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Structure and function of root systems at different altitudes of a south Ecuadorian montane forest

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Abstrakt

Es wurden Wurzelsysteme auf 1900, 2400 und 3000 m eines südecuadorianischen Bergregenwaldes untersucht. Ziel war es, ein besseres Verständnis über den Einfluss der Höhenstufe auf die Wurzelfunktionen Nährstoffaneignung und Verankerung sowie Speicherung von C und Nährstoffen in der Wurzelbiomasse zu erlangen.

Auf 2400 und 3000 m nahmen die Wurzellängendichten (WLD) mit zunehmender Bodentiefe schneller ab als auf 1900 m. Die vertikale Verteilung der N-Aufnahme war ähnlich der Verteilung der WLD. Das Nährstoffaneignungsvermögen war also in größerer Meereshöhe deutlich mehr auf die organische Auflage konzentriert war als auf 1900 m.

Nährstoffkonzentrationen in Blättern zeigten, dass auf 1900 m das Pflanzenwachstum nicht durch Nährstoffmangel limitiert war, während auf 2400 und 3000 m v. a. N, aber auch P, S und K das Pflanzenwachstum limitierten. Die schlechte Nährstoffversorgung der Pflanzen in großer Meereshöhe war vermutlich auf langsame Mineralisation organisch gebundener Nährstoffe und auf ein geringes Nährstoffaneignungsvermögen aus tieferen Bodenschichten zurückzuführen.

Die Wurzelbiomasse war auf 3000 m höher als in niedrigerer Meereshöhe. Die Bedeutung des Wurzelsystems für die C-Speicherung stieg also mit zunehmender Höhenstufe. Auch Vorräte an N, S, K, Ca und Mg in den Wurzeln waren auf 3000 m am höchsten.

Die Grobwurzelsysteme der Bäume wiesen auf allen Höhenstufen Verankerungs-fördernde Merkmale auf. Bäume auf 3000 m bildeten flachgründigere Wurzelteller als auf 1900 m. Wurzeleigenschaften, die die horizontale Ausdehnung des Wurzeltellers fördern, waren auf 3000 m häufiger oder ausgeprägter als auf 1900 m.

Es wird gefolgert, dass eine gehemmte Tiefendurchwurzelung des Bodens in größerer Meereshöhe sowohl das Nährstoffaneignungsvermögen als auch auf die Verankerung der Bäume verringerte. Die hohe Biomasseallokation in die Wurzeln in größerer Meereshöhe weist darauf hin, dass Umweltbedingungen hier besondere Anforderungen an die Wurzelfunktionen stellen.

Schlagwörter:
Kohlenstoffsequestrierung
Nährstoffaufnahme
Nährstoffspeicherung
Verankerung
Wurzelarchitektur

Abstract

Root systems at 1900, 2400 and 3000 m of a south Ecuadorian montane forest were investigated. The aim of this study was to improve our knowledge on the impact of altitude on the root functions nutrient acquisition, anchorage and storage of C and nutrients in root biomass.

At 2400 and 3000 m, the decrease of root length densities (RLD) with increasing soil depth was more pronounced than at 1900 m. The vertical distribution of N uptake was similar to the vertical distribution of RLD. Thus, the ability for nutrient uptake was more concentrated to the organic surface layer at high altitudes than at 1900 m.

Foliar nutrient concentrations showed that plant growth at 1900 m was not limited by nutrient deficiency. In contrast, at 2400 and 3000 m especially N, but also P, S and K limited plant growth. The decreased nutritional status of plants at high altitudes was caused by low mineralization rates of nutrients as well as low ability for nutrient acquisition from deeper soil layers.

At 3000 m, root biomass was higher than at low altitudes. Hence, the importance of root systems for C sequestration increased with increasing altitude. Similarly, pools of N, S, K, Ca and Mg were higher at 3000 m than at 1900 and 2400 m.

At all altitudes, coarse root systems of trees showed traits that are supposed to improve anchorage. At 3000 m, root soil plates were more superficial than at 1900 m. Root traits that improve the horizontal extension of root soil plates were more pronounced or occurred more often at 3000 m than at 1900 m.

It is concluded that impeded rooting in deeper soil layers at high altitudes decreased both the ability for nutrient acquisition and anchorage. At high altitudes, the high allocation of biomass to the root systems showed that at these sites, environmental conditions enhanced the requirements to the functions of roots.

Keywords:
anchorage
carbon sequestration
nutrient acquisition
nutrient storage
root architecture

„Den Äquator messen, fuhr Pater Zea fort. Also eine Linie ziehen, wo nie eine gewesen sei. Ob sie sich dort draußen umgesehen hätten? Linien gebe es woanders. Mit seinem knochigen Arm zeigte er auf das Fenster, das Gestrüpp, die von Insekten umschwärmten Pflanzen. Nicht hier!“

aus Daniel Kehlmann (2005): „Die Vermessung der Welt“

Contents

Summary

Root systems are important for ecosystem functioning mainly because of regulating plant productivity, nutrient retention from soil, nutrient immobilization in biomass and organic matter production. Little is known about root systems in tropical montane forests. In tropical montane forests, temperature decreases and precipitation and wind speeds usually increase with increasing altitude. Frequencies of waterlogging in soils of high altitudes are high in tropical montane forests. In many cases, the depth of the organic layer increases with increasing altitude. It can be assumed that structure and function of root systems are markedly influenced by the change of environmental conditions along altitudinal gradients.

In the present study root systems were investigated at three altitudes (1900, 2400 and 3000 m a.s.l.) of a tropical montane forest in southern Ecuador. The aim was to examine the impact of environmental changes along the altitudinal gradient on the plant based root functions nutrient acquisition and anchorage as well as on the ecosystem based root functions nutrient retention from soil (and thus, prevention of nutrient losses from soil by leaching) and storage of carbon (C) and nutrients in root biomass.

In a first approach the ability for nutrient acquisition as well as the potential for nutrient retention by roots was investigated. It is to be expected that in deep soil layers, these functions are reduced at high altitudes in comparison to low altitudes because of unfavourable soil chemical conditions such as low soil pH, low nutrient availability in soil, and oxygen deficiency. To examine the ability for nutrient acquisition in different soil depths as well as the potential for nutrient retention from soil, root length densities (RLD) in different depths of the organic layer and the mineral soil were assessed. Additionally, the relative nitrogen (N) uptake from different soil depths was measured at 1900 and 3000 m by determining ^{15}N enrichment in leaves of different plant groups (trees, shrubs, herbs and saplings) after application of ^{15}N enriched ammonium sulphate to different soil depths.

The vertical distribution of RLD was very similar during the drier (November 2001) and the rainy season (July/August 2002). The proportion of root length in the organic layer during the drier season increased from 51 % at 1900 m to 61 % at 2400 m and 76 % at 3000 m. In the mineral soil, RLD decreased more sharply at the higher altitudes than at 1900 m. The pattern of relative N uptake closely followed root distribution confirming the more superficial ability for nutrient acquisition at higher altitudes. Relative N uptake was similar for all plant groups except saplings which obtained N only from the organic layer at both altitudes. The lower spatial exploitation of mineral soil by fine roots at higher altitudes enhanced the probability of nutrient losses from deeper soil layers by leaching.

Liming and/or fertilizing (N, phosphorus (P), potassium (K), and magnesium (Mg)) of small soil patches had no significant impact on fine root growth in deeper soil layers, indicating that impaired root growth in mineral soil of higher altitudes was neither caused by soil acidity nor by low nutrient availability.

To elucidate the impact of the plant nutritional status on the decrease of plant productivity with increasing altitude, foliar nutrient concentrations of trees, shrubs and herbs at different altitudes were assessed. Comparison of foliar nutrient concentrations of trees with reference data from literature suggested that at 1900 m tree growth was not limited by nutrient deficiency. At 2400 and 3000 m, N, P, sulphur (S) and K concentrations of tree leaves were lower than at 1900 m. A similar decrease in nutrient concentrations was observed in leaves of shrubs and herbs, indicating that altitude dependent differences in foliar nutrient concentrations were caused by differences in plant nutritional status rather than by differences in species composition between altitudes. Foliar concentrations of N, S, P and K of trees at 2400 and 3000 m fell into or near the range of nutrient deficiency given in literature. Comparison of foliar N:P ratios with reference data from literature as well as nutrient indices calculated by the “Diagnosis and Recommendation Integrated System” (DRIS; Beaufils 1973) indicated that N was the most growth limiting nutrient at higher altitudes. The decreased plant nutritional status at higher altitudes may be induced by low mineralization rates of organically bound nutrients in the organic layer and low ability for nutrient uptake from deeper soil layers.

Considerable proportions of terrestrial C are sequestered in tropical rain forests. However, little is known about the contribution of tropical montane forests to C sequestration. Also the contribution of root biomass to nutrient accumulation and turnover is poorly understood. In a third approach, the ecosystem based root function of C and nutrient storage was investigated. Storage of C and nutrients in root biomass at different altitudes was assessed for different root diameter classes, because root diameter has a substantial impact on nutrient cycling by root turnover (mainly goverened by fine roots) and long term nutrient accumulation (mainly goverened by coarse roots).

Compared to C stocks in the aboveground biomass and soil, root biomass contributed between 3 and 10 % to total C in the ecosystem, showing that root biomass stored only a small proportion of C that is sequestered in this tropical montane forest. Fine root biomass (≤ 2 mm in diameter) as well as coarse root biomass (> 2 mm in diameter) was significantly higher at 3000 m than at lower altitudes. The contribution of coarse root biomass to total root biomass increased from about 70 % at 1900 m to about 80 % at higher altitudes.

Nutrient concentrations in coarse roots of *G. emarginata* (Ruiz & Pav.) Triana (Melastomataceae) were little affected by altitude. In roots ≤ 5 mm in diameter, C concentrations slightly increased with increasing altitude while concentrations of N, P, S, K and Mg markedly decreased, reflecting the decrease in plant nutritional status with increasing altitude.

Due to the decrease in nutrient concentrations with increasing altitude in combination with increasing biomass, nutrient stocks in fine root biomass showed no uniform increase or decrease with increasing altitude. Nutrient stocks in coarse and total root biomass were estimated with help of nutrient concentrations in roots of *G. emarginata*. Stocks of all nutrients in the total root biomass but P were markedly higher at 3000 m than at 1900 and 2400 m.

At all altitudes, large proportions of total root N, S, and P (35.4-72.7 %) were stored in the fine root biomass and thus contributed to short term nutrient cycling, but only a small proportion (5.3-9.3 %) of total root Ca. Estimated amounts of nutrient that reach the litter pool in soil by dying fine roots were similar or higher than the amounts of nutrient that reach the soil by leaf litter production. At 1900 m, estimated amounts of annual nutrient release from fine root turnover was similar to nutrient input into soil via throughfall of rain from canopy.

Steep slopes, shallow soils and high wind speeds might increase the requirements for anchorage of trees growing in tropical montane forests. In a fourth approach, the coarse root architecture of tree typical tree species growing at 1900 m (*G. emarginata*, *Clethra revoluta* (Ruiz & Pav.) Spreng. (Clethraceae), and *Vismia tomentosa* Ruiz & Pav. (Clusiaceae)) and at 3000 m (*Weinmannia loxensis* Harling (Cunoniaceae), *Clusia* spec. (Clusiacaea), and *Styrax foveolaria* Perkins (Styraceae)) was investigated in order to examine altitude and species specific root traits related to anchorage.

At 1900 m, 20 % of structural roots (> 20 mm in diameter) originated in the mineral soil, whereas at 3000 m root origin was restricted to the organic layer. Root asymmetry increased significantly from 1900 to 3000 m. This was accompanied by a significant decrease in the number of dominant roots (largest roots that contributed 80 % to total cross sectional area of all structural roots) from 1900 m to 3000 m. At 1900 m, 92 % of the trees grew upright in comparison to 52 % at 3000 m. At 3000 m, 48 % were inclined, lying or even partly uprooted, indicating that tree anchorage was hampered at this altitude. At this altitude, all trees with tap roots or with shoots connected by coarse rhizomes, 83 % of the trees with stilt roots, and 50 % of trees in which stems of roots were supported by other trees grew upright, suggesting that these traits were relevant for tree stability. Differences between coarse root architecture at

1900 and 3000 m indicate that root traits that improve the horizontal extension of the root soil plate (root asymmetry, low numbers of dominant roots, belowground connection of stems by rhizomes, stilt roots) are more pronounced or occur more frequently, when deep rooting is impeded.

It can be assumed that tree species that occur on broad altitudinal gradients are characterized by a high phenotypic plasticity. In a fifth approach the branching patterns of coarse root systems of *G. emarginata* growing at 1900 and 2400 m were investigated in order to examine phenotypic plasticity in coarse root architecture. Branching pattern were quantified by (i) the allocation factor (*q*), that classes branching pattern between the extremes “herringbone” and “dichotomous”, (ii) the proportionality factor, as a measure for the taper of a root axis, (iii) length of root segments between two branching points, and (iv) the number of root segments after a branching event following van Noordwijk and Mulia (2002).

Root systems at 1900 m were characterized by vertically growing roots similar to sinkers, whereas root systems at 2400 m were more superficial and concentrated on the organic layer. The allocation factor was the only branching parameter that was significantly affected by altitude, indicating more herringbone like branching pattern at 2400 m than at 1900 m. Differences in *q* between altitudes were not caused by differences in root growth directions. In fact, higher *q* values at 2400 m than at 1900 m may partly be interpreted as a trait to improve the rigidity of horizontal growing roots where deep rooting is impaired.

In conclusion, altitude had a marked impact on the structure and functions of roots, both on a plant level and on an ecosystem level. Impaired root growth in deeper soil layers at high altitudes was accompanied by (i) a decreased ability for nutrient acquisition from these layers, causing a decrease in plant nutritional status and - on an ecosystem level - enhancing the probability of nutrient leaching in soil and by (ii) a decreased contribution to anchorage by deeper growing coarse roots, increasing the importance of an extensive horizontal root-soil plate to provide tree rigidity. Despite the decrease in shoot biomass with increasing altitude, root biomass was increased at higher altitudes. The high proportion of total biomass in roots indicated that at higher altitudes, trees were exposed to high environmental stress affecting root system functioning. Due to the high total root biomass at high altitudes, large amounts of N, S, K, Ca and Mg were immobilized in roots at higher compared to lower altitudes and thus, were prevented from leaching from the soil. Furthermore, the importance of coarse root biomass for long term accumulation of nutrients increased with increasing altitude.

Zusammenfassung

Wurzeln haben einen erheblichen Einfluss auf ökosystemare Prozesse, insbesondere durch die Regulierung der pflanzlichen Produktivität, durch Nährstoffretention im Boden, durch Immobilisierung von Nährstoffen in der Biomasse und durch Produktion von organischer Substanz. Über Wurzelsysteme in tropischen Bergregenwäldern ist bislang wenig bekannt. Tropische Bergregenwälder erstrecken sich über große Höhenstufengradienten und sind damit einem kleinräumigen Wechsel klimatischer Bedingungen ausgesetzt. Eine Zunahme der Meereshöhe geht mit abnehmender Temperatur und oftmals zunehmenden Niederschlagsmengen und Windgeschwindigkeiten einher. Böden in größerer Meereshöhe sind häufig wassergesättigt, die Mächtigkeit der organischen Auflage nimmt tendenziell mit zunehmender Höhenstufe zu. Es ist zu vermuten, dass der Wechsel der Klima- und Bodenbedingungen entlang von Höhenstufengradienten einen erheblichen Einfluss auf die Struktur und Funktion von Wurzelsystemen hat.

In der vorliegenden Arbeit wurden Wurzelsysteme auf drei Höhenstufen (1900, 2400 und 3000 m) eines südecuadorianschen Bergregenwaldes untersucht. Ziel der Arbeit war es, den Einfluss der Umweltfaktoren entlang eines Höhenstufengradienten auf die Pflanzenbezogenen Wurzelfunktionen Nährstoffaneignung und Verankerung als auch auf die Ökosystembezogenen Wurzelfunktionen Nährstoffretention im Boden (und damit Verminderung von Nährstoffauswaschung) und Speicherung von Kohlenstoff (C) und Nährstoffen in der Wurzelbiomasse zu untersuchen.

In einem ersten Ansatz wurden die Funktionen Nährstoffaneignungspotential von Wurzeln und Nährstoffretentionsvermögen durch Wurzeln behandelt. Es ist zu vermuten, dass diese Funktionen in größerer Meereshöhe, im Vergleich zu niedrigerer Meereshöhe, in tieferen Bodenschichten gehemmt sind, und zwar aufgrund ungünstiger Bodenchemischer Bedingungen im Mineralboden, z.B. niedriger pH-Werte, geringer Nährstoffverfügbarkeit und Sauerstoffmangel. Nährstoffaneignungs- und Nährstoffretentionsvermögen von Wurzeln wurden indirekt abgeschätzt durch die Verteilung von Wurzellängendichten (WLD) in verschiedenen Bodentiefen. Zusätzlich wurde das relative Aufnahmevermögen von Stickstoff (N) aus verschiedenen Bodentiefen direkt gemessen, indem nach Applikation von ^{15}N angereichertem Ammoniumsulfat in verschiedene Bodentiefen die ^{15}N Anreicherung in Blättern verschiedener Pflanzengruppen (Bäume, Sträucher, Kräuter und Jungwuchs) bestimmt wurde.

Die vertikale Verteilung der WLD während der trockeneren Jahreszeit (November 2001) war der Verteilung der WLD während der Regenzeit (Juli/August 2002) sehr ähnlich. Der Anteil

der Wurzellängen in der organischen Auflage stieg von 51 % auf 1900 m auf 61 % auf 2400 m und 76 % auf 3000 m. Im Mineralboden nahmen die WLD in größerer Meereshöhe mit zunehmender Bodentiefe schneller ab als auf 1900 m. Die relative Verteilung der ^{15}N Aufnahme aus verschiedenen Bodentiefen war ähnlich der relativen Verteilung der WLD, was bestätigt, dass sich das Nährstoffaneignungsvermögen in größerer Meereshöhe deutlich mehr auf die organische Auflage konzentrierte als auf 1900 m. Bäume, Sträucher und Kräuter unterschieden sich nicht in der vertikalen Verteilung der N-Aufnahme, während der Jungwuchs auf beiden Höhenstufen N nur aus der organischen Auflage aufnahm.

Kalkung und/oder Düngung (N, Phosphor (P), Kalium (K) und Magnesium (Mg)) kleinräumiger Stellen im Mineralboden hatte keinen signifikanten Einfluss auf das Feinwurzelwachstum. Dies lässt vermuten, dass gehemmtes Wurzelwachstum im Mineralboden in größerer Meereshöhe, und das damit verbundene verminderte Nährstoffaufnahmepotential und die erhöhte Nährstoffauswaschungsgefahr in tieferen Bodenschichten, weder durch niedrige pH-Werte noch durch Nährstoffarmut in diesen Bodenhorizonten begründet war.

In einem weiteren Ansatz wurde der Frage nachgegangen, ob sich die Abnahme pflanzlicher Produktivität mit zunehmender Meereshöhe durch eine Abnahme des Nährstoffversorgungszustandes der Pflanzen begründen lässt. Dazu wurden Nährstoffgehalte in den Blättern von Bäumen, Sträuchern und Kräutern ermittelt.

Der Vergleich von Nährstoffgehalten in Baumblättern mit Referenzwerten aus der Literatur lässt den Schluss zu, dass das Pflanzenwachstum auf 1900 m nicht durch Nährstoffmangel limitiert war. Auf 2400 und 3000 m waren die Gehalte an N, P, Schwefel (S) und K in Baumblättern deutlich niedriger als auf 1900 m. Eine ähnliche Abnahme der Nährstoffgehalte mit zunehmender Meereshöhe war auch in den Blättern von Sträuchern und Kräutern zu verzeichnen, was die Annahme bestärkt, dass unterschiedliche Blattnährstoffgehalte eine Verschlechterung des Nährstoffversorgungszustandes widerspiegeln und nicht durch eine unterschiedliche Artenzusammensetzung auf verschiedenen Höhenstufen zu begründen ist. Die N-, S-, P- und K-Gehalte in Baumblättern auf 2400 und 3000 m waren identisch oder ähnlich mit den Nährstoffgehalten die laut Literatur bei anderen Baumarten auf Nährstoffmangel hinweisen. Sowohl der Vergleich der N:P Verhältnisse in Baumblättern mit Referenzdaten aus der Literatur, als auch Nährstoffindizes, errechnet aus Blattnährstoffgehalten nach dem „Diagnosis and Recommendation Integrated System“ (DRIS; Beaufils 1973), wiesen darauf hin, dass N das am stärksten Wachstumslimitierende Nährelement in größerer Meereshöhe war. Der geringe Nährstoffversorgungszustand von

Pflanzen in größerer Meereshöhe ist zum einen auf eine geringe Mineralisation organisch gebundener Nährstoffe zurückzuführen, zum anderen auf ein geringes Nährstoffaneignungsvermögen aus tieferen Bodenschichten.

In einem dritten Ansatz wurde die C- und Nährstoffspeicherfunktion von Wurzeln untersucht. Beträchtliche Anteile des terrestrischen C sind in tropischen Tieflandregenwäldern festgelegt. Bislang ist allerdings wenig über das C-Speichervermögen von tropischen Bergregenwäldern bekannt. Ebenso wurde bislang in tropischen Bergregenwäldern der Beitrag der Wurzelbiomasse zum Nährstoffumsatz und zur -festlegung kaum untersucht.

Die Mengen an C und Nährstoffen, die in der Wurzelbiomasse gespeichert sind, wurden für verschiedene Wurzeldurchmesserklassen bestimmt. Der Wurzeldurchmesser hat einen erheblichen Einfluss auf den Nährstoffumsatz durch Wurzelturnover (vorwiegend bestimmt durch Feinwurzeln) und die langfristige Nährstofffestlegung in der Biomasse (vorwiegend bestimmt durch Grobwurzeln).

Insgesamt wurden in der Wurzelbiomasse lediglich zwischen 3 und 10 % des gesamten im Ökosystem festgelegten C gespeichert. Sowohl die Fein- (≤ 2 mm im Durchmesser) als auch die Grobwurzelbiomasse (> 2 mm im Durchmesser) waren signifikant höher auf 3000 m als in niedrigerer Meereshöhe. Hierbei nahm der Anteil der Grobwurzeln an der Gesamtwurzelbiomasse von etwa 70 % auf 1900 m auf etwa 80 % in größerer Meereshöhe deutlich zu.

Die Nährstoffgehalte der Grobwurzeln von *G. emarginata* (Ruiz & Pav.) Triana (Melastomataceae) waren kaum von der Meereshöhe beeinflusst. In Wurzeln mit einem Durchmesser von ≤ 5 mm stiegen die C-Gehalte mit zunehmender Meereshöhe leicht an, während die Gehalte an N, P, S, K und Mg deutlich abnahmen. Dies spiegelte die Verschlechterung des Nährstoffversorgungszustandes mit zunehmender Höhenstufe wider.

Aufgrund abnehmender Nährstoffkonzentrationen in Kombination mit zunehmender Biomasse mit zunehmender Höhenstufe zeigten die Nährstoffvorräte in der Feinwurzelbiomasse keine eindeutige Zu- oder Abnahme entlang des Höhenstufengradienten. Nährstoffvorräte in der Grob- und Gesamtwurzelbiomasse wurden mit Hilfe von Nährstoffkonzentrationen in Grobwurzeln von *G. emarginata* geschätzt. In beiden Wurzelfraktionen waren, mit Ausnahme der P-Vorräte in der Gesamtwurzelbiomasse, alle Nährstoffvorräte auf 3000 m deutlich höher als auf 1900 und 2400 m.

In der Feinwurzelbiomasse war auf allen Höhenstufen ein hoher Anteil des gesamten Wurzel-N, -S und -P (35.4-72.7 %), aber nur ein geringer Anteil (5.3-9.3 %) des gesamten Wurzel-Ca festgelegt und damit am kurzfristigeren Nährstoffkreisumsatz beteiligt. Die geschätzte Menge an Nährstoffen, die jährlich durch Absterben von Feinwurzeln der Streufraktion im Boden zugeführt wurde, war ähnlich oder größer als die in der jährlich anfallenden Blattstreu. Auf 1900 m war die geschätzte Menge an jährlich freigesetzten Nährstoffen durch Feinwurzelumsatz ähnlich dem jährlichen Nährstoffeintrag durch Nährstoffauswaschung aus dem Blätterdach durch Regen. Dies demonstriert dass durch Feinwurzelumsatz ein beträchtlicher Beitrag zum Nährstoffeintrag in den Boden geleistet wird.

Steile Hänge, flachgründige Böden und hohe Windgeschwindigkeiten lassen vermuten, dass die Ansprüche an die Verankerungsfunktion von Baumwurzeln in tropischen Bergregenwäldern sehr ausgeprägt sind. In einem vierten Ansatz wurde daher die Grobwurzelarchitektur von drei typischen Baumarten auf 1900 m (*G. emarginata*, *Clethra revoluta* (Ruiz & Pav.) Spreng. (Clethraceae) und *Vismia tomentosa* Ruiz & Pav. (Clusiaceae)) und auf 3000 m (*Weinmannia loxensis* Harling (Cunoniaceae), *Clusia* spec. (Clusiacaea) und *Styrax foveolaria* Perkins (Styraceae)) auf Höhenstufen- und Artspezifische Eigenschaften hin untersucht, die laut Literatur eine Verbesserung der Verankerung bewirken. Auf 1900 m zweigten 20 % der Strukturwurzeln (> 20 mm im Durchmesser) von der Stammbasis im Mineralboden ab und 80 % in der organischen Auflage. Auf 3000 m hingegen zweigten alle Wurzeln in der organischen Auflage von der Stammbasis ab, d.h. die Wurzelteller auf dieser Höhenstufe waren deutlich flachgründiger als auf 1900 m. Auf 3000 m war eine signifikant höhere Asymmetrie von Wurzelsystemen zu verzeichnen als auf 1900 m. Die stärker ausgeprägte Wurzelasymmetrie auf 3000 m ging einher mit einer geringeren Anzahl von dominanten Wurzeln (die größten Wurzeln die zusammen 80 % der gesamten Querschnittsfläche aller Strukturwurzeln ausmachen) als auf 1900 m. Auf 1900 m wuchsen 92 % aller Bäume aufrecht, im Gegensatz zu 52 % auf 3000 m. 48 % aller Bäume auf 3000 m wiesen einen schrägen Wuchs auf, lagen mit der Stammbasis auf dem Boden auf oder waren teilweise entwurzelt. Auf dieser Höhenstufe wuchsen alle Bäume aufrecht, die eine Pfahlwurzel besaßen oder deren Stämmen unterirdisch durch verholzte Rhizome verbunden waren, sowie 83 % aller Bäume mit Stelzwurzeln und 50 % aller Bäume, die durch Stämme oder Wurzeln benachbarter Bäume gestützt wurden. Es ist daher zu vermuten, dass diese Eigenschaften besonders zur Baumstabilität beitragen. Unterschiede in der Grobwurzelarchitektur zwischen 1900 und 3000 m verdeutlichen, dass Wurzeleigenschaften, die die horizontale Ausdehnung des Wurzeltellers fördern (Wurzelasymmetrie, geringe Anzahl dominanter Wurzeln, Stelzwurzeln, Verbindung von einzelnen Stämmen durch verholzte Rhizome), ausgeprägter sind oder öfter vorkommen, wenn die Tiefendurchwurzelung des Bodens gehemmt ist.

Es ist anzunehmen, dass Baumarten, deren Verbreitungsgebiet sich über weite Höhenstufengradienten hinweg erstreckt, eine allgemein hohe phenotypische Plastizität aufweisen. In einem fünften Ansatz wurde daher die phenotypische Plastizität der Grobwurzelarchitektur von *G. emarginata* untersucht, indem Wurzelverzweigungsmuster dieser Art auf 1900 und 2400 m miteinander verglichen wurden. In Anlehnung an van Noordwijk und Mulia (2002) wurden diese Verzweigungsmuster charakterisiert durch (i) den Allokationsfaktor (*q*), welcher Verzweigungmuster zwischen den Extremen „Fischgrätmuster“ und „dichotomes Verzweigungsmuster“ einordnet, (ii) den Proportionalitätsfaktor, der die Verjüngung von Wurzeln quantifiziert, (iii) die Länge von Wurzelsegmenten zwischen zwei Verzweigungen und (iv) der Anzahl an Wurzelsegmenten nach einer Verzweigung.

Die Wurzelsysteme auf 1900 m wiesen vertikal wachsende Lateralwurzeln auf, die Ähnlichkeit mit Senkerwurzeln hatten. Wurzeln auf 2400 m waren vorwiegend oberflächenparallel ausgerichtet, Wurzelsysteme waren oberflächlicher und konzentrierten sich auf die organische Auflage. Der Allokationsfaktor war der einzige Verzweigungsparameter, der sich signifikant mit der Höhenstufe änderte. Höhere *q*-Werte auf 2400 m als auf 1900 wiesen auf Fischgrätähnlichere Verzweigungsmuster in größerer Meereshöhe hin. Unterschiede in *q* zwischen den Höhenstufen ließen sich nicht durch Unterschiede in der Wachstumsrichtung von Wurzeln begründen. Vielmehr können Fischgrätähnlichere Verzweigungsmuster teilweise als ein Mechanismus interpretiert werden, der die horizontale Ausrichtung des Wurzelballens fördert, wenn das Tiefenwachstum von Wurzeln gehemmt ist.

Es kann geschlussfolgert werden, dass die Meereshöhe einen erheblichen Einfluss auf die Funktionen von Wurzelsystemen hatte, sowohl auf Pflanzenebene als auch auf Ökosystemebene. Gehemmte Tiefendurchwurzelung des Bodens in größerer Meereshöhe ging einher mit (i) einem geminderten Nährstoffaneignungsvermögen aus tieferen Bodenhorizonten und damit (a) einer gehemmten Nährstoffversorgung von Pflanzen und (b) einem erhöhten Nährstoffauswaschungspotential aus tieferen Bodenschichten, als auch (ii) einem geringeren Beitrag zur Verankerung durch tief wachsende Grobwurzeln. Im Gegensatz zur abnehmenden Sprossbiomasse stieg die Wurzelbiomasse mit zunehmender Höhenstufe. Die erhöhte Allokation von Biomasse in die Wurzeln in größerer Meereshöhe verdeutlichte, dass Bäume hier hohen Stressbedingungen ausgesetzt waren, die besondere Anforderungen an die Pflanzenbezogenen Funktionen von Wurzelsystemen stellten. Aufgrund der steigenden Biomasse mit zunehmender Meereshöhe waren in großer Meereshöhe im Vergleich zu niedrigerer Meereshöhe beträchtliche Mengen an N, S, K, Ca und Mg festgelegt und damit vor Auswaschung aus dem Boden geschützt. Desweiteren stieg mit zunehmender Meereshöhe die Bedeutung der Grobwurzelbiomasse für die Langzeitakkumulation von C und Nährstoffen.

Resumen

Los sistemas de raíces son importantes para el funcionamento del ecosistema, sobre todo porque están regulando la productividad vegetal, la retención de nutrientes del suelo, los nutrientes en la biomasa y la producción de materia orgánica.

Los sistemas radiculares de las plantas que crecen en bosques tropicales de montaña han sido muy poco investigados. En bosques tropicales de montaña, la temperatura disminuye y normalmente la precipitación y la velocidad del viento aumentan con el incremento altitudinal. Muchas veces, los suelos en zones altas están saturados con agua, y la profundidad de la capa organica crece con el incremento altitudinal. Se puede asumir que el cambio del clima y del suelo con el incremento altitudinal influye directamente sobre la estructura y la función de las raíces.

En la presente investigación, los sistemas de raíces fueron investigados en tres diferentes altitudes (1900, 2400 y 3000 ms.n.m.) en un bosque tropical de montaña en el sur del Ecuador. El objetivo fue examinar el impacto del cambio del medio ambiente en la gradiente altitudinal de las funciones de adquisición de nutrientes y anclaje, que se refieren al funcionamiento de la planta, y a las funciones de retención de nutrientes del suelo, y de almacenamiento de carbono (C) y nutrientes en la biomasa de raíces, que se refiere al funcionamiento del ecosistema.

En un 1er enfoque, se investigaron la capacidad de toma de nutrientes y el potencial de retención de nutrientes en el suelo por las raíces. Se puede asumir, que en grandes altitudes, comparando con altitudes menores, estas funciones de raíces están impedidas en el suelo mineral, debido a desfavorables condiciones quimicas como valores de pH bajas, poca disponibilidad de nutrientes o falta de oxygeno. Para examinar la habilidad de la toma de nutrientes en diferentes profundidades del suelo y para examinar el potencial de retención de nutrientes en el suelo, densidades de la longitud de raíces (DLR) en diferentes profundidades de la capa organica y del suelo mineral fueron determinados. Adicionalmente la toma relativa del nitrógeno (N) de diferentes profundidades del suelo fue medida en 1900 ms.n.m. y en 3000 ms.n.m.. Para eso, se determinó el enriquecimiento de ^{15}N en hojas de diferentes tipos de vegetación (árboles, arbustos, hierbas y plántulas), tras aplicar en el suelo sulfato de amonio enriquecido con ^{15}N a distintos profundidades.

La distribución vertical de DLR fue muy similar durante la temporada de lluvia (Noviembre 2001) y la temporada más seca (Julio/Agosto 2002). El porcentaje de la longitud de raíces situada en la capa orgánica, se aumentó de 51 % en 1900 ms.n.m. hasta 61 % en 2400 ms.n.m. y 76 % en 3000 ms.n.m.. En el suelo mineral, DLR disminuyó marcadamente en las altitudes

crecientes comparando con 1900 ms.n.m.. La distribución de la toma relativa de N fue muy similar a la distribución de raíces, confirmando la más superficial habilidad de la toma de nutrientes en altitudes crecientes. La toma relativa de N fue similar para árboles, arbustos y hierbas pero más superficial para plántulas, que obtenian todo su N de la capa orgánica. La más baja explotación espacial del suelo mineral por raíces finas en alturas altas que en 1900 ms.n.m. aumenta la posibilidad que los nutrientes en el suelo mineral están perdidos por filtración.

Se agregó (i) cal, (ii) fertilizante (N, fosforo (P), potassio (K) y magnesia (Mg)) o (iii) cal y fertilizante en el suelo mineral, lo cual tuve ningún impacto significante en el crecimiento de raíces, indicando que el crecimiento inhibido de raíces en altitudes altas no estuvo causado por suelos ácidos, ni por la poca disponibilidad de nutrientes en el suelo.

Para enfocar el impacto del estado nutricional de las plantas en la disminución de la productividad vegetal con relación a la creciente altitudinal, la concentración de nutrientes en hojas de árboles, arbustos y hierbas fue evaluada. La comparación de la concentración en hojas de árboles con valores de referencias de la literatura propone que en 1900 ms.n.m. el crecimiento de arboles no era limitado por falta de nutrientes. En 2400 y 3000 ms.n.m., las concentraciónes de N, P, sulfur (S) y K en las hojas arbóreas fueron más bajos que en 1900 ms.n.m.. Lo mismo fue observado en hojas de arbustos y hierbas, indicando que las diferentes concentraciónes de nutrientes en 1900, 2400 y 3000 ms.n.m. fueron causados por diferencias en el estado nutricional de plantas y no por diferentes composiciones de especies en cada altitud. Concentraciones de N, S, P y K en hojas arbóreas en 2400 y 3000 ms.n.m. eran dentro del rango o muy cerca del ambito donde falta de nutrientes ocurre en especies referidas en la literatura. Las relaciones N - P en la comparación de hojas con valores referidos en la literatura y la comparación de índices de nutrientes calculados por el “Diagnosis and Recommendation Integrated System” (DRIS; Beaufils 1973) indica que el crecimiento de plantas en zonas altas fueron más inhibidos por N que por otros nutrientes. La perdida del estado nutricional de las plantas en zonas altas fue inducida por la poca mineralización de nutrientes que están incorporadas en la masa orgánica, y por poca habilidad en la toma de nutrientes en el suelo mineral.

Un 3er enfoque se refiere a la función del almacenamiento de C y nutrientes en la biomasa radicular. Grandes porcentajes del C terrestre estan sequestrados en la selva tropical. Todavia se save poco sobre las cantidiades de C que estan sequestrados en bosques tropicales de montaña. Ademas, la importancia de la biomasa radicular para el ciclo de nutrientes en bosques tropicales de montaña está poco entendido. El almacenamiento de C y nutrientes en

la biomasa de raíces estuvo determinado por raíces de diferentes clases de diametros. El diametro de las raíces tiene un impacto marcado en el ciclo de nutrientes (principalmento por raíces finas) y en la inmovilización de nutrientes (principalmente por raíces gruesas).

Comparando las reservas de C en el suelo y en la biomasa vegetal, la biomasa subterránea contribuye entre 3 y 10 % de todo el C que está almacenado en el ecosistema. Eso significa que la biomasa subterránea almacena solo pequeñas partes del C en este bosque tropical de montaña. La biomasa de raíces finas (≤ 2 mm de diámetro) y de raíces gruesas (> 2 mm en diámetro) era significantemente mas grande en 3000 m que en zonas bajas. El porcentaje de biomasa de las raíces gruesas en el todal de la biomasa radicular aumentó del 70 % en 1900 ms.n.m. al 80 % en 2400 y 3000 ms.n.m.

Las concentraciones de nutrientes en raíces gruesas de *Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae) con un diámetro > 5 mm estuvieron muy pocos afectados por la altitud. En raíces ≤ 5 mm de diámetro las concentraciones de N, P, S, K y Mg decrecieron con el incremento altitudinal, reflejando el bajo estado nutricional de plantas. Debido al crecimiento de la biomasa y el decrecimiento de las concentraciones de nutrientes, las reservas de abastecimiento de nutrientes en la biomasa de raíces finas no crecieron ni decrecieron con el incremento altitudinal. Al contrario, en la biomasa de raíces gruesas y en la biomasa total de raíces, reservas de todos los nutrientes con excepción de P eran más grandes en 3000 ms.n.m. que en 1900 y 2400 ms.n.m..

En todas las altitudes, grandes porcentajes de N, S y P en raíces (35.4-72.7 %) eran almacenados en la biomasa de raíces finas, contribuyendo al ciclo corto de decomposición de nutrientes, pero solo 5.3-9.3 % de todo el Ca en raíces. La cantidad estimada de nutrientes que entraba al suelo con los residuos de raíces cada año, era muy similar o mas grande a la cantidad de nutrientes que entra al suelo con el residuo de hojas. En 1900 ms.n.m. cantidades estimadas de la liberación anual de nutrientes a través de la descomposición de raíces finas fueron similar a la cantidad de nutrientes que entran al suelo por filtración del dosel.

Se puede asumir que, debido a los fuertes pendientes, los suelos superficiales y las grandes velocidades del viento, en los arboles que crecen en bosques tropicales de montaña, los mecanismos que fomentan el anclaje son muy marcados. La arquitectura de tres especies arboreos, típicos para 1900 ms.n.m. (*G. emarginata*, *Clethra revoluta* (Ruiz & Pav.) Spreng. (Clethraceae) y *Vismia tomentosa* Ruiz & Pav. (Clusiaceae)) y de tres especies creciendo en 3000 ms.n.m. (*Weinmannia loxensis* Harling (Cunoniaceae), *Clusia* spec. (Clusiacaea) y *Styrax foveolaria* Perkins (Styraceae)) fue investigada para examinar altitudinal y intra especificas diferencias en las características de raíces que, según la literatura, fomentan el

anclaje. En 1900 ms.n.m., el 20 % de las raíces estructurales (> 20 mm en diámetro) originaban en el suelo mineral, mientras en 3000 ms.n.m. el origen de raíces estaba limitado a la capa orgánica. La asimetría de raíces creció significantemente en 1900 hasta 3000 ms.n.m.. Eso fue acompañado por un decrecimiento del número de raíces dominantes (las raíces mas gruesas que contribuyen 80 % de la área en sección de todas raíces estructurales) de 1900 m a 3000 ms.n.m.. En 1900 ms.n.m., el 92 % de los árboles crecieron rectos en comparación a 52 % en 3000 ms.n.m.. En esta altitud el 48 % estaban inclinados o parcialmente desarraigados, indicando que el anclaje de arboles era impedido en esta altitud. En la misma altitud, todos los árboles con raíces pivotantes o con troncos conectados por rizomas leñosas crecieron rectos, ademas 83 % de los árboles con raíces zancos y 50 % de los árboles que se apoyaron en troncos o raíces de otro árboles. Eso indica que estas características eran importante para la estabilidad de árboles. Las diferencias entre la arquitectura de raíces gruesas en 1900 y 3000 ms.n.m. demonstraron que estas características que fomentan la extensión horizontal del plato del suelo y de las raices (asimetría de raíces, pocas raíces dominantes, la coneción de troncos por rizomas leñosas, raíces zancos) están mas pronunciadas o ocurren mas frecuentemente, si el crecimiento de raíces en horizontes mas profundos esta inhibido.

Se puede asumir que especies de arboles con una extensa area de distribución tienen una marcada plasticidad fenotípica. En un quinto enfoque, la arquitectura de raíces gruesas de *G. emarginata* creciendo en 1900 m y 2400 ms.n.m., fue investigado para examinar la plasticidad fenotípica en la muestra de la ramificación. Esta muestra fue caracterizada por (i) el factor de distribución (*q*) que clasifica la muestra entre los dos extremos "dicotomo" y "espinas de pescado", (ii) el factor de la proporcionalidad, para quantificar el releje de las raíces, (iii) la longitud de las raíces entre dos puntos de ramificación, y (iv) el número de raíces originando en un punto de ramificación. Estos parámetros se refieren a van Noordwijk y Mulia (2002). Los sistemas de raíces en 1900 ms.n.m., se caracterizaron por raíces laterales que entraron verticalmente al el suelo mineral. En 2400 ms.n.m., los sistemas de raíces se encontraron mas superficiales y se concentraron en la capa orgánica. El factor de distribución fue el único parámetro que estaba afectado por la altitud. En 2400 ms.n.m., *q* indicaba una muestra de ramificación que fue mas similar al la muestra de "espinas de pescado" que en 1900 m. Diferencias altitudinales en *q* no estuvieron causadas por diferencias en la dirección del crecimiento de raíces. De hecho los valores mas altos de *q* en 2400 ms.n.m. que en 1900 ms.n.m., pueden ser parcialmente interpretados como un mecanismo para fomentar la estabilidad de raíces horizontales si el crecimiento vertical de raíces esta impedído.

En conclusion, la altitud tuvo un marcado afecto sobre las funciones de raíces, las cuales se refieren al nivel de la planta y al nivel del ecosistema. El impedimento del crecimiento de raíces en horizontes mas profundos del suelo en zonas altas estuvo acompañado por (i) una menor habilidad en la toma de nutrientes en estos horizontes, causando un decrecimiento del estado nutricional de plantas y en el nivel del ecosistema subiendo la posibilidad de perder nutrientes en el suelo por filtración y (ii) una menor contribución de raíces profundos al anclaje de los árboles, elevando la necesidad de construir un extenso plato de raíces horizontal para mejorar la estabilidad de los árboles. A pesar del decrecimiento de la biomasa sobre el suelo, la biomasa de raíces se disminuyo en crecientes altitudes. El gran porcentaje de biomasa en las raíces indicaba que en zonas altas, los árboles estuvieron expuestos a gran estrés ambiental, afectando el funcionamiento del sistema radicular, especialmente la habilidad de la toma de nutrientes y el anclaje. Por causa de la gran biomasa total de raíces, gran cantidades de N, S, K, Ca y Mg fueron inmovilizados y por eso fueron protegidos de la filtración en zonas altas en comparacion con zones bajas.

1 General Introduction

1.1 Characterization of tropical montane forests

Worldwide 15 % of tropical forests are located in mountain areas (FAO, 1993). The border of tropical lowland and montane forests varies between 750 and 1650 m (Jacobs, 1988). The montane forests are distinguished from lowland forests by a decline in canopy height, a change in species composition, thicker leaves that are heavily covered with epiphylls, a higher abundance of epiphytes but lower numbers of large woody climbers. Further up the mountains, lower tropical montane forests change into elfin forests (cloud forests or upper montane forests). This vegetation type is a dense, low, microphyllous forest with the trees overloaded with mosses, filmy ferns and lycopods. Where tropical mountains are sufficiently high, a sparse and open vegetation type called páramo follows the elfin forests at their upper limit (Harling, 1979; Jordan 1985). Tropical montane forests are characterized by high species diversity. The tropical Andes belong to the worldwide "hottest hotspots" of diversity of vascular plants (Brummit and Lughadha, 2003).

Due to their topography, montane forests are characterized by marked abiotic gradients whereby one of the most important is the altitudinal gradient. Average temperature decreases by about 0.61 K per 100 m increase of elevation. Mountains cause the winds to ascend to cooler layers where the vapour condenses. Often, mountain summits are covered by clouds during the greater part of the day (Jacobs, 1988). Besides an increase in precipitation with increasing altitude, continual cloud cover and high air humidity at high elevation slow down evapotranspiration. In contrast to forests from lower regions, tropical montane forests often have thick organic surface layers that may even increase with increasing altitude (Schrumpf et al. 2001; Wilcke et al., 2006). Mineral soils have usually very low pH and low base saturation (Schrumpf et al., 2001). Oxygen deficiency due to water logging, but also high wind speeds are typical stress factors for plant communities at high elevation (Jordan, 1985; Cordero, 1999).

1.2 The need for investigating tropical montane forests

Investigation of the ecosystem tropical montane forest has markedly increased in the last two decades (Nadkarni and Wheelwright, 2000; Beck and Müller-Hohenstein, 2001). Concurrently large areas of tropical mountain forests disappear due to human activities. About 90 % of the original forest in the Ecuadorian Andes is already lost. The deforestation rate of the Ecuadorian lowland and montane forests between 1990 and 2000 amounted for 1.2 % per year (FAO, 2000). On a global scale, the amount of carbon that is sequestered in forests of tropical mountain areas receives increasing attention (Fehse et al., 2002). The contribution of different ecosystem compartments such as soil, aboveground and belowground biomass to carbon sequestration in tropical montane forests is poorly understood.

Human activities may further affect the functioning of ecosystem processes in montane forests, e.g. by increased atmospheric deposition due to biomass burning in lowland areas (Fabian et al., 2005). When high biodiversity in tropical montane forests shall be maintained on a long term, a better understanding of the interaction between biodiversity and ecosystem processes is essential. Still the impact of ecosystem processes on species composition, but also the impact of biodiversity on ecosystem processes such as productivity is poorly understood (Wright, 1996, 2002). Functioning of root systems plays a major role in regulating ecosystem processes.

1.3 Structure and functions of root systems in tropical montane forests

Woody dicotyledonous species represent a large proportion of plants in forest ecosystems. Different to monocotyledonous and some herbaceous species, elements of root systems of woody dicots are characterized by secondary thickening (Lauenroth and Gill, 2003). This implies that roots in forests occur in a wide range of diameters. Roots of woody species markedly differ in their functions both on a plant level and an ecosystem level.

On a plant level root systems perform two primary functions. One is the acquisition of soil based resources such as water and nutrients. The ability for resource acquisition usually decreases with increasing distance from the root apex (Marschner, 2003). The second function is anchorage which is predominantly provided by basal coarse roots in woody root systems (Robinson et al., 2003). Other root functions, e.g. storage, synthesis of growth regulators, propagation and dispersal can be regarded as secondary functions (Fitter, 2002).

It has never been reported that plants in tropical montane forests exhibit adaptive mechanisms to improve water acquisition. Even though, low soil water availability may occur occasionally in the upper soil layers (own observation) soil water contents in these forests are usually sufficient due to high precipitation and low temperatures in comparison with lowland regions.

In contrast, nutrient availability in soils of tropical montane forests is often low (e.g. Tanner et al., 1990; Tanner et al. 1992; Vitousek et al., 1993; Vitousek and Farrington, 1997). In several studies fine root biomass or fine root length density (RLD) in tropical lowland and montane forests was inversely related to soil P and/or Ca availability (Gower, 1987; Cavalier, 1992;

Coomes and Grubb, 2000; Ostertag, 2001), supporting the hypothesis of Hertel and Leuschner (2006) that high fine root biomass in tropical montane forests is attributed to low nutrient supply.

It is often assumed that nutrient input from the canopy, either by leaching from leaves, mineralization of canopy held organic matter or from the trapping of mist and rain and from dry deposition is an important source of plant available nutrients in tropical montane forests (Vance and Nadkarni, 1992; Cavalier, 1992). This assumption is partly based on the occurrence of dense root mats within the surface layers, and the notable abundance of fine roots in canopy. Less than 0.1% of ^{45}Ca and ^{32}P that had been applied to the soil surface in a tropical lowland forest in Venezuela was leached through the root-organic mat and most of the tracer was taken up by living roots, indicating that the densely rooted surface layers may efficiently take up dissolved nutrients before they percolate to mineral soil (Stark and Jordan, 1978). In tropical montane forests direct measurements of the ability for nutrient acquisition have never been performed. Little is known about the abundance of fine roots in deeper soil layers and the contribution of roots in mineral soil to nutrient acquisition (Ostertag, 2001).

In many tropical montane forests trees are exposed to strong winds such as hurricanes (Arraiga, 2000; Weaver, 2002). The small tree stature is often related to high wind speeds (Lawton, 1982; Cordero, 1999) or early failure of trees when growing on steep slopes (Edwards and Grubb, 1982). Thus, it can be expected that tree species growing in tropical montane forests possess a variety of adaptive mechanisms to cope with enhanced mechanical stress. Accordingly, saplings of *Cecropia schreberiana*, a native tree species from an elfin forest in Puerto Rico had higher root/shoot ratios on a wind exposed than on a wind protected site (Cordero, 1999). Specific traits of coarse root architecture to improve tree anchorage in tropical montane forests are poorly understood.

On an ecosystem level, root systems contribute to processes such as carbon (C), nutrient and water cycling and productivity (McClaughtery et al., 1982; Robinson et al., 2003). The spatial distribution of roots has an impact on landslides (Roering et al., 2003) that frequently occur in tropical montane forests. Furthermore, roots may affect biodiversity, e.g. by influencing the competitive advantage of plants for acquisition of soil resources (Schnitzer et al., 2005; Barbaris and Tanner, 2005) or by species specific symbioses with other organisms such as mycorrhizal fungi (Haug et al., 2004; Mummey et al., 2005).

Root systems contribute to element cycling by immobilisation, storage and release of C and nutrients. As shown by their high turnover rates fine roots are much more dynamic than coarse roots (Gill and Jackson, 2000) and thus constitute the main root fraction contributing to element fluxes. As mentioned above fine roots in upper soil layers may efficiently retain nutrients that reach the soil from above ground (Stark and Jordan, 1978). Information is lacking about the potential of roots to retain nutrients from deeper soil layers.

Standing root biomass and nutrient concentrations in root tissue basically affects the function of roots as a storage organ for C and nutrients within the ecosystem. Both in the Paleotropis and Neotropis Hertel and Leuschner (2006) registered a similar average fine root biomass in tropical lowland and lower montane forests (about 230-400 g m^{-2}), but significantly higher fine root biomass in upper montane forests (about 950-1100 g m^{-2}). Ranges of coarse root biomass were similar for mature forests in tropical lowland (945-7500 g m^{-2}) and montane regions (945-7200 g m^{-2}) (Klinge, 1975; Edwards and Grubb, 1977; Vance and Nadkarni, 1992; Cavalier, 1992; Vogt et al., 1996; Cairns et al. 1997; Pavlis and Jenik, 2000). However, only one of the latter studies was performed in an upper montane forest. Priess et al. (1999) reported that nutrient concentrations in fine root biomass of a tropical submontaneous and a tropical cloud forest were similar to those in tropical lowland forests.

Roots release carbon by respiration, rhizodeposition, and death of entire root segments (Farrar and Jones, 2003). Rhizodeposition and root litter production are associated with nutrient release to soil. It has been hypothesised that due to high root litter production a large fraction of the high C stocks accumulated in soils of tropical montane forests originate from dying fine roots (Hertel et al., 2003; Röderstein et al., 2005). The decomposition rate of fine root litter in tropical montane forests decreased with increasing lignin and decreasing N concentrations in root tissue, decreasing soil nutrient availability, and increasing mean annual precipitation associated with increasing oxygen deficiency (Ostertag and Hobbie, 1999; Schuur, 2001). Little is known about the impact of fine root turnover on nutrient cycling in tropical montane forests (Ostertag and Hobbie, 1999).

In summary, the role of the “hidden half” (Waisel et al., 2002) for the regulation of ecosystem processes in tropical montane forests is still poorly understood.

1.4 Objectives

The present study was realized within the scope of the DFG - research unit FOR 402 “Functionality in a tropical mountain rain forest” which joins projects from a wide range of disciplines (www.bergregenwald.de). General aims of this research unit are (i) evaluation of biodiversity (ii) investigation of species interactions and ecosystem processes (iii) development of sustainable land use systems and forest recovery models.

The aim of the present study was to improve our knowledge about root systems in tropical montane forests. It was conducted in close cooperation with another working group that examined further parameters of below- and aboveground biomass (M. Röderstein, G.Moser, D. Hertel, C. Leuschner, Göttingen). Investigations of the two working groups were realized at the same sites along an altitudinal gradient and focused on the root functions nutrient uptake, anchorage, C and nutrient cycling.

The chapters 2-4 comprise studies on roots and leaves that were conducted on a community level. Chapter 2 refers to the functions nutrient uptake and nutrient retention from soil. The ability for nutrient uptake was measured (i) directly by the application of ^{15}N enriched ammonium sulphate to different soil depths and subsequent measurement of ^{15}N enrichment in leaves and (ii) more indirectly by the determination of RLD in different soil depths that gives an estimate of the exploitation of soil by roots. In an experiment to investigate possible causes for the observed rooting pattern chemical properties of small patches in mineral soil were modified by liming and fertilization, and *in situ* root growth in these soil patches was measured.

In chapter 3 plant nutritional status is examined as a possible reason for decreased aboveground productivity (Röderstein et al., 2005) and tree stature with increasing altitude (G. Moser, pers. comm.). The nutritional status of plants was estimated by comparison of foliar nutrient concentrations with reference data given in literature and by the "Diagnosis and Recommendation Integrated System" (DRIS), using nutrient ratios. The nutritional status was related to nutrient concentrations in soil and the spatial exploitation of soil by roots.

Chapter 4 is addressed to the storage of C and nutrients in root biomass. Concentrations and stocks of C and nutrients in roots of different diameter classes were determined. Belowground biomass was compared with aboveground biomass estimated by G. Moser (unpublished data). The contribution of fine root biomass to C and nutrient cycling was estimated with help of fine root turnover rates as assessed by Röderstein et al. (2005).

Studies in the chapters 5 – 7 were conducted on coarse root systems of selected tree species. In chapter 5 several characteristics of root architecture related to anchorage were described for typical tree species in an elfin forest and typical tree species in a lower montane forest.

In chapter 6 the phenotypic plasticity of coarse root architecture of a tree species growing at two different altitudes was examined. Following van Noordwijk and Mulia (2002) several fractal branching parameters were assessed that allow characterization of root system architecture by the measurement of a representative number of branching points.

Additionally, empirical scaling relations between proximal root diameters and other root system parameters were determined.
Chapter 7 describes a methodological approach, in which the information value of one specific fractal branching parameter, the proportionality factor (Van Noordwijk and Mulia, 2002) was elucidated.

Hypotheses:

(1) In tropical montane forests, root distribution is more superficial at higher than at lower altitudes. This is due to (i) very low pH in mineral soil at higher altitudes and thus, increased risk of Al toxicity and due to (ii) slow nutrient release in deeper soil layers from litter decay and weathering and thus, a higher importance of input of readily available nutrients into soil from the canopy by precipitation.

(2) Higher proportions of plant biomass are allocated belowground at higher altitudes than at lower altitudes. High root to shoot ratios at higher altitudes are caused by (i) increased requirements for nutrient acquisition because low temperatures at high altitudes are associated with low mineralization rates, and by (ii) increased requirements for anchorage because of high wind speeds.

(3) Coarse root architecture is modified by the prevailing soil conditions at each altitude. These modifications are adaptive traits to improve anchorage under given environmental conditions.

Additionally, the present study is addressed to following hypothesis of the DFG-research unit:

(RU 1) The high plant diversity in tropical montane forests is maintained by low nutrient availability.

1.5 The investigation area

The Podocarpus National Park is located in the provinces Loja and Zamora Chinchipe and has an area of 1460 km^2 (Calderón, 2002). On the northern fringes of the Podocarpus National Park in the valley of the Rio San Francisco which connects the province capitals Loja and Zamora, borders the Reserva San Francisco (RSF) (Figure 1.1). This reserve with an area of about 1000 ha is owned by the foundation Nature and Culture International (NCI). The Podocarpus National Park and the RSF protect typical mountain ecosystems of southern Ecuador in an altitude between 900 and 3700 m a.s.l.. They compass the largest interconnected forest area of the country in medium altitudes (Madsen and Øllegaard, 1994).

Figure 1.1: Lower and upper montane forest in the Reserva San Francisco, situated between with 1800 and 3100 m a.s.l..

The Podocarpus National Park extents on the western and eastern side of the Cordillera Real, which is the eastern chain of the Andes in southern Ecuador. The RSF is located on the northern slope of the Cordillera del Consuelo which is a foothill of the Cordillera Real. The Cordillera Real is formed by paleazoic rocks of the Loja Terrane containing mainly phyllits, weakly metamorphosed sandstones and quartzites (Litherland et al., 1994). Recent soils are developed from periglacial cover beds (Wilcke et al., 2001). The landscape is characterized by steep slopes and small ridges. Landslides are very common both in the forests and along roads. The watershed between the Pacific and the Atlantic ocean is mainly formed by the Cordillera Real (Sauer, 1971). The area of the RSF and largest parts of the Podocarpus National Park lay within the catchment area of the Amazone.

Climatic conditions in the region are characterized by a high spatial variability of cloudiness, rainfall and temperature. The Cordillera Real forms the south Ecuadorian meteorological divide between the moist Amazone basin in the east and the dry inter Andean valley in the west (Richter, 2003). The eastern slopes (including the RSF and most of the Podocarpus National Park) have higher cloudiness than the lowlands of the Amazon basin. Precipitation rates show a strong altitudinal gradient. In the RSF annual rainfall increases from 2453 l m^{-2} at 1860 m to 7786 l m^{-2} at 3185 m. The fog water fraction of total water input increases from about 5% at 1800 m to 30 % at 3185 m (Fabian et al., 2005). Mean annual temperature at 1950 m in the RSF is 15.5 °C. With an increasing altitude mean annual temperature decreases by 0.59 K / 100 m (Richter, 2003).

The course of the innertropical convergence zone in Ecuador is conspicuously modified by regional conditions such as the topography of the Andean mountain system. In the study area the prevailing easterly flow causes very frequent precipitation in the season from May to August. From September to April the less frequent westerly flow cause heavy convective rainfall at the western slope of the Cordillera, resulting in a drier period in the study area at the eastern slopes (Bendix and Lauer, 1992). Mean temperature in the warmest month (November) and in the coldest month (August) differ only by 1.9-2.4 K (Röderstein et al., 2005).

The vegetation type in the lower parts of the Podocarpus National Park and the RSF is classified as lower montane rain forests. Plant families with highest abundance of tree species are Euphorbiaceae, Lauraceae, Melastomataceae and Rubiaceae (Homeier et al., 2002). The lower montane forest continues to about 2500 m were it changes into cloud forest (upper montane forest or elfin forest). Important plant families among others are Cunoniaceae, Ericaceae, Melastomataceae, Rubiaceae and Clusaceae. The timberline is reached at 3100 m ± 200 m (Richter, 2003).

1.6 Choice of study sites

To investigate the impact of environmental changes along altitudinal gradients on root systems, our study should be realized at three different altitudes. We decided that an altitudinal difference of at least 1000 m was necessary between the highest and the lowest site to recognize remarkable altitudinal differences in the structure and function of roots. The majority of the investigations of the research unit FOR 402 are conducted within the RSF. To allow cooperation with other working groups, two study sites (at 1900 m and 2400 m) were selected along an altitudinal transect within this area (Figure 1.2). It was not possible to select a third forest stand at higher altitudes within the RSF, since the timber line within the RSF is exceptionally low. Thus, as the highest study site a forest stand at 3000 m at the north western entrance (Cajanuma) of the Podocarpus National Park was chosen (Figure 1.2 and Figure 1.3).

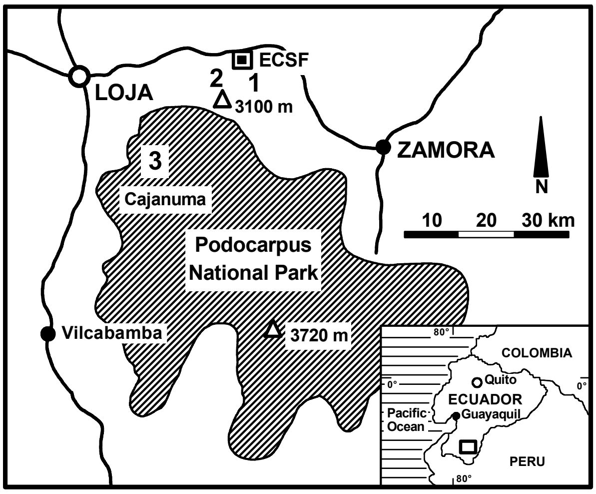

Figure 1.2: Location of the three study sites. 1 = 1900 m, 2 = 2400 m, and 3 = 3000 m. The research station (ECSF) and the Podocarpus National Park are also indicated (Röderstein et al., 2005).

All stands were located on moderate slopes, with average inclinations between 27-31° facing north-east or north-west. Vegetation represented the typical closed forest communities of the respective altitude. The selection of sites with high abundance of bamboo was avoided since bamboo was considered as an indicator for former disturbance of the stands. All stands were considered as old growth forests. Detailed information about climate, vegetation and soil properties of the study sites are given in the following chapters.

Figure 1.3: Area of the study plot at 3000 m in Cajanuma, Podocarpus National Park. With decreasing distance to the ridges, elfin forest vegetation is displaced by páramo.

2 The vertical pattern of rooting and nutrient uptake at different altitudes of a south Ecuadorian montane forest

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Abstract

The vertical pattern of root length densities (RLD) and nitrogen (N) uptake potential were determined at different altitudes (1900, 2400, and 3000 m a.s.l.) of a tropical montane forest in order to improve our knowledge about the role of fine roots for nutrient cycling in this ecosystem. At higher altitudes, precipitation rates and frequencies of fog were higher than at lower altitudes while mean annual air temperatures decreased with increasing altitude. Soils were always very acid with significantly lower pH_{CaCl2} in the 0.0-0.3 m depth of mineral soil at 3000 m (2.8-2.9) than at 1900 and 2400 m (3.1-3.5). The vertical distribution of RLD was very similar during the drier and the rainy season. The percentage of root length in the organic layer during the drier season increased from 51 % at 1900 m to 61 % at 2400 m and 76 % at 3000 m. At 3000 m, RLD were markedly higher in the upper 0.05 m than in the remaining organic layer, whereas at 1900 m and 2400 m RLD were similar in all depths of the organic layer. In mineral soil, RLD decreased more sharply with increasing soil depth at the upper two study sites than at 1900 m.

The relative N uptake potential from different soil layers (RNUP) was determined by ^{15}N enrichment of leaves after application of ^{15}N enriched ammonium sulphate at various soil depths. RNUP closely followed root distribution confirming the more superficial pattern of nutrient uptake at higher altitudes. RNUP was very similar for trees, shrubs and herbs, but more superficial for saplings which obtained N only from the organic layer at both altitudes. Liming and fertilizing (N, P, K, Mg) of small patches in mineral soil had no significant impact on fine root growth. It is concluded that substantially lower exploitation of mineral soil by fine roots at higher altitudes in comparison to 1900 m enhances the probability for nutrient losses from soil by leaching. The more superficial nutrient uptake ability at higher altitudes may be partly related to increased nutrient input from canopy by leaching. However, the specific constraints for root growth in the mineral soil of tropical montane forests warrant further investigations.

Keywords: ability for nutrient uptake, ingrowth cores, ^{15}N, nutrient retention, root length densities, season.

Abbreviations: RLD = root length density, RNUP = relative nutrient uptake potential.

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2.1 Introduction

The spatial pattern of nutrient acquisition by plant roots has a large impact on nutrient fluxes within forest ecosystems. Both, the acquisition of soil resources by plants, and nutrient losses from the ecosystem by leaching strongly depend on the exploitation of the soil by roots (Stark and Jordan, 1978). Horizontal and vertical root distribution in forest soils is much more heterogeneous than in arable land (George and Marschner, 1996). The vertical distribution is related to soil and plant characteristics including nutrient availability (e.g. Sainju and Good, 1993; Leuschner et al., 1998), soil pH (Murach, 1984; Godbold et al., 2003) access to water (Lopez et al., 2001; Bouillet et al., 2002), waterlogging (Santiago, 2000), bulk density (Carvalheiro and Nepstad, 1996), stand age (John et al., 2001; Bouillet et al., 2002), species composition (Silva and Rego, 2003; Davis et al., 2004; Göransson, 2006), and the type of mycorrhizal symbiosis (Moreno-Chacón and Lusk, 2004). Many forest ecosystems are characterized by a densely rooted surface layer (Godbold et al., 2003; Yang et al., 2004; Claus and George, 2005). In other cases, e.g. more arid regions, fine root density is highest several centimetres underneath the soil surface (Lopez et al., 2001).

Most climatic zones are characterized by marked seasons, which have great impact on root growth (John et al., 2001; Yang et al., 2004). Also the relative importance of understorey and tree layer for nutrient retention may differ throughout the year (Tessier and Raynal, 2003). In the tropics, seasonal changes of environmental conditions are confined to more or less pronounced dry and rainy seasons. Here, seasonal changes in soil water content may affect nutrient uptake activity of roots (Roy and Singh, 1995; Lehmann et al., 2001; Lehmann, 2003), and root distribution with soil depth (Yavitt and Wright, 2001; Lehmann, 2003). However, seasonal changes of nutrient uptake and rooting pattern have never been examined in moist tropical montane forests.

Tropical montane forests are mostly developed on steep slopes. Precipitation may reach several thousand mm per year (Richter, 2003). Hence, nutrients are subjected to leaching. Acid soil reaction (Stewart, 2000; Wilcke et al., 2001), anaerobic soil conditions (Santiago, 2000) and high mycorrhizal abundance (Kottke et al., 2004) are further important features related to nutrient acquisition by roots in tropical montane forests. With increasing altitude temperatures decrease, while rain and fog precipitation usually increase in tropical montane forests (e.g. Holder, 2003). The depth of the organic surface layer that stores high amounts of nutrients is often considerably larger at higher than at lower altitudes (Schrumpf et al., 2001; Wilcke et al., 2002). Thus, the pattern of rooting and nutrient acquisition may change along altitudinal gradients.

Determination of root distribution in tropical montane forests was mostly restricted to the organic layer and upper layers of mineral soil (Vance and Nadkarni, 1992; Cavalier, 1992; Hertel et al. 2003). We are aware of only one study in tropical mountains assessing root length distribution down to the parent soil material (Ostertag, 2001). No data are available on direct measurements of nutrient uptake by fine roots in tropical montane forests, though they are necessary for the understanding of nutrient fluxes. Nutrient uptake depends on nutrient supply to the root surface and active absorption by root cells (Chapin, 1980). It is influenced by various factors, such as exploitation of soil by roots, nutrient concentrations in soil solution, soil water content, soil temperature, soil compaction or mycorrhizal symbiosis (Chapin, 1980; Engels, 1993; Arvidsson, 1999; Lehmann, 2003). The ability for nutrient uptake can be assessed directly, e.g. by tracer experiments (Rowe et al., 1999; Lehmann and Muraoka, 2001; Lehmann et al., 2001) or indirectly, e.g. by measurement of root length densities (RLD) (Lopez et al., 2001; Lehmann, 2003), i.e. root length per unit soil volume, which provides an estimate of the exploitation of the soil by roots.

The first objective of this study was to assess the ability for nutrient uptake by fine roots in two seasons and at three different altitudes of a South Ecuadorian montane forest. Therefore, the nutrient uptake activity of roots growing *in situ* was assessed by measuring ^{15}N enrichment in leaves after application of ^{15}N-labelled N fertilizer. As the nutrient concentration of the soil solution was increased by the fertilizer application, this method gives an estimate of N uptake potential under conditions with no N limitation. Root length densities were determined to a maximal mineral soil depth of 1.1 m or down to a depth where root growth was confined by the parent soil material. The second objective of the present study was to investigate possible causes for the rooting pattern. For that, chemical soil properties of soil cores were modified by liming and fertilization, and *in situ* root growth in these soil cores was measured.

It was hypothesised that root length distribution and N uptake potential becomes more superficial with increasing altitude. Superficial rooting at high altitude may be caused by high subsoil acidity due to increased precipitation and by enhanced accumulation of nutrients at the soil surface in comparison with lower altitudes. Furthermore, it was hypothesised that root distribution is more superficial during the rainy season than during the drier season due to low water availability in the organic layer during the drier season and oxygen deficiency in the deeper mineral soil during the rainy season.

2.2 Materials and methods

Study sites

The investigations were done at three study sites on the northern and north western fringes of the Podocarpus National Park on the eastern Andes slope. The two lower study sites (1900 m and 2400 m a.s.l.) were situated in the Reserva San Francisco (RSF). The highest site (3000 m) was located in Cajanuma near the north western entrance of the Podocarpus National Park. The sites were all situated on slopes (20-50°) facing north-east or north-west.

Plant communities represented typical vegetation types of montane forests and changed with increasing altitude. Species compositions are listed in Röderstein et al. (2005). Maximum tree height decreased from 19 m at 1900 m to 12 m at 2400 m and 9 m at 3000 m. The upper site was located close to the timber line and was a typical elfin forest with crooked stem forms. The soils were developed on metamorphic shale, quartzite or sandstone bedrock and were classified as gleyic Cambisols (1900 and 2400 m) and Podzols (3000 m) according to FAO taxonomy (S. Iost, pers. comm.). The average depth of the organic layer increased from 0.15 m at 1900 m and 0.16 m at 2400 m to 0.31 m at 3000 m. The average depth of the Ah decreased from 0.70 m at 1900 m to 0.15 m at 2400 m and 0.20 m at 3000 m. Bedrock was often deeper than 1.1 m at 1900 m, about 0.6 m at 2400 m and between 0.4 and 0.6 m at 3000 m.

Table 2.1: Location and climatic characteristics of the study sites.

Altitude (m)	Location	Rainfall (mm y^{-1})[a]	Mean air temperature (°C)[a]
3000	S 04°06′ W 79°10′	4500	8.6
2400	S 03°59′ W 79°04′	5000	12.3
1900	S 03°58′ W 79°04′	1950	14.9

[a]Data by Röderstein et al. (2005).

Annual rainfall increased from 1900 m to the upper two sites (Table 2.1). Within the RSF, annual fog water input increased from 55 l m^{-2} at 1800 m to 2747 l m^{-2} at 3185 m (Fabian et al., 2005). Rainfall input was higher from April to August 2002 than from October 2001 to March 2002. At a climatic station at 1950 m lowest precipitation was recorded in January 2002 (58 mm) and a rainfall peak in July 2002 (299 mm) (P. Emck, pers. comm.). Mean annual temperature decreased markedly with increasing altitude (Table 2.1). Seasonality in temperature was low (difference of 1.9-2.4 K) with the warmest month in November 2001 during the drier season and the coldest in August 2002 at the end of the rainy season (Röderstein et al., 2005).

For studies of root abundance and soil properties, one 20 m x 20 m plot in representative sections of the closed forest was established at each altitude. Tracer experiments were performed in representative places of a more widespread area around the plots.

Determination of root length densities

Root length densities were determined during the dry season in November/December 2001 and at the end of the rainy season in July/August 2002. At each altitude, samples were taken from 20 locations using a random-block design. From the organic layer a quadratic sample of 100 mm x 100 mm was taken from the upper 0.05 m (O1) and the rest (O2). A soil corer with a diameter of 80 mm was used to sample mineral soil in the layers 0 - 0.1, 0.1 - 0.3, 0.3 - 0.5, 0.5 - 0.7, 0.7 - 0.9 and 0.9 - 1.1 m. When parent soil material was reached above 1.1 m, coring was stopped earlier.

Roots within soil samples were dissected with scissors to homogenize the samples. Afterwards, roots > 2 mm were sorted out from a sub-sample of 20-50 g (organic layer) or 100-200 g (mineral soil) of each sample using a 0.6 mm mesh sieve for washing and tweezers for the separation of roots and remaining soil residue. In a previous test it was shown that the variation of root length between sub-samples from one homogenized sample was much less than the variation between samples. Under a binocular living and dead roots were separated by colour, root elasticity and the degree of cohesion of cortex, periderm and stele (Persson, 1978). Roots were deep frozen for storage. In Germany, length densities of living roots were determined using the WinRhizo programm (Régent Instruments, Quebec, Canada).

Measurement of the nitrogen uptake potential at different soil depths

Nitrogen (N) uptake potential from different soil depths was assessed at 1900 and 3000 m. Five plots (3 x 3 m) per altitude were established for every soil depth (surface of organic layer, 0.05 m and 0.40 m depth of mineral soil). These plots were obtained randomly with a minimal distance of 10 m in between. Tracer was applied during the drier season in December 2003. In the organic layer, the tracer solution was applied with a syringe, and in 0.05 m and 0.40 m depth of mineral soil using a syringe and plastic tubes installed in holes pre-augered to the requested depth. Tracer solution, corresponding to 1.7 kg ^{15}N ha^{-1} (17 kg total N ha^{-1}), was placed in a grid of 41 regularly arranged application points (8 ml per point) within the plots (Figure 2.1) to obtain uniform distribution of ^{15}N within the respective soil depth. The

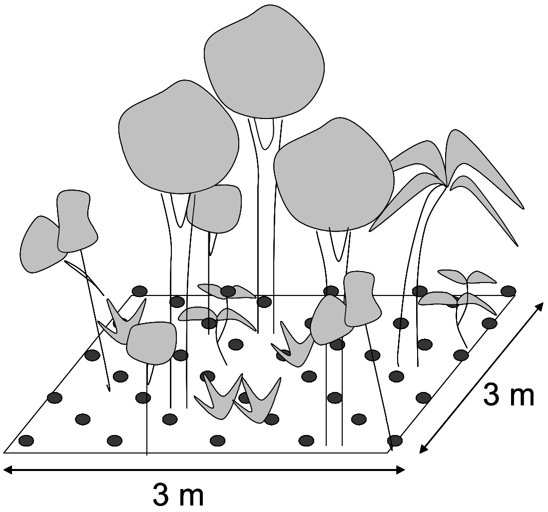

Figure 2.1: Design of the 15N experiment. Filled circles represent the horizontal distribution of application points. For each treatment (tracer application in (i) organic layer, (ii) 0.05 m depth and (iii) 0.40 m depth of mineral soil) there were 5 replications per altitude.

solution contained 216 g l^{-1} ammonium sulfate (10 atom % ^{15}N) and 850 g l^{-1} glucose (corresponding a C:N ratio of 7.4:1). In a preceding experiment that was conducted at 1900 m following a protocol of Rowe et al. (1999), it was shown that the addition of glucose diminished ^{15}N leaching in soil during the uptake study. Ten, 20, 30, and 60 days after tracer application 20 young leaves (i.e. the youngest fully developed leaves or younger leaves) per plot were collected from trees (lignified, > 3 m height), shrubs (lignified, 0.5 – 3 m height), saplings (lignified, < 0.5 m height) and herbs (not lignified), respectively. For herbs and saplings, often less than 20 young leaves were available. Leaves were dried at 50 °C and ground. The ^{15}N enrichment in plant tissue was determined with a mass spectrometer (DELTA E/NA 1500, Finnigan MAT, Thermo Electron Corporation, USA). ^{15}N enrichment is expressed in $\delta^{15}N$, calculated as:

$$\delta^{15}N(‰) = 1000x \frac{(\text{atom\%}_{\text{sample}} - \text{atom\%}_{\text{reference}})}{\text{atom\%}_{\text{reference}}}$$

where atom% is the proportion of ^{15}N in total N and $\text{atom\%}_{\text{reference}}$ is 0.3662 %. For the calculation of ^{15}N excess, natural ^{15}N levels of each plant group at each altitude were used as background levels:

$$\delta^{15}N_{\text{excess}}(‰) = \delta^{15}N_{\text{sample}}(‰) - \delta^{15}N_{\text{reference}}(‰)$$

where $\delta^{15}N_{\text{reference}}$ is the natural ^{15}N level.

The relative ^{15}N uptake potential (RNUP) from a specific soil depth in relation to N uptake potential from the surface of organic layer was calculated by:

$$^{15}N_{Xi}(\%) = 100x\frac{\delta^{15}N_{excessXi}(‰)}{\delta^{15}N_{excessOL}(‰)}$$

where $^{15}N_X$ is the RNUP from soil depth X (surface of organic layer, 0.05 m or 0.40 m depth of mineral soil), *i* is *i*th replication from this soil depth, and $\delta\ ^{15}N_{excessOL}$ is the average ^{15}N excess obtained by tracer application in organic layer at the same altitude.

Soil analyses

The concentrations of mineral nitrogen (N_{min}) and soil pH were measured in the same soil layers as RLD. For the determination of N_{min}, soil samples were taken by soil coring in February 2003 (end of dry season). Twelve randomly distributed replicate sub-samples were taken at 1900 m, and 9 at 2400 m and 3000 m, respectively. Three sub-samples each were combined to one sample. Fresh soil samples were extracted by 12.5 mM $CaCl_2$ (ratio soil:solution = 1:2 for the mineral soil and 1:4 for the organic layer). Nitrate concentrations in the extracts were assessed with a spectral photometer (Lambda 2S, Perkin Elmer, Milano, Italy) from the difference of the extinction at 210 and 275 nm. Ammonium was measured photometrically at 636 nm after staining with the indophenol blue procedure (Bundy and Meisinger, 1994). The soil pH was determined electrometrically on three replicate air dried samples per soil depth and altitude using a 1:2.5 (w:w) mixture of soil and a 0.01 M $CaCl_2$ solution.

Measurement of root growth into soil cores with altered chemical properties

An ingrowth core experiment was performed at 1900 m and 3000 m between October 2002 and October 2003. Natural substrate from mineral soil (Ah and B horizon) from each altitude was sieved with a mesh of 7 mm for homogenization and removal of fine roots. The soil was divided into 4 quarters. One quarter was limed with $CaCO_3$ until pH 5 was reached. One quarter was fertilized with 30 mg N, P, K, and Mg kg^{-1} dry soil. One quarter was both limed and fertilized. One quarter was left as a control. Per altitude and treatment, ten gauze tubes with a length of 0.4 m and a diameter of 35 mm were filled with these substrates. To position these tubes vertically in the upper 0.4 m of mineral soil, a soil corer with a diameter of 35 mm was used at 1900 m. At 3000 m, a more rigid soil corer with a diameter of 80 mm had to be used because of the rocky mineral soil. The space between gauze tubes and the soil was filled with untreated soil. After insertion of the gauze tubes, the mineral soil was covered with the original substrate from the organic layer. After 12 months, the gauze tubes were removed from the mineral soil. All living roots were sorted out and RLD were determined as described above.

Statistical analyses

The non-parametric H-test was used to assess significant differences of RLD between altitudes, of different soil treatments in ingrowth cores and of differences in N uptake pattern between plant groups. Post-hoc analysis for RLD between altitudes was performed by the Dunn test for unequal numbers of replicates. Differences of RLD between seasons and between the O1 and O2 layer were determined by the Mann Whitney test. Differences in N_{min} concentrations and pH values between altitudes were assessed by ANOVA and Tukey post-hoc test.

2.3 Results

Root length densities

At all altitudes, RLD was highest in the organic layer (Figure 2.2). While RLD at 1900 and 2400 m were similar in the O1 and O2 layer ($p > 0.05$), RLD at 3000 m was significantly higher in the O1 than in the O2 layer ($p < 0.001$). With increasing depth in mineral soil, RLD decreased more sharply at 3000 m and 2400 m than at 1900 m. At 2400 m and 3000 m, RLD decreased to values lower than 0.5 cm cm^{-3} already at soil depths below 0.1 m and 0.3 m, respectively, while at 1900 m RLD fell below 0.5 cm cm^{-3} only at a soil depth of 0.7-0.9 m. In 0.1-0.5 m depth (drier season) or 0.3-0.7 m depth of mineral soil (rainy season) RLD was significantly higher at 1900 m than at the upper two sites. Below these depths low numbers of replicates did not allow statistical analysis. At 3000 m, 76% of fine root length was located in the organic layer during the drier season, as compared to 61% at 2400 m, and 51% at 1900 m. Thus, fine root distribution was more superficial at higher altitudes.

There was no change in the vertical distribution of RLD from the drier season to the rainy season, with the exception of the upper 0.3 m in mineral soil at 3000 m, where RLD was significantly higher during the rainy season. Accordingly, the percentage of root length in the organic layer decreased to 69 % during the rainy season.

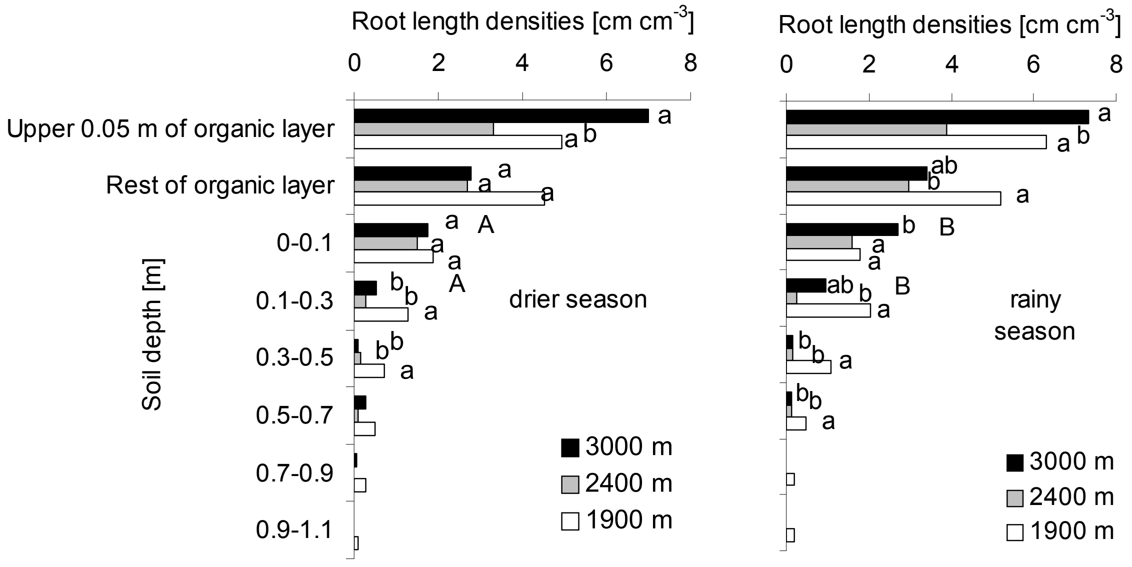

Figure 2.2: Vertical distribution of RLD at different altitudes and seasons. Lower case letters indicate significant differences of RLD between altitudes (Dunn-test; $p < 0.05$); upper case letters indicate significant differences between seasons (Mann Withney test; $p < 0.05$; $n = 8\text{-}20$).

There was no consistent trend of total fine root length with increasing altitude. Total fine root length in the drier season was 15.5 km m^{-2} at 1900 m, 7.4 km m^{-2} at 2400 m and 13.9 km m^{-2} at 3000 m. In the rainy season fine root lengths were 20.2 km m^{-2}, 7.6 km m^{-2} and 16.8 km m^{-2} at 1900 m, 2400 m and 3000 m, respectively.

Relative N uptake potential from different soil layers

^{15}N excess of young tree leaves increased with increasing time after application of the tracer into the soil (Table 2.2). This was true independently of altitude and soil depth of tracer application. For the estimation of N uptake potential only the data obtained at 60 days after tracer application were considered.

Table 2.2: ^{15}N excess (in ‰) of young tree leaves at different times after tracer injection into different soil depths ($n = 5$). Values are means ± standard errors.

Soil depth	Days after tracer injection			
(m)	10	20	30	60
3000 m				
Organic layer	2.3 ± 0.6	16.6 ± 9.4	90.6 ± 47.1	373.5 ± 121.7
0.05	3.0 ± 1.0	4.8 ± 4.0	9.3 ± 5.4	113.7 ± 51.3
0.40	2.0 ± 0.9	2.0 ± 0.7	6.8 ± 5.0	13.9 ± 5.8
1900 m				
Organic layer	3.9 ± 1.4	10.9 ± 10.0	51.8 ± 20.7	163.0 ± 61.3
0.05	2.7 ± 0.4	-2.4 ± 0.5	38.9 ± 14.7	91.7 ± 32.5
0.40	3.7 ± 1.0	-0.9 ± 1.4	-1.0 ± 2.2	17.9 ± 15.3

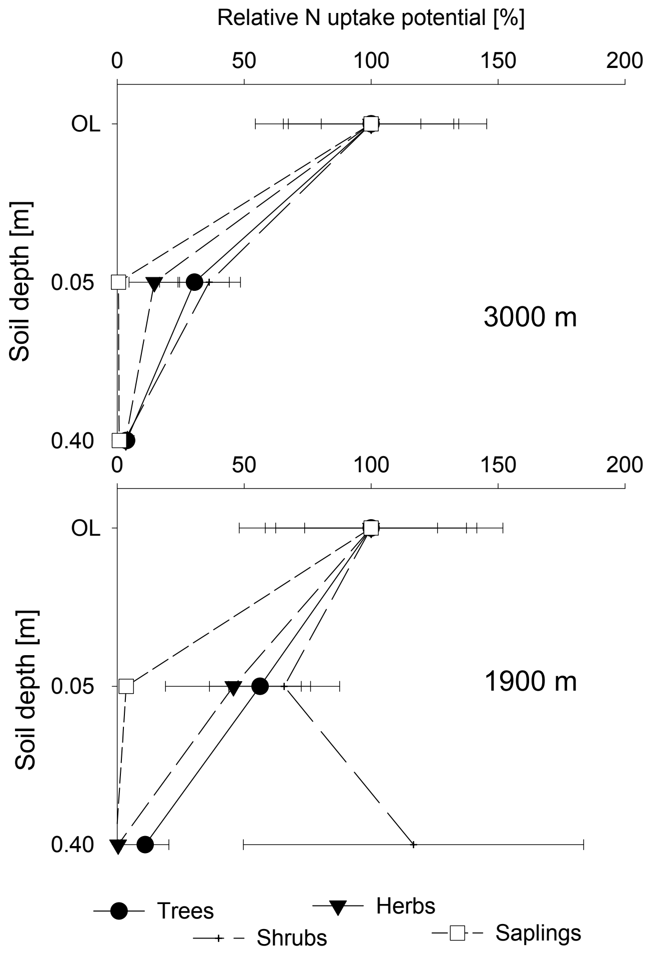

Figure 2.3: Vertical pattern of the RNUP of different plant groups at 1900 m and 3000 m. OL = organic layer. Error bars represent standard errors (*n* = 5). Differences between RNUP of different plant groups within one soil depth were not significant (H-test, p < 0.05).

The RNUP was highest in the organic layer (Figure 2.3). At 3000 m, it decreased more sharply with increasing soil depth than at 1900 m. On average of all plant groups, 43 % of the N obtained from the organic layer was acquired from 0.05 m depth at 1900 m, but only 19 % at 3000 m. From 0.4 m depth 32 % of the N obtained from organic layer was acquired at 1900 m, in comparison to 2 % at 3000 m.

Due to the high standard errors, the pattern of N uptake potential did not significantly differ between plant groups. At both altitudes however, there was a trend that for saplings the RNUP was most strongly reduced already at a depth of 0.05 m in the mineral soil.

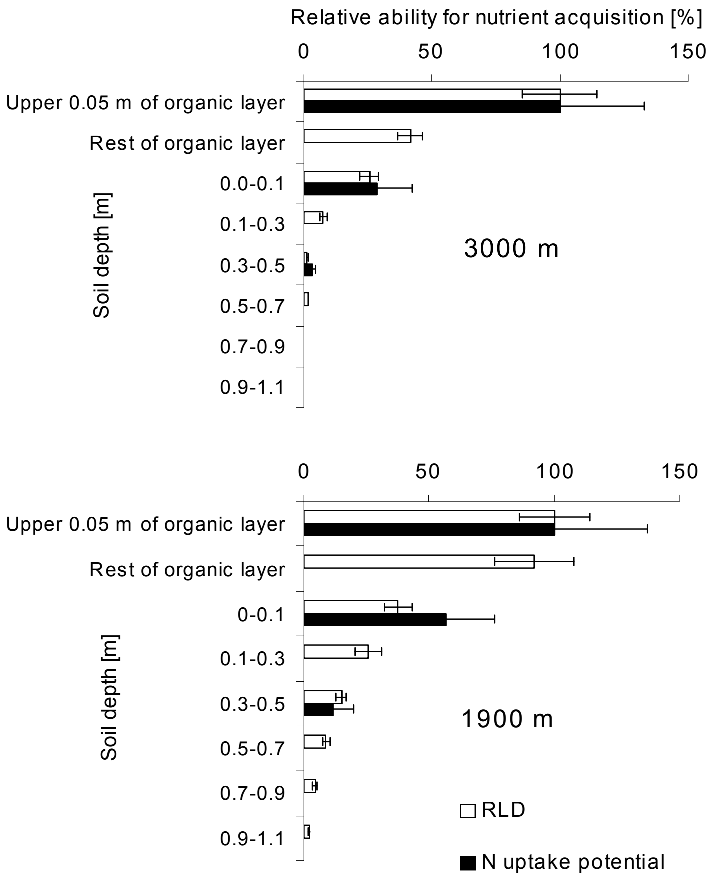

Figure 2.4: Effect of soil depth on the relative ability for nutrient acquisition as assessed by two independent methods

In Figure 2.4 estimates of the relative nutrient acquisition ability in various soil layers as obtained by two different methods are shown. The relative distribution of the Nuptake potential was very similar to the relative distribution of RLD. This implies that for the site conditions in this study, N uptake potential can be reasonably well estimated from RLD.

Soil chemical parameters

N_{min} concentrations were always very low and did not differ significantly ($p > 0.05$) between altitudes (Figure 2.5). Pools of N_{min} in the organic layer and the upper 0.7 m of mineral soil were 9.1 kg ha^{-1} at 1900 m, 5.5 kg ha^{-1} at 2400 m and 5.7 kg ha^{-1} at 3000 m. Due to high variations between replicates, these differences were not significant ($p > 0.05$). The percentage of nitrate as a fraction of total N_{min} ranged between 24 and 84 % and was not dependent on altitude and soil depth.

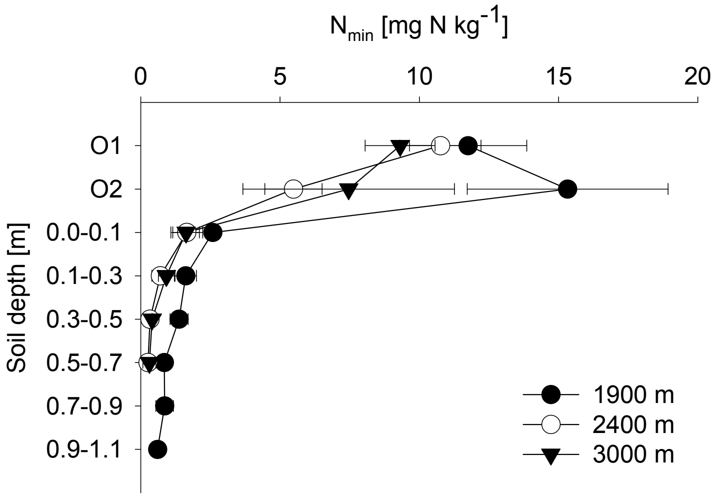

Figure 2.5: N$_{min}$ concentrations (mg N kg^{-1}) in different soil layers at three altitudes. Error bars represent standard errors (*n* = 4 at 1900 m, *n* = 3 at 2400 and 3000 m). Differences between N$_{min}$ concentrations at different altitudes within one layer were not significant (ANOVA, $p < 0.05$). O1 = upper 0.05 m of organic layer, O2 = rest of organic layer.

Soil reaction was very acid at all altitudes and in all soil layers (Figure 2.6). At 1900 m and 2400 m, pH values were lowest in the O2 layer and increased again with increasing depth in mineral soil to values near 4. At 3000 m, pH values up to a soil depth of 0.3 m were even lower than at 1900 m and 2400 m. Below that depth, pH values also increased to about 4.

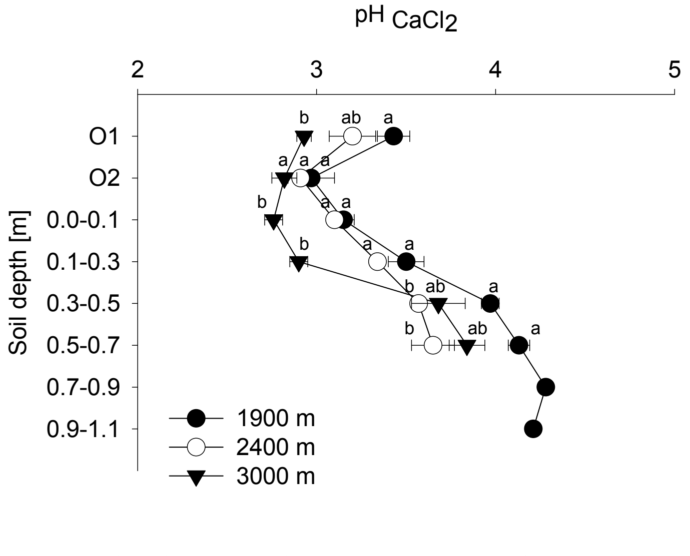

Figure 2.6: Values of pH$_{CaCl2}$ in different soil layers at three altitudes. Error bars represent standard errors (*n* = 3); lower case letters indicate significant differences between altitudes within one layer (Tukey-test, $p < 0.05$). O1 = upper 0.05 m of organic layer, O2 = rest of organic layer.

Effect of altered soil properties on fine root growth in mineral soil

At 1900 m, RLD in ingrowth cores of all treatments were similar in all soil depths, whereas at 3000 m, there was a sharp decrease in RLD with increasing depth (Figure 2.7). At 3000 m, RLD was always markedly lower than at 1900 m (note the differences in the scale). This difference may be attributed to the described discrepancies in the methodological procedure of ingrowth core installation. Differences of RLD between the treatments were not significant at any altitude (H-test, $p > 0.05$). However, at 1900 m and at 3000 m, ingrowth cores with limed soil showed trends of higher RLD than the untreated control. A trend of increasing RLD after addition of nutrients occurred only in 0.0-0.2 m depth at 3000 m.

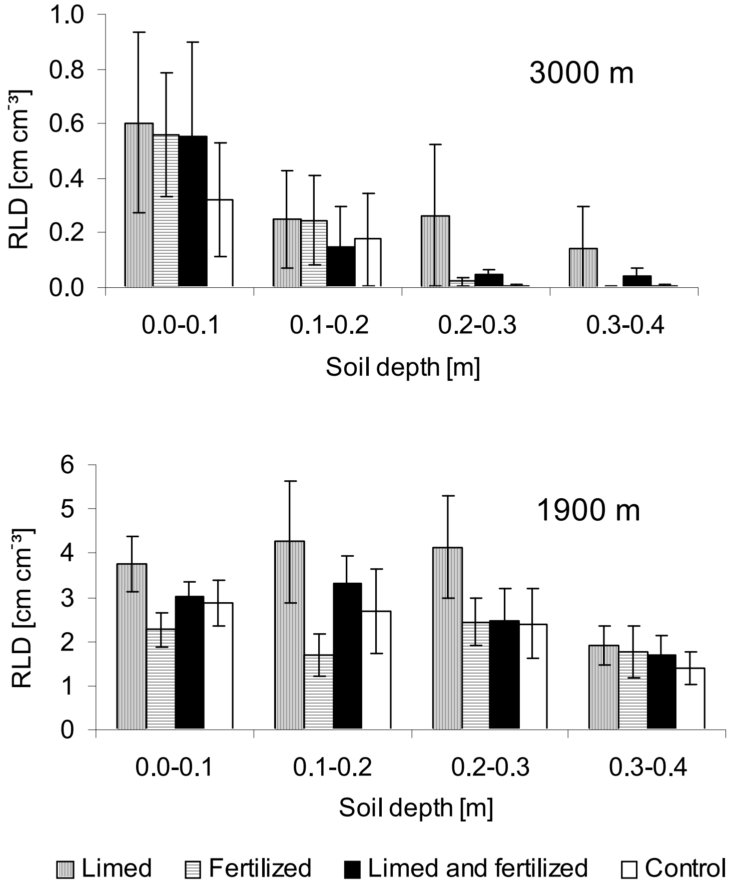

Figure 2.7: Root length densities in ingrowth cores with different soil treatments at 1900 m and 3000 m one year after installation. Error bars represent standard errors ($n = 10$).

2.4 Discussion

Seasonal changes of the nutrient uptake ability

The vertical rooting pattern in the present study was not affected by the season, except for an unexpected increase of RLD in the upper 0.3 m of mineral soil at 3000 m in the rainy in comparison to the drier season (Figure 2.2). Seasonal changes in root densities in a lowland forest in Panama were explained by changes in soil water contents and nutrient availability (Yavitt and Wright, 2001). However, in the lowland forest the dry period was much more pronounced than in the forest of the present study. In a study by Huxley et al. (1974), low topsoil water availability during the dry in comparison to the wet season in Kenya was associated with a decrease of tracer uptake from the topsoil by coffee trees, whereas root mass distribution was similar in both seasons. This indicates that tracer uptake is more sensitive to seasonal changes of water availability than fine root distribution. The lack of substantial seasonal effects on root distribution in the present study is presumably due to the fact that the seasonal fluctuations of temperature, precipitation and soil water contents were only small in the studied tropical montane forests.

Vertical pattern of nutrient uptake ability at different altitudes

In the present study, the ability for nutrient acquisition from different soil depths was estimated by two independent methods. Length densities of living fine roots are primarily an estimate for the spatial exploration of the soil by plant roots, and thus, for the ability of plants to access nutrients at different soil depths (Bouillet et al., 2002; Lehmann, 2003). It should be noted, however, that the spatial availability of nutrients is also dependent on soil characteristics regulating nutrient transport to the root surface by diffusion (Arvidsson, 1999), and on root characteristics such as root hair formation (Wissuwa and Ae, 2001) or mycorrhization (Muthukumar et al., 2003). Furthermore, RLD is commonly poorly correlated with the ability for nutrient acquisition under conditions where the physiologically based ability of roots for nutrient uptake is impaired by factors such as lack of soil moisture (Buljovcic and Engels, 2001; Lehmann, 2003) or oxygen deficiency (Morard et al., 2000) or altered by differences in the functionality of roots (Göransson, 2006). ^{15}N enrichment in leaves after application of ^{15}N labelled fertilizer to different soil depths is a measure that integrates spatial availability of nutrients in soil by plant roots and the physiologically related ability of roots for nutrient absorption. As neither total plant biomass nor mean ^{15}N enrichment in the total biomass were determined, our data can only be taken for assessment of the relative distribution of nutrient acquisition ability in different soil depths. The close correspondence of our estimates of the ability of nutrient acquisition obtained by the two methods (Figure 2.4) indicates that the physiologically based ability for nutrient uptake was similar in all soil depths.

At all three altitudes the organic layer was the horizon which was most densely rooted (Figure 2.2). This has also been reported for an old tropical montane forest (Hertel et al., 2003) and a lower montane forest in Costa Rica (Vance and Nadkarni, 1992) and is in accordance with Ostertag (2001) who found highest root lengths in the upper soil layers of a Hawaiian tropical montane forest. RLD in the organic layer in this study were two times higher than in several tropical lowland sites (Powers et al., 2005).

In our study, there was no consistent effect of increasing altitude on RLD in the organic layer. In mineral soil, RLD below 0.1 m soil depth were substantially lower at the upper study sites in comparison to 1900 m. The reduced access of roots to nutrients in mineral soil at high altitudes may imply that the potential risk of nutrient leaching is increased. Nitrate in soil is almost fully dissolved in soil solution (Jungk, 2002) and is therefore predisposed to leaching. However, at all altitudes RLD in all soil layers were high enough to assume effective nitrate retention by roots (Claassen and Steingrobe, 1999). Complete access to other nutrients such as Ca^{2+}, K^{+} or Mg^{2+} requires RLD of at least 0.7 cm roots cm^{-3} (recalculated from Claassen and Steingrobe, 1999 and Yanai et al., 2003). Root length densities fell below this value in 0.5 m depth at 1900 but already in 0.1 m depth at the upper sites. Taking into account the higher precipitation rates at higher altitude, the decrease of RLD in mineral soil from 1900 m to 2400 and 3000 m suggests nutrient retention by roots to be less efficient at 2400 and 3000 m.

In many ecosystems, the retention of nutrients from deeper soil layers and thus the prevention of nutrient losses from the ecosystem by leaching may be attributed to specific plant groups due to clear species differences in the vertical stratification of root systems (Van Noordwijk et al., 1996). For example, in a South African savannah grasses had more superficial root systems than trees (Knoop and Walker, 1985). In a seasonal tropical forest in the eastern Amazon herbaceous species had deeper root systems than trees (Sternberg et al., 1998). At our study sites, the vertical pattern of N uptake potential was very similar for all plant groups except for saplings, which obtained nearly their entire N from the organic layer (Figure 2.3). Thus, nutrient retention from deeper soil layers in these forests can be ascribed to both trees and the understorey.

Possible mechanisms for the observed pattern of nutrient uptake ability

There are several possible reasons for the sharp decrease in RLD and N uptake potential in mineral soil at higher altitudes. As reported for other tropical montane forests (Cavalier, 1992; Santiago, 2000), mineral soils at 3000 m were often waterlogged, which may have caused oxygen deficiency in deep soil layers. Other impacts include shallower mineral soils at 2400 and 3000 m than at 1900 m, less favourable soil chemical properties at higher altitude and differences in species composition between sites.

It is well known that rooting depth varies depending on plant species (Coners et al., 1998; Silva and Rego, 2003; Claus and George, 2005). The species composition of the forests in the present study changed significantly along the altitudinal gradient. However, plant diversity was extremely high (Homeier et al., 2002), suggesting a high genetic potential for complementary use of biotope space (Dimitrakopoulos and Schmid, 2004) at all altitudes. It is therefore more likely that the vertical root distribution of the entire forest communities was governed by soil factors.

The soil pH was very low not only in the organic layer, but also in mineral soil, particularly at high altitudes (Figure 2.6). Subsoil acidity has been shown to reduce vertical rooting intensity of *Picea abies* (Jentschke et al., 2001). The reduction of root growth in acid soil is usually related to high Al^{3+} and H^{+} concentrations and low Ca/Al ratios in soil solution (Murach and Ulrich, 1988; de Graaf et al., 1997). However, liming of the mineral soil did only marginally increase root growth at 1900 m and 3000 m (Figure 2.7). The lack of a clear effect of liming on RLD in the soil cores may have been caused by methodological problems. The initial difference in soil pH induced by liming was reduced during the one year period of the experiment from 1.0 to 0.3 pH units (decrease from pH 5 to pH 4.3) at 1900 m and from 2.2 to 0.7 pH units (from pH 5 to pH 3.5) at 3000 m. Furthermore, the lack of a significant rooting response may also indicate low susceptibility of root growth to low soil pH. Phytotoxic effects of low soil pH are usually reported for ecosystems exposed to anthropogenic induced soil acidification due to emissions of air pollutants (Murach and Ulrich, 1988; de Graaf et al., 1997; de Wit et al., 2001; Jentschke et al., 2001). Native plant species growing on naturally acid soils are often adapted to low soil pH, e.g. by mycorrhizal symbiosis, rhizosphere alkalinization, Al chelation or by accumulating Al in extra-cytoplasmic compartments of root or shoot tissue (Cuenca et al., 1990; de Wit et al., 2001). In some cases plant growth of species adapted to acid soils is even increased by Al application (Watanabe and Osaki, 2002). In the present study, the average leaf Al concentrations of lignified plants were always higher than 1000 ppm (data not shown), indicating that many woody species were Al accumulators (Cuenca et al., 1990). Accordingly, many Al accumulating species have also been observed in a tropical cloud forest in Venezuela (Cuenca et al., 1990). At least at 1900 m and 3000 m, high organic carbon contents in mineral soil (data not shown) suggest high degrees of Al-complexation with organic compounds and thus, low toxicity of Al for root growth (Jentschke et al., 2001). In summary, indirect evidence suggests that the differences in rooting depth at different altitudes are not caused by soil pH.

The N_{min} concentrations in mineral soil were very low, particularly at high elevations (Figure 2.5). It is well documented, that external N_{min} concentrations have a strong impact on root growth (Stitt and Scheible, 1998; López-Bucio et al., 2003). The variation of vertical fine root distribution in a montane rain forest in Panama was explained by the concentration of N in soil (Cavalier, 1992). However, fertilization did not significantly modify rooting into ingrowth cores (Figure 2.7). This may be due to nutrient leaching during the one year of the study period or to low rooting response of the forest plant community to fertilization.

Not only vertical fine root distribution in mineral soil but also in the organic layer showed different patterns between altitudes (Figure 2.2). Whereas at 1900 m and 2400 m RLD were similar in the O1 and O2 layer, at 3000 m RLD was two times higher in the O1 layer than in the O2 layer. At 3000 m, it was often observed that roots grew upwards along the trunk of their own or neighbouring trees, covered by thick moss layers. This was also observed in other tropical montane forests and is usually interpreted as a strategy to improve competition for nutrients that are leached from the canopy (Stewart, 2000). The more superficial root distribution at higher altitudes supports the assumption of Cavalier (1992) that especially at higher altitudes of wet tropical regions more nutrients are absorbed directly from litterfall, throughfall and stemflow. At a higher altitude, nutrient input from above ground is increased not only due to leaching from canopy (Wilcke et al., 2001) but also due to atmospheric nutrient input that is closely and positively related to fog and precipitation (R. Rollenbeck, pers. comm.).

Conclusions

In this tropical montane forest, the organic layer was always the preferred layer for nutrient acquisition. A substantially lower exploitation of mineral soil by fine roots at higher altitudes in comparison to 1900 m enhanced the probability for nutrient losses from soil by leaching. The more superficial fine root distribution within the organic layer at 3000 m than at lower altitudes was presumably related to increased nutrient input from canopy by leaching. The specific constraints for root growth in the mineral soil of tropical montane forests warrant further investigations.

Acknowledgements

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3 Nutritional status of plants growing at different altitudes of a tropical montane forest in Ecuador

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Abstract

Plant growth and aboveground net primary productivity of forest ecosystems may be constrained by nutrient limitation. We measured the foliar composition of macronutrients and soil nutrient availability at different altitudes (1900, 2400, and 3000 m a.s.l.) of a tropical montane forest to assess the role of mineral nutrition for the decrease of growth and tree height at high altitudes. Leaf concentrations of N, P, S and K in trees were lower at 2400 and 3000 m than at 1900 m, whereas the concentrations of Ca and Mg were not significantly affected by altitude. Comparison of our data with reference concentrations from the literature indicated that at 1900 m growth was not limited by nutrients. However, at higher altitudes the leaf concentrations of N, P, S and K fell into or near the range of nutrient deficiency. The N:P ratio in leaves was lowest at 3000 m indicating strong N deficiency. The calculation of DRIS (Diagnosis and Recommendation Integrated System) indices based on the leaf nutrient ratios found at 1900 m, confirmed that N was the most growth limiting nutrient at the highest altitude. The decrease of the N, P and S leaf concentrations with increasing altitude was associated with higher C:N, C:P and C:S ratios in the organic surface layer suggesting lower availability of these nutrients from mineralization of plant litter. In contrast, stocks of plant available nutrients in the mineral soil were similar at all altitudes (N) or even increased at high altitudes (P, K, Ca, Mg), but due to impaired root growth in the oxygen deficient mineral soil at higher altitudes these nutrient stocks were hardly accessible to plants. Our results indicate that plant growth at high altitudes of Ecuadorian tropical montane forests may be limited by several nutrients whereby nutrient deficiency may be induced by low mineralization of organically bound nutrients and low ability of plants for nutrient acquisition from mineral soil.

Keywords: DRIS, foliar nutrient analysis, nutrient availability, nutrient uptake, root length density.

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3.1 Introduction

The decrease of aboveground net primary productivity (ANPP) and tree stature with increasing altitude in tropical montane forests is poorly understood. Several explanations for low growth and stature of trees at high altitudes are given in the literature: (1) Low photosysnthesis due to persistent cloudiness and thus, low radiation input (Bruijnzeel and Veneklaas, 1998) or due to low temperatures (Kitayama and Aiba, 2002); (2) direct impact of low temperatures on growth (Hoch and Körner, 2003); (3) exposure to strong winds (Lawton, 1982; Cordero, 1999); (4) low nutrient availability due to water saturated soils, low temperatures and high concentrations of phenolic compounds in soils leading to low decomposition and mineralization rates (Edwards and Grubb, 1977; Bruijnzeel et al., 1993; Tanner et al., 1998); (5) low nutrient uptake capacity due to reduced root respiration or transpiration (Bruijnzeel and Veneklaas, 1998).

Correlations between plant growth and nutrient availability have often been observed in tropical montane forests. The exceptional high tree stature in a montane forest stand in Papua New Guinea was attributed to its nutrient rich soil parent material (Edwards and Grubb, 1977). In Jamaica (Tanner et al., 1990) and Hawaii (Vitousek and Farrington, 1997) trunk diameter growth and leaf production of several native tree species in montane forests were enhanced by addition of N or P. In a Venezuelan (Tanner et al., 1992) and a Hawaiian (Vitousek et al., 1993) montane forest low N supply was likely the most important limitation to plant growth.

Vitousek and Farrington (1997) as well as Vitousek et al. (1993) observed a correlation between N and P nutrition of tropical montane forests and soil age, supporting the theory of Walker and Syers (1976) that young soils are low in N availability whereas later in soil development, P and other rock-derived nutrients are gradually lost or bound in protected forms, but N continues to enter the system via biological N_2 fixation. Tanner et al. (1998) hypothesized that in tropical montane forests N limitation is more common than P limitation whereas tropical lowland forests are usually P limited. The authors suggested that with regard to N, tropical montane forests appear to function more like forests from higher latitudes than like tropical lowland forests. This suggestion is based on the observation that boreal and temperate forests tend to be strongly N deficient, whereas tropical forests on old soils tend to be P deficient (Vitousek et al., 1993; McGroddy et al., 2004; Reich and Oleksyn, 2004).

The nutritional status of plants is governed both by chemical and spatial nutrient availability to plant roots (Jungk 2002). Chemical nutrient availability in tropical montane forests may be affected by parent material, weathering intensity, cation exchange capacity, the rates of litter decomposition, or extracellular phophatase activity (Treseder and Vitousek, 2001; Kitayama and Aiba, 2002; Wilcke et al., 2006). Spatial nutrient availability is dependent on the exploitation of soil by roots or mycorrhizal hyphae and the mobility of the respective nutrient in soil. It is likely to be high in the densely rooted organic surface layers of tropical montane forests (Vance and Nadkarni, 1992; Hertel et al., 2003) and may be further enhanced by high abundance of mycorrhizal fungi (Treseder and Vitousek, 2001; Kottke et al., 2004; Haug et al., 2004). At high altitudes of tropical montane forests, spatial availability of nutrients in mineral soil may be decreased due to unfavourable chemical soil properties for root growth (Santiago, 2000; Schrumpf et al., 2001).

The nutritional status of plants in tropical montane forests may be assessed by fertilization experiments (e.g. Tanner et al., 1990; Tanner et al., 1992; Vitousek et al., 1993; Vitousek and Farrington, 1997), foliar nutrient analysis (Tanner et al., 1998), root ingrowth cores (Stewart, 2000) or correlation analysis between soil nutrient contents and ANPP (Homeier, 2004). Fertilizing experiments are necessary to make definite conclusions about the limitation of ANPP by nutrients, but they are time consuming and therefore often restricted to very few nutrients. Determination of foliar nutrient concentrations allows a rapid examination of many nutrients. However, to assess potential growth limitation by nutrients, critical nutrient concentrations (leaf concentrations that indicate nutrient deficiency or sufficiency) have to be known. For native species of tropical montane forests, critical nutrient concentrations are usually not available. A further problem for the assessment of nutrient limitation by foliar analysis in tropical montane forests is their high biodiversity. Neighbouring plant species growing in one stand may differ in the degree of growth limitation by nutrients (Tanner et al., 1990) and foliar nutrient concentrations may vary among individual species (Vitousek et al., 1995).

In the present study, we examined the nutritional status of plants growing at different altitudes of a south Ecuadorian montane forest to elucidate factors that may contribute to the reduction of ANPP and tree stature with increasing altitude. The plant nutritional status was assessed by foliar nutrient analysis of various plant types (trees, shrubs, herbs). Additionally, data from foliar analysis were related to data from soil. It was hypothesized (i) that plant growth at high altitudes is limited by nutrient deficiency and (ii) that nutrient deficiency is attributed to both low chemical and low spatial nutrient availability.

3.2 Materials and methods

Study sites

Experimental work was carried out at three study sites on the fringes of the Podocarpus National Park on the eastern Andes slope. The two lower study sites (1900 m a.s.l., S 03°58′ W 79°04′ and 2400 m a.s.l., S 03°59′ W 79°04′) were situated in the Reserva San Francisco (RSF), the highest site (3000 m, S 04°06′ W 79°10′) was located in Cajanuma within the Podocarpus National Park. The sites were similar in inclination (20-50°).

Maximum tree heights at 1900 m and 2400 m were 19 m and 12 m, respectively (Röderstein et al., 2005). About 250 to 288 tree species from 25 different families occurred in the RSF. Most frequent families were Lauraceae, Rubiaceae and Melastomataceae, and species composition differed markedly between 1900 and 2400 m (Homeier, 2004). The uppermost study site in Cajanuma was located in a typical elfin forest, with a maximum tree height of 9 m (Röderstein et al., 2005). Notable tree families at this site were Clusiaceae, Cunoniaceae, Aquifoliaceae and Clorantaceae (Homeier, 2004).

Within the study area, aboveground productivity increased markedly with increasing altitude. As an estimate for annual gross leaf production, Röderstein et al. (2005) reported a decrease of average leaf litter production from 862 g m^{-2} yr^{-1} at 1900 m to 433 g m^{-2} yr^{-1} at 2400 m and 263 g m^{-2} yr^{-1} at 3000 m. The relative annual increment in stem cross sectional area declined from 1.26 % at 1850 m to 0.63 % at 2450 m (Homeier, 2004).

The soils were developed on metamorphic shale, quartzite or sandstone bedrock and were classified as gleyic Cambisols according to FAO taxonomy at 1900 and 2400 m and podzols at 3000 m (S. Iost, pers. comm.). The organic layer was markedly deeper at 3000 m (about 0.30 m) than at the lower study sites (about 0.15 m). The average depth of the Ah decreased from 0.70 m at 1900 m to 0.15 m at 2400 m and 0.20 m at 3000 m.

The mean annual rainfall at 1900 m (1950 mm) was lower than at 2400 m (5000 mm) and 3000 m (4500 mm). Mean annual temperature decreased markedly from 14.9 °C at 1900 m to 12.3 °C at 2400 m and 8.6 °C at 3000 m (Röderstein et al., 2005).

Sampling

Foliar nutrient concentrations at the community level were assessed by the following procedure: (i) Mixed samples were taken to address the problem that plant species may differ in growth limitation by nutrients and foliar nutrient concentrations; (ii) Samples were taken separately for the plant groups “trees” (lignified and higher than 3 m), “shrubs” (lignified and with a height of 0.5 – 3 m) and “herbs” (not lignified), to estimate the impact of species-specific nutrient concentrations on nutrient concentrations in the mixed samples.

Five locations were obtained randomly at each altitude. Ten plants per plant group growing most adjacent to each location were chosen. One young fully developed leaf per plant was harvested, using pruning shears for trees and shrubs. From microphyllous species more than one leaf was harvested to compensate for the reduced weight of leaf material. The ten or more replicate leaves per plant group and location were mixed together to one bulked sample and dried at 50 °C.

Soil was sampled in 20 x 20 m plots established at each altitude. Twenty replicate locations per plot were sampled. Samples from the organic layer were taken with help of a frame (100 mm x 100 mm). Samples were divided in the upper 0.05 m of the organic surface layer (O1) and the rest of the organic surface layer (O2). Mineral soil was sampled with a soil corer (80 mm in diameter) in the depths 0.0-0.1, 0.1-0.3, 0.3-0.5 and 0.5-0.7 m. Four of the 20 replicates were bulked together in each case to obtain 5 replicate samples per soil depth for analysis. Samples were air dried for storage.

For the determination of N_{min}, samples from mineral soil were taken by soil coring in February 2003 (end of dry season). Twelve randomly distributed replicate sub-samples were taken at 1900 m, and 9 at 2400 m and 3000 m, respectively. Three sub-samples each were combined to one sample to obtain four replicates for the analysis at 1900 m and three replicates at 2400 m and 3000 m. Fresh soil samples were extracted with 12.5 mM $CaCl_2$ (ratio soil:solution = 1:2).

Chemical analyses

After drying at 50 °C, leaf samples and soil samples from the organic layer were ground with a flint mill (Type MM2, Retsch-GmbH & CoKG, Haan, Germany). Concentrations of total C, N, and S were assessed with a CNS analyser (Vario Max CNS, Elementar Analysesysteme, Hanau, Germany). For determination of total P, K, Ca and Mg ground samples were digested with concentrated HNO_3 under pressure (Heinrichs et al., 1986). Phosphorus, K, Ca and Mg from the mineral horizons were extracted by the Mehlich III procedure (Mehlich, 1984). The Mehlich III reagent composition was 0.2 M CH_3COOH, 0.25 M NH_4NO_3, 0.015 M NH_4F, 0.013 M HNO_3, and 0.001 M EDTA. The extraction ratio (soil weight to extractant volume) was 1:10. Concentrations of Ca, K, and Mg from leaf and soil samples were measured by flame atomic absorption spectrometry (Perkin Elmer 4100, Perkin Elmer, Milano, Italy) and P concentrations were determined with a spectral photometer (Specord 200, Analytik Jena,

Jena, Germany) after staining with the molybdene blue procedure (Murphy and Riley, 1962). For determination of N_{min} in mineral soil, nitrate concentrations in the extracts were assessed with a spectral photometer (Lambda 2S, Perkin Elmer, Milano, Italy) from the difference of the extinction at 210 and 275 nm. Ammonium was measured photometrically at 636 nm after staining with the indophenol blue procedure (Bundy and Meisinger, 1994).

Assessment of growth limiting nutrients from foliar nutrient analysis

To address the problem that critical foliar nutrient concentrations are not known for the species growing in this forest, different approaches based on absolute nutrient concentrations and nutrient ratios were followed.

1) Foliar nutrient concentrations of trees were compared with critical concentrations of other tree species from literature.

2) Foliar nutrient ratios were compared with foliar nutrient ratios of tropical lowland forests and temperate forests from an extensive database summarized in McGroddy et al. (2004). Tropical lowland forests were regarded as representative for typical P limited forest ecosystems and temperate forests for typical N limited forest ecosystems.

3) Foliar nutrient ratios at different altitudes were compared according to the “Diagnosis and Recommendation Integrated System” (DRIS) developed by Beaufils (1973) by calculating DRIS indices. DRIS indices give an indication of the relative deficiency (negative indices) or excess (positive indices) of a nutrient in a specific plant population in comparison with a high yielding population. Thus, they can be interpreted as a measure for the relative importance to yield (Walworth and Sumner, 1987). Nutrient ratios of a given population are compared with standard norms which are derived from a favourable, i.e. high yielding, population. In the present study standards were derived from foliar nutrient ratios at 1900 m, where plant productivity was highest (Homeier, 2004; Röderstein et al., 2005). DRIS indices of all nutrients were calculated for 2400 m and 3000 m according to Walworth and Sumner (1987).

Calculations and statistical analyses

To calculate nutrient stocks in soil, average bulk densities of each soil layer were used. Significant differences of foliar nutrient concentrations, nutrient stocks in soil and C to nutrient ratios in soil between different altitudes were assessed by ANOVA and Tukey post-hoc test.

3.3 Results

Nutrient concentrations in leaves

The effect of altitude on foliar nutrient concentrations of trees varied depending on the specific nutrient (Table 3.1). While concentrations of Ca and Mg were not affected by altitude, the concentrations of all other nutrients were lower at 2400 and 3000 m than at 1900 m. The decrease of the concentrations of N, P, S, and K at higher altitudes was similar for N, P, S and K, ranging from 30 to 48 %.

The effect of altitude on foliar nutrient concentration of shrubs and herbs was similar to that on foliar nutrient concentration of trees (Table 3.1). The concentration of N, P, and S were markedly lower at 2400 and 3000 m than at 1900 m. The concentrations of K decreased at higher altitudes in herbs but not in shrubs. The concentrations of Ca were significantly reduced only in herbs at 2400 m.

At 1900 m, foliar nutrient concentrations of trees were within the ranges of nutrient sufficiency given in textbooks for temperate broadleaved tree species and concentrations of N, P, S, K and Mg were in the ranges of sufficiency for tropical tree species (Table 3.1; Bergmann, 1993). At this altitude, foliar concentrations of all nutrients were higher than the ranges of nutrient deficiency found in other studies for trees of tropical montane forests (Vitousek et al., 1995; Vitousek and Farrington, 1997) and tropical lowland forests (Drechsel and Zech, 1991). In contrast, at 2400 and 3000 m, foliar concentration of N, S and K fell below the ranges of sufficiency according to all reference data given by Bergmann (1993). Concentrations of N, P and K were within or only slightly higher than the ranges indicating deficiency in tropical forests (Drechsel and Zech, 1991; Vitousek et al., 1995; Vitousek and Farrington, 1997).

Table 3.1: Nutrient concentrations in youngest fully developed leaves of trees, shrubs and herbs at three altitudes ($n = 5$) and data from literature (N = number of tree species). Upper case letters indicate significant differences in nutrient concentrations between altitudes (Tukey-test; $p < 0.05$).

Plant group	Location	N	P	S	K	Ca	Mg
		Nutrient concentrations (mg g-1)					
Trees	This study						
	1900 m	21.7 (1.3)^{A}	2.2 (0.2)^{A}	1.9 (0.1)^{A}	10.0 (1.2)^{A}	6.2 (1.7)^{A}	3.4 (0.6)^{A}
	2400 m	13.5 (1.2)^{B}	1.2 (0.1)^{B}	1.1 (0.1)^{B}	7.0 (0.4)^{AB}	7.4 (1.0)^{A}	2.7 (0.2)^{A}
	3000 m	11.3 (0.3)^{B}	1.4 (0.1)^{B}	1.2 (0.1)^{B}	5.3 (0.4)^{B}	4.9 (0.3)^{A}	3.2 (0.2)^{A}
	Ranges of nutrient sufficiency						
	Temperate zones[a]	17 – 40 ($N = 7$)	1.5 – 3.0 ($N = 7$)	-	10 – 18 ($N = 7$)	2 – 18 ($N = 7$)	1.5 – 4.0 ($N = 7$)
	Tropical zones[a]	14 – 30 ($N = 5$)	1.0 - 2.5 ($N = 5$)	1.5 - 2.5 ($N = 4$)	10 – 23 ($N = 5$)	9 - 40 ($N = 5$)	2.5 - 8.0 ($N = 5$)
	Ranges of nutrient deficiency						
	Tropical montane forest[b]	8.7 – 14.2 ($N = 1$)	0.6 – 1.0 ($N = 1$)	-	-	-	-
	Tropical zones[c]	6 – 20 ($N = 17$)	0.3 – 1.1 ($N = 16$)	0.3 – 0.5 ($N = 1$)	1.0 – 5.7 ($N = 9$)	-	0.7 – 0.9 ($N = 3$)
Shrubs	This study						
	1900 m	22.3 (2.6)^{A}	2.0 (0.4)^{A}	1.8 (0.2)^{A}	10.2 (1.2)^{A}	9.2 (2.4)^{A}	3.6 (0.6)^{A}
	2400 m	14.9 (0.9)^{B}	1.3 (0.1)^{A}	1.3 (0.2)^{A}	7.7 (0.8)^{A}	9.7 (1.4)^{A}	2.8 (0.3)^{A}
	3000 m	13.4 (0.7)^{B}	1.7 (0.1)^{A}	1.2 (0.1)^{A}	9.4 (0.6)^{A}	6.4 (0.9)^{A}	3.5 (0.5)^{A}
Herbs	This study						
	1900 m	23.7 (1.9)^{A}	3.3 (0.4)^{A}	2.2 (0.2)^{A}	22.4 (1.6)^{A}	10.0 (1.5)^{A}	4.5 (0.5)^{A}
	2400 m	15.2 (1.2)^{B}	1.5 (0.1)^{B}	1.4 (0.4)^{B}	15.4 (1.3)^{B}	5.9 (0.6)^{AB}	2.6 (0.1)^{B}
	3000 m	12.3 (0.7)^{B}	1.5 (0.1)^{B}	1.1 (0.1)^{B}	11.8 (1.4)^{B}	5.6 (0.8)^{B}	3.5 (0.4)^{AB}

[a] **Bergmann (1993): Ranges of foliar nutrient concentrations where neither deficiency nor toxicity occurs on temperate or tropical broadleaved tree species, respectively.**

[b] **Vitousek et al. (1995), Vitousek and Farrington (1997): Ranges of foliar nutrient concentrations of the tree species *Metrosideros polymorpha* growing in Hawaiian tropical montane forests on sites where the respective nutrient was limiting plant growth.**

[c] **Drechsel and Zech (1991): Ranges of foliar nutrient concentrations where deficiency symptoms occurred at several tropical broadleaved tree species.**

Nutrient ratios in leaves

With increasing altitude, there was a marked increase of C:N and C:P ratios in tree leaves, resulting in significantly higher C to nutrient ratios at 2400 and 3000 m than at 1900 m (Table 3.2). Highest C:N ratios occurred at 3000 m and highest C:P ratios at 2400 m. Accordingly, N:P ratios were significantly higher at 2400 m than at 3000 m.

Table 3.2: Nutrient ratios (weight to weight) in leaves of trees ($n = 5$) compared with data from literature. Values in parentheses are standard errors; upper case letters show significant differences between altitudes (Tukey-test, $p < 0.05$); N = number of studies.

Location	C:N	C:P	N:P
This study			
1900 m	23.3 (1.2)^{A}	232 (21)^{A}	10.0 (0.9)^{AB}
2400 m	38.2 (3.8)^{B}	430 (44)^{B}	11.3 (0.3)^{A}
3000 m	44.7 (1.1)^{B}	372 (19)^{B}	8.3 (0.4)^{B}
Temperate broadleaved forests[a]	30.4 ($N = 29$)	357 ($N = 28$)	12.7 ($N = 28$)
Tropical lowland forests[a]	30.1 ($N = 7$)	951 ($N = 12$)	19.6 ($N = 7$)

[a] **McGroddy et al. (2004)**

Both, the C:N and the C:P ratio at 1900 m were low in comparison with ratios in tree leaves from temperate broadleaved and tropical lowland forests (McGroddy et al., 2004; Table 3.2). In contrast, C:N ratios at 2400 and 3000 m markedly exceeded C:N ratios in these forest biomes. The C:P ratio at 2400 and 3000 m was higher than that usually found in temperate forest biomes that are expected to be rather N than P limited, but substantially lower than the ratio found in lowland forests from the tropics that are expected to be rather P limited. The N:P ratios of leaves in the present study were similar or slightly lower than in temperate forests but markedly lower than in tropical lowland forests.

DRIS indices

Ranges of DRIS indices were similar at 2400 and 3000 m (from -12.5 to 14.7), with exception of the high Mg index of herbs at 3000 m (24.2) (Table 3.3). Within each altitude, there were some similarities in the orders of DRIS indices. At 2400 m, P had always negative indices and, in trees and herbs, was the nutrient being most deficient relative to the P nutritional status at 1900 m. Nitrogen and S showed negative indices in trees and shrubs but indices were positive in herbs. Calcium, Mg and K had always positive indices at 2400 m. At 3000 m N exhibited always the most negative indices. At this altitude, P indices of trees and herbs were negative whereas P indices of shrubs were positive. Sulphur indices were negative in two plant groups and equalled zero in one plant group. While Ca and Mg indices were always positive at 3000 m, indices of K varied within a broad range. On average of all plant groups and altitudes, N was the nutrient with the most negative index, followed by P and S, whereas K, Ca and Mg exhibited positive indices.

Table 3.3: Order of DRIS-indices of different plant groups at 2400 m and 3000 m. Data in parentheses show the index of the respective nutrient.

Altitude (m)	Plant group	Order of DRIS-indices
2400	Trees	**P** (-12.5) < **S** (-7.4) < **N** (-4.7) < **Mg** (4.4) < **K** (5.6) < **Ca** (14.7)
	Shrubs	**N** (-3.4) < **S** (-1.4) < **P** (-0.4) < **Mg** (1.2) < **K** (1.3) < **Ca** (2.8)
	Herbs	**P** (-11.3) < **Mg** (0.2) < **N** (1.5) < **Ca** (1.8) < **S** (2.4) < **K** (5.3)
3000	Trees	**N** (-12.4) < **K** (-7.6) < **P** (-0.3) < **S** (0.0) < **Ca** (6.9) < **Mg** (13.3)
	Shrubs	**N** (-11.2) < **S** (- 5.4) < **Ca** (0.4) < **Mg** (4.7) < **P** (5.7) < **K** (5.9)
	Herbs	**N** (-8.5) < **S** (-8.1) < **P** (-6.7) < **K** (-2.4) < **Ca** (1.5) < **Mg** (24.2)
Mean		**N** (-6.4) **<** **P** (-4.3) **<** **S** (-3.3) **<** **K** (1.4) **<** **Ca** (4.7) **<** **Mg** (8.0)

Nutrients in the organic layer

There was no uniform effect of altitude on total nutrient stocks in the organic layer (Figure 3.1). The stocks of N, S and Mg were significantly affected by altitude, whereby the largest stocks were found at 3000 m. The stocks of P, K and Ca were not significantly affected by altitude. At all altitudes the bulk of all nutrients were located in the O2 layer.

Ratios of C:N, C:P, and C:S in the O1 and O2 layer increased significantly with increasing altitude (Table 3.4). The extent of this increase (about 50 % from 1900 to 3000 m) was similar in both layers. The C to nutrient ratios were significantly higher in the O1 than in the O2 layer (Student´s T-test, $p<0.05$), except for C:N and C:S ratios at 2400 m, and C:P ratios at 3000 m, which were not significantly different between the two layers.

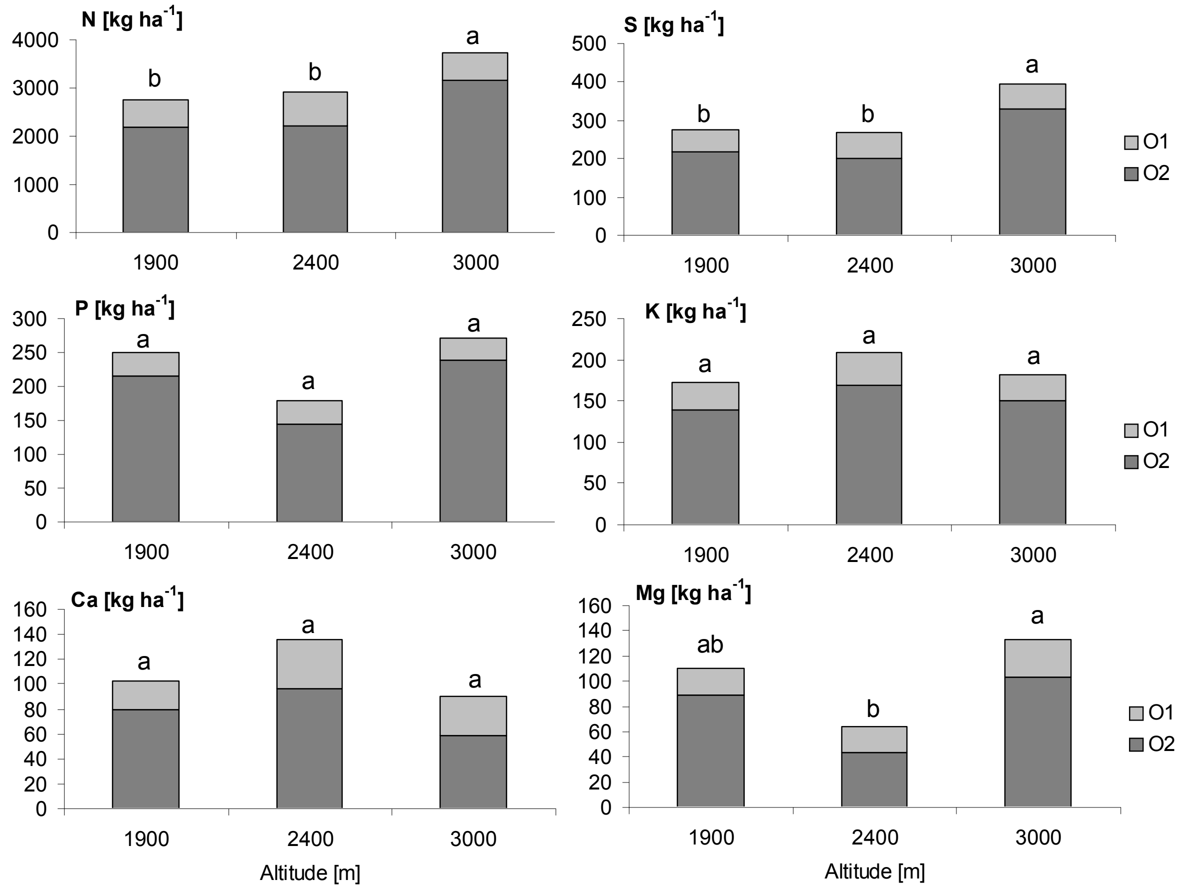

Figure 3.1: Total nutrient stocks in the upper 0.05 m (O1) and the rest (O2) of the organic layer at three altitudes (n = 5). Different lower case letters indicate significant differences in nutrient stocks between altitudes (Tukey test, $p < 0.05$).

Table 3.4: Carbon to nutrient ratios (weight to weight) in different depths of the organic layer from three different altitudes (n = 5). Upper case letter indicate significant differences between altitudes within one layer (Tukey-test; $p < 0.05$). O1 = upper 0.05 m of organic layer, O2 = rest of organic layer.

Soil layer	Altitude (m)	C:N	C:P	C:S
O1	1900	21 (1) ^{C}	351 (28) ^{B}	207 (5) ^{C}
	2400	25 (1) ^{B}	605 (88) ^{A}	265 (8) ^{B}
	3000	34 (1) ^{A}	620 (47) ^{A}	315 (11) ^{A}
O2	1900	19 (1) ^{C}	205 (32) ^{B}	186 (3) ^{B}
	2400	23 (1) ^{B}	352 (26) ^{AB}	249 (11) ^{A}
	3000	28 (1) ^{A}	432 (80) ^{A}	269 (11) ^{A}

Nutrients in mineral soil

In mineral soil, average stocks of N_{min} in the upper 0.7 m were about two times higher at 1900 m than at 2400 and 3000 m (Figure 3.2). However, differences between altitudes were not significant. The proportion of NO_3^- in total N_{min} stocks ranged between 24 and 84 %, irrespectively of soil depth and altitude. The stocks of Mehlich III extractable P, K, Ca and Mg increased markedly with increasing altitude. This was most pronounced for available Mg stocks which increased about 8 times from 1900 to 3000 m, and least for available P stocks which increased about 3 times. The increase of available P, Ca, Mg, and K stocks in mineral soil was especially pronounced in the deeper soil layers below 0.3 m.

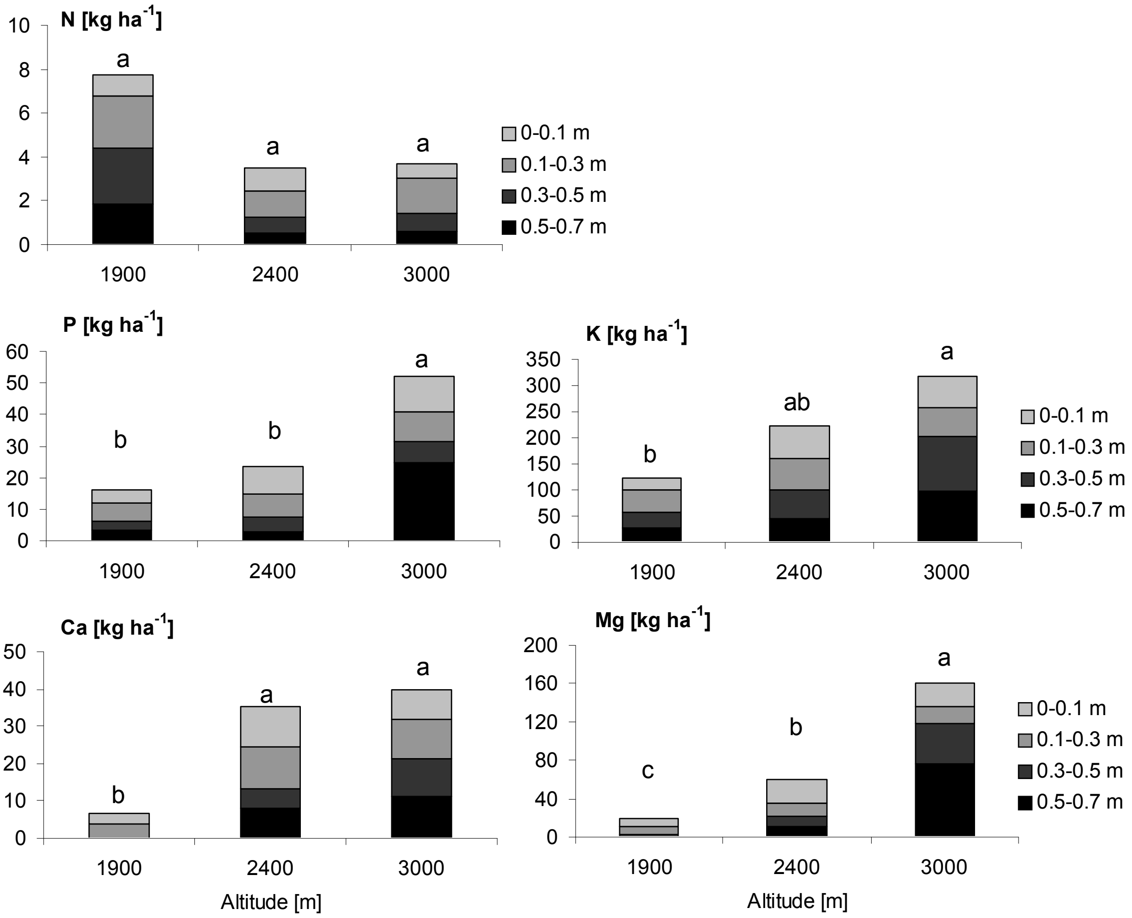

Figure 3.2: Stocks of N_{min} (n = 3-4) and Mehlich III extractable nutrients (n = 5) in different depths of mineral soil at three altitudes. Different lower case letters indicate significant differences in nutrient stocks between altitudes (ANOVA, Tukey test, $p < 0.05$).

3.4 Discussion

Plant nutritional status at 1900 m

At 1900 m, tree leaf concentrations were within the range of sufficiency for all plant macronutrients (Table 3.1). Also foliar micronutrient concentrations were within the range of sufficiency given in textbooks (N. Soehte, J. Lehmann and C. Engels, unpublished data). This indicates that at this altitude growth limitation due to nutrient deficiency is not to be expected.

This is in contrast to other tropical forest sites where growth limitation by N or P has been suggested (Tanner et al., 1990; Vitousek and Farrington, 1997). In the present study foliar C:N and C:P ratios were substantially lower than those reported from the literature for temperate broadleaved and tropical lowland forests (Table 3.2; McGroddy et al., 2004) substantiating the suggestion that at 1900 m, growth was not limited by N or P. In comparison to lower altitudes, however, forest growth at 1900 m was also reduced in the studied South Ecuadorian montane forests. Since nutrient limitations are unlikely at 1900 m given the results shown in this study, possible causes for reduced growth in these forests include increased cloudiness (Bruijnzeel and Veneklaas, 1998) and direct growth reduction by low temperatures (Hoch and Körner, 2003).

Effect of altitude on plant nutritional status

In Table 3.1, nutrient concentrations were based on leaf dry matter to allow comparisons with ranges of sufficiency or deficiency given in the literature. Leaf anatomy changed with increasing altitude, whereby leaves became thicker and more xeromorphic with increasing altitude. Edwards and Grubb (1982) suggested that decreasing foliar N concentrations at high altitudes of tropical montane forests reflects the development of thicker cell walls, which may not be related to N shortage but e.g. aid in minimizing the infestation by fungi under cool and moist conditions. It has been found that foliar N and P concentrations increased with increasing altitude when expressed on a leaf area basis, whereas concentrations decreased when based on leaf dry matter (Vitousek et al., 1992; Kitayama and Aiba, 2002). In the present study, foliar N and P concentrations decreased with increasing altitude regardless of whether the concentrations were based on leaf dry matter or leaf area.

The effect of increasing altitude on foliar nutrient concentrations of trees was dependent on the specific nutrient (Table 3.1). The concentrations of Mg and Ca were not significantly affected by altitude. This is in accordance with the studies reviewed by Tanner et al. (1998). The foliar concentrations usually did not decrease below the ranges of sufficiency given in textbooks indicating that growth limitation by Mg and Ca is not to be expected at higher altitudes. In contrast, the concentrations of N, P, S and K were substantially lower at 2400 and 3000 m than at 1900 m, whereby the concentrations at 2400 and 3000 m were similar. This shows that at higher altitudes nutrient acquisition of plants was even more affected than biomass growth leading to dilution of nutrients in the leaf dry matter. Furthermore, for nearly all these nutrients the foliar concentrations at higher altitudes decreased below the ranges of sufficiency given in textbooks. This strongly indicates limitation of growth by deficiency of several nutrients at higher altitudes. It has been suggested that many wild plants respond to nutrient deficiency by growth reduction rather than by reduction in nutrient concentrations (Chapin, 1980). This may explain the observation that foliar concentrations at 2400 and 3000 m were similar despite of the lower growth at 3000 m than at 2400 m.

There is no general agreement about the specific nutrients likely to be most limiting in tropical forests. Most often either N or P is supposed to be growth limiting (Tanner et al., 1998; McGroddy et al., 2004). In our study N:P ratios were substantially lower than those commonly found in tropical lowland forests (Table 3.2; McGroddy et al., 2004) and significantly decreased with increasing altitude suggesting that at high altitudes N was more limiting than P. However, our data indicate that in addition to N and P, also the S and K nutritional status of plants was substantially below the optimum, and thus growth reduction by these nutrients is also to be expected.

The "Diagnosis and Recommendation Integrated System" (DRIS) uses a series of foliar nutrient ratios for each nutrient (e.g. N:P, N:K, N:S, N:Ca, and N:Mg for N) to assess the order of the relative limitation by several nutrients. The assessment of the relative limitation is based on a standard population that is supposed to be well supplied with nutrients. We defined the forest at 1900 m as the standard population. The DRIS-indices which were derived from differences in nutrient ratios between the standard population and the forest sites at 2400 m and 3000 m, respectively, indicate N on average of all plant groups and two altitudes as the most limiting nutrient followed by P and S (Table 3.3). However, it has to be noted that low DRIS-order of K for nutrient limitation at higher altitudes may be due to the low foliar concentrations in the standard population at 1900 m.

It is well known that foliar nutrient concentrations vary between plant species (Tanner et al., 1990; Vitousek et al., 1995); e.g. foliar N concentrations are higher in leguminous species than in non-leguminous species (Drechsel and Zech, 1991). Slow-growing species adapted to nutrient-poor habitats usually show higher foliar nutrient concentrations than fast-growing species when growing under nutrient poor conditions (Chapin, 1980). The species composition at our forests sites completely changed with increasing altitude (Homeier, 2004). However, compared with the effect of altitude, the effect of plant group (trees, shrubs, herbs) on foliar nutrient concentrations was negligible (with the exception of increased K concentrations in herbs at all altitudes and increased P concentrations of herbs at 1900 m). This indicates that the differences of foliar nutrient concentrations at different altitudes were not due to the occurrence of specific species, and supports the assumption that the decrease of nutrient concentrations at 2400 and 3000 m in comparison to 1900 m was induced by environmental effects on nutrient availability or nutrient acquisition of plants.

Possible mechanisms for the effects of altitude on plant nutritional status

Increasing altitude may affect the plant nutritional status by modification of soil nutrient availability and the ability of plants for nutrient acquisition. In montane forests, high amounts of soil nutrients are stored in the organic surface layer (Wilcke et al., 2002). In the present study, spatial exploitation of the organic layer by fine roots was high, ranging between 2.6 and 7.2 cm fine roots cm^{-3} soil (Chapter 2). Total amounts of nutrients in the organic surface layer were not affected by altitude for P, K and Ca and were highest at 3000 m for N, S and Mg (Figure 3.1). Therefore, the decrease of leaf nutrient concentrations at high altitudes was not related to nutrient stocks in the organic layer.

In the organic layer, most N, P and S are incorporated into the organic matter, and their availability is governed by the mineralization rates (Stevenson and Cole, 1999; Wilcke et al., 2002). Assuming an average turnover time for N and P in the organic layer of 14 and 11 years, respectively (Wilcke et al., 2002), annual nutrient release at 1900 m would roughly amount to 197 kg ha^{-1} yr^{-1} for N and 23 kg ha^{-1} yr^{-1} for P. These amounts would exceed nutrient uptake by the vegetation as measured in other studies (Lodhiyal and Lodhiyal, 2003). However, it may be expected that mineralization of organic matter is reduced at higher altitudes because of higher C to nutrient ratios (Table 2.1), lower soil pH, lower temperatures and less oxygen availability due to waterlogging (Wilcke et al., 2002; Wegner et al., 2003; McGroddy et al., 2004; Chapter 2). Therefore, plant availability of N, P and S from the organic surface layer may be reduced at high altitudes despite of similar or higher total nutrient stocks in this layer (Figure 3.1).

The amount of available nutrients in the mineral soil, as determined by Mehlich III extraction, increased at higher altitudes (Figure 3.2). Furthermore, at high altitudes the amounts of plant available nutrients except N in the mineral soil were high in comparison to the annual requirements of plants (Lodhiyal and Lodhiyal, 2003). However, the low foliar P and K concentrations let assume that chemically available nutrient stocks from mineral soil were hardly accessible to plants. At 2400 and 3000 m, root growth in mineral soil was reduced at high altitudes in comparison to 1900 m, presumably by unfavourable soil conditions such as oxygen deficiency (Chapter 2). In 0.3-0.7 m depth were highest stocks of available P and K occurred at higher altitudes, root length density was 0.1-0.2 cm cm^{-3} at 2400 and 3000 m in comparison to 0.5-0.7 cm cm^{-3} at 1900 m. Thus, spatial availability of nutrients in mineral soil was lower at higher altitudes. The spatial availability of soil nutrients in deeper soil layers may have been further decreased by reduction of the abundance of mycorrhizal hyphae, e.g. due to lower soil aeration (Schack-Kirchner et al., 2000; Wallander et al., 2004; Powers et al., 2005). That is, soil conditions may have reduced the ability of plants for nutrient acquisition, and thus, impaired the plant nutritional status, despite of high chemical availability of nutrients in the mineral soil.

Conclusions

Plant growth at 1900 m was not limited by mineral nutrients. At higher altitudes, foliar nutrient analysis indicated that growth may become limited by N, P, S and K supporting the hypothesis that low ANPP and tree stature at high altitudes in tropical montane forests can be attributed to low nutrient supply. Low nutrient supply at high altitudes may be due to slow mineralization of organically bound nutrients and poor ability of plants for nutrient acquisition from the mineral soil.

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4 Carbon and nutrient stocks in roots at different altitudes of an Ecuadorian tropical montane forest

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Abstract

Carbon and nutrient stocks in belowground biomass have rarely been investigated in tropical montane forests. In the present study, the amounts of carbon, nitrogen, phosphorus, sulphur, potassium, calcium, and magnesium in root biomass were determined at three different altitudes (1900, 2400 and 3000 m) of a tropical montane forest in Ecuador. Root biomass increased markedly from 2761 g m^{-2} at 1900 m and 3996 g m^{-2} at 2400 to 6508 g m^{-2} at 3000 m. The contribution of coarse roots (> 2 mm in diameter) to total root biomass increased from about 70 % at 1900 to about 80 % at higher altitudes. In fine roots (≤ 2 mm in diameter) concentrations of nutrients except calcium markedly decreased with altitude. Therefore, the nutrient stocks in fine roots were similar at 1900 m and 3000 m for nitrogen and sulphur, and were even lower at higher altitudes for phosphorus, potassium and magnesium. In coarse roots of *Graffenrieda emarginata* (Ruiz & Pav.) Triana, concentrations of nutrients were substantially lower than in fine roots, and were little affected by altitude. The data suggest that the importance of coarse roots for long-term carbon and nutrient accumulation in total plant biomass increases with increasing altitude.

Key words: Carbon sequestration; fine root biomass; nutrient concentrations; nutrient immobilisation; root diameter; short term nutrient cycling.

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4.1 Introduction

In the debate about the global carbon (C) cycle the role of forest biomes as potential carbon sources and sinks receives increasing attention (Malhi et al., 1999; Fehse et al., 2002). Considerable amounts of terrestrial C are sequestered in tropical forests (Vogt et al. 1996; Mahli et al. 1999). In 1994, these forests contributed 37 % of total C sequestered worldwide in forest ecosystems. About 50 % of total C in tropical forests is bound in biomass (Dixon et al., 1994). Roots contribute 7-34 % to total biomass in tropical lowland forest ecosystems (Vogt et al. 1996). Thus, C stocks in root systems of tropical lowland forests are important components of the C budget on a global scale.

Within forest biomes, roots have a large impact on C and nutrient fluxes (Ostertag and Hobbie, 1999; Chen et al., 2001). Here, the amounts of C and nutrients returned to soil from fine root turnover may equal or exceed that from leaf litter (Joslin and Henderson, 1987; Raich and Nadelhoffer, 1989). Besides root tissue composition, e.g. the concentration of N, lignin, and non-structural carbohydrates, and environmental factors such as temperature, root diameter is a key factor that governs the nutrient return to soil via root turnover (McClaughtery et al., 1982; Nambiar, 1987; Ostertag and Hobbie, 1999; Janisch et al., 2005). Therefore, fine and coarse roots differ substantially in their contribution to ecosystem C and nutrient dynamics. Nambiar (1987) reported that root turnover of *Pinus radiata* is largely confined to roots < 1 mm in diameter. On the other hand root biomass contributes to nutrient immobilization and may thus diminish nutrient losses from the ecosystem by leaching. This is especially true for tropical lowland forests with high precipitation rates where most potassium (K) and calcium (Ca) are stored in biomass, whereas the soil is often impoverished in these nutrients (Jordan, 1985).

Data on total belowground biomass as well as C and nutrient stocks in the belowground biomass of tropical montane forests are scarce (Edwards and Grubb, 1977; Edwards and Grubb, 1982; Vance and Nadkarni, 1992). An important difference to lowland forests is that montane forests extend over large altitudinal gradients. Thus, they are characterized by high spatial heterogeneities in climatic conditions. Usually with increasing altitude temperatures decrease while precipitation increases, causing a decrease in mineralization rates (Marrs et al., 1988; Holder, 2003; Fabian et al., 2005). As a result, the amounts of C stored in the organic layer and mineral soil of montane regions are usually higher than in the lowlands (Edwards and Grubb, 1977). It is likely that also the amounts of C and nutrients in belowground biomass may be affected by the climatic changes along altitudinal gradients.

Carbon and nutrient stocks in the root biomass are dependent on nutrient concentrations in root tissue. These concentrations are governed by several internal and external factors. The impact of different diameter classes of tree roots on nutrient concentration is well documented. Nitrogen (N) and phosphorus (P) concentrations generally decrease with increasing root diameter, while Ca, Mg and K concentrations were found either to decrease, or to increase, or to remain constant with increasing diameter (Klinge, 1975; Edwards and Grubb, 1982; Nambiar, 1987; Gordon and Jackson, 2000; John et al. 2002). Furthermore, it was shown that in forest ecosystems nutrient concentrations in fine roots are influenced by season (Guevara and Romero, 2004), soil age (Ostertag and Hobbie, 1999), stand age (Meier et al., 1985) and stand density (Barron-Gafford et al., 2003). In many cases an increase in root nutrient concentrations is explained by an increase in soil nutrient availability (Yin and Perry, 1991; Ostertag and Hobbie, 1999; Hendricks et al., 2000).

In this study, we measured C and nutrient stocks in roots differing in diameter. We use the term “nutrient” for the nutrient elements N, sulphur (S), P, K, Ca and Mg, and the term “element” to encompass nutrients as well as C. It may be expected that nutrient stocks in fine roots constitute a significant source of nutrient supply for plants via fine root turnover, whereas C and nutrient stocks in coarse roots contribute to long term sequestration of elements in plant biomass. The investigation was performed in tropical montane forests of Ecuador at 1900, 2400 and 3000 m. We hypothesized that root biomass and root C and nutrient stocks increase with altitude because nutrient limitation of plant growth increases biomass and nutrient partitioning to roots.

4.2 Methods

Study sites

We selected three stands in an Ecuadorian tropical montane forest close to the provincial capital Loja. The lower stands (1900 m and 2400 m) were situated in the Reserva San Francisco at the northern fringes of the Podocarpus National Park that protects typical mountain ecosystems of southern Ecuador. The highest stand (3000 m) was located in the Cajanuma area in the north western edge of the National Park.

The three sites were similar in inclination (ranging between 20° and 50°) and were exposed north east or north west. Precipitation was markedly lower at 1900 m than at the upper sites and temperature decreased with increasing altitude (Table 4.1).

Table 4.1: Characteristics of the study sites

Altitude (m)	Location	Mean annual precipitation ($mm\ y^{-1}$)	Mean air temperature (°C)	Soil type
1900	S 03°58′ W 79°04′	1950	14.9	gleyic Cambisol
2400	S 03°59′ W 79°04′	5000	12.3	gleyic Cambisol
3000	S 04°06′ W 79°10′	4500	8.6	Podzol

*** Data from Röderstein *et al.* (2005).**
**** S. Iost (pers. comm.).**

Soils were acid ($pH_{(CaCl2)}$ < 3.5 to a depth of 0.3 m in mineral soil) and covered by organic layers that were deeper at 3000 m (an average of 0.31 m) than at 1900 and 2400 m (an average of 0.15 m and 0.16 m, respectively). Maximum tree height decreased from 1900 to 2400 and 3000 m (19, 12 and 9 m, respectively). Further information on plant species composition that changed considerably with altitude, is given in Röderstein et al. (2005).

Sampling of roots ≤ 5 mm in diameter

Sampling of roots ≤ 5 mm in diameter was conducted during the dry season of November/December 2001. At each altitude, one 20 m x 20 m plot in the closed forest was established. Samples were taken from 20 locations using a random-block design. From each location, a quadratic sample of 100 mm x 100 mm was taken from the organic layer. Mineral soil was sampled with a soil corer (80 mm in diameter) at depths of 0.0 m - 0.1 m, 0.1 m - 0.3 m, 0.3 m - 0.5 m, 0.5 m - 0.7 m, 0.7 m - 0.9 m and 0.9 m - 1.1 m. When parent soil material was reached above 1.1 m, sampling was finished earlier.

Sampling of roots > 5 mm in diameter

Sampling of roots > 5 mm in diameter was conducted in the dry season from December 2002 until January 2003. Since the sampling procedure was very destructive and the 20 x 20 m plots had to be maintained for further investigations, sampling was performed on 15 randomly distributed locations around the plots. Both soil properties and vegetation around the plots were similar to those within the plots (unpublished data), allowing a comparison of roots ≤ and > 5 mm in diameter. At each of the 15 sampling locations a hole of 0.4 m x 0.4 m was dug. Roots within the hole were cut or sawed off and separated into roots from the organic layer, and from 0.0-0.1 and 0.1-0.3 m depth of mineral soil. In soil layers deeper than 0.3 m no coarse roots were found. Roots that grew at the interface between organic layer and mineral soil were added to the roots from the organic layer.

Analysis of roots ≤ 5 mm in diameter

For determination of root biomass, roots were sorted out from a sub sample of 20-50 g (organic layer) or 100-200 g (mineral soil) of each sample. For washing of each sub sample, a 0.6 mm mesh sieve was used. From a small bowl filled with water, roots and remaining soil residue were separated with tweezers. Under a binocular, living and dead roots were separated by colour, root elasticity and the degree of cohesion of cortex, periderm and stele (Persson, 1978). Living roots were separated into the diameter classes ≤ 1 mm, > 1-2 mm, > 2-5 mm. Following Röderstein et al. (2005) who determined fine root turnover at the same study sites, root ≤ 2 mm were classified as fine roots, whereas roots > 2-5 mm were included to the coarse root fraction. Roots were deep frozen for storage to allow further analysis in Germany. Afterwards, roots were dried at 50°C for 24 h and weighted.

For the analysis of elemental composition, additional root material was sorted out from the remaining soil material of every sample. After washing, roots were sorted out directly from the mesh. This procedure allowed a shorter contact of the roots with water and a collection of sufficient root material for nutrient analysis. In a preceding analysis it was shown, that this procedure was associated with negligible losses of nutrients during sample preparation (unpublished data). Roots for nutrient analysis were separated into the same diameter classes as described above, dried at 50°C for 24 h and ground with a flint mill (Type MM2, Retsch-GmbH & CoKG, Haan). Concentrations of C, N, and S were determined with a CNS analyser (Vario Max CNS, Elementar Analysesysteme, Hanau). For determination of P, K, Ca, and Mg, ground samples were digested with concentrated HNO_3 under pressure (Heinrichs et al., 1986). Concentrations of K, Ca, and Mg were measured by flame atomic absorption spectrometry (Perkin Elmer 4100, Perkin Elmer, Milano) and P concentrations were assessed with a spectral photometer (Specord 200, Analytik Jena, Jena) using the molybdene blue procedure (Murphy and Riley, 1962).

Analysis of roots > 5 mm in diameter

For determination of coarse root mass, roots from each soil layer were separated into the diameter classes >5-10 mm, >10-20 mm, >20-50 mm, and >50 mm. Root samples were dried at 50°C until weight constancy was achieved. Carbon and nutrient concentrations in coarse roots were assessed only exemplarily from *Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae), a frequent tree species in the lower parts of the study area. Samples were obtained from the 1900 and 2400 m stands from 3 trees per altitude. Roots of each tree were divided in the same diameter classes as described above without considering soil depth.

Subsamples of about 20 g were taken from every diameter class. Therefore smaller coarse roots were hackled with a hedge clipper. From thicker coarse roots, representative sub samples from the bark to the root centre were taken with a boring machine. Carbon and nutrient analyses from these sub samples were performed as described above.

Determination of soil C stocks

Soil C stocks were determined from the 20 replicate soil cores per altitude and soil depth taken for determination of root biomass ≤ 5 mm in diameter. Therefore, four equal sub samples of the 20 replicates were bulked together in each case to obtain 5 replicate samples per soil depth for analysis. Samples were air dried for storage. Concentrations of total C were assessed with a CNS analyser (Vario Max CNS, Elementar Analysesysteme, Hanau).

Calculations and statistics

Root biomasses at different altitudes within one soil depth were compared by non-parametric Kruskall Wallis test for not normally distributed replicates and subsequent Dunn test for unequal numbers of replicates (roots ≤ 5 mm in diameter) or Nemenyi test for equal numbers of replicates (roots > 5 mm in diameter).

Nutrients stocks in different root diameter classes ≤ 5 mm were calculated from the average root biomass of the respective diameter class and the replicate nutrient concentrations within this diameter class. ANOVA and Tukey test or student´s t-test were used to assess significant differences in total fine and coarse root biomass, nutrient stocks or nutrient concentrations between altitudes or between diameter classes. Additionally, two-way ANOVA was applied to nutrient concentrations in roots to compare the impact of altitude and diameter class. Data were log-transformed when necessary.

4.3 Results

Root biomass

Total root biomass steadily increased from 1900 to 3000 m (Table 4.2). At 3000 m, biomass of fine roots and coarse roots was significantly higher than at 2400 and 1900 m. The fraction of fine roots in total root biomass decreased from 32 % at 1900 m to 18 % at 2400 m and 22 % at 3000 m. In contrast to root biomass, above ground biomass as estimated from diameter at breast height, tree height and wood density (Chave et al., 2005) decreased with increasing altitude (G. Moser, C. Leuschner and D. Hertel, unpublished data). Correspondingly, the proportion of root biomass in total biomass strongly increased with increasing altitude (Table 4.2).

Table 4.2: Root biomass (g m^{-2}) at different altitudes (*n* = 20 for fine roots, *n* = 15 for coarse roots). Data in parenthesis show standard errors. Different lower case letters indicate significant differences between altitudes (Tukey test, $p < 0.05$).

Altitude (m)	Fine root biomass (g m^{-2})	Coarse root biomass (g m^{-2})	Total root biomass (g m^{-2})	Proportion of root biomass in total biomass* (%)
1900	890 (70)^{a}	1910 (264)^{a}	2800	14
2400	729 (90)^{a}	3286 (567)^{a}	4015	29
3000	1503 (127)^{b}	5340 (473)^{b}	6843	37

*** Data on above ground biomass were derived from G. Moser (pers. comm.).**

At all altitudes, the largest proportion of root biomass was located in the organic layer (Figure 4.1). This was most pronounced at 3000 m and 2400 m, where about 80 % of total root biomass were located in this layer, in contrast to about 59 % at 1900 m. Below 0.1 m depth of mineral soil, about 10 % of total coarse root and 38 % of total fine root biomass were found at 1900 m, compared with only 1 % of total coarse root and about 6 % of total fine root biomass at 2400 and 3000 m. This indicates that nutrient cycling between plant roots and soil via fine roots and, in the long term, release of C and nutrients into the soil by decaying coarse roots, are mainly confined to the uppermost soil layers particularly at high altitudes.

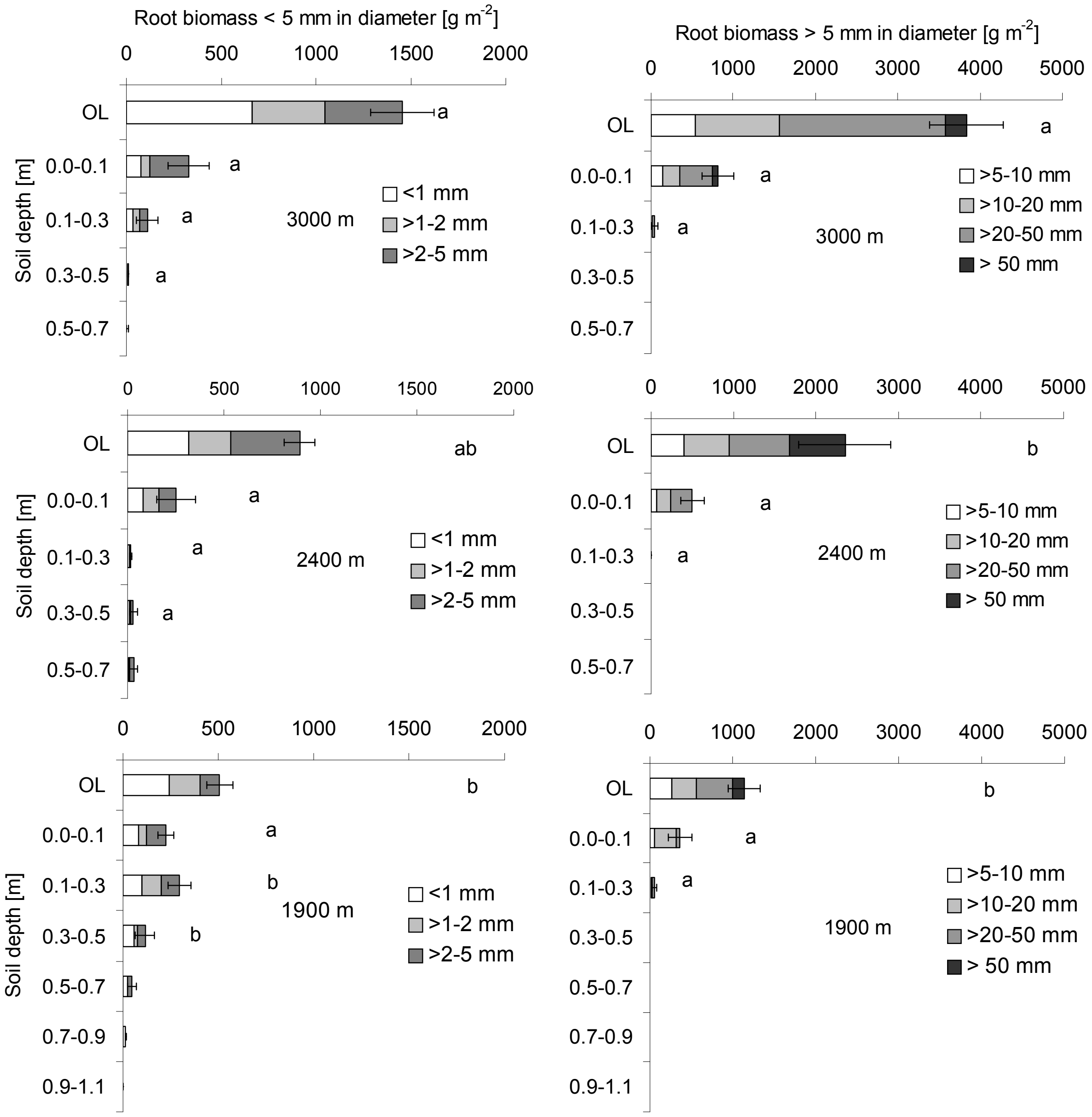

Figure 4.1: Root biomass (g m^{-2}) of different diameter classes in different soil depths at 1900 m, 2400 m, and 3000 m; OL = organic layer. Error bars indicate standard errors. Different lower case letters indicate significant differences of root biomass between altitudes within one soil depth (root biomass ≤ 5 mm in diameter: n = 9-20, Dunn test, p<0.05; root biomass > 5 mm in diameter: n = 15, Nemenyi test, p < 0.05).

Element concentrations in roots

The element concentrations of roots ≤ 5 mm in diameter were not affected by the soil layer or soil depth (data not shown). Thus, only element concentrations in roots from the organic layer are shown in this study. The root concentrations of elements with the exception of Ca were significantly ($p < 0.05$) influenced by altitude (Table 4.3).

Table 4.3: Significance levels for differences in root element concentrations (≤ 5 mm in diameter) from root diameter and altitude calculated by two-way ANOVA (*n* = 5).

	C	N	S	P	K	Ca	Mg
Altitude	<0.001	<0.001	<0.001	<0.001	<0.001	0.175	0.001
Diameter	0.001	<0.001	<0.001	<0.001	<0.001	0.021	0.106
Diameter*Altitude	0.039	0.692	0.461	0.439	0.787	0.371	0.916

Table 4.4: Element concentrations (mg g^{-1}) in roots ≤ 5 mm in diameter (*n* = 5). Data in parentheses are standard errors.

Element	Altitude (m)	Diameter class (mm)			
		≤ 1	>1-2	>2-5	**Mean**
C	1900	500 (3)	504 (5)	500 (2)	**501 (1)**
	2400	511 (1)	514 (3)	501 (1)	**509 (4)**
	3000	544 (1)	532 (3)	513 (1)	**530 (9)**
	Mean	**519 (12)**	**517 (8)**	**505 (4)**	
N	1900	15.4 (0.6)	12.0 (1.1)	9.1 (0.7)	**12.2 (1.8)**
	2400	12.3 (0.1)	9.1 (1.0)	8.0 (1.0)	**9.8 (1.3)**
	3000	10.4 (0.6)	6.4 (0.2)	4.9 (0.4)	**7.2 (1.6)**
	Mean	**12.7 (1.5)**	**9.1 (1.6)**	**7.3 (1.3)**	
S	1900	1.82 (0.10)	1.40 (0.09)	1.22 (0.15)	**1.48 (0.18)**
	2400	1.18 (0.14)	1.02 (0.08)	0.88 (0.09)	**1.03 (0.09)**
	3000	1.13 (0.05)	0.87 (0.08)	0.60 (0.06)	**0.87 (0.15)**
	Mean	**1.38 (0.22)**	**1.10 (0.16)**	**0.90 (0.18)**	
P	1900	1.03 (0.06)	0.85 (0.19)	0.61 (0.08)	**0.83 (0.12)**
	2400	0.57 (0.09)	0.28 (0.07)	0.29 (0.06)	**0.38 (0.10)**
	3000	0.55 (0.05)	0.26 (0.02)	0.22 (0.03)	**0.34 (0.10)**
	Mean	**0.72 (0.16)**	**0.46 (0.19)**	**0.37 (0.12)**	
K	1900	3.43 (0.27)	5.09 (0.75)	6.57 (0.96)	**5.03 (0.91)**
	2400	1.99 (0.09)	3.15 (0.75)	4.31 (0.87)	**3.15 (0.67)**
	3000	1.70 (0.14)	2.13 (0.29)	3.52 (0.73)	**2.45 (0.55)**
	Mean	**2.37 (0.53)**	**3.45 (0.87)**	**4.80 (0.91)**	
Ca	1900	2.32 (0.81)	2.35 (0.59)	2.62 (0.56)	**2.43 (0.10)**
	2400	2.14 (0.41)	3.50 (0.38)	5.65 (2.32)	**3.76 (1.02)**
	3000	1.80 (0.64)	3.88 (0.54)	4.14 (1.37)	**3.27 (0.74)**
	Mean	**2.08 (0.15)**	**3.24 (0.46)**	**4.14 (0.87)**	
Mg	1900	1.49 (0.28)	1.32 (0.19)	2.03 (0.45)	**1.61 (0.23)**
	2400	0.94 (0.04)	2.26 (0.66)	1.27 (0.23)	**1.49 (0.40)**
	3000	0.79 (0.05)	1.06 (0.14)	1.25 (0.17)	**1.03 (0.13)**
	Mean	**1.08 (0.21)**	**1.55 (0.36)**	**1.52 (0.26)**	

The C concentration slightly increased with altitude (less than 10 % increase from 1900 m to 3000 m), whereas the concentrations of N, S, P, K and Mg strongly decreased (decrease by 40 to 60 % from 1900 to 3000 m) with increasing altitude (Table 4.4). Furthermore, the root concentrations of elements with the exception of Mg were significantly influenced by root diameter (Table 4.3). The concentrations of C slightly decreased, and the concentrations of N, S and P strongly decreased with increasing diameter, whereas the concentrations of K and Ca markedly increased with increasing root diameter (Table 4.4). For root C concentrations, a significant interaction between root diameter and altitude was found (Table 4.3) as root C concentrations at 1900 m, in contrast to 2400 and 3000 m, were not influenced by root diameter.

The concentrations in roots > 5 mm, which were only measured in *G. emarginata*, with the exception of Ca were not significantly influenced by altitude (Table 4.5). The Ca concentrations were higher at 2400 than at 1900 m (Table 4.6). Coarse root diameter significantly influenced the concentrations of N, S and P (Table 4.5). The concentrations of these nutrients decreased with increasing root diameter, whereas concentrations of other elements were not affected by root diameter (Table 4.6).

The concentrations of N, S, P and Mg in coarse roots > 5 mm of *G. emarginata* were markedly lower than concentrations of these elements in roots ≤ 5 mm that were bulked from all species growing in the forests stands (compare data in Table 4.6 and Table 4.4). Concentrations of C and K did not strongly vary between these root pools, whereas Ca concentrations were substantially higher in roots > 5 mm than in roots with smaller diameter.

Table 4.5: Significance levels for differences in element concentrations in coarse roots > 5 mm in diameter of *G. emarginata* from root diameter and altitude calculated by two-way ANOVA ($n = 3$).

	C	N	S	P	K	Ca	Mg
Altitude	0.619	0.664	0.302	0.540	0.114	< 0.001	0.262
Diameter	0.168	0.001	0.015	0.043	0.073	0.128	0.209
Diameter*Altitude	0.580	0.128	0.386	0.275	0.139	0.030	0.408

Table 4.6: Element concentrations (mg g^{-1}) in coarse roots > 5 mm in diameter of *G. emarginata* ($n = 3$). Data in parentheses are standard errors.

Element	Altitude	Diameter class (mm)				
	(m)	>5-10	>10-20	>20-50	>50	**Mean**
C	1900	495 (1)	491 (4)	490 (1)	486 (2)	**490 (2)**
	2400	490 (4)	491 (3)	488 (1)	488 (1)	**489 (1)**
	Mean	**493**	**491**	**489**	**487**	
N	1900	4.3 (0.4)	4.6 (1.4)	2.3 (0.2)	2.4 (0.1)	**3.4 (0.6)**
	2400	5.2 (0.3)	3.0 (0.3)	2.6 (0.1)	2.1 (0.1)	**3.2 (0.7)**
	Mean	**4.8**	**3.8**	**2.5**	**2.2**	
S	1900	0.70 (0.04)	0.72 (0.26)	0.33 (0.00)	0.31 (0.01)	**0.51 (0.11)**
	2400	0.76 (0.28)	0.33 (0.01)	0.30 (0.02)	0.26 (0.01)	**0.41 (0.12)**
	Mean	**0.73**	**0.52**	**0.32**	**0.29**	
P	1900	0.081 (0.012)	0.086 (0.033)	0.040 (0.005)	0.037 (0.002)	**0.061 (0.013)**
	2400	0.087 (0.012)	0.042 (0.001)	0.033 (< 0.001)	0.056 (0.026)	**0.054 (0.012)**
	Mean	**0.084**	**0.064**	**0.036**	**0.046**	
K	1900	3.0 (0.2)	3.2 (0.7)	2.0 (0.1)	1.9 (0.1)	**2.5 (0.3)**
	2400	4.5 (1.0)	2.4 (0.1)	2.5 (0.4)	3.2 (0.7)	**3.2 (0.5)**
	Mean	**3.7**	**2.8**	**2.3**	**2.6**	
Ca	1900	9.2 (0.8)	15.7 (6.9)	6.8 (1.1)	7.7 (0.3)	**9.9 (2.0)**
	2400	11.8 (0.8)	12.5 (0.9)	13.2 (1.4)	18.8 (3.1)	**14.1 (1.6)**
	Mean	**10.5**	**14.1**	**10.0**	**13.2**	
Mg	1900	0.78 (0.40)	0.22 (0.05)	0.23 (0.04)	0.66 (0.24)	**0.47 (0.14)**
	2400	0.43 (0.21)	0.35 (0.04)	0.24 (0.01)	0.26 (0.04)	**0.32 (0.04)**
	Mean	**0.61**	**0.29**	**0.23**	**0.46**	

Stocks of carbon and nutrients in root biomass

In fine roots up to 2 mm in diameter, stocks of all elements except Ca were significantly influenced by altitude (Table 4.7). Element stocks in fine roots were lowest at 2400 m, i.e. at the altitude, were lowest fine root biomass was associated with medium element concentrations (Table 4.4). Carbon stocks in fine roots were highest at 3000 m where highest biomass was associated with highest C concentration. The stocks of N, S and Mg were not significantly different between 3000 m and 1900 m because higher root biomass at 3000 m in comparison to 1900 m was balanced by lower nutrient concentrations. The stocks of P and K in fine roots were even lower at 3000 m in comparison to 1900 m because of very low concentrations of these nutrients in the fine root biomass.

Table 4.7: Element stocks (g m^{-2}) in fine roots ≤ 2 mm in diameter (n = 5) and coarse roots > 2 mm in diameter and data from other tropical forests. Different lower case letters indicate significant differences in nutrient stocks between altitudes (Tukey test, $p < 0.05$).

Root fraction	Altitude	Element stocks (g m^{-2})						
	(m)	C	N	S	P	K	Ca	Mg
Fine roots	1900	431^{b}	12.0^{a}	1.42^{a}	0.82^{a}	3.49^{a}	1.99^{a}	1.53^{a}
	2400	379^{c}	8.1^{b}	0.82^{b}	0.33^{c}	1.83^{b}	2.01^{a}	0.81^{b}
	3000	680^{a}	11.2^{a}	1.31^{a}	0.55^{b}	2.34^{b}	3.24^{a}	1.12^{ab}
Coarse roots*	1900	938	8.6	1.18	0.31	6.69	19.40	1.27
	2400	1621	12.7	1.64	0.29	9.75	36.21	1.63
	3000	2630	17.9	2.39	0.38	14.70	54.21	4.19
Total root biomass*	1900	1369	20.6	2.60	1.13	10.18	21.40	2.81
	2400	1999	20.8	2.46	0.62	11.58	38.22	2.44
	3000	3310	29.1	3.70	0.93	17.04	57.45	5.31
Total root biomass	*Lower montane*							
	New Guinea[1]	-	13.7	-	0.6	18.6	33.3	6.1
	Puerto Rico[1]	-	30.0	-	1.6	23.0	30.0	8.5
	Lowland							
	Brazil[2]	-	55.3	-	0.7	6.2	8.3	5.5
	Ghana[1]	-	32.6	-	2.4	14.3	26.8	6.5
	Brazil[3]	1023-1260	11-40	-	0.3-1.1	-	-	-

*** Data are estimated with help of element concentrations in coarse root biomass of *G. emarginata*.**

[1] From Edwards and Grubb (1982).

[2] From Klinge (1975).

[3] From Silver et al. (2000).

To obtain a rough estimate of element stocks in coarse roots > 2 mm in diameter, coarse root biomass of forest stands was multiplied with average element concentrations from 1900 and 2400 m measured in coarse roots of *G. emarginata*. To obtain a rough estimate of element stocks in total root biomass, measured element stocks in fine roots and estimated element stocks in coarse roots were summed up. Element stocks in coarse root and total root biomass increased with altitude (Table 4.7). The only exception was the root stocks of P in total root biomass which were very similar at 1900 and 3000 m.

In Table 4.7, element stocks in roots from lower montane (Edwards and Grubb, 1982) and lowland tropical forests (Klinge, 1975; Edwards and Grubb, 1982; Silver et al., 2000) were also listed. Compared to these data from literature, carbon stocks at 3000 m were about three times higher. At 3000 m, also Ca stocks were substantially higher, whereas the stocks of all other elements in the present study were similar to the range found for the other tropical forests.

Carbon stocks in soil

Carbon stocks differed significantly between altitudes (Table 4.8). Higher C stocks at 1900 and 3000 m than at 2400 m were the result of the high C concentrations in mineral soil at these altitudes. In the upper 0.3 m of mineral soil, C concentrations were 7.7 and 7.2 %, respectively, in comparison to 1.6 % at 2400 m. Despite the deep organic layers, most C was stored in mineral soil at all altitudes. This was most pronounced at 1900 and 3000 m with more than 75 % of total soil C in mineral soil. At 2400 m, about 45 % of total soil C was stored in the organic layer.

Table 4.8: Carbon stocks (t ha^{-1}) in soil at different altitudes (n = 5). Data in parentheses show standard errors. Different lower case letters indicate significant differences between altitudes (Tukey test, p < 0.05).

Altitude (m)	Soil C stocks (t ha^{-1})
1900	342 (41)^{a}
2400	131 (4)^{b}
3000	402 (82)^{a}

4.4 Discussion

Impact of altitude on root biomass

Fine and coarse root biomass were substantially higher at 3000 m than at 1900 and 2400 m. This is in agreement with results of Röderstein et al. (2005) obtained from the same study sites. The absolute increase of total root biomass with increasing altitude was accompanied by increased biomass partitioning to roots at high altitudes (Table 4.2). It is well documented that biomass partitioning between above- and belowground organs is dependent on environmental conditions, such as light intensity (Sultan, 2003), soil moisture content (Bell and Sultan, 1999), root zone temperature (Engels, 1993) and wind speeds (Cordero, 1999). According to theories, plants regulate biomass partitioning to optimize capture of resources (McConnaughay and Coleman, 1999; Farrar and Jones, 2003). At high altitudes, capture of belowground resources may be reduced by low soil nutrient availability (Edwards and Grubb, 1977; Bruijnzeel et al., 1993; Tanner et al., 1998) and low nutrient uptake ability of roots due to low oxygen availability in soil (Bruijnzeel and Veneklaas, 1998). Capture of above ground resources may be reduced by increased cloudiness, i.e. low light intensity (Bruijnzeel and Veneklaas, 1998) and low photosynthetic activity of leaves due to low air temperatures

(Kitayama and Aiba, 2002). Increased biomass partitioning to roots at high altitudes may indicate that environmental conditions at high altitudes limit nutrient uptake activity more than photosynthetic activity. In accordance with this conclusion, oxygen deficiency, lower temperatures and higher C to nutrient ratios likely reduced nutrient availability in soil at high in comparison to low altitudes, and foliar nutrient concentrations of several plant groups were reduced at high in comparison with low altitudes indicating nutrient deficiency (Chapter 3.4). Furthermore, stem concentrations of non-structural carbohydrates were generally high and similar at 1900 m (90-166 mg g^{-1}) and 3000 m (81-149 mg g^{-1}). Thus, there was no evidence for a deficiency in C supply at high altitude.

The fraction of coarse root biomass in total root biomass was higher at 2400 and 3000 m than at 1900 m (Table 4.2). Little is known about the regulation of biomass partitioning between coarse roots and fine roots. Fine roots mainly contribute to nutrient acquisition whereas coarse roots contribute to plant anchorage in soil. Plant anchorage at high altitudes is hampered by reduced deep rooting and high wind speeds (Chapter 5). Thus, increased biomass partitioning to coarse roots possibly indicates that the importance of the anchorage function of roots increases at high altitudes. In accordance with this assumption, it was found that morphological root traits leading to better anchorage and tree stability are particularly frequent at high altitudes (Chapter 5).

Contribution of biomass to total forest C

Soil C stocks at 2400 m were slightly higher than the average of tropical forests (123 t ha^{-1}) as reviewed by Mahli et al. (1999). The amounts of C in soils at 1900 m and 3000 m even exceeded average C stocks in boreal forests (343 t ha^{-1}) as reported by the authors, emphasizing the high potential for C sequestration of tropical montane forest soils.

The amount of biomass C in the study area was estimated by total root biomass (Table 4.2), aboveground biomass (G. Moser, unpublished data) and a proxy of 500 mg/g as average C concentrations in biomass (Gordon and Jackson, 2000; Wilcke et al., 2005). By comparison of C stocks in soil and biomass, the fraction of biomass C amounted for 22 % of total forest C at 1900 m, for 35 % at 2400 m and for 17 % at 3000 m. This is somewhat lower than in a tropical montane forest in New Guinea (29-41 %) reported by Edwards and Grubb (1977). In a global comparison, the C distribution at 1900 m and 3000 m was more similar to C distribution in boreal forests where most C (about 84 %) is stored in soil organic matter than to C distribution in tropical lowland forests, where about half of C is stored in biomass (Dixon et al., 1994; Malhi et al., 1999). Accordingly, root systems in the present study, while storing similar or higher amounts of C than in some tropical lowland forests (Table 4.7) contributed little to total C sequestration in the forest (3% at 1900 m, 10% at 2400 m and 7 % at 3000 m).

The impact of altitude on nutrient stocks in roots

Biomass as well as stocks of N, P and Mg stored in fine root biomass (Table 4.7) were similar (Biomass: 1613, N: 13.7, P: 0.24 Mg: 0.86 g m^{-2}) to a tropical lowland forest (Klinge, 1975) whereas stocks of K and Ca in fine roots were several times higher (K: 0.6 g m^{-2}, Ca: 0.5 g m^{-2}). In contrast to the significantly increased fine root biomass in high in comparison to low altitudes, nutrient stocks in fine roots showed no consistent increase or decrease with increasing altitude. This was due to a decrease in the concentrations of N, S, P, K and Mg in fine roots with increasing altitude (Table 4.4), counteracting the increase in nutrient stocks by increasing biomass. Decreasing root N concentration with increasing altitude was also detected in different grass species growing in New Zealand between 45 and 1205 m (Craine and Lee, 2003). The authors suggested that the decrease in N concentrations with increasing altitude was attributed to a decrease in nutrient availability. Accordingly, Ostertag and Hobbie (1999) observed lower P concentrations in fine roots at a P deficient site than at a site with sufficient P supply in a tropical montane forest in Hawaii. As indicated by foliar nutrient concentrations, increasing altitude led to a decrease in N, P, S and K nutrition of plants (Chapter 3). It is suggested that the decrease in nutrient concentrations in root tissue with increasing altitude was mainly caused by a decrease in the nutritional status of plants.

Different to nutrient stocks in fine root biomass, estimated nutrient stocks in total root biomass followed the increase in root biomass with increasing altitude (Table 4.7). This was due to the absence of an impact of altitude on nutrient concentrations in coarse roots of *G. emarginata*. The impact of environmental conditions on nutrient concentrations in coarse roots is poorly understood. Differences in the impact of altitude on nutrient concentrations in fine and coarse root biomass in the present study may either be caused by the differences in the methodological approaches or may indicate that nutrient concentrations in coarse root biomass are less sensitive to changes of environmental conditions such as nutrient availability than nutrient concentrations in fine root biomass.

Implications for element cycling

Root turnover is a central component of ecosystem element cycling (Gill and Jackson, 2000). The turnover rate of roots as the reciprocal of the average time span from appearance to total decomposition of root segments is governed by average root longevity and decomposition rate of root litter. Shorter live spans and higher decomposition rates for roots of smaller than larger diameter classes emphasize the importance of the fine root fraction for short term element cycling. E.g. published values for average fine root longevity fluctuate between several days and a few years (Priess et al., 1999; Gill and Jackson, 2000; Rasse et al., 2001). In contrast, for roots > 1 mm in diameter, Kurz et al. (1996) suggested an average longevity of 50 years. Average decomposition time of fine root litter in a tropical montane forest ranged between 2.5 and 6.3 years (Ostertag and Hobbie, 1999), whereas estimated decomposition time of root debris >10 mm diameter in a conifer forest was more than 43 years (Janisch et al., 2005). In the present study, the contribution of fine and coarse root biomass to element storage in total root biomass varied largely between nutrients. Considerable proportions (between 33.3 and 72.7 %) of total root N, S and P were stored in fine root biomass < 2 mm in diameter, but only small proportions of Ca (between 5.3 and 9.3 %). This implies that in the present study large proportions of root N, S and P were included in short term nutrient cycling, i.e. these nutrients were returned to soil within a few years, whereas most Ca in roots was immobilised on a long term.

Large parts of C and nutrients in forests are returned to soil by leaf and fine root litter production (Edwards, 1977; Röderstein et al., 2005). Since root litter production may equal or even exceed leave litter production (Röderstein et al., 2005), considerable proportions of nutrients in biomass that are returned to the soil litter pool may origin from dying fine roots. Nutrient stocks in fine roots from the present study were slightly lower than nutrient stocks in leaf biomass of a montane cloud forest in Costa Rica (N: 149.5, P: 7.1, K: 69.6, Ca: 63.1, and Mg:19.5 kg ha^{-1}), which had a similar leaf biomass (6.5 t ha^{-1}) as the forests of the present study (G. Moser, unpublished data). While in leaves large amounts of nutrients (up to 90 % N and P and up to 70 % K but no Ca) are re-translocated before shedding (Chapin, 1980; McGroddy et al., 2004), it is assumed that re-translocation of nutrients from senescing roots is negligible (Nambiar, 1987; Gordon and Jackson, 2000). Thus, the amount of nutrients that is stored in fine root biomass may be a good indicator for the amount of nutrients that is admitted to soil via fine root litter production. Annual fine root litter production in the study area was only about half of leaf litter production at 1900 m, but about 2-fold higher than leaf litter production at 2400 m and even 8-fold higher than leaf litter production at 3000 m (Röderstein et al., 2005). That means that especially at the upper two altitudes, nutrient return to soil via fine root litter production exceeds nutrient return via leaf litter production.

Due to the high precipitation rates, large amounts of plant available nutrients reach soils of tropical rain forests by leaching from canopy and atmospheric deposition (Wilcke et al., 2001;

Chuyong et al., 2004). However, decaying litter may also be an important source for this nutrient fraction in soil. This may especially be true at lower altitudes, where precipitation rates are reduced and mineralization rates of organically bound nutrients are higher (Chapter 3) in comparison with higher altitudes. Nutrient release from fine roots at 1900 m may be estimated with the help of an average fine root longevity of 0.8 years assessed at the 1900 m site by Röderstein et al. (2005) and a decomposition time of 2.5 years as determined by Ostertag and Hobbie (1999) in a tropical montane forest in Hawaii with a comparable mean annual temperature (16°C). The parameters from these studies were obtained from the organic layer and not from the deeper soil layers. However, they may give satisfactory estimates for nutrient release by fine root decay in the present study, since most fine roots were located in the organic layer (Figure 4.1). Estimated annual nutrient release from fine root turnover (N: 3.5, P: 0.2, S: 0.4, K:1.0, Ca: 0.6, and Mg: 0.5 g m^{-2} y^{-1}) was similar to the amounts of nutrients that enter the soil from above via through fall of rain from canopy in adjacent forest sites within the Reserva San Francisco (N: 1.6, P: 0.5, S: 0.3, K: 12.2, Ca: 1.6 and Mg: 1.0 g m^{-2} y^{-1}) (Wilcke et al., 2001).

Conclusions

Higher root biomass at higher than at lower altitudes reflected the increased allocation of biomass to the root system, presumably as a response to decreased nutrient availability in soil and high mechanical stress affecting trees growing at high altitudes. Higher C and nutrient stocks in coarse roots at higher than at lower altitudes suggest that the importance of this root fraction for long term nutrient accumulation is increased at high altitudes. Due to the response of nutrient concentrations in fine roots to the change of environmental conditions such as soil nutrient availability along the altitudinal gradient, nutrient stocks in this root fraction did not follow the marked increase of root biomass with increasing altitude. Root biomass of this tropical montane forest may particularly contribute to short term nutrient cycling by fine root turnover. However, the contribution of root biomass to C sequestration within this forest is rather low.

Acknowledgements

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5 Root morphology and anchorage of six native tree species from a tropical montane forest and an elfin forest in Ecuador

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Abstract

Root architecture of tree species was investigated at two different altitudes in tropical forests in Ecuador. Increasing altitude was accompanied by higher wind speeds and more shallow soils, while slope angles of both sites were comparable (20-50°). Three tree species typical for the montane forest at 1900 m (*Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae), *Clethra revoluta* (Ruiz & Pav.) Spreng. (Clethraceae), *Vismia tomentosa* Ruiz & Pav. (Clusiaceae)) and for the elfin forest at 3000 m (*Weinmannia loxensis* Harling (Cunoniaceae), *Clusia* spec. (Clusiacaea) *Styrax foveolaria* Perkins (Styraceae)) were examined. At 1900 m, 92 % of the trees grew upright, in comparison to 52 % at 3000 m. At 3000 m, 48 % of the trees were inclined, lying or even partly uprooted. At this altitude, all trees with tap roots or with shoots connected by coarse rhizomes, 83 % of the trees with stilt roots, and 50 % of the trees in which stems or roots were supported by other trees grew upright, suggesting that these characteristics were relevant for tree stability. Root system morphology differed markedly between altitudes. In contrast to 1900 m, where 20 % of structural roots originated in the deeper mineral soil, root origin at 3000 m was restricted to the forest floor. The mean ratio of root cross sectional area to tree height decreased significantly from 6.1 x 10^{-3} m^2 m^{-1} at 1900 m to 3.2 x 10^{-3} m^2 m^{-1} at 3000 m. The extent of root asymmetry increased significantly from 0.29 at 1900 m to 0.62 at 3000 m. This was accompanied by a significantly lower number of dominant roots at 3000 m (2.3 compared to 3.8 at 1900 m). In conclusion, native tree species growing in tropical montane and elfin forests show a variety of root traits that improve tree stability. Root system asymmetry is less important for tree stability where anchorage is provided by a deep and solid root-soil plate. When deep rooting is impeded, root traits improving the horizontal extension of the root-soil plate are more pronounced or occur more frequently. Furthermore, mutual mechanical support of roots and stems of neighbouring trees seems to be an appropriate mechanism to provide anchorage in soils with low bulk density and in environments with high wind speeds.

Keywords: Aspect ratio, buttress, root architecture, root asymmetry, slope, stilt root.

Abbreviations: AR = aspect ratio; CSA = cross sectional area; DBH = diameter at breast height; ZRT = zone of rapid taper.

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5.1 Introduction

Tropical montane forests are often characterized by steep slopes and soil creeping (Hagedorn, 2001) and anchorage of trees is rendered difficult by shallow soils (Arraiga, 2000; Schrumpf et al., 2001). High wind speeds can cause additional mechanical loads. Hurricanes occur frequently in lower montane forests of Puerto Rico (Weaver, 2002) and were the main cause for tree mortality in a Mexican cloud forest (Arraiga, 2000). The combination of high mechanical stress and shallow soils typically leads to a short and stunted appearance of trees in such forests (Cavalier and Mejia, 1990; Cordero, 1999). Thus, trees require strategies to improve stability.

In mountain regions, trees are usually affected by wind loadings and “self loadings”. “Self loading” was defined by Chiatante et al. (2003a) as the mechanical stimulus due to the weight of a plant growing on a slope. To achieve anchorage, the tree transfers the loading forces experienced by the stem into the ground *via* roots (Chiatante et al., 2003a). Forces that trees and soil have to resist to maintain stability are mainly bending stress (within roots and stem), tension (within roots), compression (within and between roots and soil), and shearing forces (between root and soil and within soil) (Coutts, 1983; Nielsen, 1990; Nicoll and Ray, 1996; Stokes and Matthek, 1996; Crook et al., 1997; Czarnes et al, 1999). Therefore, roots contribute to plant stability by forming rigid elements in the root system, e.g. deep tap roots, or by forming a rigid root-soil plate.

Tree anchorage may also be related to various architectural root characteristics. Mechanical stress may cause an increase of total root cross sectional area (CSA) (Crook and Ennos, 1996; Mickovski and Ennos, 2003a,b). Another common response to mechanical stress is the modification of the shape of root cross sections (Coutts et al., 1999; Chiatante et al., 2003a,b). Often cross sections are T- or I-beam shaped (Rigg and Harrar, 1931; Nicoll and Ray, 1996) and eccentric (Mickovski and Ennos, 2003b). An extreme case of eccentric roots are buttresses (Crook et al., 1997). When the mechanical stress is not homogenously distributed around the root system, root growth and development may be increased in the direction of maximal stress intensity influencing the symmetry of anchorage rigidity around the stem (Coutts, 1983; Nicoll and Ray, 1996; Chiatante et al., 2003b). Coutts et al. (1999) describe two types of root system asymmetry. Type I shows regular arrangement of individual roots around the stem center, but roots vary in diameter. In type II, roots are evenly sized but not uniformly arranged. In tree root systems both types of asymmetry may occur together. The direction of root clustering (windward/up-slope or leeward/down-slope) differs between studies (Nicoll and Ray, 1996; Watson, 2000; Chiatante et al., 2003b). Root asymmetry is often assessed by the "center of mass" of all lateral roots. The "center of mass" is calculated by the sum of growth directions weighted by diameter or CSA of roots (Nicoll and Ray, 1996; Mickovski and Ennos, 2003b).

Most studies on root anchorage have concentrated on species of economical interest, particularly conifers (Crooks and Ennos, 1996; Nicoll and Ray, 1996; Stokes, 1999; Moore, 2000; Watson, 2000; Polomski and Kuhn, 2001; Cucchi and Bert, 2003; Mickovski and Ennos, 2003a,b). More knowledge about root morphology and architecture of other species is necessary to provide further insight into the way in which the form is related to the function of root systems (Mickovski and Ennos, 2003b). While the impact of strong winds in the elfin forest on the aboveground appearance of trees has been described by several authors (e.g. Lawton, 1982; Cordero, 1999), coarse root morphology of trees in this ecosystem has never been investigated. Very few studies deal with anchorage mechanisms of tropical plants and with anchorage mechanisms of plants growing on slopes (Chiatante et al., 2003a,b; Di Iorio et al., 2005). For tropical lowlands, architectural root traits of forest species are table roots and stilt roots (Jenik, 1978; Crook et al., 1997) as well as deep tap roots (Förster, 1970).

The aim of this study was to test the hypothesis that native species growing on steep slopes and exposed to high wind velocity are adapted to mechanical forces by the development of architectural root characteristics that improve anchorage in soil. Furthermore, it was expected that these root characteristics differ between altitudes because of differences in wind speed and in physical and chemical soil properties affecting root growth. To test this hypothesis, root architecture of three of the most frequent species growing in a tropical montane forest in the South of Ecuador at an altitude of 1900 m (montane forest) and 3000 m (elfin forest) was compared.

5.2 Materials and methods

Study sites and species

Experimental work was carried out at the Estacion Científica San Francisco (ECSF) near the Podocarpus National Park in the South of Ecuador. The lower study site (1900 m a.s.l.; 03°58´S, 79°04´W) was located in a montane forest in the area of the ECSF. Thermally induced mountain breezes, i.e. valley winds during the day and mountain winds during the night, were typical for this region. Mean wind speeds measured at 2.5 m above soil surface in an open space outside of the forest were less than 2 ms^{-1}. Down-slope winds reached maximum speeds of 8 ms^{-1} (M. Richter, pers. comm.). The soils had low $pH_{(CaCl2)}$ in the range of 3 to 3.5, an average depth of the organic surface layer of 0.15 m and of the mineral soil of > 0.9 m. Average bulk densities are listed in Table 5.1.

Table 5.1: Bulk densities at different soil depths at 1900 m and 3000 m a.s.l..

Soil depth (m)	Bulk density (g cm^{-3})	
	1900 m a.s.l.	3000 m a.s.l.
Upper 0.05 m of forest floor	0.05	0.07
Rest of forest floor	0.09	0.09
0.0 – 0.1	0.44	0.38
0.1 – 0.3	0.77	0.93
0.3 – 0.5	0.81	1.60
0.5 – 0.7	0.90	1.64

Slope angles varied from 25° – 50°. At this altitude, the tree species *Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae), *Clethra revoluta* (Ruiz & Pav.) Spreng. (Clethraceae) and *Vismia tomentosa* Ruiz & Pav. (Clusiaceae) were selected because of their widespread occurrence.

The upper study site (3000 m a.s.l.; 04°06´S, 79°10´W) was located in the elfin forest close to the timber line in the Podocarpus National Park. This area belonged to the elevated parts of the eastern Cordilleras and was exposed to gusty eastern winds (Richter, 2003). Wind speeds were generally higher than in the montane forest, with mean wind speeds between 4 – 5 ms^{-1}, and maximal values up to 24 ms^{-1} (M. Richter, pers. comm.). The soils were often waterlogged and characterized by low pH$_{(CaCl2)}$ between 2.7 and 3.0, deep organic surface layers (average of 0.3 m) and shallow mineral soils (average of 0.4 m). Average bulk densities are listed in Table 5.1. Slope angles varied from 20° to 50°. At this altitude the tree species *Weinmannia loxensis* Harling (Cunoniaceae), *Clusia* spec. (Clusiacaea) and *Styrax foveolaria* Perkins (Styraceae) were selected for measurements.

Table 5.2: Morphological parameters related to tree stability of typical tree species growing at 3000 m and 1900 m a.s.l..

	Extent of root asymmetry *R* (angle β)	Aspect ratio ($m\ m^{-1}$)	Ratio of CSA_{root} to tree height ($10^{-3}\ m^{2}\ m^{-1}$)	Number of dominant roots	Tree height (m)	Crown diameter (m)	DBH (m)	Ratio of DBH to tree height ($10^{-2}\ mm^{-1}$)
3000 m a.s.l.								
W. loxensis (*n* = 9)	0.7 ± 0.1 ^{a}	1.4 ± 0.1	3.5 ± 0.8 ^{a}	2.7 ± 0.4 ^{a}	4.5 ± 0.3 ^{a}	1.2 ± 1.0	0.11 ± 0.01 ^{a}	2.4 ± 0.1 ^{a}
Clusia spec.(*n* = 7)	0.6 ± 0.1 ^{a}	1.1 ± 0.1	2.8 ± 0.8 ^{a}	2.4 ± 0.3 ^{a}	3.6 ± 0.3 ^{a}	1.0 ± 1.2	0.11 ± 0.03 ^{a}	2.9 ± 0.7 ^{a}
S. foveolaria (*n* = 7)	0.6 ± 0.1 ^{a}	1.4 ± 0.2	3.2 ± 0.9 ^{a}	1.9 ± 0.1 ^{a}	4.0 ± 0.6 ^{a}	1.2 ± 1.0	0.08 ± 0.01 ^{a}	2.1 ± 0.2 ^{a}
1900 m a.s.l.								
C. revoluta (*n* = 10)	0.3 ± 0.0 ^{ab}	1.8 ± 0.1	6.8 ± 1.2 ^{a}	3.5 ± 0.2 ^{a}	10.1 ± 0.5 ^{a}	4.0 ± 0.5 ^{a}	0.23 ± 0.05 ^{a}	2.2 ± 0.4 ^{a}
V. tomentosa (*n* = 8)	0.4 ± 0.1 ^{a}	1.2 ± 0.1	7.1 ± 0.8 ^{a}	4.0 ± 0.4 ^{a}	13.2 ± 0.4 ^{b}	5.4 ± 1.0 ^{a}	0.17 ± 0.01 ^{a}	1.3 ± 0.1 ^{a}
G. emarginata (*n* = 7)	0.2 ± 0.0 ^{b}	1.6 ± 0.2	4.5 ± 0.4 ^{a}	3.9 ± 0.3 ^{a}	10.2 ± 0.8 ^{a}	4.8 ± 0.5 ^{a}	0.16 ± 0.01 ^{a}	1.6 ± 0.2 ^{a}

Values are means ± standard errors. Different letters indicate significant differences between species within one altitude (by Scheffé-test or H-test; $p < 0.05$).

Measurements

Sampling design

Measurements of root and stem morphology were performed on seven to ten individuals per species (Table 5.2). Trees were either dominant (i.e. protruding from the canopy) or co-dominant (i.e. reaching the height of the canopy). To record the features that may improve tree anchorage, the entire root ball with all structural roots (defined as roots with a diameter > 0.020 m at 1900 m, and > 0.015 m at 3000 m, respectively) was excavated within a radius of 0.3 m (1900 m) or 0.2 m (3000 m) around the stem. The minimal root diameter and the radius of the excavation were modified depending on altitude because of the differences in tree size between these two sites.

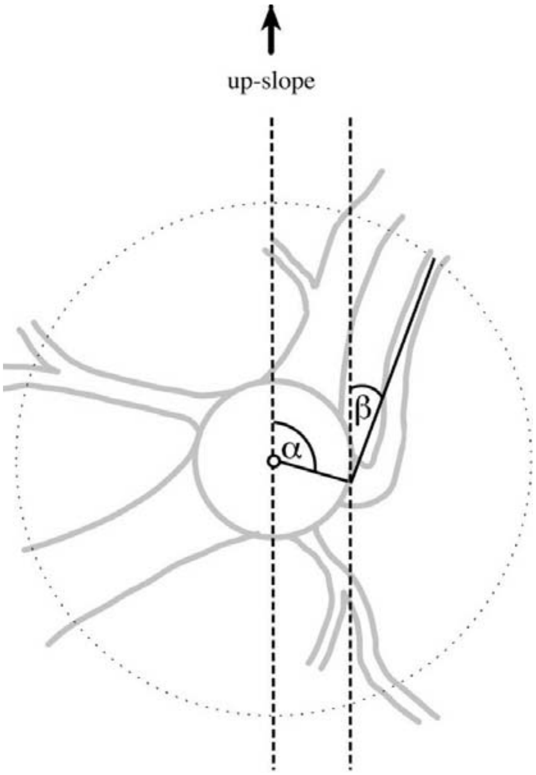

Figure 5.1: Description of different methods to assess root orientation; angle α: orientation of root origin; angle β: root growth direction; angels were always measured clockwise against up-slope direction (dotted lines); inner circle represents stem cross section, outer circle (dotted) represents outer limit of root excavation and measuring.

Spatial arrangement of roots

The depth where structural roots originated from the stem or the tap root, was assigned to the following classes: (i) above soil surface (stilt roots), (ii) within organic surface layer, (iii) at the interface between organic surface layer and mineral soil, (iv) within 0-0.1 m depth, (v) 0.1-0.2 m depth, and (vi) 0.2-0.3 m depth of mineral soil. The cross sectional area was measured separately for all roots growing in a specific soil depth by using the equation:

$$CSA = \pi \cdot \left(\frac{d_h + d_v}{4} \right)^2 ,$$

where d_h is the horizontal and d_v is the vertical diameter of the respective root, measured with callipers near the stem base after the zone of rapid taper (ZRT; Wilson, 1975). Root system asymmetry was measured with a technique similar to the one described by Nicoll and Ray (1996). Orientation of tap roots at their deepest branching point with structural lateral roots was also included in the measurement, because on slopes, tap roots were often not vertically orientated. The horizontal orientation of all structural roots was recorded in two different ways: (a) For the orientation of the root origin the azimuth angle α was measured between the line that is oriented in slope direction and the line that connects the point of origin with the center of the stem (Figure 5.1); (b) For the orientation in which the root had developed, the azimuth angle β was measured between the line that is oriented in slope direction and the line that connects the root at a distance of 0.2 or 0.3 m to the stem with the point of origin of this root (Figure 5.1). In the case of branching, the weighted center of the emerging daughter roots was estimated. The center of the CSA, which is a measure for the average orientation of roots, has the coordinates

$$X = \sum_{i=1}^{n} X_i \qquad Y = \sum_{\mathrm{i}=1}^{n} Y_i \ ,$$

where the Cartesian coordinates of the i_{th} root ($i = 1 \ldots n$) weighted by the CSA are

$$X_i = \left(\frac{\mathrm{CSA}_i}{\mathrm{CSA}_{\mathrm{total}}} \right) \sin \alpha \, ; \; Y_i = \left(\frac{\mathrm{CSA}_i}{\mathrm{CSA}_{\mathrm{total}}} \right) \cos \alpha$$

or,

$$X_i = \left(\frac{\mathrm{CSA}_i}{\mathrm{CSA}_{\mathrm{total}}} \right) \sin \beta \, ; \; Y_i = \left(\frac{\mathrm{CSA}_i}{\mathrm{CSA}_{\mathrm{total}}} \right) \cos \beta \, ,$$

where α is the angle of root origin, β is the angle of root growth direction and CSA_i is the cross sectional area of the i_{th} root and $\mathrm{CSA}_{\mathrm{total}}$ is the sum of cross sectional area of all structural roots. For the center of root origin the CSA was assessed directly after the ZRT, as described in the previous section. For the center of root growth direction CSA was assessed at a distance of 0.3 m (1900 m) or 0.2 m (3000 m) from the stem.

The extent of asymmetry R is represented by the distance between the center of root CSA and the origin of the coordinate system. It is a relative value between 0 and 1 that increases when roots cluster in a preferred direction. R is calculated using the equation

$$R = \left(X^2 + Y^2 \right)^{1/2} .$$

Proportions within roots and stem

To describe the shape of CSA at the root origin close to the stem after the ZRT, aspect ratios (AR) were calculated according to Mickovski and Ennos (2003b):

$$\mathrm{AR} = \frac{\mathrm{d_v}}{\mathrm{d_h}}\,.$$

To compare root CSA of trees differing in size, the ratio between root CSA and tree height was calculated. All structural roots were considered for the calculation of the CSA. For every tree the number of dominant roots was recorded. Dominant roots were defined as the largest roots summing up to 80% of total CSA of all structural roots (Coutts et al., 1999).

Other root traits influencing tree stability

The presence or absence of the following qualitative features that were supposed to improve tree stability, were recorded: (a) vertically growing tap roots, (b) stilt roots, (c) support of stem, stem base or coarse roots by stems or coarse roots of neighbouring trees, (d) trees with two or more shoots which were connected by structural rhizomes and (e) I-beam and T-beam shaped roots and other shapes of root CSA.

Shoot characteristics

For every excavated tree several shoot characteristics were determined. Tree height was assessed with a hypsometer (Vertex, Forestor Instruments, Sweden) at 1900 m and a tape measure at 3000 m. Crown diameter was assessed visually by estimating crown radius in four directions with an accuracy of 0.5 m. Additionally, diameter at breast height (DBH) and its relation to stem height was assessed. The inclination of all stems was classified as upright, inclined, lying or partly uprooted (Table 5.2). When trees were lying or partly uprooted, the length of the stem positioned in or on the forest floor was determined with a tape measure.

Statistical analyses

For the depth of root origin, the extent of root asymmetry *R*, aspect ratio, the ratio of $\mathrm{CSA_{root}}$ to tree height, the number of dominant roots, and the stem parameters differences between the two altitudes were assessed using a student´s t-test. At 1900 m, the three means of *G. emarginata*, *C. revoluta* and *V. tomentosa*, and at 3000 m, the three means of *W. loxensis*, *Clusia* spec. and *S. foveolaria* were used as replicates for the t-test. For *R*, aspect ratio, ratio of

CSA_{root} to tree height, tree height, crown diameter and ratio of DBH to tree height, one way ANOVA and Scheffé-test for uneven samples sizes were used to assess differences between species within one altitude. For the number of dominant roots and DBH, the non-parametric H-test was used to assess differences between species within one altitude.

Table 5.2: Classification of stem inclination.

Category	Explanation
Upright	upright to 15° inclination from the vertical
Inclined	> 15° inclination from the vertical
Lying	lower part of stem lying on soil surface, all structural roots anchoring in soil
Partly uprooted	lower part of stem lying on soil surface; structural roots partly uprooted

5.3 Results

Spatial arrangement of roots

Roots were initiated at a higher position above soil or within soil at 3000 m than at 1900 m (Figure 5.2).

At 1900 m, 53 % of root CSA derived from roots originating at the interface between forest floor and mineral soil or in the mineral soil. At 3000 m, no roots were initiated in mineral soil and 78 % were initiated in the forest floor.

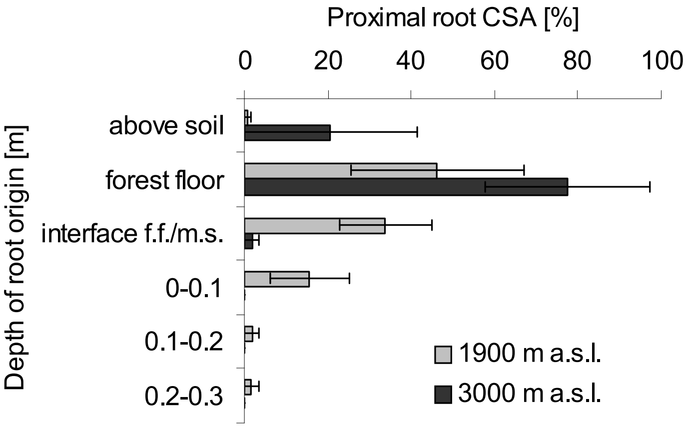

Figure 5.2: Origin of the lateral roots in trees growing at 1900 m and 3000 m a.s.l. (means and standard errors); f.f. = forest floor, m.s. = mineral soil.

Stilt roots summed up to 21 % of root CSA at this altitude. At 1900 m, root CSA in the zone of root initiation (angle α) did not cluster in a specific direction as indicated by the uniform distribution of the closed symbols around the centre of the diagram in Figure 5.3a.

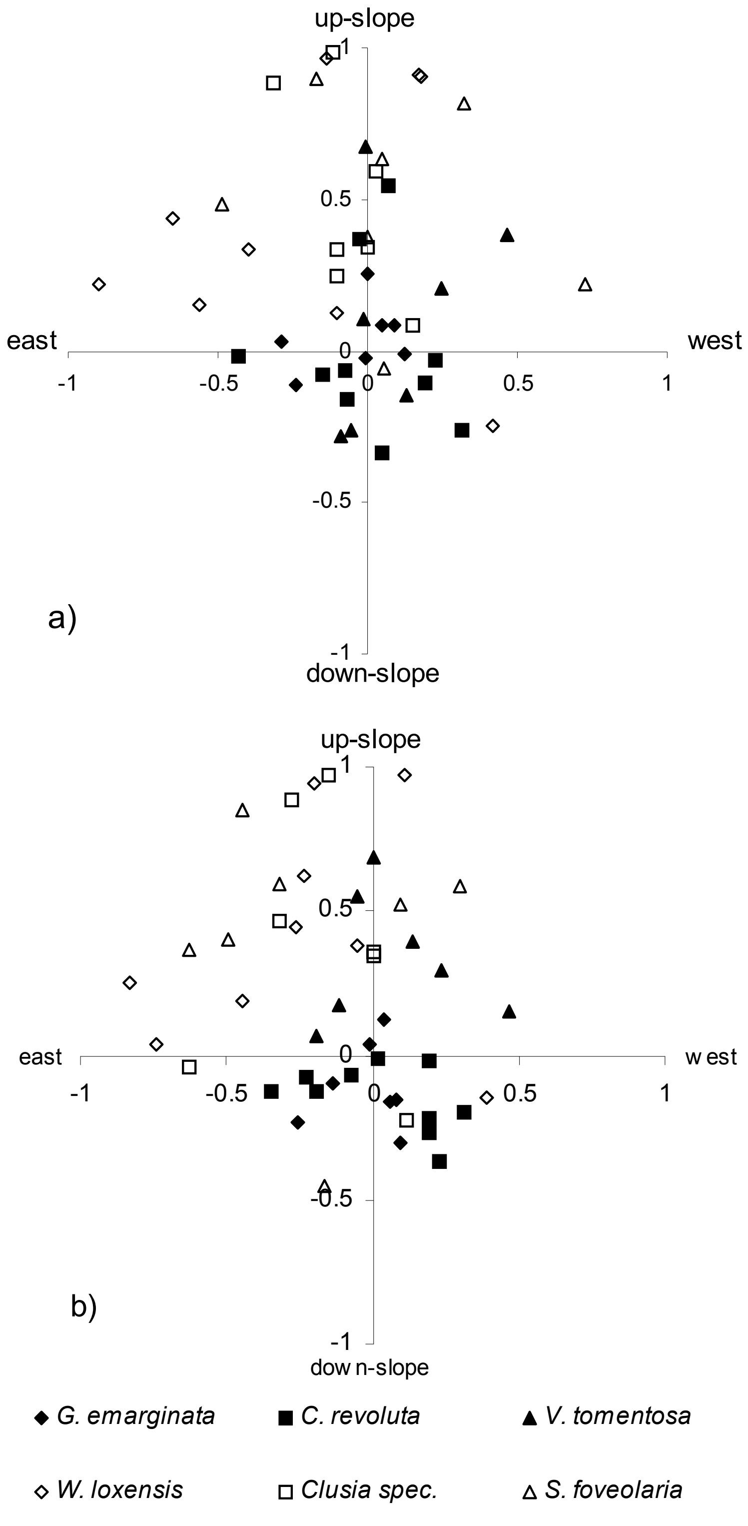

Figure 5.3: Average orientation of root CSA relative to slope direction; (a) average orientation of root origin, center represents stem center (b) mean direction of root growth, center represents respective point of origin of every root. Axes show a scale for the dimension of asymmetry R. Its distance to the center has a norm of 0 when there is no root clustering and a norm of 1 when 100% of root CSA is orientated in the same direction. Filled symbols: tree species at 1900 m, open symbols: tree species at 3000 m.

In contrast, at 3000 m there was conspicuous root clustering in up-slope direction. This is shown by the distribution of the open symbols, which are located mainly in the upper two quadrants in nearly all trees (Figure 5.3a).

When root CSA was measured further away from stem surface and when orientation of CSA was defined as the direction of root growth (angle β), root clustering became even more distinct (Figure 5.3b). Roots at 3000 m were markedly clustered in an up-slope direction with a clear deviation to the eastern side. At 1900 m, differences in the orientation of root clustering between species became apparent (Figure 5.3b). Roots of *C. revoluta* only clustered down-slope, but those of *V. tomentosa* only up-slope. The root system of *G. emarginata* was oriented down-slope in 5 of 7 trees.

The extent of root asymmetry *R* was significantly higher (p = 0.012; *n* = 3) at 3000 m than at 1900 m. The minimal diameter of roots included in the measurements was 0.020 m at 1900 m and 0.015 m at 3000 m. However, at 3000 m roots with a diameter < 0.020 m contributed less than 3 % to the total CSA in 17 of the 23 trees measured. This shows that the effect of altitude on *R* was not caused by the method of root sampling. *R* was not correlated with slope gradient (Figure 5.4a).

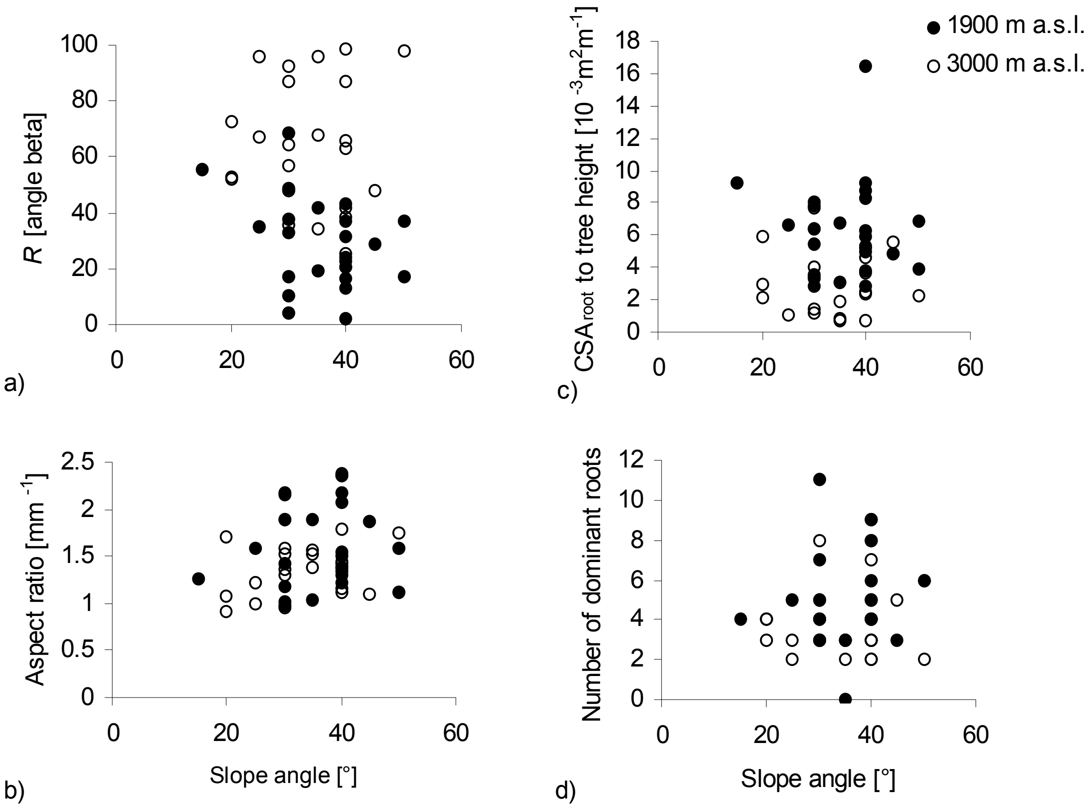

Figure 5.4. a) Root asymmetry *R* (angle ß), b) aspect ratio, c) ratio of CSA_{root} to tree height, and d) number of dominant roots at 1900 m and 3000 m in relation to slope angle.

Proportions within roots and stem

After the ZRT, structural roots of *Clusia* spec. and *V. tomentosa* had aspect ratios close to 1, i.e. they were nearly circular in cross section (Table 5.2). Thus, the shape of their root CSA was not influenced by mechanical stress. Roots of *C. revoluta* had the highest aspect ratios, i.e. here, the response to mechanical stress was most pronounced. The formation of small buttresses was typical for this species. Aspect ratios differed significantly between species within 1900 m. There was no effect of altitude on aspect ratio.

In relation to tree height, root CSA was higher at 1900 m than at 3000 m ($p = 0.025$; $n = 3$), i.e. tree anchorage was favoured by large ratios of $\mathrm{CSA}_{\mathrm{root}}$ to tree height at lower altitude. This parameter did not differ significantly between species within one altitude (Table 5.2). Tree species at 3000 m had a significantly lower number of dominant roots ($p = 0.006$; $n = 3$) than tree species at 1900 m. There was no consistent difference between species within one altitude (Table 5.2). None of the parameters aspect ratio, ratio of $\mathrm{CSA}_{\mathrm{root}}$ to tree height and number of dominant roots was correlated to slope angle (Figure 5.4b - d).

Qualitative traits of root anatomy

All six species differed markedly in their root architecture (Figure 5.5). *Clusia* spec. (at 3000 m) was characterized by the development of stilt roots up to 1 m height. Stilt roots were also found on species of *Clusia* at 1900 m, but there, they were only initiated close to the base of the trunk. *Clusia* spec. (at 3000 m) and *V. tomentosa* (at 1900 m) were the only species forming tap roots. The vertical extension of tap roots, however, was much more limited at 3000 m than at 1900 m (Figure 5.5). At 3000 m, the tap roots penetrated only the organic surface layer. At 1900 m, vertical extension of tap roots was impeded at depths of about 0.5-0.8 m in the mineral soil. Thus, all tap roots changed growth direction at certain soil depths. *W. loxensis* (at 3000 m) was the only species that had the ability to propagate by rhizomes, i.e. creeping underground stems with the ability to produce new shoots (Figure 5.5). Up to three shoots were connected by large structural rhizomes. Since the root systems were not completely excavated horizontally, it can be expected that even more shoots belonged to one plant. The CSA of structural roots near the stem of *S. foveolaria* (at 3000 m) and *C. revoluta* (at 1900 m) often deviated clearly from a circle. For *C. revoluta*, this has already been shown by the aspect ratio (Table 5.2).

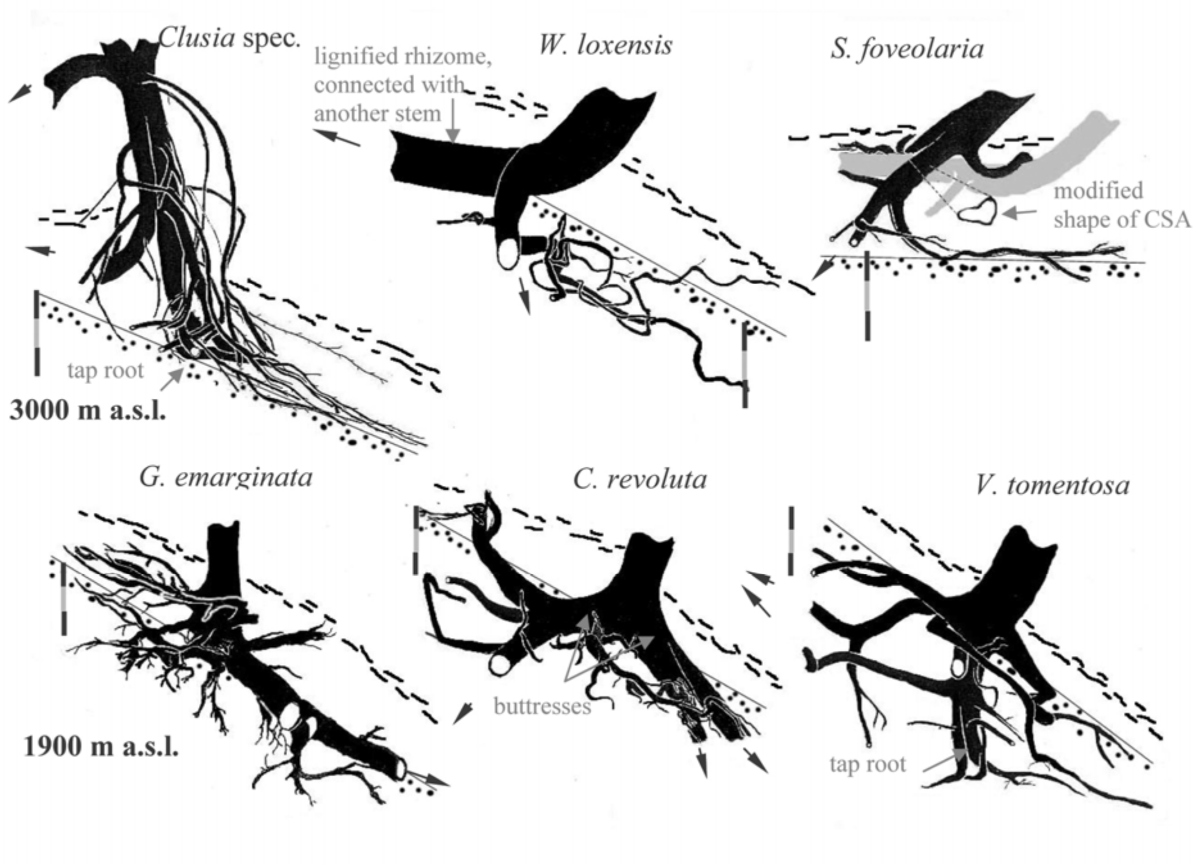

Figure 5.5: Typical appearance of coarse root systems of the investigated tree species, derived from photographs; black arrow = skeleton root continues; grey figure = stem of other tree; dots = surface of mineral soil; dashed lines = surface of forest floor; scale sections = 0.1 m.

Buttresses were often I- and T-beam shaped. Eccentric root CSA with typical I- and T-beam shapes were rarely found in *S. foveolaria*. The shape of CSA of this species was especially modified at the locations where the stem base was supported by roots of other trees, increasing the contact area between stem base and root (Figure 5.5).

Root systems of *G. emarginata* growing at 1900 m were characterized by vertically growing laterals similar to sinker roots (Figure 5.5). High branching frequencies resulted in a relatively small root system radius and thus, in small horizontal extension of the potential root-soil plate.

Shoot characteristics

Tree height, crown diameter and DBH were significantly higher at 1900 m than at 3000 m (p = 0.002, p = 0.001 and p = 0.020, respectively; *n* = 3). Ratios of DBH to tree height were slightly, but not significantly higher at 3000 m, i.e. at this altitude, trees had higher stem taper (Table 5.2). At both altitudes, stem inclination was oriented in down-slope direction, but there were marked differences in the extent of inclination between altitudes. At 1900 m, 92 % of trees grew upright or slightly inclined (Figure 5.6a), in comparison with 52 % at 3000 m (Figure 5.6b). At 3000 m, 48 % of trees were inclined, lying or partly uprooted. Between 0.3 m and 0.8 m of the stem were positioned within or on forest floor when trees were lying or partly uprooted. At this altitude, most trees grew upright when shoots were connected by rhizomes or in the presence of tap roots or stilt roots (Figure 5.7). In contrast, most trees with roots showing either modifications of the CSA or no special root feature were lying or even partly uprooted (Figure 5.7).

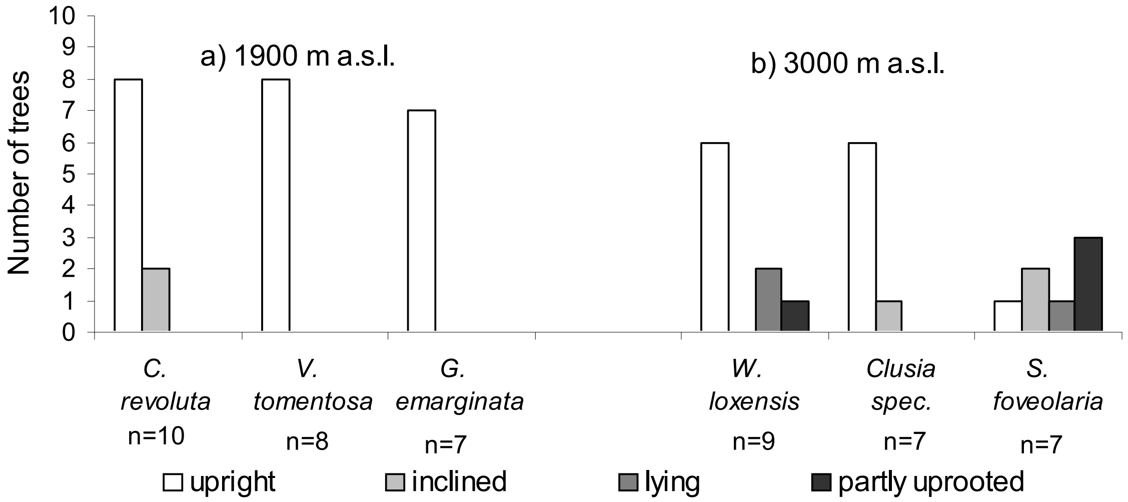

Figure 5.6: Appearance of tree stems with respect to tree rigidity at a) 1900 m and b) 3000 m; *n* = number of trees of the respective species.

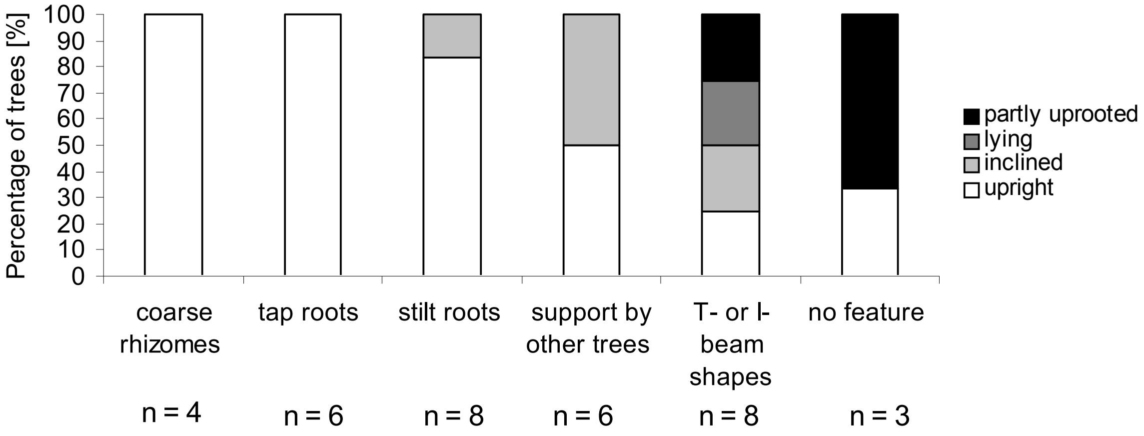

Figure 5.7: Relationship between the occurrence of a specific root trait (coarse rhizomes, tap roots, stilt roots, support by other trees, T- or I-beam shapes of root cross sections, no specific trait) and tree rigidity as assessed by the percentage of trees in different classes of stem inclination (upright, inclined, lying, partly uprooted) for trees growing at 3000 m; *n* = number of trees showing specific root traits.

5.4 Discussion

Importance of the observed morphological root traits for tree anchorage

In the montane and elfin forest of Southern Ecuador, a variety of root traits was observed that improve tree anchorage in soil. The extent of root asymmetry *R* with respect to both the direction of root origin and the direction of root growth at both altitudes was higher than in a study on Sitka spruce (*Picea sitchensis* Bong. Carr.) trees growing on slopes ≤14° (Nicoll and Ray, 1996). In the elfin forest, the extent of root asymmetry was higher than in a study on *Pinus peuce* (Mickovski and Ennos, 2003b). Root asymmetry influences root system stiffness in different directions. For example, winching stems of mature Sitka spruce sideways resulted in tree failure in the directions where main roots were less well developed (Coutts, 1983). Thus, root asymmetry is important for tree stability when mechanical forces e.g. wind loading are not evenly distributed around the stem.

Root asymmetry and root clustering can also be caused by physical obstructions of roots or the spatial variability of water and nutrient availability in soil (Coutts et al., 1999; Mickovski and Ennos, 2002). The occurrence of root clustering in the eastward up-slope direction in the elfin forest (Figure 5.3b) was accompanied by eastern winds, while root clustering in either up-slope or down-slope direction in the montane forest was accompanied by mountain and valley winds. This indicates that root asymmetry in the present study was mainly caused by mechanical loads and reflects the importance of horizontally growing roots for tree anchorage in shallow but also in deeper soils. However, this study does not allow to quantify the contribution of wind loading and “self loading” on root system asymmetry. It can be assumed that at 3000 m, the gusty winds have a major impact on root system asymmetry while at 1900 m, “self loading” forces get more important because of lower wind speeds and higher biomass of the trees.

The main direction of mechanical forces was related to the direction of root growth (Figure 5.3b) rather than to the orientation of root origin (Figure 5.3a). This indicates that roots reoriented, e.g. as a result of soil creeping or tree movement, or that some roots tapered or died and new branches formed in a different direction. According to our observations reorientation of roots was a very common feature. Thus, it is also possible that in several cases root asymmetry is a result of tree or soil movement rather than a mechanism to improve tree stability.

Buttresses as well as I- and T-beam shapes were most pronounced in *C. revoluta*, i.e. the species with the most superficial root system at 1900 m. The formation of buttresses or cross sections with an I- or T-beam shape may further improve anchorage by maximizing the bending resistance of the roots with a minimum of biomass costs (Mattheck, 1992; Coutts et al., 1999). For example, anchorage strength of buttressed tree species of the tropical lowlands was almost doubled in comparison to unbuttressed species (Crook et al., 1997). These modifications in the shape of root cross sections are usually found in superficial roots or root systems (Nicoll and Ray, 1996; Mickovski and Ennos, 2003b). In contrast to *C. revoluta*, structural roots of *V. tomentosa* and *Clusia* spec. were nearly circular in cross section. In these two species, horizontally growing roots were less important for tree stability because of the presence of tap roots and stilt roots. Tap roots moderate external forces by shifting the hinge point from the soil surface to deeper soil zones (Polomski and Kuhn, 2001). Together with windward sinkers they contributed to 75 % of anchorage strength in *Larix* spec. (Crook and Ennos, 1996). The functioning of stilt roots is similar to a guy rope, increasing the lever arm lateral to the stem (Mattheck, 1992). Results from the present study support the assumption that modifications in root cross sections are most pronounced in the absence of other root traits that improve tree stability.

In the present study, the impact of these root traits on tree rigidity was not measured. Rather, their effectiveness to improve anchorage was estimated by stem inclination. The uniform direction of stem inclination shows that inclination is the result of mechanical loadings acting on the trees. Inclination of stems at 3000 m suggests that tap roots, stilt roots and rhizomes enabled trees to resist mechanical forces (Figure 5.7). In contrast, inclination of trees with the formation of I- and T-beam shaped root CSA suggest that this trait was not sufficient to prevent stem inclination in the elfin forest. However, information is lacking on the time of the formation of these root traits. It is possible that in several cases I- and T-beam shaped root CSA formed after stem inclination.

Site specific differences in root and stem morphology

Even though root traits related to plant anchorage were often species specific, root system architecture was also significantly influenced by the different environmental conditions prevailing at different altitudes. Altitudes differed in wind speed and soil conditions, while slope angles were comparable. There was no correlation between slope angle and the extent of any root trait related to tree anchorage, suggesting that the extent of these traits is governed by other factors such as heterogeneities in wind loadings or the weight of the tree. The results of this study are in contrast to the results of Di Iorio et al. (2005) who found lower numbers of first order roots and higher basal CSA as well as higher extents of root asymmetry in *Quercus pubescens* Willd. and *Quercus cerris* L. trees growing on steep slopes (14° - 34°) than growing on shallow slopes (4° - 5°). The authors explained the impact of slope angles on root morphology by higher turning moments acting on the shoot on steep slopes.

Rooting depth affects the vertical extension of the root soil plate. In contrast to 3000 m, at 1900 m many structural roots originated in the mineral soil (Figure 5.2) which had higher bulk densities (Table 5.1) and thus, provided more stability than the forest floor. In comparison to 3000 m, at 1900 m dissipation of forces to mineral soil was further improved by the presence of rigid main tap roots in *V. tomentosa* and by vertically growing lateral roots similar to sinkers in *G. emarginata* (Figure 5.5). Thus, at this altitude the vertical extension of the root-soil plate may be of special importance for anchorage. The restriction of root origin to the forest floor at 3000 m (Figure 5.2) was accompanied by poor development of tap roots of *Clusia* spec. in comparison to good tap root development of *V. tomentosa* growing at 1900 m (Figure 5.5). The final extension of tap roots and root systems in general is strongly influenced by soil conditions and groundwater level (Rigg and Harrar, 1931; Kodrik and Kodrik, 2002; Cucchi et al., 2004). Investigations on the effect of vertical root growth restriction on anchorage strength led to contradictory results (Schaetzl et al., 1989; Cucchi et al., 2004). In the present study, vertical root extension at 3000 m was possibly restricted by waterlogged and shallow mineral soils (Schrumpf et al., 2001). As the bulk density in the forest floor is low, the concentration of root growth to the forest floor at 3000 m is expected to reduce tree stability (Rigg and Harrar, 1931; Ray and Nicoll, 1998).

Several root traits were supposed to have an impact on the horizontal extension of the root-soil plate. At 1900 m, strains might be transmitted to the soil closer to the stem than at 3000 m because of a larger root surface area (Ennos, 1990). A relatively larger root surface area at 1900 m is derived from higher ratios of CSA_{root} to tree height and higher numbers of dominant roots (Table 5.2) as well as high branching frequencies near the stem in *G. emarginata* (Figure 5.5). When trees have little anchorage from deeper growing roots, the horizontal extension of the root-soil plate becomes more important for tree anchorage (Mickovski and Ennos, 2003b; Cucchi et al., 2004). In accordance to this, the extent of root system asymmetry *R* was significantly higher in the elfin forest than in the montane forest (Table 5.2). The high extent of root system asymmetry in the elfin forest was accompanied by small numbers of dominant roots at this site (Table 5.2). Dominant roots, i.e. the largest roots summing up to 80 % of total CSA, are considered to be the most relevant roots for plant anchorage, because the stiffness of roots increases with the fourth power of their diameter (Coutts et al., 1999). The distribution of 80 % of total root CSA to a lower number of dominant roots may be regarded as the optimum investment of biomass with respect to rigidity (Coutts, 1983).

Another very effective trait to improve the horizontal extension of the root-soil plate and thus, tree stability is the propagation of *W. loxensis* by lignified rhizomes (Figure 5.7). It is possible that this trait results in a marked resistance to uprooting and that it is one reason for the high abundance of this species in the elfin forest. Support of the stem base or roots, either by nurse logs or by aboveground parts of the trees also occurred quite frequently in the elfin forest but was never observed in the montane forest. The development of trees on fallen logs or wood fragments is a typical feature of tropical montane forests with waterlogged soils and can be explained by a more favourable oxidation-reduction potential in these locations than in the underlying soil horizons (Santiago, 2000). In the present study, this mutual support was always accompanied by upright or just inclined stems (Figure 5.7). In combination with the high coarse root density support of the stem base or roots might be an important factor for tree stability at this site, because the low bulk density of the forest floor reduces its function as a hard bearing subsurface (Stokes and Mattheck, 1996). Furthermore, contact between roots and stems of neighbouring trees might improve anchorage by damping the effect of swaying due to high wind speeds. This damping effect was also found to be a function of crowns being in contact with each other in dense stands (Cucchi and Bert, 2003).

Besides root morphology above ground tree architecture also differed between altitudes (Table 5.2). Shorter stems with smaller crown areas in the elfin forest in comparison with the montane forest reduce wind induced turning moments (Nielsen, 1990) and may be thigmomorphogenetic responses to high wind speeds (Cordero, 1999). Higher taper of stems in the elfin forest causes more resistance to bending (Moore, 2000) and is another typical adaptation to high wind speeds (Lawton, 1982). This elfin tree stature may reduce wind loadings on the root systems enabling trees to grow on the shallow soils of this site.

In conclusion, native tree species growing on steep slopes of a south Ecuadorian tropical montane and elfin forest showed a variety of root traits related to plant stability. These traits were both species and site specific, but were not related to slope angle. Generally, mechanical loads caused a marked root asymmetry in these forests. Root traits improving the horizontal extension of the potential root-soil plate became even more important at higher altitudes, where deep rooting was markedly impeded by soil properties. Furthermore high coarse root densities and mutual support of roots and stems seemed to improve tree rigidity in elfin forests where bulk densities of the rooted soil horizons were low and wind speeds were high.

Acknowledgements

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6 Phenotypic plasticity in coarse root architecture of the tree species *Graffenrieda emarginata* (Ruiz & Pav.) Triana growing in an Ecuadorian tropical montane forest

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Summary

Coarse root systems of *Graffenrieda emarginata* (Ruiz & Pav.) Triana, a native tree species from the Ecuadorian tropical montane forest were investigated at two different altitudes (1900 m and 2400 m) in order to determine the extent to which root architecture of this species is modified by environmental conditions. Allocation factor (q), proportionality factor (p), length of root segments (l) and number of root segments after branching events ($Nsub$) were measured on a representative number of branching points and root segments. These parameters are typically used in fractal root system analysis for the modelling of scaling relations. Furthermore, scaling relations for entire roots of the same trees were assessed empirically. While p, l, and $Nsub$ were not influenced by altitude, q was significantly higher at 2400 m, indicating a more explorative growth strategy at this altitude. While root systems at 1900 m were characterized by vertically growing roots similar to sinkers, root systems at 2400 m grew more superficially and concentrated in the organic layer. These differences in spatial orientation had a conspicuous impact on l. In contrast q was not modified by growth direction. Altitude dependent differences in q suggested that with increasing altitude root biomass and root length as well as the proportion of total root length in the root main axis increased at a given proximal root diameter. However, these differences were not reflected by empirical scaling relations. It is suggested that the fractal parameter q is more sensitive to environmental changes than scaling relations.

Keywords: allocation factor, altitude, fractal branching parameter, proportionality factor, scaling relations, topology.

Also submitted to *Tree Physiology.*

6.1 Introduction

Complex environmental gradients are typical for the tropical mountains. Besides topography, exposition and parent rock also elevation affects environmental conditions such as temperature, soil humidity and nutrient availability (McGroddy and Silver, 2000; Takyu et al., 2002; Sklenar and Laegaard, 2003). Soils of tropical montane forests are often superficial with deep organic layers that may even increase with altitude (Arraiga, 2000; Schrumpf et al., 2001). At high altitudes, soils are often waterlogged (Grubb, 1977; Schrumpf et al., 2001). The change of environmental conditions along the altitudinal gradient may have a great impact on spatial root distribution and thus, on root system architecture (Spek, 1997).

Root architecture describes the explicit geometric deployment of the root axes and can be dissected into a number of measurable variables. One important variable is root topology that refers to how individual root axes are connected to each other (Lynch, 1995). Topology places root systems in between the dichotomous and the herringbone branching pattern (e.g. Fitter, 1987; van Noordwijk et al., 1994; Taub and Goldberg, 1996; Bouma et al., 2001a,b). Further variables are root radius and the degree of tapering (Danjon et al., 2005) as well as the geometry of a root system which comprises the length of root segments (the root subdivision between two branching points or between branching point and root tip) and their spatial orientation (Fitter, 1987; Fitter and Stickland, 1991; Bouma et al., 2001a,b; Smith, 2001).

The architecture of a root system is closely linked to its functions, e.g. resource acquisition and anchorage. It may be regarded as optimal, when root functions are provided with a minimum of carbon costs for the establishment of the root system (Coutts et al., 1999; Lynch and Ho, 2005). The wide variations in root system architecture indicate that plants benefit from different growth strategies. Such growth strategies may be e.g. exploitative, leading to high root densities within a given soil volume or explorative, providing access to a large soil volume (Spek and van Noordwijk, 1994; van Noordwijk et al., 1994; Hughes et al., 1995). It could be shown that an exploitative growth strategy is achieved by a dichotomous branching pattern and short root segments, whereas root systems with a herringbone character and long root segments exhibit a more explorative growth strategy (Spek and van Noordwijk, 1994; Oppelt et al., 2001). The benefit of the one or the other growth strategy e.g. for resource acquisition depends on many factors, such as the mobility of the resource in soil (Fitter, 1996), temporal and spatial heterogeneity of resource availability within soil (Oppelt et al., 2001; Dunbabin et al., 2004) or competition by other plants (Fitter et al., 1991).

It is well known that variations in root system architecture contain both genotypic and environmental components (Fitter, 1987; Taub and Goldberg, 1996; Bouma et al., 2001a,b;

Oppelt et al., 2001). Phenotypic plasticity of root system architecture had been observed in response to alterations in soil structure and competition (Gautam et al., 2003), inundation frequency and nitrogen availability (Bouma et al., 2001a,b), soil bulk density (Goodmann and Ennos, 1998), the depth of the water table (Ray and Nicoll, 1998), the depth of a hard pan in soil (Danjon et al., 2005), the slope angle (Chiatante et al., 2003b; Di Iorio et al., 2005), and wind-induced mechanical stress (Stokes et al., 1995; Nicoll and Ray, 1996). It has been proposed that phenotypic plasticity of root system architecture is presumably pronounced in those species that inhabit broad ranges of environmental conditions (Sultan, 2003; Fitter, 1996).

Due to the high efforts in measuring tree root systems, phenotypic plasticity of root system architecture was mostly investigated in herbal species or tree saplings (Fitter et al., 1991; Taub and Goldberg, 1996; Bouma et al., 2001a; Chiatante et al., 2003b). In the recent years, many studies have focused on the fractal pattern of root systems (e.g. van Noordwijk et al., 1994; Berntson, 1996; Eshel, 1998; Smith, 2001). In fractal branching pattern the same rules govern branching at each subsequent level (Spek and van Noordwijk, 1994), i.e. that architectural variables such as topology, tapering and geometry do not change with increasing root diameter. Based on this assumption, tree root architecture can be characterized quantitatively by the measurement of a representative number of root segments and branching points. However, phenotypic plasticity of fractal branching parameters in tree root systems has never been examined.

Fractal branching parameters are usually used in models or equations that provide tree specific scaling relations (Van Noordwijk und Mulia, 2002; Richardson and zu Dohna, 2003). Scaling relations allow e.g. the estimation of root biomass, total root length or the length of the longest root axes by measuring the proximal root diameter (Oppelt et al., 2001). Similar to architectural variables, species specific scaling relations of root systems may be affected by environmental conditions, but this has rarely been tested in literature (Ritson and Sochacki, 2003).

The aim of the present study was to examine phenotypic plasticity in the coarse root architecture of the native tree species *Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae), which occurs on a broad altitudinal gradient within an Ecuadorian tropical montane forest. Therefore, coarse root architecture of trees growing at two different altitudes was compared. It was hypothesised that both fractal parameters and empirical scaling relations of tree root systems differ between altitudes.

6.2 Materials and methods

The study was carried out at two altitudes in a lower tropical montane forest within the Reserva San Francisco, close to the south Ecuadorian province capitals Loja and Zamora. The lower study site (03°58′ S, 79°04′ W) was located at 1900 m a.s.l.. The soils had low $pH_{(CaCl2)}$ and low bulk densities (Table 6.1).

Table 6.1: Soil characteristics at different soil depths at 1900 m and 2400 m a.s.l..

Soil depth (m)	Bulk density (g cm^{-3})		$pH_{(CaCl2)}$	
	1900 m a.s.l.	2400 m a.s.l.	1900 m	2400 m a.s.l.
Organic layer	0.1	0.1	3.2	3.1
0.0 – 0.1	0.4	0.7	3.2	3.1
0.1 – 0.3	0.8	1.2	3.5	3.1
0.3 – 0.5	0.8	1.4	4.0	3.3
0.5 – 0.7	0.9	1.4	4.1	3.6

Average depth of the organic layer on the soil surface was 0.15 m and average depth of the mineral soil was > 0.90 m. The upper study site (2400 m a.s.l., 03°59′ S, 79°04′ W) had acid soils and higher bulk densities in mineral soil than at 1900 m. Average depth of the organic layer was 0.16 m, but due to high amounts of cavities it appeared deeper than at 1900 m. The mineral soil was more superficial with an average depth of about 0.60 m. Soils at both sites were classified as gleyic Cambisols according to FAO taxonomy (S. Iost, pers. comm.). Both sites were situated on moderately steep slopes facing north east. *G. emarginata* was one of the most frequent tree species at 1900 m, ranging in height between 10.2 and 11.7 m. At 2400 m, *G. emarginata* was less abundant and much smaller in stature (6.3 - 6.9 m). This tree species was selected for the examination of coarse root architecture because it was the only tree species that occurred at both altitudes.

Coarse root systems of three trees per altitude were excavated in a semicircle of 1 m radius at one side of the stem, parallel to slope direction. Additionally, one root of every tree was excavated entirely. With a hedge clipper the organic layer was removed carefully, leaving all coarse roots (≥ 5 mm in diameter) intact as well as all roots with a diameter ≥ 2 mm that originated from those coarse roots. Afterwards, roots growing in the organic layer were signed and the mineral soil was removed with the help of a screwdriver. Excavation ended in the depth, where no more coarse roots were growing. For the calculation of fractal parameters and scaling relations, the length and the diameter at the beginning and at the end of every root segment were measured, recording its number and the number of its parent root.

Calculation of fractal parameters

Fractal parameters were calculated according to van Noordwijk and Mulia (2002) (Figure 6.1).

As a measure for topology, the allocation factor (q) was determined. This parameter defines the partitioning of biomass between the new root segments after a branching point and is expressed as:

$$q = \frac{\left(\max \mathrm{D}_{\mathrm{after\_branching}}\right)^2}{\sum\left(\mathrm{D}_{\mathrm{after\_branching}}\right)^2}$$

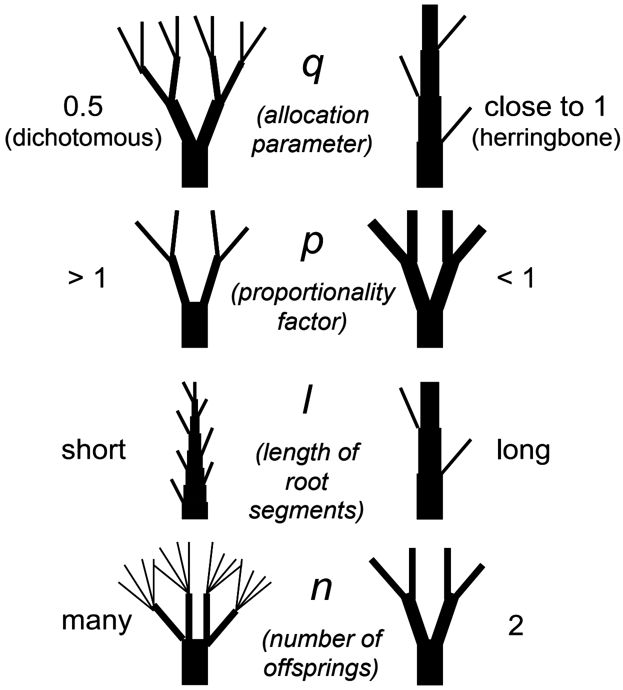

Figure 6.1: Fractal branching parameters as assessed in this study.

where D is the diameter at the beginning of the respective root segments and max $\mathrm{D}_{\mathrm{after\_branching}}$ is the diameter of the largest root segment after branching. While the q value of a dichotomous branching pattern is 0.5 it approaches to unity in a herringbone branching pattern.

The proportionality factor (p) characterizes tapering by quantifying the change of the cross sectional area (CSA) by branching. It is calculated as follows:

$$p = \frac{\left(\mathrm{D}_{\mathrm{before\_branching}}\right)^2}{\sum\left(\mathrm{D}_{\mathrm{after\_branching}}\right)^2}$$

In the case of maintenance of CSA, factor p equals 1, in the case of rapid taper, the value increases. Further parameters were the average number of offsprings that emerge from a branching point (*Nsub*) and average length of all root segments (l). The latter was calculated only for root segments with a diameter of 5 – 50 mm, because l may change with root diameter. For the parameters q, p and *Nsub* all parent roots with a diameter $\geq$ 5 mm and all offsprings with a diameter $\geq$ 2 mm were considered. Average q, p, *Nsub* and l values of one altitude were calculated by the means of the three excavated trees at this altitude.

Calculation of empirical scaling relations

Scaling relations were obtained separately for each tree by adding length or biomass of the respective root segments of the entirely excavated roots. For the calculation of the biomass of a root segment its volume was assessed by root length and the mean of distal and proximal diameter. The volume was multiplied by a wood density of 0.5 g cm^{-3}. This density had formerly been assessed by drying root segments with a known volume at 70°C until constant weight had been achieved.

Diameters of all root segments of the main axis were related to (i) total biomass distal to the respective root segment, (ii) the length of all root segments distal to the respective root segment and (iii) the proportion of total distal root length that was formed by the main axis. The main axis was defined as the root that had the largest root segment diameters at every branching point from the beginning at the stem base until the minimal diameter was reached.

Statistic analyses

Average values of the fractal parameters q, p, $Nsub$ and l at both altitudes were compared by student´s t-test for independent samples. For the comparison of means from different soil layers or different root diameter classes the t-test procedure for paired samples (two values per tree) was realized. Scale dependence of fractal parameters was assessed by correlation analysis.

6.3 Results

Fractal parameters and appearance of the root systems

Factor q was the only fractal parameter that differed significantly between altitudes (Table 6.2). At 2400 m, the value was higher than at 1900 m, i.e. at 2400 m, root systems exhibited a branching pattern that was better characterized by a herringbone structure. As indicated by the stability index, correlation between fractal parameters and root segment diameter were very weak (Figure 6.2), justifying the assumption of fractal branching patterns.

Table 6.2: Fractal branching parameters at two different altitudes (Mean ± standard deviation, $n = 3$). Lower case letters indicate differences between altitudes at a significance level of $p < 0.05$.

Altitude (m)	Allocation factor (q)	Proportionality factor (p)	Mean link length [mm]	Number of offsprings ($Nsub$)
2400 m	0.83 ± 0.02^a	1.07 ± 0.05^a	111.1 ± 21.6^a	2.35 ± 0.13^a
1900 m	0.73 ± 0.04^b	1.10 ± 0.10^a	109.3 ± 14.3^a	2.27 ± 0.07^a

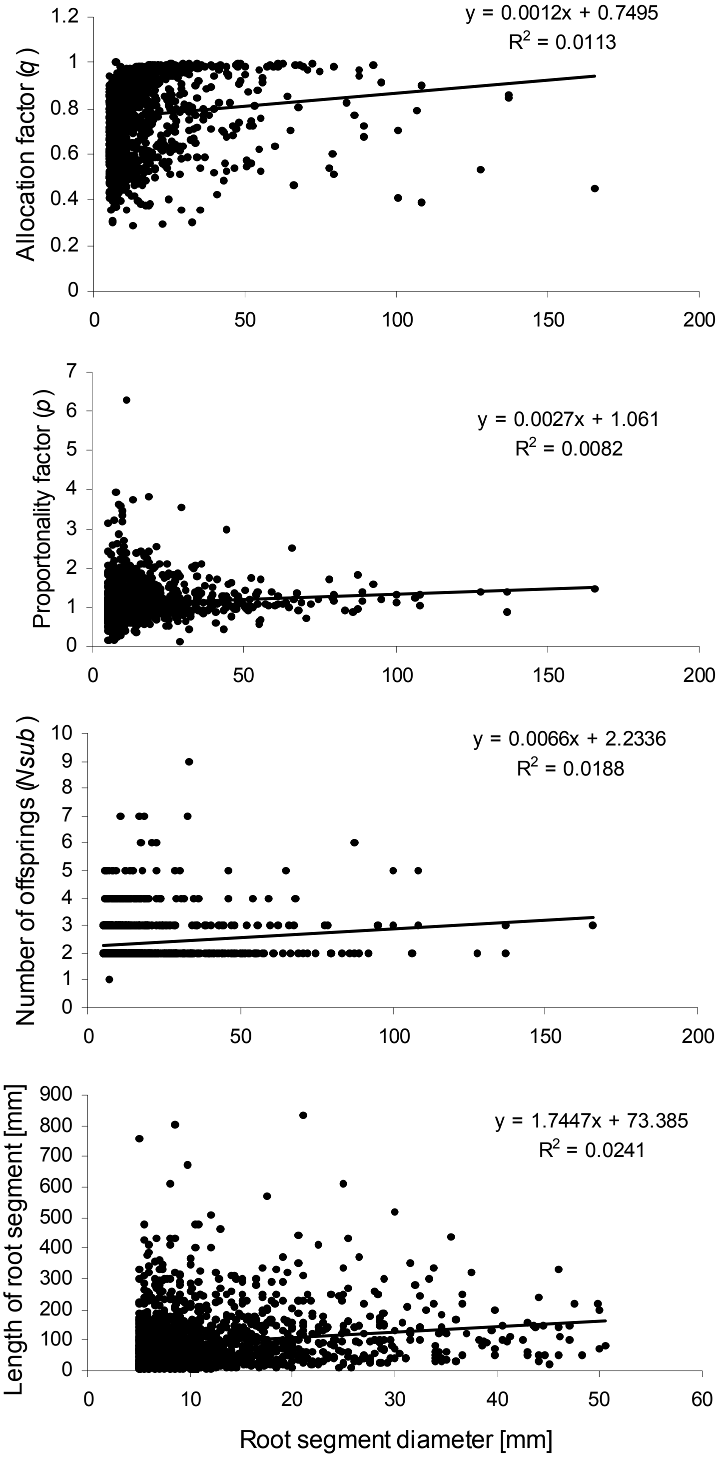

Figure 6.2: Fractal parameters *q*, *p*, *Nsub* and *l* for all trees plotted against root segment diameter and the respective linear regression line. For *p*, *q* and *Nsub, n* = 1586, for *l, n* = 1670.

Nevertheless, slight increases in fractal parameters with increasing root segment diameter could be observed. To test if differences in factor q between altitudes were the result of this weak scale dependence, average q was assessed for defined root diameter classes (Table 6.3).

At 2400 m, *q* from roots ≥ 15 mm in diameter was significantly ($p < 0.05$) higher than from roots < 15 mm in diameter, i.e. thick coarse roots had more herringbone character. The same trend was observed at 1900 m. Nevertheless, differences of factor *q* between altitudes remained in roots < 15 mm in diameter (Table 6.3), indicating that altitude dependent differences of *q* were not the result of scale dependence.

Table 6.3: Allocation factor *q* for different root diameter classes (Mean ± standard deviation, *n* = 3). Ø = root segment diameter. Lower case letters indicate differences between altitudes and upper case letters indicate differences between root diameter classes at a significance level of p < 0.05.

Altitude (m)	Ø < 15 mm	Ø > 15 mm
2400 m	0.78 ± 0.01^{aA}	0.87 ± 0.03^{aB}
1900 m	0.73 ± 0.03^{bA}	0.79 ± 0.08^{aA}

Coarse root systems at 1900 m and 2400 m differed markedly in their appearance (Figure 6.3). This was most noticeable in the orientation of root growth. At 2400 m, coarse roots were concentrated on the organic layer with many roots growing horizontally on the surface of the mineral soil. At 1900 m, more vertically growing roots similar to sinkers penetrated the mineral soil, especially near to the stem base.

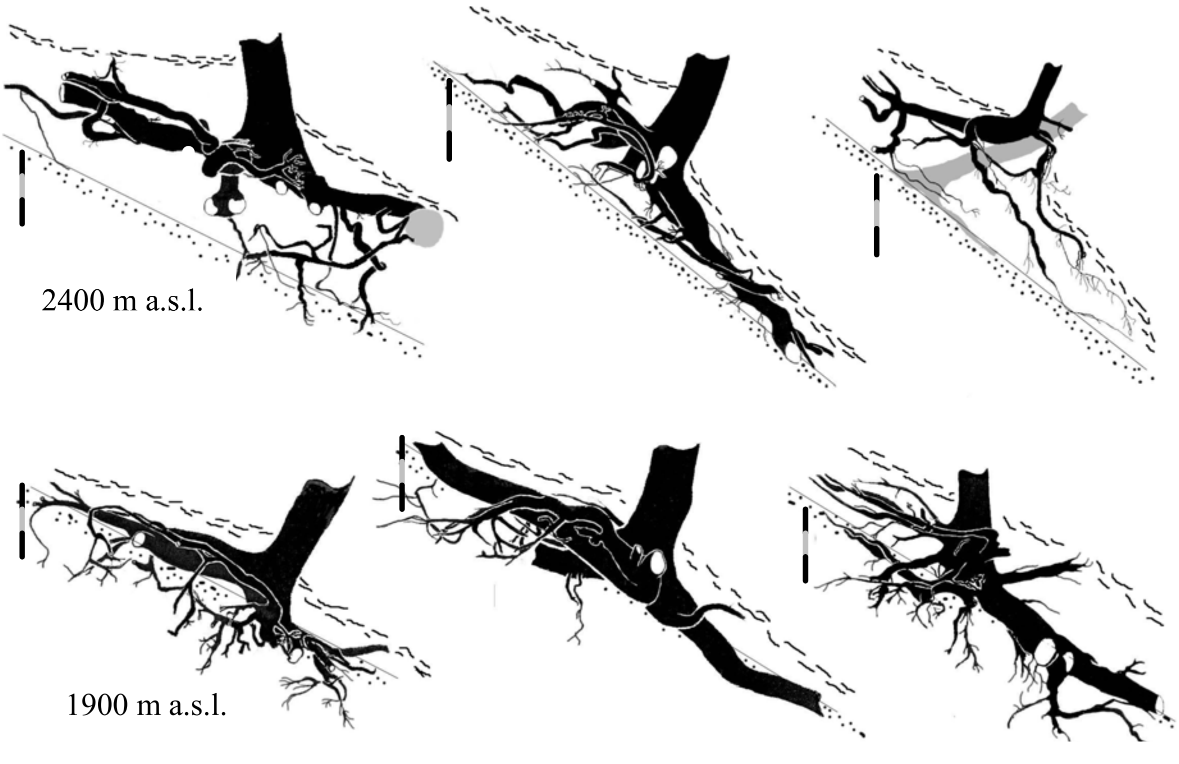

Figure 6.3: Appearance of coarse root systems of *G. emarginata* growing at two altitudes, derived from photographs; dashed lines = upper limits of organic layer, dots = surface of mineral soil, scale section = 0.1 m. Grey figures represent neighbouring trees.

To test if root growth directions had an impact on fractal parameters, root segments of the trees at 1900 m were divided in those growing in the organic layer and those growing in mineral soil. Only *l* was significantly affected by rooting depth, i.e. root segments growing in mineral soil (that were more often orientated downward) were shorter than more horizontally orientated root segments growing in the organic layer (Table 6.4). In contrast, factor *q* was similar in both soil layers. In the organic layer, its mean was still lower, i.e. more dichotomous, than the total mean at 2400 m, indicating that an altitude dependent plasticity occurred also within superficially growing roots.

Table 6.4: Fractal branching parameters of trees at 1900 m for two different soil layers (Mean ± standard deviation, *n* = 3). Lower case letters indicate differences between soil layers at a significance level of p < 0.05.

Soil layer	Allocation factor (*q*)	Proportionality factor (*p*)	Mean link length [mm]	Number of offsprings (*Nsub*)
Organic layer	0.74 ± 0.05^a	1.17 ± 0.19^a	10.97 ± 3.94^a	2.25 ± 0.09^a
Mineral soil	0.72 ± 0.03^a	1.23 ± 0.14^a	8.11 ± 2.69^b	2.39 ± 0.14^a

Scaling relations

With increasing proximal root segment diameter there was a linear increase of distal root biomass (Figure 6.4a). For root segments of small diameters this increase was better described by a potential equation (data not shown). The distal length of the root main axis (Figure 6.4b) increased logarithmically and the proportion of the root main axis in total root length (Figure 6.4c) decreased potentially with increasing proximal root segment diameter. The relation between proximal root segment diameter and absolute distal root length exhibited the broadest scattering of all scaling relations. Distal root biomass and the relative length of the root main axis were tightly correlated with root segment diameter. None of the empirical scaling relations differed between trees growing at 1900 m and 2400 m.

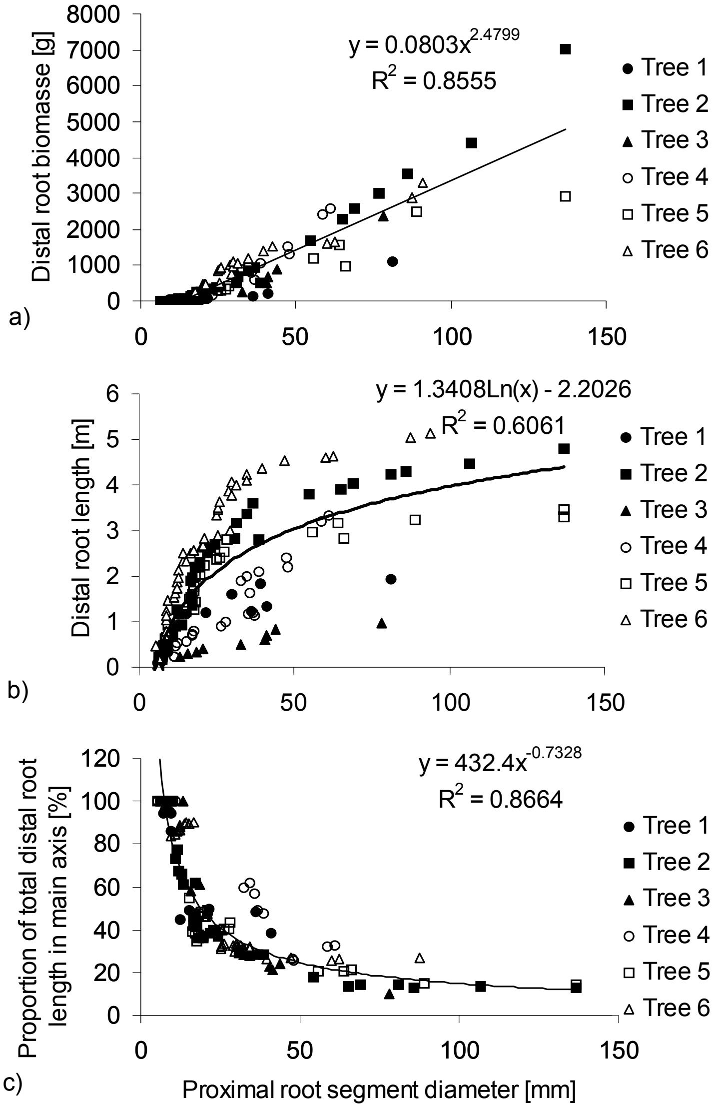

Figure 6.4: (a) Biomass, (b) length of the main axis and (c) proportion of total root length in the main axis distal to a root link plotted against its diameter. White symbols: trees at 2400 m, black symbols: trees at 1900 m.

6.4 Discussion

Phenotypic plasticity of fractal branching parameter and scaling relations

Our *q* values at 1900 m (0.73) lay in the middle range and at 2400 m (0.83) in the upper range in comparison to *q* values of tree root systems from other studies (0.64 to 0.86) (Van Noordwijk and Purnomosidhi, 1995; Ozier-Lafontaine et al., 1999; Richardson and zu Dohna, 2003). The *q* value of *G. emarginata* at 1900 m was the lowest observed in six different tree species growing in the forest of the present study, whereas the *q* value of *G. emarginata* at 2400 m was similar to the highest (0.85, unpublished data), indicating that *G. emarginata* had a high phenotypic plasticity in the topology of coarse roots.

Changes in q were not accompanied by changes in empirical scaling relations (Figure 6.2). These results disagree with theoretical approaches of Spek and van Noordwijk (1994) which showed that at a given proximal diameter total root volume as well as the length of the longest root increased with increasing q. The results also disagree with approaches on herbaceous species (Bouma et al., 2001) where the proportion of total distal root length in the main axis increased when the root systems resembled more herringbone type. It is suggested that scaling relations in tree root systems are less sensitive to changes in environmental conditions than the fractal parameter q. This assumption is supported by Oppelt et al. (2001) who observed that differences in root architecture of four African tree species were reflected by topological indices, although the empirical scaling relations were the same for all species. In a sensitivity analysis for root systems modelling, the average factor p and the distribution of root length had a greater effect on total root biomass and root length than the average q (Ozier-Lafontaine et al., 1999; van Noordwijk and Mulia, 2002) supporting the hypothesis that topology in tree root systems has a minor impact on scaling relations. The influence of average q on scaling relations in natural root systems may be further diminished by the broad scattering of single q values (Spek, 1997).

Possible reasons for differences in root system architecture between altitudes

It is likely, that the scarce root development in mineral soil at 2400 m was caused by unfavourable growth conditions such as oxygen deficiency (Chapter 2) and thus, is an inevitable effect of suboptimal environments rather than an adaptive plasticity to enhance root system functioning (Sultan, 2003).

It could be shown that altitude dependent differences in q were not related to differences in the spatial orientation of root systems between altitudes. Thus, the increase of q with increasing altitude may hardly be a response to vertical heterogeneities in soil. Changes in topology, as estimated by q, are often regarded as an adaptive trait to improve the efficiency of nutrient uptake or to diminish carbon costs for the construction of a root system (Fitter, 1987; Fitter, 1996; Taub and Goldberg, 1996). In the following, possible impacts of these aspects on coarse root architecture are discussed.

- *Nutrient availability*

  Nutrient availability is likely decreased at 2400 m due to lower mineralization of soil organic matter than at 1900 m (Chapter 3). Even though coarse roots do not contribute to nutrient uptake, nutrient availability might also affect coarse root architecture because every coarse root had been a fine root in its early stage of development. When seedlings of dicotyledons were grown under nutrient-poor conditions the herringbone character of root systems was more pronounced and length of root segments were higher, i.e. root systems were more explorative than under high nutrient availability (Fitter and Stickland, 1991; Taub and Goldberg, 1996). This can be explained by a more effective capture of mobile resources such as nitrate ions, because in explorative root systems depletion zones around the roots do not overlap as they would in root systems following an exploitative growth strategy (Fitter, 1987; Fitter et al., 1991). In contrast to the seedling experiments that were conducted with single plants growing in pots, trees growing in the montane forest had to compete with other plants for nutrient acquisition. Because of this competition in natural nutrient limited habitats, the impact of topology on the overlapping of depletion zones may be reduced or even reversed compared to pot experiments (Fitter et al., 1991; Bouma et al., 2001). It can therefore be suggested that nutrient limitation at 2400 m did not explain the more pronounced herringbone-like root systems at 2400 m.

- *Carbon costs*

Persistent cloudiness (Bruijnzeel and Veneklaas, 1998) or low temperatures (Kitayama and Aiba, 2002) may reduce photosysnthesis at high altitudes of tropical montane forests and thus, the amount of C that is located to the root systems. However, it might not be expected that C-supply to coarse root systems governs growth strategy in the present study, because (i) the concentration of reducing sugars in twig tissue of *G. emarginata* was very high at both altitudes (unpublished data), suggesting that C assimilation rates do not limit plant growth (Körner, 2003); and (ii) the amount of C needed for coarse root growth may be very low in comparison with total C demand of root systems due to very low coarse root turnover (Kurz et al., 1996; Gill and Jackson, 2000).

Root topology has rarely been related to anchorage (Fitter, 1996). It is noticeable that at 2400 m q values were significantly higher in coarse roots ≥ 15 mm in diameter than in coarse roots < 15 mm in diameter (Table 6.3). High q values are associated with a slow taper of the main root axis (Spek and van Noordwijk, 1994). Rigidity of root systems is predominantly increased by a slow taper, when it occurs close to the stem base, i.e. at the thickest coarse roots (Nielsen, 1990; Coutts et al., 1999). It might be expected that at 2400 m, where deep rooting is hampered, the rigidity of superficial coarse roots becomes more evident for anchorage than at 1900 m, where tree stability is improved by deeper growing roots (Coutts, 1983; Chapter 5). However requirements to tree anchorage may not be the only reason for the significant changes of q with increasing altitude, because (i) requirements to anchorage may affect only few (the thickest) branching points that have only little influence on average q;

and (ii) altitude dependent differences of q were more pronounced in roots < 15 mm than in roots ≥ 15 mm in diameter (Table 6.3).

Conclusion

The fractal parameter q as a measure for root topology differed significantly in coarse root systems of *G. emarginata* when growing at two different altitudes. Differences in q were not reflected by empirical scaling relations, suggesting that root system topology is more sensitive to environmental changes than scaling relations. The reason for phenotypic plasticity in the topology of coarse root systems requires further investigation.

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7 Root tapering between branching points should be included in fractal root system analysis

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Abstract

The proportionality factor (*p*) is a parameter used for fractal root system modelling. It describes tapering along root axes and is calculated by the ratio of total cross sectional area (CSA) before and after branching. The exact point where the area of the parent branch is measured is often not defined. By measurement of the CSA adjacent to a branching point tapering without branching is not included in factor *p*.

In this study *p* was measured on 6 tropical tree species (*Clethra revoluta, Graffenrieda emarginata, Vismia tomentosa, Weinmannia loxensis, Clusia* sp. and *Styrax foveolaria*). The measurement was conducted in three different ways, quantifying (i) tapering of roots by branching (p_{branch}), (ii) tapering without branching (p_{within}), and (iii) total root tapering (p_{total}). For five species p_{total} was significantly higher than p_{branch} ($p<0.05$). For three species p_{within} contributed significantly more to p_{total} than p_{branch}. There was only a weak correlation between *p* and root segment diameter. The slope of the regression line was often higher for p_{within} than for p_{branch}. The results suggest that the exclusive use of p_{branch} in fractal branching models leads to an underestimation of total root system tapering and to an overestimation of total root system biomass and root length in fractal branching models. Furthermore in some species self similarity decreases when tapering without branching is included in the proportionality factor *p*. This may imply that models should allow *p* to change with increasing diameter.

Keywords: Leonardo´s rule, proportionality factor, root architecture, root biomass, self similarity, WanFBA.

Also submitted to *Ecolgical Modelling.*

7.1 Introduction

Leonardo da Vinci claimed in his notebook that the cross sectional area (CSA) of a tree trunk is equal to the sum of the CSA of branches at any higher level (Richter, 1970). In some cases, the assumption of area preserving branching was also confirmed for tree root systems even though variations between single branching points were large (Oppelt et al., 2001; Richardson and Dohna, 2003).

When branching at each subsequent level of a root system is governed by the same rules, the root system can be described as a self similar or fractal network (Spek and van Noordwijk, 1994; Richardson and Dohna, 2003). In fractal branching models, tree specific scaling rules are assessed on the basis of easily observable parameters (Van Noordwijk and Mulia, 2002; Richardson and Dohna, 2003). The change of CSA during branching is often quantified by a proportionality factor (p) that is calculated as the ratio of total CSA before and after branching (Van Noordwijk and Mulia, 2002). Factor p affects the tapering of root systems and thus, influences total root length and biomass at a given proximal diameter (Spek and van Noordwijk, 1994).

To test the assumption of the preservation of cross-sectional area or to quantify the rate of tapering along root axes for root system modelling, the exact point where the diameter of the parent root segment (segment between two branching points) is measured is often not defined (Ozier-Lafontaien et al., 1999; Oppelt et al., 2001). In other cases, root segment diameters are measured adjacent to the branching point (Smith, 2001). This method may underestimate tapering along the root axes since tapering without branching is not included.

In this study, the effect of the measuring point on factor p was tested on 6 different tree species growing in a tropical montane forest. It was hypothesized that the location of this point (at the beginning or at the end of the parent root segment) influences the predicted degree of root tapering.

7.2 Methods

The study was perfomed at the Estacion Científica San Francisco (ECSF) near to the Podocarpus National Park in the South of Ecuador. The selected tree species grew at two different altitudes because measurements were part of another study. At the lower study site (1900 m a.s.l.; 03°58´S, 79°04´W) the species *Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae), *Clethra revoluta* (Ruiz & Pav.) Spreng. (Clethraceae) and *Vismia tomentosa* Ruiz & Pav. (Clusiaceae) were investigated. Here, average vegetation height was about 11 m. Soils were very acid, with an $\mathrm{pH}_{(\mathrm{CaCl2})}$ about 3 and had an average depth of the forest floor of 0.15 m and a mineral soil > 0.9 m depth.

At the upper study site (3000 m a.s.l.; 04°06´S, 79°10´W), the species *Weinmannia loxensis* Harling (Cunoniaceae), *Clusia* sp. (Clusiacaea) and *Styrax foveolaria* Perkins (Styraceae) were investigated. Average vegetation height was about 4 m. The soils were often waterlogged and characterized by deep forest floors (average of 0.3 m), shallow mineral soils (average of 0.4 m) and pH about 3.

Three individuals of every species were investigated at the lower altitudes, four individuals each at 3000 m. The coarse root systems were excavated in a semicircle of 1 m radius at one side of the stem, parallel to slope direction. Additionally one primary root of every tree was excavated entirely. With a hedge clipper the organic layer was carefully removed, leaving all coarse roots (≥5 mm in diameter) intact as well as all roots with a diameter ≥2 mm that originated from those coarse roots. Because of the dense vegetation at 3000 m it was not always possible to conserve this procedure at this altitude. In this case, as many coarse roots of a tree as possible were excavated. The diameter at the beginning and at the end of every root segment was measured. With help of the WanFBA helpfile (Van Noordwijk and Mulia, 2002), factor *p* was calculated in three different ways:

$$p_{\text{branch}} = \frac{D^2_{\text{before branching dist}}}{\sum D^2_{\text{after branching prox}}} \qquad (1)$$

$$p_{\text{within}} = \frac{D^2_{\text{before branching prox}}}{D^2_{\text{before branching dist}}} \qquad (2)$$

$$p_{\text{total}} = \frac{D^2_{\text{before branching prox}}}{\sum D^2_{\text{after branching prox}}} \qquad (3)$$

where D is the diameter at the beginning (prox) or at the end (dist) of the respective root segment (Figure 7.1).

Statistical analysis

Statistical analyses were realized with SPSS 11.0. For each species, $p_{(\text{total})}$, $p_{(\text{within})}$, and $p_{(\text{branch})}$ values were compared pair wise by the nonparametric Wilcoxon-test.

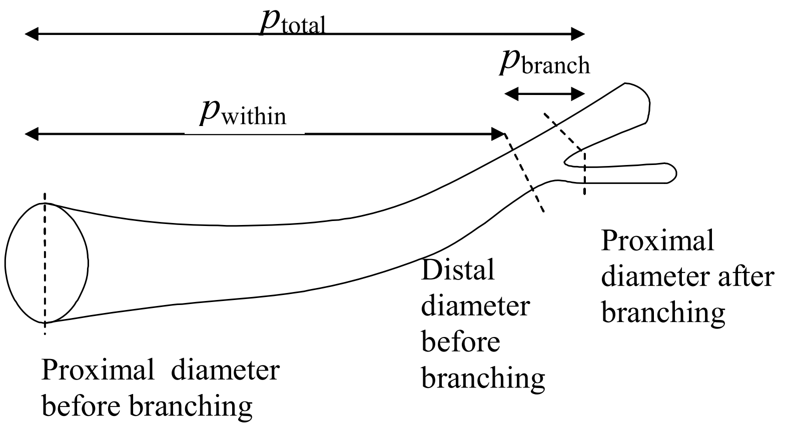

Figure 7.1: Measuring points of the parameters p_{total}, p_{within} and p_{branch}.

7.3 Results

For the calculation of average p_{branch}, p_{within} and p_{total}, 100 branching points per tree species were obtained randomly from all replicate observations, allowing a better comparability of standard errors between tree species than unequal numbers of replicates. Average data of p_{branch} ranged between 1.00 and 1.17 (Table 7.1).

Table 7.1: Proportionality factor for different species measured by three different methods (n = 100).

Tree species	Proportionality factor		
	p_{branch}	p_{within}	p_{total}
C. revoluta	1.17 (0.04)^{a}*	1.21 (0.09)^{a}	1.38 (0.08)^{b}
Clusia sp.	1.00 (0.02)^{a}	1.13 (0.03)^{b}	1.13 (0.04)^{b}
G. emarginata	1.09 (0.04)^{a}	1.02 (0.02)^{a}	1.12 (0.04)^{a}
S. foveolaria	1.16 (0.09)^{a}	1.30 (0.12)^{a}	1.50 (0.15)^{b}
V. tomentosa	1.06 (0.02)^{a}	1.31 (0.08)^{b}	1.40 (0.09)^{c}
W. loxensis	1.02 (0.03)^{a}	1.13 (0.04)^{b}	1.15 (0.05)^{b}

*** Data in parenthesis show standard errors. Lower case letters show differences between the methods at a 5% level (Wilcoxon Test).**

When tapering without branching was included (p_{total}), averages ranged from 1.12 to 1.50. Except for *G. emarginata*, p_{total} was always significantly higher than p_{branch}. In three cases p_{within} was higher than p_{branch}. The p_{branch} of *Clusia* sp. and *W. loxensis* was close to 1. Here, tapering of the root system was predominantly caused by tapering without branching. In general, the contribution of p_{within} and p_{branch} to total tapering was highly dependent on tree species, but usually the impact of p_{within} was higher than the impact of p_{branch}.

For the determination of scale dependence p_{total} and p_{within} were plotted against the proximal root segment diameter of the parent root while p_{branch} was plotted against its distal root segment diameter. Stability indices showed no correlation between p and root segment diameter (Table 7.2).

Table 7.2: Equation for the regression (R.E.) of p_{total} against the proximal root segment diameter D_{prox} (mm) and of p_{branch} against distal link diameter D_{dist} (mm) for different tree species and stability index (R^2).

Tree species	D_{dist} against p_{branch}		D_{prox} against p_{within}		D_{prox} against p_{total}		
	R.E.	R^2	R.E.	R^2	R.E.	R^2	*n*
C. revoluta	Y = 0.0022x + 1.12*	0.0256	Y = 0.0010x + 1.23	0.0012	Y = 0.0012x + 1.36	0.0017	317
Clusia sp.	Y = 0.0023x + 0.96	0.0078	Y = 0.0031x + 1.08	0.0146	Y = 0.0045x + 1.03	0.0196	295
G. emarginata	Y = 0.0030x + 1.07	0.0092	Y = 0.0000x + 1.04	0.0003	Y = 0.0027x + 1.12	0.0060	953
S. foveolaria	Y = 0.0077x + 0.98	0.0268	Y = 0.0179x + 0.88	0.0910	Y = 0.0232x + 0.92	0.1027	133
V. tomentosa	Y = 0.0022x + 1.02	0.0133	Y = 0.0175x + 1.17	0.0499	Y = 0.0188x + 1.18	0.0636	344
W. loxensis	Y = 0.0044x + 0.97	0.0299	Y = 0.0103x + 1.01	0.0614	Y = 0.0149x + 0.98	0.0755	268

***Y = link diameter, x = proportionality factor.**

However, for *S. foveolaria*, *V. tometosa* and *W. loxensis* the slopes of the regression lines were markedly higher for p_{within} and p_{total} than for p_{branch}. Thus, p_{within} increased more with increasing diameter than p_{branch}.

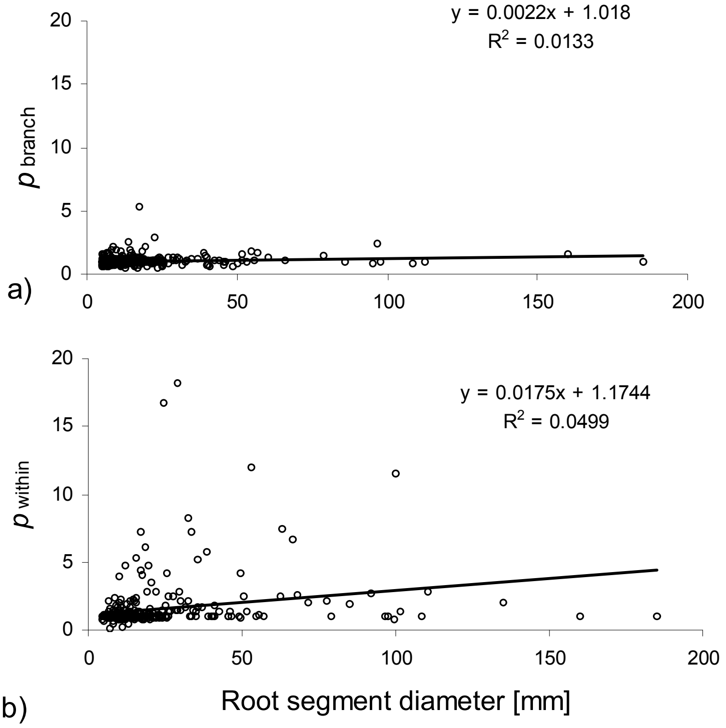

Figure 7.2: The impact of root segment diameter D on (a) tapering by branching and (b) tapering without branching from all root segments (n = 345) of *V. tomentosa.*

This is illustrated in Figure 7.2 for *V. tomentosa* showing that tapering without branching occurred especially in the thick coarse roots while tapering by branching was more evenly distributed along the gradient of root segment diameters.

7.4 Discussion

Means of p_{branch} were consistent with those of tree root systems from other studies, which lay between 1.09 and 1.33 (Van Noordwijk and Purnomosidhi, 1995; Ozier-Lafontaine et al., 1999; Smith, 2001). Also the broad scattering of single p values is in accordance with these studies. By including tapering without branching (p_{total}), means obtained in this study were often higher than p_{branch} (Table 7.1). With increasing deviation of p from 1, the assumption of area preservation looses its validity. Thus, even if it may be true for the average of single branching points expressed by p_{branch} (Richardson and Dohna, 2003), it is not necessarily true for the entire root system. From a functional point of view this means that flow velocity or the proportion of xylem to total CSA may vary with root diameter (Van Noordwijk et al., 1994; Oppelt et al., 1999).

Scaling rules for tree biomass (Y) normally follow the equation $Y=aD^b$. Branching parameters used in fractal branching models especially influence the constant b (Van Noordwijk and Mulia, 2002). The smaller p, the more branching events are needed until a minimum diameter is reached (Spek and van Noorwijk, 1994). When p_{branch} is much lower than p_{total}, the exclusive use of p_{branch} in fractal branching models may overestimate constant b and thus total root system biomass. For example the WanFBA software for fractal branching analysis (Van Noordwijk and Mulia, 2002) suggests a decrease in root biomass of up to 61 % when p is increased from 1 to 1.2 (unpublished data). Richardson and Dohna (2003) included a separate factor for the rate of tapering between two branching points (the inverse of p_{within}) in their model, but in other models tapering without branching was neglected (Ozier-Lafontaine et al., 1999; van Noordwijk and Mulia, 2002).

The lack of correlation between p and root segment diameter is in accordance with other studies (Van Noordwijk and Purnomosidhi, 1995; Smith, 1999). However, in the present study the slope of the regression line p against root diameter was often higher for p_{total} than for p_{branch}. If the dependency of the factor p on root size is pronounced, models have to be modified to allow p to change with root diameter (Van Noordwijk and Mulia, 2002; Richardson and Dohna, 2003). The possible decrease in self similarity when using p_{total} instead of p_{branch} should be taken into account for root system modelling.

Conclusions

Depending on tree species, root tapering without branching can have a great impact on total root system tapering. Thus, when tapering without branching is not included in fractal branching models total root biomass may be overestimated. Self similarity of p_{total} is often lower than of p_{branch}. The use of several p values for different root diameter classes might be necessary when using p_{total}.

Acknowledgements

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8 General discussion

8.1 Discussion of the overall hypotheses

(1) In tropical montane forests, root distribution is more superficial at higher than at lower altitudes. This is due to (i) very low pH in mineral soil at higher altitudes and thus, increased risk of Al toxicity and due to (ii) slow nutrient release in deeper soil layers from litter decay and weathering and thus, a higher importance of input of readily available nutrients into soil from the canopy by precipitation.

It could be shown that the distribution of RLD (Figure 2.2), the N uptake potential (Figure 2.3), the biomass of fine and coarse roots (Figure 4.1), and the origin of roots at the stem base (Figure 5.2) were more superficial at higher than at lower altitudes. Furthermore, the vertical extension of tap roots was more limited at 3000 m than at 1900 m (Figure 5.5) and lateral roots of *G. emarginata* frequently penetrated into the mineral soil at 1900 m, but hardly did so at 2400 m (Figure 6.3). Thus, distribution of fine and coarse roots was always more superficial at higher than at lower altitudes.

In literature, vertical root distribution is mostly presented for fine root biomass. At 1900 m, distribution of fine root biomass (62 % in the upper 0.25 m) was similar to temperate and tropical lowland forests, where 45-69 % and 42-57 % of total fine root biomass occurred in the upper 0.3 m (Jackson et al., 1997; Moreno Chacón and Lusk, 2004). It was in the range of several temperate broadleaved and coniferous forests where fine root biomass above 0.1 m depth of mineral soil contributed between 42 and 72 % of all fine roots to a depth of 0.3 m (Claus and George, 2005). The pattern of N uptake at 1900 m (Figure 2.3) that resembled the pattern of fine root distribution in the present study was similar to that of a well drained temperate forest where the amount of ^{15}N acquired from 0.50 m soil depth by mature *Quercus robur* trees was about 25 to 40 % of the amount acquired from the upper 0.15 m depth (Göransson et al., 2006). Thus, distribution of fine root biomass resembled fine root distribution in other forest biomes.

In contrast, distribution of fine root biomass at 2400 m (94 % in upper 0.25 m) and at 3000 m (83 % in upper 0.30 m) was more superficial than in most other studies. Distribution at these altitudes was similar to boreal forests (83% in upper 0.30 m) (Jackson et al., 1997) which are dominated by soil types, e.g. Podzols and Histosols (Zech and Hintermaier-Erhard, 2002), that occurred frequently at 3000 m. Sporadically, similar shallow rooting pattern were observed in tropical lowland forests (Klinge, 1973; Pavlis and Jeník, 2000). At 3000 m, the pattern of ^{15}N uptake was similar to the pattern of ^{45}Ca uptake by *Betula* ssp. and *Picea abies* trees growing on frequently water saturated and thus, oxygen deficient soils (Brandtberg et al., 2004).

The results of the present study illustrate that rooting in tropical montane forests is not always very superficial. The high abundance of fine roots in the acid mineral soils at 1900 m support the assumption that species growing in tropical montane forests are adapted to low soil pH (Chapter 2.4). It has to be considered that the methodological approach of the present study (one stand per altitude) enhanced the probability that factors unrelated to altitude affected the observed pattern of root growth. Different to the other altitudes, the forest at the 1900 m site had developed on an old landslide profile. In soils developed on landslides nutrient availability (Wilcke et al., 2003) as well as soil pH may be increased (Schrumpf et al, 2001). However, both parameters had little impact on root growth in the present study (Figure 2.7). In contrast, oxygen deficiency in soil was likely an important factor for superficial rooting at high altitudes (Chapter 2.4). The frequencies of oxygen deficiency were particularly increased at high altitudes because of increased precipitation and decreased evapotranspiration due to lower temperatures.

(2) Higher proportions of plant biomass are allocated belowground at higher altitudes than at lower altitudes. High root to shoot ratios at higher altitudes are caused by (i) increased requirements for nutrient acquisition because low temperatures at high altitudes are associated with low mineralization of nutrients in soil, and by (ii) increased requirements for anchorage because of high wind speeds.

Despite the decrease in aboveground biomass with increasing altitude, the increasing allocation of plant biomass to the root system was accompanied by an increase in absolute root biomass (Table 4.2), supporting the assumption that plants at high altitudes were exposed to high environmental stress related to root system functioning. This is further supported by the finding that the proportion of root biomass in total biomass at 3000 m was at the upper range (5 - 41 %) observed in many tropical, temperate and boreal forests (Vogt et al., 1996; Cairns et al., 1997).

Classically, the root to shoot ratio reflects the relative abundance of different resources, being larger when a resource utilized by roots is low (Farrar and Jones, 2003). Understanding of biomass allocation to the root systems by trees is very low (Vogt et al., 1996; Cairns et al., 1997). Fine roots are often a minor fraction of total belowground biomass in trees (Table 4.2, Vance and Nadkarni, 1992), but their contribution to total biomass may be more affected by nutrient availability in soil than root to shoot ratios, since resource acquisition is generally restricted to fine roots. Concurrent to the decrease in nutrient supply from the organic layer with increasing altitude (Chapter 3.4), the proportion of fine root biomass in total biomass increased from 4.4 % at 1900 m to 5.2 % at 2400 m and 8.4 % at 3000 m. Increased allocation of biomass to fine roots also resulted in an absolute increase in fine root biomass from 1900 and 2400 m to 3000 m (Table 4.2). This is in accordance with the findings from other studies from tropical montane forests where fine root biomass was negatively correlated with nutrient contents in soil (Gower, 1987; Coomes and Grubb, 2000; Powers et al., 2005). Low foliar nutrient concentrations (Table 3.1) at high altitudes support the hypothesis that increased biomass allocation to the fine root system is the result of low nutrient supply but illustrate at the same time that decreased nutrient availability at high altitudes was not offset by increased fine root biomass.

The significant increase in coarse root biomass, associated with an increase in coarse root to shoot ratios from 0.11:1 at 1900 m to 0.33:1 at 2400 m and 0.48:1 at 3000 m suggests that increased belowground biomass at high altitudes is at least partly a response to increased mechanical stress. This assumption stands to reason since wind speeds increased with increasing altitude (Chapter 5.2), rooting depth and thus the depth of a potential root soil plate decreased with altitude (Figure 5.2, Figure 5.5, Figure 6.3), the proportion of coarse root biomass in total root biomass increased with increasing altitude (Table 4.2), and coarse root systems at 3000 m exhibited a large range of traits that were supposed to improve anchorage (Chapter 5.4). In tree saplings and annual species, root to shoot ratios were increased by exposure to wind (Cordero, 1999; Henry and Thomas, 2002). The root to shoot ratio of mature *Picea sitchensis* (Bong.) Carr. trees was negatively related to the depth of the root-soil plate (Nicoll and Ray, 1996). Both, high wind speeds and decreased rooting depth may contribute to high allocation of biomass to coarse roots at high altitude.

Summarized, enhanced allocation of biomass to the root systems at high altitudes and the resulting high absolute root biomass may be attributed to low nutrient availability and enhanced mechanical stress.

<u>(3) Coarse root architecture is modified by the prevailing soil conditions at each altitude. These modifications are adaptive traits to improve anchorage under given environmental conditions.</u>

Coarse root architecture varied considerably between altitudes. As discussed in the chapters 5.4 and 6.4, high requirements to anchorage at high altitudes may contribute to the observed modifications in coarse root architecture. Modifications were attributed to phenotypic plasticity (Table 6.2) as well as to changes in the composition of species showing specific traits related to anchorage (Chapter 5.3).

It could be shown that phenotypic plasticity of coarse root architecture between altitudes was pronounced in the factor *q* that describes the topology of a root system. Variations in the branching parameter *p*, *Nsub* and *l* of one tree species (*G. emarginata*) growing at different altitudes (Table 6.2) were much smaller than variations in average *p* (Table 7.1), *Nsub* (2.16-2.35) and *l* (103-319 mm) between six different tree species growing in the area of the present study, highlighting the genotypic impact on these parameters. Since these parameters affect tapering along root axes and branching intensity they might also influence the species ability to adapt to increased mechanical stress. However, it remains unclear whether plasticity in these parameters was not detected in the present study because of their genotypic determination or because the differences in environmental conditions between 1900 and 2400 m were relatively small.

As discussed in chapter 5.4, stilt roots and the connection of stems by coarse rhizomes were supposed to improve tree stability at 3000 m, where deep rooting was hampered and wind speed was increased in comparison to deeper altitudes. Both traits occurred only on one species, respectively. It is reported from literature that the ability to propagate by rhizomes is at least partly genetically governed and is a frequent trait of woody species occurring in humid and cold environments (Kutschera and Lichtenegger, 2002). The ability to develop stilt roots, is also genetically governed (Jeník, 1978). Thus, species composition at different altitudes may affect the resistance of the forest stands to enhanced mechanical stress.

(RU1) "The high plant diversity in tropical montane forests is maintained by low nutrient availability."

The reason for the high numbers of plant species that coexist on small spatial scales in tropical forests is poorly understood (Wright, 2002). Possible explanations for high tree diversity in tropical forests include (i) large heterogeneity in habitats influencing the development of tree seedlings and thus, the spatial distribution of tropical trees (Palmiotto et al. 2004; Dalitz et al., 2004; Hood et al, 2004), (ii) negative density dependence, that constrains locally abundant species, e.g. by allelopathy, intraspecific competition or pest facilitation (Wright 2002), and (iii) maintenance of the coexistence of competing species by disturbance (Molino and Sabatier, 2001; Kelly and Bowler, 2002; Sheil and Burslem, 2003). Several studies summarized in Givnish (1999) show that tree species diversity in tropical forests is positively correlated with the rates of rainfall and tree turnover, the time following catastrophic disturbances, and forest stature across lowland sites and negatively correlated with diameter at breast height and latitude. An increase in soil fertility along gradients in tropical forests was accompanied with an increase (Gentry, 1988; Aiba and Kitayama, 1999) or decrease (Huston, 1994) in tree species diversity. Ecological theory suggests that intermediate fertility should allow greatest biodiversity, because on fertile sites competitive exclusion of species may be enhanced by one or a few species with characteristics that improve light interception while on infertile sites competitive exclusion may be caused by species with superior nutrient acquisition characteristics (Herbert et al., 2004).

Tree species diversity in montane forests of the tropics is usually lower than in lowland forests (Haber, 2000; Homeier, 2004). On an altitudinal gradient in the RSF the numbers of tree species > 0.1 m in diameter at breast height decreased significantly from 17 species per 400 m^{-2} at 1900 m to 2 species per 400 m^{-2} at 2500 m. Also total numbers of tree species declined significantly with increasing altitude (Homeier, 2004). As suggested by foliar nutrient analysis, soil fertility in the RSF was high at 1900 m, but lower at higher altitudes (Chapter 3). These results do not support the hypothesis that high tree diversity at lower altitudes in this tropical montane forest is maintained by low nutrient availability.

8.2 Conclusions

The change of environmental conditions along the altitudinal gradient had a marked impact on the functions of root systems both on the plant level and the ecosystem level. Large impacts on root functioning were attributed to the shallower root distribution at higher in comparison with lower altitudes. On a plant level, low fine root abundance in deeper soil layers together with decreased nutrient supply in the organic layer impaired nutrient uptake at higher altitudes as indicated by lower concentrations of N, S, P and K in fine roots and leaves. Furthermore, hampered root growth in deeper soil layers and high wind speeds at high altitudes substantially modified coarse root architecture, whereby those root traits were improved that increased the horizontal extension of the potential root-soil plate. Concurrent to the decrease in shoot biomass with increasing altitude, root biomass was increased at higher altitudes. The high proportion of total biomass in roots supports the finding that at higher altitudes, trees were exposed to high environmental stress affecting root system functioning.

On an ecosystem level, decreased fine root abundance in deeper soil layers in combination with high precipitation rates at high altitudes increased the probability of nutrient losses from soil by leaching. On the other hand, large amounts of N, S, K, Ca and Mg were immobilized in roots at higher in comparison with lower altitudes and thus, were prevented from leaching. Furthermore, the importance of coarse root biomass for long term accumulation of nutrients increased with increasing altitude.

8.3 Outlook

The present study provides a large pool of data that serve for modelling of ecosystem processes such as productivity as well as C, nutrient and water fluxes in tropical montane forests. Modelling of ecosystem processes allows an estimation of the impact of possible natural or anthropogenic changes on the functions of tropical montane forests, e.g. their habitat function or on a global scale their function in C sequestration.

For a better understanding of the impact of abiotic and biotic factors on the functioning of root systems in tropical montane forests the investigation of root systems along further environmental gradients is necessary. Important gradients beside altitude are soil age (Chapter 3), topography as well as disturbance and subsequent succession.

Topography has been found to affect both vegetation and soil properties. Soils on ridges and slopes have usually deeper organic surface layers than in valleys, lower water contents and lower concentrations of nitrate and base cations (Silver et al., 1994; Wilcke et al., 2002; Scowcroft et al., 2004). Vegetation on ridges and slopes differs markedly in species composition, and average tree height is larger in valleys than on slopes and ridges (Homeier, 2004). Leeward sides of mountains are exposed to lower precipitation rates than wind sides and differ in species composition and vegetation structure (Sklenar and Laegaard, 2003).

Disturbances in tropical montane forests may be natural or induced by humans and include the establishment of gaps due to tree failure, thinning or landslides and the conversion of forest to pasture, which is mostly initiated by biomass burning. Disturbances may mainly affect vegetation properties or may additionally destroy the organic surface layer or even deeper soil layers.

In treefall gaps, soils may be similar as in the closed forest, but light levels are higher (Zanne and Chapman, 2005). In the RSF, soils that developed on landslide material with high contents of weakly weathered rocks had higher pH values and effective exchange capacity and were richer in exchangeable cations (Schrumpf et al., 2001). Forest burning may cause a destruction of the organic surface layer and an increase in P, K and Ca concentrations in soil directly after burning (Kauffman et al., 1995). Conversion of forest to pastures can lead to a decrease in the rates of N mineralization and the fraction of nitrate in total N_{min} (Reiners et al., 1994; Scowcroft et al., 2004).

It can be expected that both natural and anthropogenic gradients have a marked impact on the structure of root systems and thus on their functions related to C, water and nutrient cycling.

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Erklärung

Hiermit erkläre ich, dass ich die Arbeit selbständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.

Ferner erkläre ich, dass ich nicht anderweitig versucht habe, diese Dissertation, weder in Teilen noch als Ganzes, einzureichen. Ich habe keine gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden und besitze keinen entsprechenden Doktorgrad.

Nathalie Soethe Berlin, den 04. April 2006