by slow-growing tree species of small stature (Moser, unpublished data).

Does high soil moisture act as a stressor for fine root growth at high elevations?

High soil water contents pose stress on the root system and increase the mortality of fine roots due to oxygen deficiency (Jackson and Ricard 2003) or increased concentrations of toxic ions such as S^{2-}, Mn^{2+} and Fe^{2+} in the soil solution (Raynal et al. 1990). High soil moisture is further limiting decomposition and nutrient mineralization, which often may be the case in upper montane rainforests (Benner et al. 2008). By reducing soil moisture experimentally, we tried to prove that anoxia was the cause of elevated fine root mortality as it was observed by Graefe et al. (2008) in the stand at 3060 m.

However, the desiccation experiment conducted in the upper-montane stand did not lead to reduced fine root mortality in the organic layer as it was postulated in our third hypothesis. In contrast, turnover was slightly, but not significantly, enhanced under the drier conditions. This was not due to an increased loss (mortality) of fine roots under the roofs, but was mainly caused by reduced root length production under the desiccation treatment.

Several studies have examined the influence of altered soil moisture on fine root activity in tropical and temperate forests (e.g. Persson et al. 1995; Joslin et al. 2000; Yavitt and Wright 2001; Romero-Saltos et al. 2005). However, the aim of these studies was to examine the influence of water-limiting conditions on the root system, but not to reduce soil moisture in water-logged soils to a “moderate” level, as it was done in our experiment. Therefore, our results can hardly be compared to other experiments of similar design. The dry conditions that were created by means of the roofs can not be referred to as real “drought” conditions; rather, soil moisture in the organic layer was reduced to a moderate level (about 15 instead of 40 vol%). It appears that waterlogging with partial anoxia was not the primary cause of elevated root mortality at this site; alternative possible stressors that were not investigated in our experiment are elevated concentrations of toxic ions in a reducing environment, or aluminium.

Both Persson et al. (1995) and Romero-Saltos et al. (2005) found a shift in root activity to deeper soil layers through the experimental exclusion of rainfall in Swedish and Brazilian forests, respectively. Consequently, more dead fine roots were observed in the surface soil. This could also explain the reduced root length increase under the roofs of our desiccation experiment, but data on soil moisture and root growth in deeper soil layers are not available. Green et al. (2005) observed a decrease of fine root biomass during the dry season in a lowland rainforest in Malaysia. In their study, root birth decreased and root loss increased when soil water content decreased. Joslin et al. (2000), on the other hand, found fine root turnover to be highest in the wet treatment of a throughfall displacement experiment in Tennessee, USA, which they attributed to a higher nutrient availability, which may shorten root lifespan. However, fine root production was not significantly higher with a better water availability in their experiment. Similarly, Yavitt and Wright (2001), who conducted a dry season irrigation experiment in Panama, could not detect an effect of irrigation on fine root biomass.

We assume that the fine root system in the upper montane elfin forest of the South Ecuadorian transect has partly adapted to the specific conditions of these soils with high moisture, low nutrient availability and potentially toxic ions. In fact, Soethe et al. (2006) found increasing root length densities during wetter compared to drier periods in this forest stand. They further observed a more superficial nutrient uptake at 3060 m than in lower elevation stands, which indicated unfavourable root growth conditions in the mineral soil. Increasing superficial rooting and nutrient uptake is a characteristic feature of trees growing on water-logged soils.

Moser et al. (2008) found an extraordinary high fine root biomass in the superficial organic soil layers of the stand at 3060 m, which exceeded root biomass at 1050 and 1890 m by a factor of 3. Apparently, poor nutrient supply requires a high standing crop of fine root biomass to meet the nutrient demand of the trees. Minirhizotron observations showed that the turnover of fine rootlets in this root system is remarkably high (Graefe et al. 2008), even though fine roots are slow in exploring new soil patches as is evidenced by the very low ingrowth rates of fine roots into the ingrowth cores of this study (see Fig. 1B). From these observations we conclude that nutrient shortage at this upper montane site stimulates the built-up of a very large fine root system which suffers from high root mortality due to putative chemical stress and probably also temporal anoxia. Despite low temperatures, the trees must be capable to allocate sufficient carbohydrates to this active belowground carbon sink. On the other hand, adverse growing conditions seem to hamper the formation of fast growing long roots which could explore nutrient-rich patches as it is visible in the fertilizer experiment. The trees seem to compensate this limited flexibility of root growth by forming thick and dense fine root systems in the organic layer.

Conclusions

We observed decreasing concentrations of major nutrients in fine root tissue with increasing altitude, indicating a limited availability of N, but also of P, K, Ca and Mg at higher altitudes. P seemed to be short in supply also at lower pre-montane elevations, which is supported by the fertilizer experiments. Despite low soil temperatures in the upper montane forest stand, fine roots did not show a reduced N uptake capacity, suggesting that the tree species growing at this altitude may compensate for low temperatures by increased specific nitrate and/or ammonium uptake capacities, and possibly by slower translocation of N from roots to above ground plant organs. According to the throughfall exclusion experiment, anoxia in water-logged soils at the upper montane site is not the primary cause for slow root growth; rather, adverse soil chemical conditions seem to be limiting. By forming dense, superficial fine root mats in the organic layer, replacing dead fine rootlets rapidly, and maintaining a sufficiently high N uptake capacity in the nutrient-poor, cool and very wet high elevation soil, the upper montane trees have developed successful strategies to cope with this unfavourable environment. The lower montane forests, in contrast, are primarily limited by low P supply, which may favour a symbiosis with P-efficient arbuscular mycorrhizal fungi.

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CHAPTER 5

Low temperature effects on root water absorption of trees in a tropical mountain forest

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Abstract

Tropical mountain rainforests cover large elevational gradients over short distances and are characterised by diverse climatic conditions. Little is known about the influence of environmental factors on root water uptake at different altitudes in these forests. We applied miniature heat balance sap flow gauges in three tropical mountain rainforest stands between 1050 and 3060 m asl in the South Ecuadorian Andes, in order to measure water flow in coarse roots with a diameter of 10 mm in situ. We further analysed the anatomical characteristics of the conducting vessel area of root cross-sections. In all three forest stands, root sap flow followed marked diurnal courses and varied between the seasons. Root sap flow decreased roughly by a factor of three between 1050 and 3060 m. A reduced sap flow was observed when VPD was above average for several days. We identified VPD as the most influential environmental factor controlling root water uptake, but its significance decreased with increasing altitude. In contrast, the influence of temperature increased along the elevational transect, and was identified as the most influential factor determining root sap flow at 3060 m close to the alpine timberline. Anatomical analyses of root cross-sections provided evidence for decreasing vessel diameters with increasing altitude. Theoretical hydraulic conductivity was found to decrease more than ten fold from 50.2 m^2 MPa^{-1} s^{-1} at 1050 m to 4.0 m^2 MPa^{-1} s^{-1} at 3060 m. We conclude that the temperature decrease with increasing altitude acts on water uptake through several pathways, (i) on the physics of water flow in the soil-plant-atmosphere continuum (increasing viscosity of water, decreasing VPD), (ii) by reducing vessel cell growth, (iii) by restricting nutrient availability (which may lead to smaller vessels), and (iv) possibly by lowering aquaporine activity in the roots.

Keywords: altitude, Ecuador, miniature sap flow gauges, root anatomy, root sap flow, theoretical hydraulic conductivity, tropical mountain rainforests, VPD

Introduction

Tropical mountain rainforest extend over large altitudinal differences and thus occupy a wide range of environmental conditions (Cavelier 1996). A main characteristic of these forests is a decrease in tree height and above ground biomass with increasing elevation (Leuschner et al. 2007; Moser et al. 2007). Roots and leaves are the main interfaces between plant and environment in the soil-plant-atmosphere continuum (SPAC) of water flow in ecosystems, as water is taken up by roots and transpired to the atmosphere by leaves. Water dynamics in tropical mountain rainforests are not yet fully understood, but need further attention given the importance for water budgeting at the tree and ecosystem level in view of global climate change. Much research has been undertaken on above ground processes such as canopy transpiration and xylem sapflow (Cavelier 1990; Meinzer et al. 1993; Goldstein et al. 1998; Santiago et al. 2000; Motzer et al. 2005), whereas until now little information is available on root water uptake and its control by environmental conditions, especially low temperatures (Bruijnzeel and Proctor 1995). Likewise, not much is known about anatomical characteristics of roots at different elevations, which represent the physical limitations of water flow and determine the risk of xylem dysfunction. However, there is evidence that warm environments tend to favour species with larger vessel diameters compared to colder environments (Tyree and Ewers 1996). Thus, low temperature in high-elevation tropical forests most likely will influence root water uptake in three ways, (i) by increasing the viscosity of water which may slow down water flow in soil and root, (ii) by decreasing axial hydraulic conductivity due to smaller vessel sizes, and (iii) by putative reduction of aquaporin activity in a colder environment.

In this study, we used miniature heat balance sap flow gauges after Senock and Leuschner (1999) and Coners and Leuschner (2002) for measuring sap flow of roots under field conditions in South Ecuadorian tropical mountain rainforest at different elevations. The aim of our study was (1) to measure seasonal changes of sap flow in small-diameter roots (d = 10 mm) at elevations of 1050, 1890 and 3060 m; (2) to examine the dependence of root water uptake on temperature and atmospheric and soil water status; and (3) to analyse anatomical characteristics of root cross sections in relation to measured sap flow.

Material and methods

Study sites

Sap flow measurements 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. Stand Nº 1 (1050 m) is located close to the village of Bombuscaro inside Podocarpus National Park representing a pre-montane tropical moist forest. Stand Nº 2 (1890 m) is situated in the forest reserve of the Estación Cientifica San Francisco (ECSF) which consists of a mid-montane tropical moist forest. The uppermost stand Nº 3 represents an elfin forest in the upper montane Cajanuma region of Podocarpus National Park at 3060 m. Data on tree species composition are given in Homeier et al. (2008). Mean tree height decreases from 15.6 m in the lowermost stand to 5.2 m at the uppermost site (Moser et al. 2008). All sites are 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 averages about 2000 mm yr^{-1}, whereas precipitation is about 4500 mm yr^{-1} at 3060 m (P. Emck & M. Richter, unpublished data, Moser et al. 2008). Annual mean air temperature measured at 1.5 m above the forest floor in the stands decreases from 19.4°C at 1050 m to 15.7°C at 1890 m and 9.4°C at 3060 m. The volumetric water content of the organic layer measured during sap flow measurements increased from 29.7 to 49.1 vol% along the elevational transect.

At all three sites, the soils are acidic and nutrient-poor. The pH($CaCl_2$) value in the upper mineral soil (0-30 cm) ranges from 3.9 at 1050 m to 2.9 at 3060 m (S. Iost, unpublished data). The transect is characterized by a strong upslope increase in the C/N ratio of the organic layer (22 - 28 - 63 g g^{-1}) and in organic layer thickness (48 - 305 - 435 mm) (S. Iost, unpublished data).

Table 1. Location and characteristics of the study sites. Temperature and air humidity were measured 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 1050 m (measuring period May 2003 - May 2004, Moser et al., 2008), and from measurements at 1950 and 3170 m (three-year means, P. Emck & M. 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 S. Iost & F. Makeschin (unpublished data). Soil type description according to FAO taxonomy.

Plot Nº	1	2	3
Elevation (m asl)	1050	1890	3060
Slope (°)	26	31	27
Annual mean air temperature (°C)	19.4 ± 0.1	15.7 ± 0.1	9.4 ± 0.03
Mean air humidity (%)	88.7 ± 0.3	90.8 ± 0.2	93.5 ± 0.1
Rainfall (mm yr-1)	2230	1950	4500
Soil type	Alumic Acrisol	Gleyic Cambisol	Podzol
Organic layer thickness (mm)	48	305	435
Mean soil moisture (vol%)	9.9 ± 0.001	11.6 ± 0.001	45.3 ± 0.002
pH-CaCl2 (organic layer)	3.9	3.5	2.9
C/N (organic layer)	22	28	63
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
Viscosity of water (10-3 Pa s)	1.019583	1.119042	1.333986

Sap flow measurements

Root sap-flow rates were measured on roots with a diameter of ca. 10 mm by means of the constant power heat-balance method according to Senock and Leuschner (1999) and Coners and Leuschner (2002). Sap flow gauges were based on the design of Sakuratani (1981) and Senock and Ham (1993), where heater, thermocouples and thermopile are embedded in a flexible cork jacket providing good contact between the gauge and the root. The gauges were heated continuously with 0.04-0.07W by a Kapton film resistance heater (Heater Designs Inc., Bloomington, CA, USA), which was placed directly on the root periderm. Two pairs of thermocouples and a thermopile recorded the axial and radial dissipation of heat. Battery-powered CR10X data loggers with AM16/31 multiplexers (Campbell, Cambridge, UK) recorded gauge signals every 30s, of which 60-min-averages were calculated. Based on these data, the heat balance of the system was solved for the mass flow term, i.e. the heat transported with water flow in the xylem in axial direction. Sap flow rates were calculated based on the heat capacity of water (4187 J kg^{-1} K^{-1}) to convert heat flow (in W) to mass flow (in g h^{-1}). For calculating the gauge heat conductance K_g, conditions of zero flow were required. We therefore recalculated K_g by assuming that sap flow approaches zero before dawn. On days with significant night flow, i.e. during dry and windy nights, K_g was adjusted by extrapolating from preceding and subsequent days by means of a graphical interactive software tool (H. Coners, unpublished).

Synchronously to sap flow measurements, air temperature and relative air humidity were recorded at hourly intervals and soil moisture at 6-hourly intervals, respectively. Temperature and air humidity data were further used to calculate vapour pressure deficit (VPD). This allowed relating daily sap flow densities to cumulative daily VPD values.

Measurements were performed during three consecutive periods of 2-4 weeks between October 2006 and January 2007. During each measuring period, 10 gauges were installed in each of the three forest stands on roots in the organic layer, which ranged in diameter between 9.5 and 10.5 mm. For mounting the gauges, root segments of ca. 8 cm were uncovered from the surrounding soil. After installation, the gauges were wrapped with polyurethane foam insulation and fixed to the root with a metal clip. The pits were finally covered with polystyrene wrapped in aluminium foil in order to minimize temperature fluctuations in the gauge surroundings. At the end of the measuring periods, each root segment, on which sap flow measurements were conducted, was cut and conserved in 70% ethanol. This allowed for a subsequent microscopic analysis of root cross-sections.

Root anatomical analyses

Conserved root segments were immersed for several hours in liquefied polyethylenglycol (PEG) at 50-55°C, which removed the ethanol from the samples. PEG-blocs with the embedded root segments were cooled down to solidify and were stored at 5°C until further processing. For cross-sectional analysis, cuttings with a thickness of ca. 20-25 µm were sliced with a rotary microtome (Leica Reichert-Jung 2030 BIOCUT) from each root segment. Root cross-sectional images were captured from a microscope (Olympus AX 70) equipped with a digital camera (Canon PowerShot A620). The number and size of vessels was analyzed with the ImageJ software (http://rsb.info.nih.gov/ij/). Vessels with a diameter > 25 µm were analyzed from images taken at 25x magnification covering the whole root cross-section. Vessels with a diameter < 25 µm were analyzed at 100x magnification in four representative sub-areas of 0.86 mm² each. The obtained values were then extrapolated to the entire cross-section. The results from the cross-sectional analysis where further used to convert sap flow values (in g h^{-1}) to sap flow densities related to the conducting vessel area of each root (in g mm^{-2} h^{-1}).

Theoretical hydraulic conductivity

To determine the possible maximum water flow through the analyzed root segments, theoretical hydraulic conductivity (K_h^{theor}) was calculated by means of the Hagen-Poiseuille-equation (Lösch 2001):

$K_h^{theor} = (\pi \Sigma r^4) / (8 \eta)$ [m^4 MPa^{-1} s^{-1}]

with r = vessel radius [m] and η = viscosity of water [Pa s] (which is 10^{-3} Pa s^{-1} at 20°C).

The specific viscosity of water at each study site was calculated on the basis of the mean air temperature (Table 1):

$\eta = 498.36 + \exp(-0.0472 \cdot (Temp – 151.95)$ [μPa s]

Statistical analyses

After applying a Shapiro-Wilk test to test for normality, a non-parametric global analysis of significant effects (Kruskal-Wallis test) and a Mann-Whitney two-sample test (U-test) were used to analyse significant differences in root anatomical characteristics between the three study sites. Multiple regression analyses were performed to detect environmental variables (i.e. vapor pressure deficit, air temperature, soil moisture) and root anatomical parameters (i.e. theoretical hydraulic conductivity) with a significant influence on root water uptake. In regressions with a stepwise reduction of variables, daily totals of sap flow densities were regressed on daily cumulative values of VPD and daily means of temperature and soil moisture. The daily cumulative VPD values (VPD_{cum}) were calculated by adding the 24 hourly VPD means of a day (unit: mPa d^{-1}). All calculations were done with SAS software (SAS Institute, Cary, NC, USA). Significance was determined at $p < 0.05$.

Results

Daily and seasonal courses of sap flow density at different altitudes

Sap flow density in 10 mm roots showed marked diurnal courses which closely followed the diurnal change in VPD (Fig. 1). Peak flow rates were recorded between 11 a.m. and 4 p.m. Sap flow ceased during the evening and the night, as well as on days with low VPD in the forest stand at 3060 m.

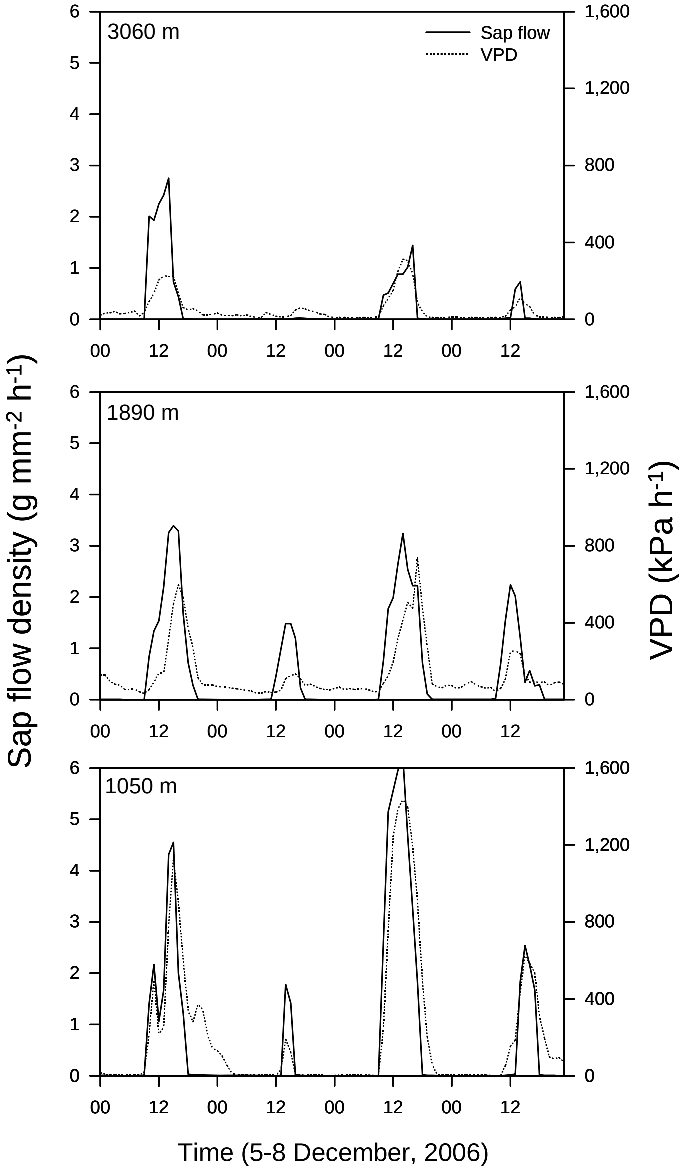

Fig. 1. Daily course of sap flow density of individual roots and VPD on four consecutive days at altitudes of 1050, 1890 and 3060 m asl. Sap flow per root (g h^{-1}) was related to the cross-sectional sap conducting vessel area (cva) at the measuring point. Data represent hourly means.

The first measuring period from mid-October to mid-November 2006 was characterised by highly variable VPD_{cum}, ranging from 170 to 3230 mPa in the forest stand at 1890 m, and from 70 to 2000 mPa in the forest stand at 3060 m (Fig. 2). At 1890 m, roots showed peak sap flow densities of around 20 g mm^{-2} d^{-1} on days with intermediate VPD$_{cum}$ (1800 mPa). Sap flow decreased on days with extremely high VPD, and ceased when VPD$_{cum}$ was below 500 mPa. At 3060 m, where recorded sap flow was most of the time close to the resolution limit of the gauges, reliable sap flow data were only available for two individual roots. Sap flow density in theses roots was considerably lower than at 1890 m, and did not exceed 10 g mm^{-2} d^{-1} on most days. Also in this forest, stand sap flow decreased on days with very high VPD (i.e. 18-21 October 2006) and ceased on rainy days.

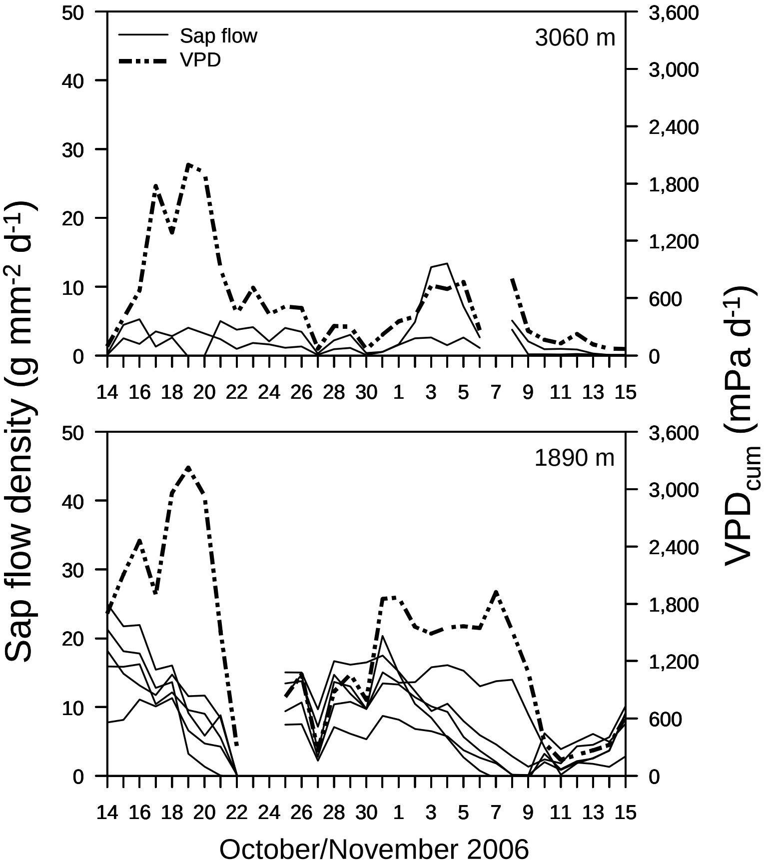

Fig. 2. Seasonal course of sap flow density in different 10 mm roots measured with miniature sap flow gauges and VPD$_{cum}$ in the forest stands at 1890 and 3060 m during measuring period 1. Sap flow per root (g day^{-1}) was related to the cross-sectional sap conducting vessel area (cva) at the measuring point. Data represent daily totals derived from hourly means. Each line represents one root.

During the second measuring period at the beginning of December 2006, VPD was rather high in the low and mid-elevation forest stand (up to 1600 mPa d^{-1}), and did not exceed 400 mPa d^{-1} at 3060 m (Fig. 3). On days with low VPD, sap flow decreased markedly in all three forest stands. A very high variability of sap flow densities was observed among individual roots in the stands at 1050 and 1890 m, which differed more than 10-fold on a given day. The third measuring period at the beginning of January 2007 was characterised by rather low VPD values in all forests stands, though individual days differed markedly in cumulative VPD values (Fig. 3). During this period, measured sap flow densities were notably high at 1050 m (up to 25 g mm^{-2} d^{-1}), especially in comparison to the second measuring period, during which considerably higher VPD was recorded. At 1890 m, again a high variability (up to eight-fold) of sap flow density was observed among different neighbouring roots, but a reduced sap flow as a response to decreasing VPD was obvious in all cases. In the uppermost stand at 3060 m, root water uptake ceased during a week with VPD of 20 to 30 mPa d^{-1}, but increased markedly when VPD rose to 150 mPa d^{-1} thereafter.

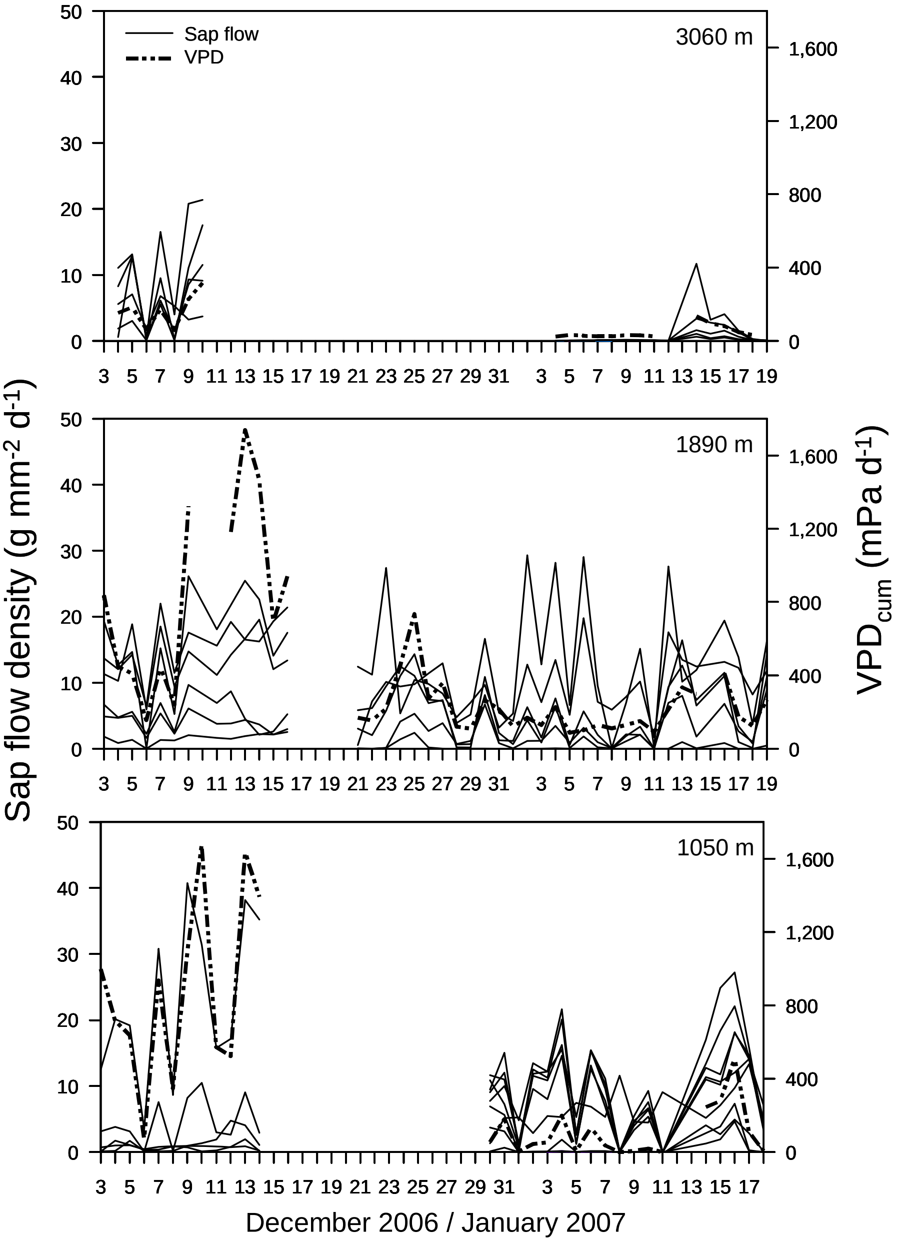

Fig. 3. Seasonal course of sap flow density in 10 mm roots measured with miniature sap flow gauges and VPD in the forest stands at 1050, 1890 and 3060 m during measuring period 2 & 3. Sap flow per root (g day^{-1}) was related to the cross-sectional sap conducting vessel area (cva) at the measuring point. Data represent daily totals derived from hourly means. Each line represents one root.

Xylem anatomy

Anatomical analyses of xylem vessels provided evidence for decreasing vessel diameters with increasing altitude (Table 2, Fig. 4). At all three study sites, the bulk of the vessels had a diameter < 25 µm; the number of vessels in this diameter class remained more or less constant with elevation (Table 2). In the next larger diameter class (25-50 µm) the number more than doubled between 1050 and 3060 m. The highest number of vessels in the intermediate diameter class (50-75 µm) was found in the mid-elevation forest stand. In the larger diameter classes of 75-100 and > 100 µm, again a decrease of vessel numbers with increasing altitude was observed. In the forest stand at 3060 m, vessels in the largest diameter class occurred only exceptionally.

Table 2. Distribution of vessel diameters at elevations of 1050, 1890 and 3060 m of root sections on which sap flow measurements were conducted. Total root diameter was 10 mm; number of vessels per diameter class was related to 1 mm² conducting vessel area.

Diameter (µm)	Elevation (m asl)		
	1050 m	1890 m	3060 m
< 25	950	1049	1059
25-50	26	51	70
50-75	7	14	12
75-100	4	3	1
> 100	5	1	0

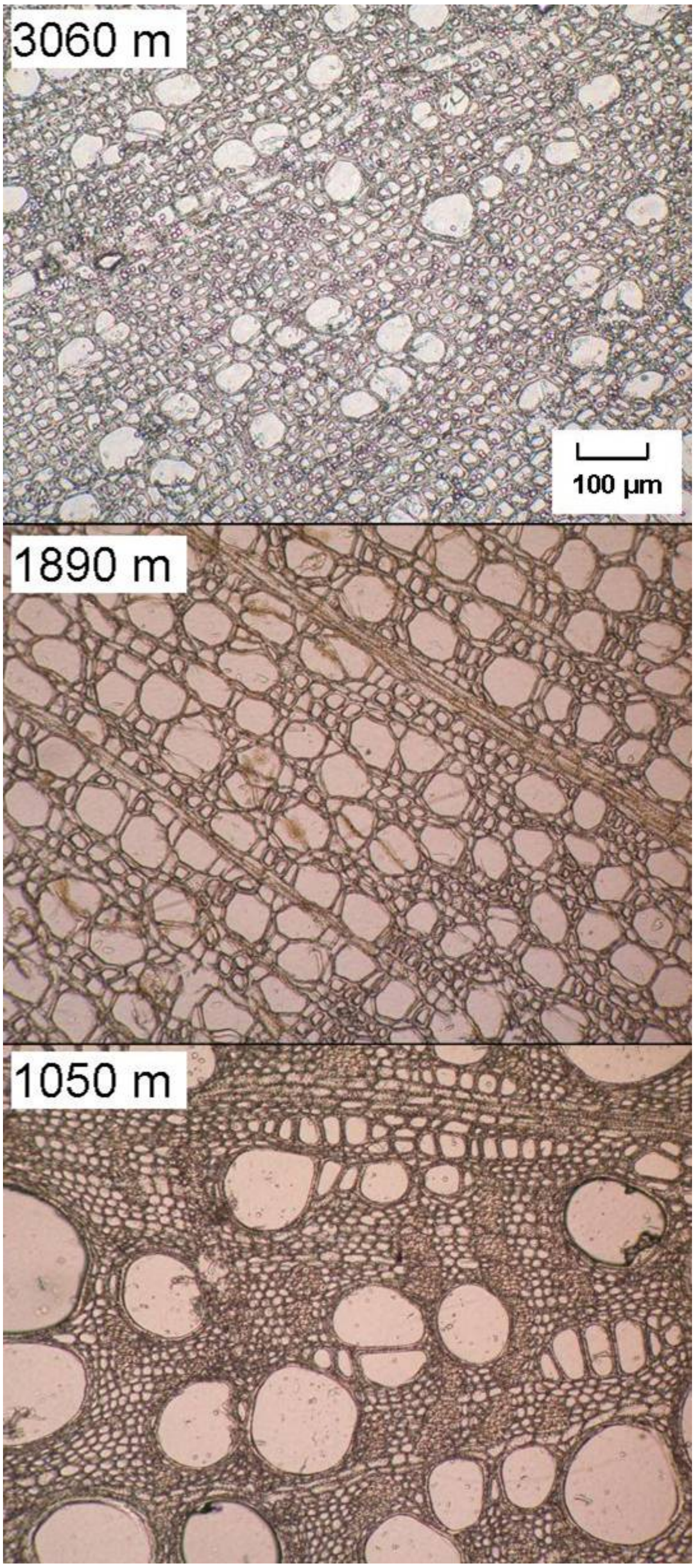

Fig. 4. Cross-sections of roots in forest stands at 1050, 1890 and 3060 m. Pictures were taken at 100x magnification.

The mid-elevation forest stand had a slightly higher sapwood cross-sectional area and also cumulative area of conducting vessels as compared to the lowermost and uppermost forest stands (Table 3); however, this difference was not significant. Overall, the conducting vessel area comprised about 20% of the sapwood area, and 10 to 12% of the total root cross section.

The theoretical root specific conductivity (k_h^{theor}) as derived from Hagen-Poiseuille's equation was found to decrease significantly with increasing altitude (Table 3). A 2.5-fold decrease of k_h^{theor} was observed from 1050 to 1890 m, and a 5-fold decrease from 1890 to 3060 m. The percental proportion of the different xylem vessel diameter classes in k_h^{theor} showed very altitude-specific characteristics (Fig. 5). In the uppermost forest stand, the diameter class 25-50 µm contributed most to k_h^{theor}, followed by the diameter class 50-75 µm. The contribution of the larger diameter classes was small at this altitude. In the mid-elevation forest stand, k_h^{theor} was more evenly distributed among the diameter classes, with the highest proportion observed in the diameter class 50-75 µm. In the lowermost forest stand, the largest diameter classes by far contributed most to k_h^{theor}. The contribution of the smaller diameter classes each did not exceed 10% at this altitude. The smallest diameter class, which included the highest number of vessels in all three forest stands, contributed only marginally to k_h^{theor}.

Table 3. Anatomical characteristics of root cross sections on which sap flow measurements were conducted at elevations of 1050, 1890 and 3060 m. All investigated roots had a diameter of 10 mm. Given are means ± 1 SE, n = 17-20 roots per elevation.

	Elevation (m asl)		
	1050	1890	3060
Sapwood cross-sectional area (mm²)	48.4 ± 3.9 a	54.4 ± 3.2 a	49.8 ± 2.8 a
% of total root cross section	*50.6*	*60.9*	*56.6*
Conducting vessel area (mm²)	9.4 ± 1.2 a	11.3 ± 1.3 a	9.3 ± 1.0 a
% of sapwood cross-sectional area	*20.0*	*20.8*	*19.3*
% of total root cross section	*9.6*	*12.4*	*10.8*
k_h^{theor} (m^2 MPa^{-1} s^{-1}) total	50.2 ± 12.3 a	20.9 ± 12.7 b	4.0 ± 1.3 c

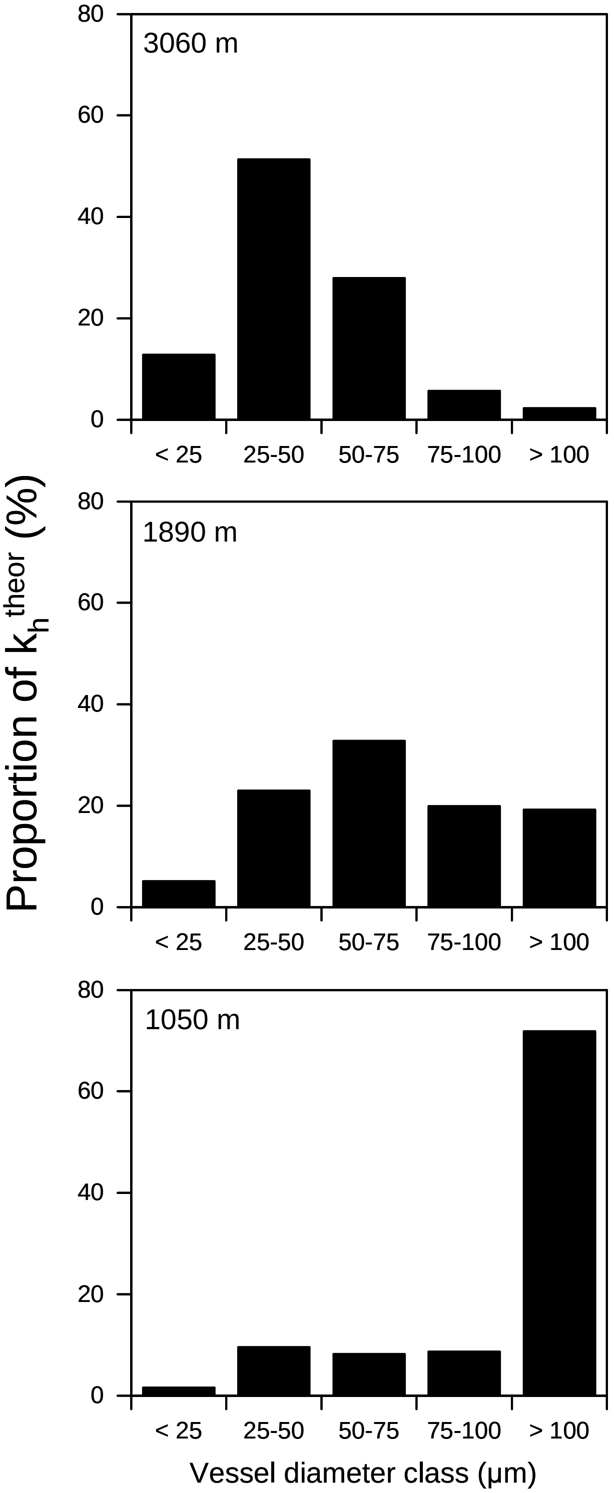

Fig. 5. Proportion of vessel diameter classes in theoretical root specific conductivity (k_h^{theor}) of roots with a diameter of 10 mm in forest stands at 1050, 1890 and 3060 m.

Environmental control of root water uptake

In all three forest stands, a highly significant correlation between sap flow density and VPD was observed (Fig. 6). Sap flow increased with increasing VPD, and reached a plateau which occurred at lower VPD levels at higher altitudes. Highest recorded daily values of sap flow density were 40 g mm^{-2} d^{-1} at 1050 m, 30 g mm^{-2} d^{-1} at 1890 m and 20 mm^{-2} d^{-1} at 3060 m. Whereas at 1050 m highest flows were observed during days with high VPD, at 3060 m sap flow ceased during high radiation days, and highest values were recorded on days with VPD of 200 to 800 mPa d^{-1}. The forest stand at 1890 showed a variable response of sap flow on days with extremely high VPD.

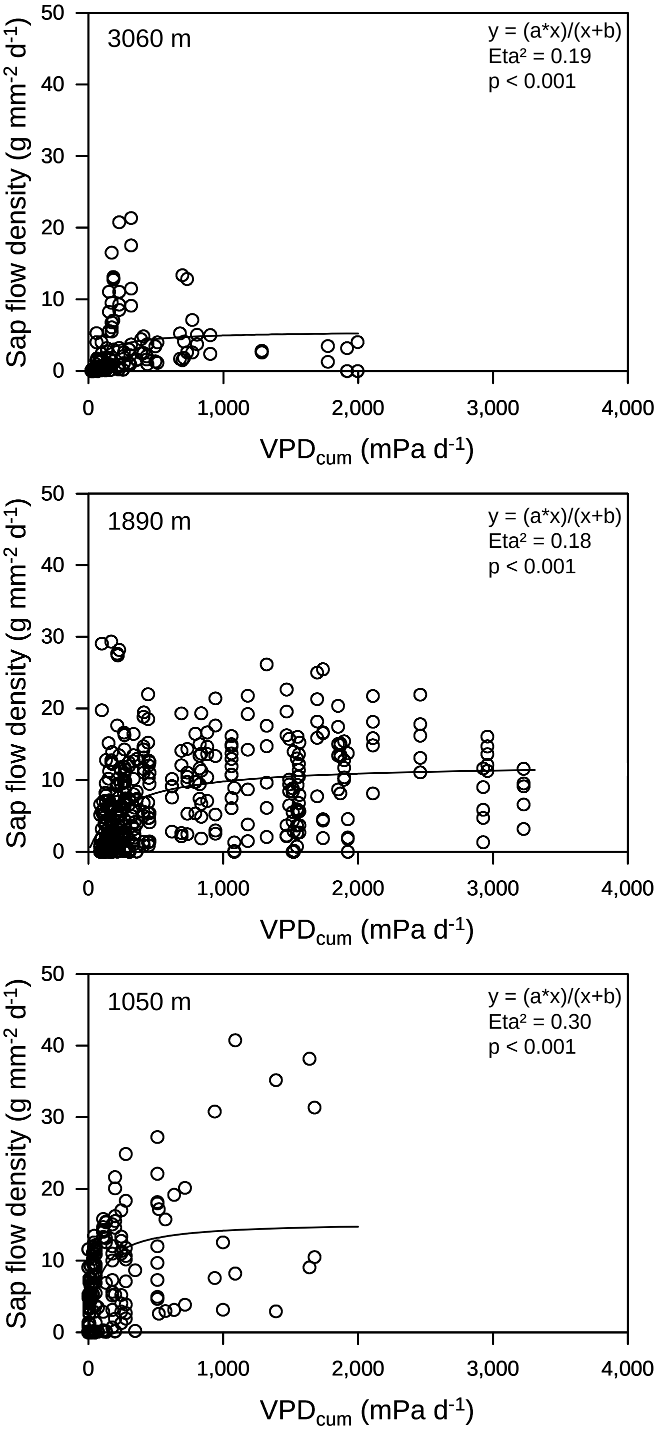

Fig. 6. Relationship between sap flow density in 10 mm roots and cumulative VPD at three elevations (n = 186 roots at 1050 m, 401 roots at 1890 m, 166 roots at 3060 m)

Multiple regression analyses on the effect of environmental parameters and k_h^{theor} on sap flow density identified VPD as the most influential factor, followed by air temperature (Table 4). As a whole, the influence of VPD decreased considerably with increasing altitude. At 1050 m VPD was selected in 75% of the measured roots as a variable with a significant influence, at 3060 m the influence of VPD was only significant in 5% of the roots. Air temperature, on the other hand, showed a reverse trend. In the uppermost stand, temperature was identified as significantly influencing the variability of water uptake in 50% of the roots; in contrast, in the lowermost stand no significant influence could be detected. Soil moisture and k_h^{theor} were only of minor importance in explaining the variability of sap flow density in the three forest stands. When the three forest stands are inspected individually, it becomes clear that at 1050 and 3060 m, VPD and temperature, respectively, were the single most influential factors explaining the variability of sap flow, whereas at 1890 m all four parameters each accounted for at least 10% of the variation.

Table 4. Variable selection in multiple regressions with stepwise variable reduction of daily totals of sap flow densities (g mm^{-2} d^{-1}) on daily totals or means of VPD, air temperature, soil moisture and theoretical root specific conductivity against. Number of observation days was 30 at 1050 m, 72 at 1890 m and 55 at 3060 m. Given is the percental frequency of variable selection.

Elevation (m asl)	1050	1890	3060
VPD (hPa d^{-1})	74.5	41.8	5.1
Air temperature (°C)	n.s.	22.0	48.6
Soil moisture$_{orglay}$ (vol%)	n.s.	11.6	6.7
K_h^{theor} (m^2 MPa^{-1} s^{-1})	n.s.	9.9	n.s.

Discussion

To our knowledge, our study is the first to provide empirical data on the processes controlling root sap flow at different elevations in tropical mountain rainforests. We identified VPD to be the most influential abiotic factor controlling root water uptake. However, its importance decreased with increasing altitude. In contrast, the influence of temperature increased with increasing altitude, explaining nearly 50% of the variability of sap flow in the highest forest stand.

VPD is regarded as the main driver for tree transpiration. An increased evaporative demand is rapidly transferred as a pressure signal to the roots where it supports a higher uptake of water by the roots. We found root sap flow closely following daily courses of VPD, as well as a strong coupling of sap flow to cumulative VPD values on a daily basis. This is in agreement with results of Coners and Leuschner (2005), who detected VPD as the single most influential environmental factor for beech and oak fine root water uptake in Central Germany. Also Senock and Leuschner (1999) found daily water flux in the root system to be closely related to rapid fluctuations of VPD in *Eucalyptus saligna* trees of Hawaii.

Even though there is not much data available on root water uptake in tropical montane forest, some research has been undertaken on the influence of VPD on above ground tree physiological processes such as stem sap flow or transpiration. Motzer et al. (2005) found stem sap flow of trees in a lower montane rainforest in South Ecuador to be mainly associated with variations in VPD and photosynthetic photon flux density (PPF). VPD seemed to impede transpiration when it exceeded 1.2 kPa, even when soil water supply was not limiting, which resulted in a saturation of sap flux density at high VPD. Cavelier (1990) observed mid-day stomatal closure in trees of a Colombian elfin cloud forest at an altitude of 865 m, which prevented water deficits under elevated VPD. Our results especially in the forest stand at 3060 m also suggest stomatal closure resulting in a reduction of root sap flow at high VPD in the perhumid climate of the study region. This response can be observed when clouds dissipate for several days in upper montane forests. Reduction of leaf conductance under elevated VPD has been observed in tropical lowland forests where VPD can be temporarily high (Meinzer et al. 1993), but it seems to play a role also in the cool and moist environment of elfin forests with an average air humidity > 93%.

In a previous study we detected a very high variability of monthly mean VPD in the pre-montane forest stand at 1050 m, which was three times greater than at 3060 m (Graefe et al. in press). Therefore, one can assume that a stomatal response and also root water uptake respond flexibly to these considerable changes in VPD in this pre-montane forest stand, where trees may possess a relatively large stem water storage capacity. Goldstein et al. (1998) found water storage capacity of canopy trees in a seasonal tropical forest of Panama to be strongly related to tree size and sapwood area, with the consequence that large trees were able to transpire at a maximum rate for a longer part of the day than smaller trees with less sapwood area. In the upper montane forest stand, on the other hand, it seems that occasionally high VPD is already perceived as drought stress, resulting in stomatal closure. However, soil moisture is always high at this site and should, in most cases, not be limiting.

If water deficits occur in upper montane forests is a matter of speculation. Bruijnzeel and Proctor (1995) suggested that the xeromorphic habit of the leaves in upper montane forests reflects an inability of the trees to transpire at the potential rate due to limited uptake, which is not caused by soil water deficiency. They related a reduced water uptake in tropical mountain forests to anaerobic and nutrient deficient soil conditions. Further, leaf area index (LAI) is a key determinant of the exchange of water between the canopy and the atmosphere. It was found to decrease by 50% along our altitudinal transect in South Ecuador (Moser et al. 2007). Santiago et al. (2000) found whole-tree transpiration to be reduced at sites with waterlogged compared to non-waterlogged soils in montane cloud forests of Hawaii, which they explained with a reduced leaf area per tree in this stands.

A key result of our study is the strong decrease of vessel diameter with increasing altitude. Consequently, k_h^{theor} was roughly 10 fold smaller at 3060 m elevation simply due to anatomical reasons. A similar reduction in vessel diameter with increasing elevation was also observed by Noshiro et al. (1994) and Noshiro et al. (1995) in *Alnus nepalensis* trunks along an altitudinal transect in Nepal. In addition, viscosity of water increased by about 30% from 1050 to 3060 m, which further slows down water flow in the roots and in the soil as well.

Despite a very high diurnal and day-to-day variability in sap flow, one can draw the conclusion that sap flow density in roots was about three fold higher at 1050 m than at 3060 m. Given the fact that the theoretical axial conductivity was more than 10 fold higher at 1050 m and VPD was, on average, much larger as well, we conclude that resistances other than root axial resistance in the soil-plant-atmosphere continuum must play a key role in reducing water flux through the roots at the lowermost stand. Among them could be radial root resistances, resistances in the soil-root interface, or an effective stomatal regulation of transpiration. Furthermore, actual axial root conductivity could be much lower than k_h^{theor}. The great relative importance of VPD in controlling root sap flow at 1050 m makes it likely that stomatal control is much more important at low than at high elevation. On the other hand, relative influence of temperature greatly increased toward the upper montane stand, which points to an inhibiting effect of low temperature on water uptake, possibly through energy limitations of aquaporine activity in root membranes in cold periods.

Apart of low soil temperature, water transport across cells is also sensitive to a lack of oxygen in waterlogged soils, especially in trees growing close to the treeline (Stevens and Fox 1991). Furthermore, Harvey and van den Driessche (1999) report about increasing vessel diameters with increasing N-supply in greenhouse-grown poplars, thus an effect of nutrient supply on root water uptake seems to be evident. This fact can also be related to our altitudinal transect study, as we observed reduced nutrient availabilities, in particular N, with increasing altitude (Graefe et al. unpublished). According to Wagner et al. (1998), mechanical strength and hydraulic conductivity per xylem transversal area are negatively related in chaparral shrubs in California. This trade-off could also be important in the tree species growing in the upper montane forest stand, where the root system needs to provide an effective anchorage, as this forest stand is subjected to high wind speeds (Soethe et al. 2006). Thus, besides low temperature, nutrient shortage, water logging and possibly wind are environmental factors that could be responsible for the small average vessel size in roots at high elevation, thereby hampering root water uptake.

We conclude that root water uptake is markedly reduced upslope along this altitudinal transect, reaching very low rates in the elfin forest close to the alpine timberline. It appears that the decrease occurs more or less continuously with increasing elevation, and is a consequence of both increasing physical limitations of water transport in the SPAC (increasing viscosity and decreasing VPD) and a decreasing axial hydraulic conductivity of the root. The continuous temperature decrease along the slope acts on water uptake through several pathways, (i) on the physics of water flow in the SPAC, (ii) by reducing vessel cell growth, (iii) by restricting nutrient availability, and (iv) by possibly lowering aquaporine activity in the roots. Our findings are support of the view that important physiological processes such as root water absorption are more or less continuously impaired by temperature decrease along tropical mountain slopes, thereby causing tree height and tree growth to decrease toward the alpine timberline.

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CHAPTER 6

Synthesis

Background

Fine roots are highly dynamic plant organs, which are responsible for the uptake of water and nutrients from soil resources. The turnover of fine roots (i.e. the replacement of existing fine root biomass by new fine root biomass) plays an important role in the cycling of carbon and nutrients in ecosystems (Gill and Jackson 2000; Clark et al. 2001). This is especially due for tropical mountain forests, which are characterised by thick organic layers and high amounts of fine root biomass (Vogt et al. 1996; Cairns et al. 1997; Hertel and Leuschner in press). It is well known that the turnover of soil organic matter decreases with increasing elevation in these forests, resulting in an increased belowground carbon sequestration at higher altitudes (Raich and Schlesinger 1992; Bird et al. 1994; Iost 2008). The knowledge about fine root dynamics and its related carbon and nutrient fluxes on the other hand is rather scarce, which is amongst others due to methodological difficulties (Vogt et al. 1998). Several authors found a pronounced increase of fine root biomass and necromass with increasing altitude in tropical montane forests (i.e. Kitayama and Aiba 2002; Hertel et al. 2003; Roederstein et al. 2005; Leuschner et al. 2007; Moser et al. 2008). Previous studies indicate a 4-fold increase of fine root biomass and an 18-fold increase of fine root necromass along an elevational transect between 1050 and 3060 m in a South Ecuadorian mountain rainforests (Moser et al. 2008), which is also the study region of the present thesis.

The study was conducted in five forest stands between 1050 and 3060 m, and aimed at answering following main questions:

1) How do environmental conditions along the elevational transect affect fine root turnover?
2) Are nutrient limitation and high soil water contents limiting factors for fine root growth?
3) Do roots show a reduced uptake of nutrients and water with increasing elevation?

Fine root turnover as affected by altitude

On a global scale, temperature was identified as the most important factor explaining fine root turnover rates, as high temperatures enhance root maintenance respiration, nutrient mineralization and the activity of root pathogens (Gill and Jackson 2000; Lauenroth and Gill 2003). The minirhizotron study yielded relatively high rates of fine root turnover in the lower, pre-montane part of the altitudinal transect, i.e. 0.9 yr^{-1} for roots with a diameter < 2 mm and 1.4 yr^{-1} for roots with diameter < 0.5 mm at an altitude of 1050 m. These results are comparable to fine root turnover rates of tropical lowland forests (Herbert and Fownes 1999; Priess et al. 1999; Gill and Jackson 2000). The turnover of fine roots in mid-montane forests of the transect at altitudes between 1500 and 2000 m was considerably lower (i.e. 0.5 yr^{-1} at

1890 m for fine roots with a diameter < 2 mm). Hence the temperature effect on fine root turnover can be also attributed to the lower part of the altitudinal transect, where a temperature decrease by 3.7 K between 1050 m and 1890 m resulted in a 40% decrease of fine root turnover.

However, the decrease of fine root turnover with increasing elevation did not follow this pattern towards the upper montane forest stands; in contrast, fine root turnover decreased significantly in the upper part of the transect. This had the consequence that at 3060 m fine root turnover rates were similar to the lowermost stand at 1050 m, resulting in a U-shaped turnover curve for the whole transect.

The upper part of the altitudinal transect is characterised by a perhumid climate with high precipitation and soil moisture, and partly waterlogged soils. Soil pH is also very low (i.e. 2.9 at an altitude of 3060 m, Iost 2008). Both oxygen deficiency and an acid soil environment are known to increase fine root turnover (Godbold et al. 2003; Jackson and Ricard 2003). Upper montane forests are further characterised by high C/N ratios in the organic layer and reduced nutrient mineralisation rates (Tanner et al. 1998; Benner et al. in press). Several authors found increased fine root turnover rates when nutrient supply, especially nitrogen, was limited (Vogt et al. 1986; Pregitzer et al. 1993; Burton et al. 2000). For the upper montane forests stands it can be assumed, that the costs for a tree in terms of carbon supply to the roots for extended periods are too high, when related to the nutrients the roots provide. In nutrient poor soils it may be more advantageous to produce new roots which are more efficient in nutrient uptake. This shift in carbon allocation to fine absorbing roots at low temperatures was also observed by Tyron and Chapin (1983) in boreal trees. It seems to be obvious, that fine root dynamics along the elevational transect in South Ecuador are controlled by several environmental factors, which counteract the influence of temperature, resulting in a non linear altitudinal trend of fine root turnover.

The combination of fine root turnover values with data on standing fine root biomass obtained from soil coring (Roederstein et al. 2005; Moser 2008) could be used to estimate absolute fine root production, as well as associated flows of carbon and nutrients. First estimates from a combination of fine root turnover and biomass data yielded a more than 4-fold increase of fine root production between 1050 and 3060 m (Moser 2008), indicating a marked shift in carbon allocation from above- to belowground biomass with increasing elevation. However, it should be considered that minirhizotron observations tend to favour the sampling of the most dynamic part of fine root populations. A further discrepancy could be the fact, that fine root turnover rates obtained during this study just refer to the first 10 cm of the organic layer, which is assumed to have a more rapid turnover than deeper soil horizons, hence total fine root production may be overestimated to some degree. For analysing larger fine roots with a slower turnover, radio carbon tracer methods (^{14}C) are considered to yield more reliable estimates. The combination of both minirhizotron and ^{14}C methods should improve the understanding of both ends of fine root age distribution (Tierney and Fahey 2002; Trumbore and Gaudinski 2003; Majdi et al. 2005; Strand et al. 2008).

Influence of adverse soil conditions on fine root activity

Phosphorous is the key nutrient limiting tree growth in tropical lowland and pre-montane rainforests growing on highly weathered soils, whereas younger and less developed soils of upper montane rainforests are rather limited by the supply of nitrogen (Vitousek and Sanford 1986; Tanner et al. 1992; Tanner et al. 1998; Paoli et al. 2005; Benner et al. in press). A fertilization experiment conducted by means of root ingrowth cores in forests stands at 1050 and 3060 m supported this assumption, as the strongest ingrowth of fine root mass at the lower altitude was observed for the P treatment, and at the higher altitude for the N treatment. As roots have high nutrient demands and react sensitively to nutrient addition, the ingrowth of roots into the treatments can be regarded as a solid indicator for nutrient limitation.

The analysis of nutrient concentrations in fine root tissue yielded decreasing concentrations of major nutrients (N, P, K, Ca, Mg) with increasing altitude, which points to a limited nutrient uptake at higher elevations. The steepest decrease in nutrient concentration was observed for nitrogen. As a result of low temperatures the decomposition of organic matter is slowed down at higher altitudes, which leads to an increased nutrient immobilisation (Marrs et al. 1988; Tanner et al. 1998). Tropical mountain rainforests are further characterised by decreasing litter production with increasing altitude (Roederstein et al. 2005; Moser et al. 2007). Extractable P was found to be positively related to litter production (Tanner et al. 1998; Paoli et al. 2005), and could be therefore short in supply at higher elevations.

Nutrient transport in mass flow and the uptake of nutrients by roots is apparently reduced by low temperatures at higher elevations in tropical montane forests. A ^{15}N tracer experiment was conducted in forest stands at 1050, 1890 and 3060 m, in order to test for a reduced N uptake activity of fine roots with increasing elevation. Indeed, the experiment did not reveal an inhibition of N uptake with increasing altitude. Five days after the onset of the experiment similar $\delta^{15}N$ values in fine root tissue were observed in all three forest stands. In the mid-elevation and the uppermost stand, 50% of the maximum $\delta^{15}N$ value was already reached in less than 2 hours after tracer application. In the lowermost stand on the other hand, 50% of the maximum $\delta^{15}N$ value was approached only after ca. 32 hours. However, the study did not yield information on how much translocation of ^{15}N labelled tracer from roots to the stem took place; it can be assumed that a rapid shift of the tracer to above ground plant parts occurred in the lowermost stand. A reason for the high ^{15}N absorption capacity at 3060 m could be due to high fine root turnover rates in this forest stand, resulting in relatively young fine root biomass with a high nutrient uptake capacity. Evidence exists for a temperature insensitive nutrient uptake in slow-growing taiga tree species, which can be explained as an adaptation to low soil temperatures (Chapin et al. 1986). This finding could be possibly also attributed to the uppermost stand of the South Ecuadorian transect, which is characterised by slow-growing tree species of small stature (G. Moser, unpublished data).

A throughfall exclusion experiment in the uppermost forest stand aimed to test the assumption that soil anoxia is a main cause for the high fine root turnover rate in this forest stand, as it was observed in the minirhizotron study. High soil water contents are known to pose stress on the root system, as they increase the concentration of toxic ions, and reduce decomposition and nutrient mineralization (Raynal et al. 1990; Jackson and Ricard 2003; Benner et al. in press). Indeed, better growing conditions for fine roots at reduced soil moisture could not be proven by the exclusion of throughfall; in contrast, root growth was reduced and turnover was slightly but not significantly higher under the desiccation treatment. It can be assumed, that the reduced root length production was possibly due to a more pronounced root growth to deeper soil layers which were not affected by desiccation, however, the experiment only yielded data about the first 10 cm of the organic layer.

The throughfall exclusion experiment allows to draw the conclusion, that the fine root system is well adapted to the wet conditions occurring in the uppermost forest stand, and that the high fine root turnover may be rather due to a limited nutrient availability, as discussed above. However, a limited nutrient supply in upper montane forests is certainly a consequence of the cold and moist soil environment. Tree species growing in upper montane forests close to the treeline may compensate for low temperatures and limited nutrients with a highly efficient nutrient uptake capacity.

Temperature effects on root sap flow

Sap flow of roots with a diameter of 10 mm was found to be strongly coupled to daily and seasonal changes in VPD. As a whole, VPD was identified as the most influential environmental factor explaining root water uptake. However, the influence of VPD on sap flow density decreased with increasing altitude. At 1050 m VPD was found to explain 75% of the variability in root sap flow, at 3060 m only 5%. The influence of temperature on the other hand increased with increasing altitude. No significant influence of temperature was observed at 1050 m, but explained nearly 50% of the variability at 3060 m. The third variable, soil moisture, was detected to have only a minor influence for explaining the variability of root sap flow density in the three forest stands.

VPD is the main driver for tree transpiration, and an increased evaporative demand will consequently increase the demand for water. However, when VPD was above average for several days, a reduction in root sap flow was observed. This pattern was found to occur more frequently with increasing elevation. A stomatal closure of leaves is known to occur at high VPD values, even when water supply is not limiting, resulting in a saturation or even reduction of sap flow (Cavelier 1990; Meinzer et al. 1993; Motzer et al. 2005). This saturation point seems to be reached faster the higher the elevation in montane forests, as tree species growing under wet and cloudy conditions are not adapted to high VPD values over longer periods. Tree species growing in pre-montane forests under high and strongly variable VPD are better adapted to fluctuations of evaporative demands.

The anatomical analysis of root cross sections revealed decreasing vessel diameters with increasing altitude, and a significant decrease of the theoretical hydraulic conductivity (k_h^{theor}) from 50.2 m² MPa^{-1} s^{-1} at 1050 m to 4.0 MPa^{-1} s^{-1} at 3060 m. The xylem hydraulic conductivity depends on the fourth power of the radius, thus large vessels contribute much more to conductivity than numerous smaller vessels (Tyree and Ewers 1991). This fact is highlighted by the distribution of vessel sizes and related k_h^{theor} at different elevations of the transect. In the lowermost stand, only 5 vessels per mm² conducting vessel area were classified into the largest diameter class (vessel diameter > 100 µm), but contributed 70% to total k_h^{theor}. The smallest diameter class (vessel diameter < 25 µm) was represented by 950 vessels mm^{-2} conducting vessel area, but the contribution to total k_h^{theor} was only marginal (< 5%). In the uppermost forest stand on the other hand, the largest share of k_h^{theor} was sustained by small diameter vessels, which yielded an overall low conductivity. The mid-elevation forest stand showed intermediate values.

Sap flow density was about three fold higher at 1050 m than at 3060 m, which leads to the conclusion, that root water absorption is markedly impaired by increasing elevation. This is certainly a consequence of both increasing physical limitations of water transport in the soil-plant-atmosphere continuum (i.e. increasing viscosity of water, decreasing VPD) and a decreasing axial hydraulic conductivity of the root (i.e. through reduced vessel cell growth).

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CHAPTER 7

Summary

Zusammenfassung

Resumen

Summary

Tropical mountain rainforests extend over large elevational gradients with diverse climatic conditions. They are characterised by a decrease of above ground biomass, and a pronounced increase of fine root biomass with increasing elevation. Forest stands at higher elevations are further characterised by thick organic layers and very moist soil conditions. The turnover of fine roots plays an important role in the cycling of carbon and nutrients in theses ecosystems. However, the knowledge about the patterns of fine root dynamics in tropical mountain rainforests is still scarce. Likewise, not much is known about water and nutrient uptake capacities of roots at different elevations.

The present study was conducted in five forests stands along an elevational transect between 1050 and 3060 m asl in a mountain rainforest of South Ecuador. It aimed (1) to analyse the effect of temperature and soil conditions on fine root turnover along the elevational transect by means of minirhizotrons; (2) to assess the role of nutrient limitation and water-logging for fine root activity by means of a fertilization and throughfall exclusion experiment, respectively; as well as to examine nitrogen uptake capacity of fine roots by ^{15}N tracer application; and (3) to investigate the dependence of root sap flow on environmental variables by means of miniature heat balance sap flow gauges, and to analyse related anatomical characteristics of root cross sections.

Fine root turnover (d < 2 mm) was significantly higher in the lowermost and the uppermost stand (0.9 cm cm^{-1} yr^{-1}) than in the three mid-elevation stands (0.6 cm cm^{-1} yr^{-1}). The turnover of finest roots (d < 0.5 mm) was higher compared to the root cohort with d < 2 mm, and exceeded 1.0 cm cm^{-1} yr^{-1} at the lower and upper elevations of the transect. Hence fine root turnover decreased from pre-montane to mid-montane forests as would be expected from an effect of low temperature on root turnover, but it decreased further upslope despite colder temperatures. It is assumed that this non linear altitudinal trend of fine root turnover originates from an overlapping of a temperature effect with other environmental gradients in the upper part of the transect. Adverse soil conditions may reduce root longevity at high elevations, and are thus additional factors besides temperature that control root dynamics in tropical mountain forests. The fast replacement of fine roots is possibly used as an adaptive mechanism by trees to cope with limiting environmental conditions.

The fertilizer study revealed highest root growth stimulation after P addition at 1050 m, and after N addition at 3060 m, thus pre-montane forests may be presumably limited by the availability of P, whereas upper montane forests are rather limited by the availability of N. The concentrations of major nutrients in fine root tissue dropped significantly along the elevational transect, with strongest reductions observed for N. This may support the assumption of a decreased nutrient availability with increasing altitude. Throughfall exclusion

at 3060 m did not reduce fine root mortality in this forest stand, hence high soil moisture contents do not seem to be a main stressor leading to high fine root turnover rates in upper montane forests. The $^{15}NO_3{}^{15}NH_4$ uptake study yielded a constantly high nitrate and ammonium uptake capacity of fine roots at altitudes at 1050, 1890 and 3060 m, suggesting that fine roots in upper montane forests compensate for low nutrient supplies with high nutrient uptake capacities.

Root sap flow followed marked diurnal and seasonal courses in the forest stands at 1050, 1890 and 3060 m. Sap flow decreased roughly by a factor of three between the lowermost and the uppermost forest stand. A reduced sap flow was observed when VPD was above average for several days. VPD was identified as the most influential environmental factor controlling root water uptake, but its significance decreased with increasing altitude. In contrast, the influence of temperature increased along the elevational transect, and was identified as the most influential factor determining root sap flow at 3060 m. Anatomical analyses of root cross-sections provided evidence for decreasing vessel diameters with increasing altitude. Theoretical hydraulic conductivity was found to decrease more than ten fold from 50.2 $m^2\ MPa^{-1}\ s^{-1}$ at 1050 m to 4.0 $m^2\ MPa^{-1}\ s^{-1}$ at 3060 m. It is concluded that the temperature decrease with increasing altitude acts on water uptake through several pathways, (i) on the physics of water flow in the soil-plant-atmosphere continuum (increasing viscosity of water, decreasing VPD), (ii) by reducing vessel cell growth, (iii) by restricting nutrient availability (which may lead to smaller vessels), and (iv) possibly by lowering aquaporine activity in the roots.

Zusammenfassung

Tropische Bergregenwälder erstrecken sich über große Höhenstufen und sind damit unterschiedlichen klimatischen Bedingungen ausgesetzt. Eine charakteristische Veränderung dieser Ökosysteme ist die Abnahme der oberirdischen und die Zunahme der unterirdischen Biomasse mit ansteigender Meereshöhe. Waldbestände in großen Höhenlagen sind zudem durch mächtige organische Auflagen und relativ nasse Bodenverhältnisse gekennzeichnet. Für den Kohlenstoff- und Nährstoffkreislauf spielt der Umsatz von Feinwurzeln eine wichtige Rolle in diesen Ökosystemen. Das Wissen über Feinwurzelumsätze in tropischen Bergregenwäldern ist bisher jedoch sehr begrenzt. Ebenso ist nicht viel über die Wasser- und Nährstoffaufnahmekapazität von Wurzeln auf unterschiedlichen Höhenstufen bekannt.

Die vorliegende Arbeit wurde in fünf südecuadorianischen Bergregenwaldbeständen entlang eines Höhengradienten von 1050 bis 3060 m üNN durchgeführt. Ziel der Studie war es, (1) den Einfluss von Temperatur und Bodeneigenschaften auf den Feinwurzelumsatz entlang des Gradienten mit Hilfe von Minirhizotronen zu untersuchen, (2) die Bedeutung von Nährstofflimitierung und Staunässe für die Aktivität von Feinwurzeln durch ein Düngungs- bzw. Austrocknungsexperiment zu testen sowie die N-Aufnahmefähigkeit von Feinwurzeln durch ein ^{15}N-Tracer-Experiment zu erfassen und (3) mit Miniatur-Saftflusssystemen die Abhängigkeit des Wurzelsaftflusses von Umweltvariablen zu untersuchen sowie anatomische Charakteristika von Wurzelquerschnitten zu analysieren.

Der Umsatz von Feinwurzeln (d < 2 mm) war in dem untersten und dem obersten Waldbestand signifikant höher (0.9 cm cm^{-1} $Jahr^{-1}$) als in den drei Bestände auf mittleren Höhenstufen (ca. 0.6 cm cm^{-1} $Jahr^{-1}$). Der Umsatz von Feinstwurzeln (d < 0.5 mm) war generell höher als der Feinwurzelumsatz (d < 2 mm) und überschritt 1.0 cm cm^{-1} $Jahr^{-1}$ an den beiden Endpunkten des Transektes. Der Feinwurzelumsatz nahm demnach vom prae-montanen zum montanen Bestand ab, wie man es vom Einfluss niedrigerer Temperatur auf physiologische Prozesse erwarten würde, nahm jedoch mit noch größerer Meereshöhe wieder zu. Dieser nicht-lineare Trend lässt sich durch ein Überlappen des Temperatureffektes mit anderen Umweltgradienten in der oberen Hälfte des Höhentransektes erklären. Neben der Temperatur sind vermutlich ungünstige Bodenbedingungen der Grund für die verkürzte Lebensdauer der Feinwurzeln in hochmontanen Bergregenwäldern. Ein hoher Feinwurzelumsatz ist offenbar eine Anpassungsstrategie von Bäumen an limitierende Umweltbedingungen in großen Höhenlagen.

Das Düngungsexperiment ergab nach einer P-Düngung das stärkste Wurzelwachstum auf 1050 m, und nach einer N-Düngung auf 3060 m, was darauf schließen lässt, dass prae-

montane Wälder P limitiert sind, während hochmontane Wälder eher N limitiert sind. Nährstoffkonzentrationen in Feinwurzeln, insbesondere N, nahmen signifikant mit zunehmender Höhe ab, was auf eine verminderte Nährstoffverfügbarkeit mit zunehmender Meereshöhe deutet. Das Austrocknungsexperiment lieferte keine Hinweise auf eine reduzierte Feinwurzelmortalität unter trockeneren Bodenbedingungen. Nässe scheint somit keine Erklärung für den hohen Feinwurzelumsatz in großen Höhenlagen zu sein. Das ^{15}N-Tracer-Experiment ergab eine konstant hohe Aufnahmerate von Nitrat und Ammonium auf allen drei Flächen (1050, 1890 und 3060 m), was annehmen lässt, dass Feinwurzeln in hochmontanen Bergregenwäldern eine verminderte Nährstoffverfügbarkeit durch eine hohe Nährstoffaufnahmekapazität kompensieren.

Saftfluss in Wurzeln folgte deutlich täglichen und saisonalen Schwankungen des Wasserdampf-Sättigungsdefizits der Luft (VPD) in den drei Waldbeständen auf 1050, 1890 und 3060 m, nahm aber etwa um den Faktor drei zwischen dem untersten und dem obersten Bestand ab. Eine verminderte Saftflussrate wurde beobachtet, wenn VPD über mehrere Tage überdurchschnittlich hoch war. VPD wurde als einflussreichster Umweltfaktor für die Wurzelwasseraufnahme identifiziert, sein Einfluss nahm aber mit zunehmender Meereshöhe ab. Dagegen stieg der Einfluss von Temperatur mit zunehmender Höhe stark an und war in dem höchstgelegenen Bestand der Faktor mit dem größten Einfluss auf den Wurzelsaftfluss. Anatomische Analysen von Wurzelquerschnitten ergaben abnehmende Gefäßdurchmesser mit zunehmender Meereshöhe. Die theoretische hydraulische Leitfähigkeit nahm dadurch um mehr als das 10-fache entlang des Höhentransektes ab. Die Temperaturabnahme mit zunehmender Meereshöhe wirkt folglich über verschiedene Mechanismen auf die Wurzelwasseraufnahme: (i) den physikalischen Wasserfluss im Boden-Pflanze-Atmosphäre-Kontinuum durch die höhere Viskosität des Wassers und eine Abnahme von VPD, (ii) durch ein vermindertes Wachstum von Zellen der leitenden Gefäße, (iii) durch eine verminderte Nährstoffverfügbarkeit und (iv) durch eine möglicherweise verminderte Aquaporin-Aktivität in den Wurzeln.

Resumen

Los bosques tropicales montañosos se extienden sobre amplios gradientes altitudinales con condiciones climáticas diversas. En estos bosques se observa una reducción de la biomasa aérea y un incremento marcardo de la biomasa de raíces con un aumento en la altitud. Además, los suelos de bosques de altitudes elevadas tienen una capa organica profunda y condiciones de alta humedad. La tasa de renovación de raíces finas juega un rol importante en el ciclo de carbono y nutrientes en estos ecosistemas. Sin embargo, aún no existe mucho conocimiento sobre la dinámica de crecimiento de raíces finas en los bosques montañosos, como tampoco sobre la capacidad de las raíces de absorber agua y nutrientes a differentes altitudes.

El presente estudio se llevó a cabo en cinco áreas de bosque no disturbado a lo largo de un gradiente altitudinal entre 1050 y 3060 m s.n.m en un bosque tropical montañoso en el sur de Ecuador. Los objetivos de este trabajo fueron (1) analizar la influencia de la temperatura y la calidad del suelo sobre la tasa de renovación de raíces finas a lo largo del gradiente altitudinal por medio de minirizotrones; (2) investigar el efecto de la limitación de nutrientes y de la saturación con agua sobre la actividad de las raíces finas mediante un experimento de fertilización y un experimento de desecamiento, respecitivamente; así como examinar la capacidad de las raíces finas de absorber nitrógeno a través de la aplicación de un marcador ^{15}N; y (3) determinar la relación entre la adquisición de agua por las raíces y las variables ambientales por medio de sensores de flujo de savia y el análisis de las characteristicas anatómicas en cortes transversales de raíces.

La tasa de renovación de raíces finas (d < 2 mm) fué más alta en los sitios de mayor y menor elevación (0.9 cm cm^{-1} $año^{-1}$) que en los tres sitios intermedios (0.6 cm cm^{-1} $año^{-1}$). Por lo general, la tasa de renovación de raíces muy finas con un diámetro < 0.5 mm fue más alta que la de las raíces con un diámetro < 2 mm, y excedió un 1.0 cm cm^{-1} $año^{-1}$ en sitios localizados en los extremos del transecto. Así, la tasa de renovación de raíces finas disminuyó de los bosques de altitud baja hacia los bosques de altitud media, lo que se puede asumir como un efecto de la disminución de la temperatura sobre la tasa de renovación. Sin embargo, al mismo tiempo tasa de renovación de raíces finas aumentó hacía la altitud más elevada a pesar de una disminución progresiva de la temperatura. Esta tendencia no linear en el aumento de la tasa de renovación de raíces finas a lo largo del gradiente altitudinal proviene probablemente de un solapamiento del efecto de la temperatura con otros gradientes ambientales en la parte más elevada del transecto. Características desfavorables de los suelos pueden disminuir el tiempo de vida de raíces finas en altitudes elevadas, y son factores adicionales además del efecto de la temperatura que controlan la dinámica de raíces finas en bosques tropicales montañosos. La renovación

rápida de raíces finas es supuestamente un mecanismo de adaptación de los árboles a las condiciones ambientales limitantes.

Los resultados del experimento de fertilización mostraron el máximo incremento en el crecimiento de raíces con la aplicación de fósforo (P) en el sitio à 1050 m y con la aplicación de nitrógeno (N) en el sitio à 3060 m. Estos resultados indican una escasez de P en los bosques de baja altitud, y una limitación de N en los bosques elevados. El contenido de nutrientes principales en la materia seca de raíces finas, sobre todo N, disminuyó claramente a lo largo del gradiente altitudinal. Este resultado sostiene la suposición de una marcada escazes de nutrientes à elevadas altitudes. Además, no se observó una reducción en la mortalidad de raíces finas en el experimento de desecamiento, entonces se puede suponer que las condiciones de alta húmedad en el suelo del bosque más elevado no son la causa de la alta tasa de renovación de raíces finas en este sitio. El ensayo de marcación con ^{15}N NH_4NO_3 indicó una alta capacidad de las raíces de absorber nitrato y amonio en todos los tres sitios (1050, 1890 y 3060 m). De estos resulatdos se puede concluir que las raíces finas en los bosques elevados compensan la aminorada disponibilidad de nutrientes con una capacidad efectiva de absorber nutrientes.

El flujo de savia en las raíces siguió claramente los cambios diarios y temporales del VPD (déficit de presión de vapor de agua) en los bosques a 1050, 1890 y 3060 m, y fué tres vecs más alto en el sitio más bajo que en el sitio más elevado. Además se observó un flujo de savia reducido cuando el VPD fue superior al promedio diario. El VPD fue el factor más influyente en la adquisición de agua, pero su importancia disminuyó con la altitud. Al contrario, la influencia de la temperatura incrementó a lo largo del gradiente altitudinal, y fue el factor más importante para el control del flujo de savia a 3060 m. El análisis anatómico de los cortes transversales de las raíces reveló una disminución del diámetro de los tubos vasculares con el aumento en altitud, sin embargo la conductividad hidraulica teorética declinó diez veces a lo largo del transecto. La disminución de la temperatura en los bosques montañosos influye sobre la captura de agua de las raíces a través de diversos mecanismos: (i) sobre las cualidades físicas del flujo de agua en el continuum planta-suelo-atmósfera mediante el aumento en la viscosidad del agua y una disminución del VPD, (ii) una supresión en el crecimiento de las células vasculares, (iii) una baja disponibilidad de nutrientes, y (iv) una actividad reducida de los aquaporines en las raíces.

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