RELATIONSHIPS BETWEEN SOIL CHEMICAL PROPERTIES AND FOREST STRUCTURE, PRODUCTIVITY AND FLORISTIC DIVERSITY ALONG AN ALTITUDINAL TRANSECT OF MOIST TROPICAL FOREST IN AMAZONIA, ECUADOR.

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Meiner Familie

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TABLE OF CONTENTS

CHAPTER

1

INTRODUCTION

1.1 GENERAL INTRODUCTION

Forest structure changes with altitude, probably the most obvious characteristic of these changes is the decreasing tree height with increasing elevation. Several hypotheses for the stunted growth of montane forest trees have been put up, e.g. reduced leaf temperatures caused by a closer and denser cloud cover with increasing elevation (Grubb 1977), direct impact of low temperatures on growth (Hoch & Körner 2003), reduced root respiration or transpiration due to more water saturated soils (Hetsch & Hoheisel 1976, Bruijnzeel & Veneklaas 1998), low decomposition and mineralization rates caused by the lower temperatures, the water-saturated soil and high concentrations of phenolic compounds in the soil (Edwards & Grubb 1977, Bruijnzeel *et al.* 1993, Tanner *et al.* 1998), limitation of photosynthesis due to persistent cloudiness and thus low radiation input (Bruijnzeel & Veneklaas 1998) or due to low temperatures (Kitayama & Aiba 2002) and increase of damaging UV-B radiation (Flenley 1995). The reasons for declining tree heights with elevation are still discussed and the underlying causes are still not completely understood (Bruijnzeel & Proctor 1995, Richards 1996, Hafkenscheid 2000).

The decrease in tree height is attended by the decrease of above-ground net primary productivity (ANPP) with increasing elevation (Weaver & Murphy 1990, Raich *et al.* 1997, Waide *et al.* 1998), but whether the above-ground productivity is closely related to above-ground biomass is still worth discussing (Keeling & Phillips 2007), though both are limited by similar ecological factors, such as temperature and precipitation and soil fertility (Churkina & Running 1998, Silver 1998, Knapp & Smith 2001, Ryan *et al.* 2006).

Montane forests are not only smaller-statured than lowland forests but also contain less tree species (Grubb 1971, 1977, Whitmore 1984, Stadtmüller 1987, Richards 1996). They also differ significantly in soil chemical properties from each other (Vitousek & Sanford 1986, Marrs *et al.* 1988, Richards 1996, Benner *et al.* (in press). Especially at landscape or regional scale, soil chemical properties play an important role in controlling the variability in forest structure and net primary productivity (Bruijnzeel *et al.* 1993, Bruijnzeel & Veneklaas 1998, Tanner *et al.* 1998, Laurance *et al.* 1999, Malhi *et al.* 2004).

The nutritional status of plants is governed by the amounts of chemically available nutrients in soil and the ability of fine roots for nutrient acquisition. This ability for nutrient acquisition implies the spatial exploitation of the soil by roots and the nutrient uptake activity. Chemical nutrient availability in tropical forests may be affected by parental substrate, weathering intensity, cation exchange capacity, extracellular phosphatase activity

and especially the rates of litter decomposition (Treseder & Vitousek 2001, Kitayama & Aiba 2002, Wilcke *et al.* 2002).

Fast rates of litter decomposition and also high mineralization rates are characterizing tree nutrition in the majority of tropical lowland forests (Jenny *et al.* 1949, Meentemeyer 1977, Anderson & Swift 1983) while in tropical montane forests, on the other hand, decomposition rates are much slower caused by the growth under lower temperatures and, often, adverse soil conditions such as partial anoxia and low pH values (Tanner 1981, Vitousek & Sanford 1986, Schuur 2001, Leuschner *et al.* 2007, Benner *et al.* (in press)). Already Jenny (1980) proposed that lower decomposition rates are linked to reduced mineralization and nutrient cycling rates per unit soil organic matter and thus could induce nutrient shortage at higher elevations.

So, alterations in forest structure are often associated with, and may partly be caused by distinct changes in soil and humus morphology from lowland to upper montane forests as well (Paoli *et al.* 2008).

But not only trees, also lianas, or woody vines, being structural parasites, have an impact on forest structure, forest ecology and ecosystem functions (Schnitzer & Bongers 2002). They amount between 15% and 45% of the woody individuals and species in tropical forests (Gentry 1991, Pérez-Salicrup *et al.* 2001, Schnitzer 2005) and contribute up to 40% of forest leaf area and leaf productivity (Hegarty & Caballé 1991). They can influence forest dynamic processes like reducing the growth of adult trees (Clark & Clark 1990), and/or lowering seedling recruitment and growth (Pérez-Salicrup 2001). Tree mortality might increase with rising liana abundance (Phillips *et al.* 2005) and lianas might alter gap-phase regeneration (Schnitzer *et al.* 2000).

Of the factors influencing liana abundance, species richness and liana distribution, tree fall dynamics together with host tree identity and abundance might be a very important factor for determining the composition of lianas (Ibarra-Manríquez & Martínez-Ramos 2002). Liana density generally increases in disturbed forests (Hegarty & Caballé 1991), being a consequence of the elevated radiation regimes in the newly formed gaps (Schnitzer *et al.* 2000). The influence of nutrient poor or fertile soil on lianas has been widely discussed, while many scientists believe there is an increase of liana abundance and biomass on more fertile forest soils (Putz & Chai 1987, Gentry 1991, Laurance *et al.* 2001, DeWalt *et al.* 2006), Macia *et al.* (2007) reported only little explanation of soil properties on liana floristic composition, while Phillips *et al.* (2005) reported a much higher dependency of lianas on the availability of suitable host trees than on soil conditions, and van der Heijden & Phillips

(2008) even postulated the hypothesis that liana density may be unrelated to soil fertility or other soil gradients in Neotropical forests.

Transect studies across tropical montane slopes can provide valuable information on elevational change in nutrient availability and altitudinal shifts in nutrient limitation of growth if a sufficiently large plot sample is investigated, to account for the substantial spatial heterogeneity in soil properties in tropical forests.

A special emphasis was put on the measurement of plant-available fractions of the five key elements, i.e. nitrogen (total nitrogen (N)) and nitrogen net mineralization rate (N_{min}-rate)), plant-available phosphorus (P_a), and salt-exchangeable calcium (Ca), magnesium (Mg) and potassium (K) concentrations. Because root distribution of trees in tropical forests is mostly restricted to the organic horizon and the upper horizons of the mineral soil (Grieve *et al.* 1990, Cavalier 1992, Tanner *et al*. 1998, Hafkenscheid 2000, Hertel *et al.* 2003, Soethe *et al.* 2006), therefore our soil analyses were focussed on the upper horizons of the soil, i.e. the organic layer horizon and the top 10 cm of the mineral soil. A distinctiveness of this study is the multitude of investigated plots (n = 80) and the high heterogeneity of the study area, covering an area of almost 100 km x 100 km with a large variety of bedrock, forest soils and tree species composition.

The present study was conducted in the context of the collaborative project Pro Benefit funded by the BMBF (Federal Ministry of Education and Science of Germany). The goal of ProBenefit (**PRO**cess-oriented development of a model for equitable (**BENEFIT**-sharing) for the use of biological resources in the Amazon Lowlands of Ecuador) is to develop a suitable procedure for equitable benefit-sharing for the use of biological resources and the associated indigenous knowledge in line with the principles of the Convention on Biological Diversity (CBD).

1.2 SOIL PROPERTIES

1.2.1 ORGANIC LAYER AND SOIL pH

Tropical montane forest soils usually have more soil organic matter per unit ground area than tropical lowland forest soils (e.g. Whitmore & Burnham 1969, Grubb & Tanner 1976, Hetsch 1976, Fölster & Fassbender 1978, Veneklaas 1991, Schrumpf *et al.* 2001, Wilcke *et al.* 2002)**,** and the depth of the organic horizon that stores high amounts of nutrients is commonly very high in tropical montane forests (Grieve *et al.* 1990, Tanner *et al.* 1998, Hafkenscheid 2000, Leuschner *et al.* 2007).

This is partly explained by changes in temperature and soil moisture (Vitousek & Matson 1988, Schrumpf *et al.* 2001, Wilcke *et al.* 2002). The change of species composition with elevation causing a variation in the quantity and quality of the litter is a further explanation for the variance of the organic layer thickness (Burghouts *et al.* 1998, Wilcke *et al.* 2002).

Soils of tropical moist forests are more often water-saturated at higher elevations (Vitousek & Sanford 1986, Kappelle 2004), and lower temperatures with increasing altitude are inhibiting the decomposition of organic matter (Vitousek & Matson 1988, Schrumpf *et al.* 2001) and increase the accumulation of organic matter with altitude. Indeed, lower decomposition is observed with increasing elevation on tropical mountains, for both litter decomposition (Bruijnzeel *et al.* 1993, Vitousek *et al.* 1994, Pendry & Proctor 1996, Kitayama & Aiba 2002) and soil organic matter turnover (Townsend *et al.* 1995).

In montane environments, this causes low pH values, oxygen depletion, and low microbial activity (Bruijnzeel & Veneklaas 1998, Silver *et al.* 1999), leading to a reduction in nutrient availability (Meentemeyer 1977, Vitousek & Sanford 1986), especially nitrogen (Vitousek & Sanford 1986, Sveijnbjörnsson *et al.* 1992, Timoney 1995, Tanner *et al.* 1998), because a large proportion of nutrients is bound up in undecayed litter or unmineralized humus (Grubb 1977). On the other side the increasing amounts of organic matter stored on top of the soil lead to larger stocks of nutrients in the topsoil (Edwards & Grubb 1977, Wilcke *et al.* 2002, Soethe *et al.* 2006), possibly mitigating negative consequences of lowered mineralization rates at high elevations.

Therefore, nutrients released from the organic layers play an important role for plant nutrition in tropical montane forests (Grubb 1977, Edwards & Grubb 1977, 1982, Edwards 1982, Cuevas & Medina 1986, 1988, Grubb 1995, Kauffman *et al.* 1998), and also in tropical lowland forests, though commonly growing on strongly weathered or inherently nutrient-poor soils and being covered by thin organic layers only, the soil organic matter contains most of the nutrients available for plants (Cuevas & Medina 1986, Grubb 1995, Kauffman *et al.* 1998).

Soil pH is strongly influencing the availability of plant nutrients but also altering the activity of certain microorganisms (Brady & Weil 2002). Macronutrients like nitrogen, phosphorus and the major cations like potassium, calcium and magnesium tend to be less available in soils with low pH (Wilcke *et al.* 2002, John *et al.* 2007), while micronutrients like aluminium, copper, manganese or zinc tend to be less available in soils with high pH (Brady & Weil 2002, John *et al.* 2007). A low pH is common in tropical montane rain forests (Bruijnzeel & Proctor 1995, Veneklaas & van Ek 1990, Grieve *et al.* 1990, Tanner *et al.*

1998). The low pH in the Ecuadorian Andes is possibly due to organic acids with low pK_a-values (acid dissociation constant) (Schrumpf *et al.* 2001), which are released into solution during organic matter decomposition and by root exudation (Schawe *et al.* 2007). This is also true for the eastern slopes of the Andes with their highly humid climate, where soil development proceeds quite rapidly, leading to acid, highly weathered soils (Schrumpf *et al.* 2001).

1.2.2 SOIL NITROGEN CONTENT AND N MINERALIZATION RATE

Total nitrogen (N) content of soil increases in parallel with total carbon, but soil stocks and available pools of other elements show no clear trend with altitude (Bruijnzeel & Proctor 1995). N availability is mainly determined by the mineralization rate, i.e. the amount of N released through the decomposition of organic matter during a certain period of time. However, neither the total amount of soil N nor the soil concentrations of ammonium and nitrate are good expressions of the fertility of soils (Ellenberg 1977, Chapin *et al.* 1986, Tamm 1991). A better way to characterize N availability for plants is ammonification and nitrification as key processes of mineral N supply.

Nitrogen ammonification is described as the conversion of organic nitrogen compounds (mostly amino groups) into ammonium-ions. This hydrolysis is controlled catalytic by enzymes of various heterotrophic microorganisms as bacteria, fungi and protozoa. This process is followed by nitrification or, if concentration of nitrogen is low, immobilization.

The nitrogen mineralization is the sum of these two processes. Because immobilization is taking place at the same time, only the net mineralization can be measured. Assuming no losses to leaching, plant uptake or gaseous N emissions, net mineralization and nitrification in this study were calculated as follows (Hart *et al.* 1994):

$$\text{Net N mineralization} = (NH_4^+\text{-}N + NO_3^-\text{ - }N)_{t+1} - (NH_4^+\text{-}N + NO_3^-\text{ - }N)_t$$

$$\text{Net nitrification} = (NO_3^-\text{ -}N)_{t+1} - (NO_3^-\text{ -}N)_t$$

The turnover rate of N is largely dependent on C availability for microbial demand (Hart *et al.* 1994, Corre *et al.* 2007, Sotta *et al.* 2008). So when the soil organic matter quality in terms of C/N ratio is constant, N mineralization is mainly controlled by temperature because a bulk of evidence shows that N mineralization slows down in cooler environments (e.g. Meentemeyer 1977, Sveinbjörnsson *et al.* 1995, Timoney 1995, Sveinbjörnsson 2000). But also soil moisture content (Marks & Bormann 1972, Stone, 1973, Harcombe 1977), and pH,

aeration and ammonium content are affecting N mineralization (Paul & Clark 1989, Swift *et al.* 1979). Lower net mineralization and nitrification rates may also result from high rates of microbial immobilization.

At very long time scales, nitrogen availability is also dependent on the balance between input from deposition and biological nitrogen fixation (Vitousek & Field 1999) vs. loss due to hydrologic export, disturbance, and denitrification (Hedin *et al.* 1995, Vitousek *et al.* 1998). Nitrogen deposition from the atmosphere is high in the moist tropics due to frequent rain showers or thunderstorms and can exceed 20 kg N ha^{-1} yr^{-1} (Phoenix *et al.* 2006).

Soil N status of old-growth tropical forests is generally influenced by forest type (lowland versus montane), soil development/age, legume abundance (distribution of woody legumes is centered in the lowland tropics (Crews 1999), degree of organic matter accumulation and climatic factors such as temperature and rainfall. Lowland forests, commonly growing on heavily weathered soils, have in general higher net N mineralization rates (Marrs *et al.* 1988, Rhoades & Coleman 1999), but also higher NO_3^- leaching losses (Hedin *et al.* 2003, Klinge *et al.* 2004, Dechert *et al.* 2005, Schwendenmann & Veldkamp 2005) than montane forests, which are likely to occur on less developed soils due to recurrence of substrate addition (volcanic ashes) and removal (erosion and slope processes) (Tanner *et al.* 1998).

Grubb (1971, 1977) and Edwards & Grubb (1982) put forward the hypothesis, that nitrogen cycling may be a mayor factor limiting plant growth on tropical mountains, and Walker & Syers (1976) came up with the assumption that soil N availability should decrease with elevation and increase with pedogenetic development in tropical forest soils, which has been the result in various studies in the tropics (e.g. Vitousek & Sanford 1986, Marrs *et al.* 1988, Riley & Vitousek 1995, Tanner *et al.* 1998).

1.2.3 SOIL PHOSPHORUS

There is substantial evidence, mostly from foliar nutrient contents, that tree growth in many tropical lowland forests is primarily limited by P while plant-available N seems to be relatively abundant (Vitousek 1984, Tanner *et al.* 1992).

A conceptual model of pedogenesis and nutrient availability postulated by Walker & Syers (1976) assumes that N supply should be poor in young soils and N fixation from the atmosphere being an important process, whereas P becomes progressively unavailable during pedogenesis. Like the major cations, P is derived by weathering from parent material, and it is often present at very low levels in old, highly weathered soils. P adsorption is generally stronger than that of cations, however.

This prediction is in line with the results of Walker *et al.* (1981), Tanner *et al.* (1998), Vitousek (2004) and Benner *et al.* (in press), that tropical montane forests most often grow on younger soils where N should be short in supply whereas P limitation of growth should be of secondary importance compared to the older lowland soils. Nutrient addition experiments in tropical mountain forests (Tanner *et al.* 1990, Tanner *et al.* 1992, Harrington *et al.* 2001, Cavelier *et al.* 2000) in fact provided evidence that montane forests are predominantly N-limited.

The phosphorus cycle in tropical soils is more complex than that of nitrogen. The major end product of chemical weathering in lowland tropical environments are aluminum and iron sesquioxides, while it is allophone (an amorphous hydrous aluminum silicate clay mineral) in otherwise fertile young volcanic soils (Uehara & Gillman 1981). Sesquioxide clays characterize oxisols and ultisols, which have a substantial anion exchange capacity in neutral or acid soils (Uehara & Gillman 1981, Fitter 2005). Such clays have a very strong affinity for phosphorus, and can bind it nearly irreversibly (Sanchez 1976, Högberg 1986), so the natural vegetation in tropical sites is more likely to be phosphorus deficient than is temperate vegetation. Phosphorus fixing soils are indeed widespread in tropical regions (Uehara & Gillman 1981, Cole & Heil 1981, Wood *et al.* 1984, Sollins *et al.* 1988, Cole *et al.* 1989). Finally, most organic phosphorus in soils is not covalently bonded directly to carbon but rather is held by ester linkages which can be cleaved by extracellular phosphates (McGile & Cole 1981). Consequently, phosphorus in soils can cycle independently of the decomposition of organic matter.

Phosphorus content of litter and soil is increasingly recognized as a potential control of mineralization (Redfield 1959, Chapin *et al.* 1978, Cole & Heil 1981). Phosphate supply may possibly control nitrification (Chase *et al.* 1968, Purchase 1974), but NH_4-N supply may be more important in some soils (Robertson & Vitousek 1981) and moisture or pH in other soils (Belser 1979, Schmidt 1982). Much circumstantial (Reich & Oleksyn 2004, Wardle *et al.* 2004) and some experimental (Hobbie & Vitousek 2000, Cleveland *et al.* 2006) evidence suggests that phosphorus plays a key role controlling leaf litter decomposition in lowland tropical forests.

1.2.4 SOIL CATIONS

Like phosphorus, the major cations are derived by weathering from parent material, and they are often present at very low levels in old, highly weathered soils. Cation adsorption is generally weaker than that of phosphorus, however, and "exchangeable" (salt-extractable)

cations represent a reasonable estimate of instantaneous cation availability. Measurements of acid-extractable cations have been proposed as a means of estimating potential cation supply from weathering (Baillie & Ashton 1983), though findings of Grieve *et al.* (1990) at their elevational gradient in Costa Rica did not affirm this trend.

Among other soil chemical characteristics that influence optimum supply of nutrients including soil pH and the pH buffering capacity, cation and anion exchange capacities and cation balance are important. Any increase in soil acidification may result in decreased cation exchange capacity (CEC) owing to protonation of variable charges, reduced nutrient retention, and increased danger of Al and Mn toxicity to plant roots (Ludwig *et al.* 1997).

To our knowledge there exists only little evidence that potassium (K), magnesium (Mg) or calcium (Ca) limit growth or effect composition in natural forests in the tropics. Cuevas & Medina (1988) carried out some root-ingrowth experiments, which showed that roots in Tierra Firme forest in southern Venezuela grew preferentially into cylinders of vermiculate, doped with Ca or K dihydrogen phosphate (Tanner *et al.* 1998). Also Raich *et al.* (1994) in a set of experiments from Hawaií, where roots were growing into bags fertilized with an element, found as a result increased growth caused by fertilization with that element (Tanner *et al.* 1998). Especially on sandy and acidic soils the cation contents of K and Mg become more relevant for plant growth (Evers 1991, Flaig & Mohr 1991).

Potassium is an essential element for healthy plant and animal growth. In plants, one of its most important functions is regulation of stomatal opening. This controls the rate of assimilation of carbon dioxide and the rate of transpiration. Except nitrogen, K is a mineral nutrient plants require in the largest amounts (Marschner 1995). The content of K declines with ongoing pedogenesis. K deficiency does not immediately cause visible symptoms, but it results in a reduction of growth rate and delays vegetative development of plants.

Magnesium is a keystone of many important plant components as chlorophyll and phytate, it is especially important for the activation of enzymes, e.g. the phosphorylation of the protein synthesis and it is regulating the cation/anion – balance inside the plants. The content of Mg, unlike potassium and phosphorus, increases in general with soil depths, except in sandy soils poor with clay (Marschner 1995).

Calcium is an element closely related to the carbonate buffering system in the soil and often shows a broader range than other cations (Baillie & Ashton 1983, Marrs *et al.* 1988, Vitousek *et al.* 1998, Wilcke *et al.* 2002). The Ca content of soils varies between 0.1 and 1.2 %, but soils rich with calcium carbonate exhibit even higher levels of Ca content, while sandy soils and very acid forest soils might even show a calcium content below 0.1 %. Especially tropical

soils rich in oxides with a variable charge (e.g. ferralsols) are poor in Ca and are widespread (Marschner 1995).

In very acidified forest soils 80 to 100 % of the exchangeable cations may be Al_3^+-ions and to a lesser extent hydrogen- (H^+) as well as iron- (Fe_3^+) and manganese- (Mn_2^+) ions. This causes pronounced nutrient deficit and toxic effects of Al- and Mn- ions on forest trees (Ulrich 1986, Zöttl & Hüttl 1986, Kaupenjohann *et al.* 1987). Concentrations above 10 mg l^{-1} of Al in the soil solution can become toxic for tree roots and their mycorrhiza system. Though Al can be found in various monomer and polymer forms in soluble and also quite stabile Al-complexes, e.g. when bound with fluorides or phosphates, the most toxic form of Al in the soil solution seem to be Al_3^+-ions.

In addition, the extent of Al-toxicity is dependent of the content of other plant-available soil nutrients as well, especially Mg and Ca. Therefore the ratios of Ca/Al and Mg/Al in the soil solution are a good measurement for possible Al-toxicity as well as Mg supply for forest trees (Ulrich 1986, Zöttl & Hüttl 1986).

1.3 FOREST STRUCTURE, FOREST GROWTH AND TREE DIVERSITY

1.3.1 ABOVE-GROUND BIOMASS AND PLANT DIVERSITY

Studies of species richness have demonstrated that tropical lowland moist or wet forests harbour the greatest number of tree species per unit area (Whitmore 1990, Richards 1996). Moreover, the Amazon Basin is a centre for tree species richness (Gentry 1982). The relatively high rainfall and more nutrient-rich soils of western Amazonia have been cited as possible contributing factors to this high tree species richness (Gentry 1982, 1988b). On the contrary montane forests are not only often containing smaller plants than lowland forests but also fewer species (Grubb 1971, 1977, Stadtmüller 1987, Richards 1996, Whitmore 1998).

But only few studies have quantified soil influences on forest structure (e.g. Laurance *et al.* 1999). In tropical rain forest there is evidence that, after controlling for moisture, the greatest richness in species of trees, treelets and shrubs is found on soils richer in available nutrients (Beadle 1966, Gentry & Emmons 1987, Grubb 1987, Gentry 1988, Wright 1992), while on nutrient poor soils tree growth is slower, but the efficiency of plant nutrient use and uptake is higher (Paoli *et al.* 2005). This may also be true for climbers and herbs (Coomes & Grubb 1996). But if richer soils are having an effect on AGB, and if this effect is increasing or decreasing the AGB, is still in debate.

1.3.2 ABOVE-GROUND BIOMASS INCREMENT

Above-ground net primary productivity (ANPP) also decreases with increasing elevation (Weaver & Murphy 1990, Raich *et al.* 1997, Waide *et al.* 1998), but whether the above-ground productivity is closely related to above-ground biomass is still worth discussing (Keeling & Phillips 2007), though both are limited by similar ecological factors, such as temperature and precipitation (Churkina & Running 1998, Silver 1998, Knapp & Smith 2001, Hoch & Körner 2003, Ryan *et al.* 2006), and low photosynthesis (Kitayama & Aiba 2002). Plant growth is often correlated with nutrient availability in tropical montane forests, e.g. attributed Edwards & Grubb (1977) the exceptionally high tree stature in a montane forest stand in Papua New Guinea to its nutrient rich soil parent material, and fertilization experiments in Jamaica (Tanner *et al.* 1990), Hawaií (Vitousek *et al.* 1993, Vitousek & Farrington 1997), and Venezuela (Tanner *et al.* 1992) found an enhanced trunk diameter growth and leaf production of several tree species by addition of N and P. Montane forests generally have reduced cycling of N and P and often K, Ca, and Mg, in comparison with lowland forests (Grubb 1977, Vitousek 1984).

Within the biome of tropical forests, above-ground net primary production (litterfall plus wood increment) ranges nearly tenfold (Clark *et al.* 2001a). Much of this variation is explained by declining productivity with increasing elevation (Proctor *et al.* 1989, Pendry & Proctor 1996), but even among lowland forests (< 500 m a.s.l.) productivity varies threefold for fine litterfall and fourfold for woody biomass increment (Clark *et al.* 2001b, Malhi *et al.* 2004). Some of these variation can be explained by the effects of annual rainfall on ANPP (Schuur 2003), but the extent of variation observed within the lowland tropics is not captured by current models of terrestrial productivity based on soil moisture only (Churkina *et al.* 1999, Houghton *et al.* 2001), therefore other factors might have an effect on AGB increment.

Based on several excellent reviews of tropical soils and plant-soil relations (e.g., Sanchez 1976, Uehara & Gillman 1981, Högberg 1986, Grubb 1989, Richter & Babbar 1991, Sollins 1998) plus more recent primary literature, a reasonable set to effect net primary productivity might be: P availability, Al toxicity, nitrogen availability and availability of base-metal cations, soil gravity and its content of sand and clay, depth to water table and micronutrients.

Clark (2007), in a review on the knowledge of biomass and productivity of tropical rainforests and their responses to climate change, pointed out, that there is still a large lack of data, especially on altitudinal gradient studies.

1.3.3 LEAF AREA INDEX

Of all environmental factors affecting plants, light is probably the most spatially and temporally heterogeneous. The light heterogeneity in space is particularly important in tropical forests where unfavourable temperatures are less significant for plant life and light is considered to be the single-most limiting resource for plant growth (Pearcy 2007). Canopy closure and the size and abundance of gaps are, therefore, important factors controlling tree regeneration, forest dynamics and forest diversity (e.g. Hartshorn 1978, Hubbell 1979, Denslow 1980, Whitmore 1984, Brokaw 1987). Tree seedlings and saplings, herbaceous plants and understorey trees have been shown to be closely keyed to variation in below-canopy light availability (Denslow 1987, Strauss-Debenedetti & Bazzaz 1991).

As the exchange surface between the photosynthetically active component of the vegetation and the atmosphere, the leaf area index (Turner *et al*. 1999, Cohen *et al*. 2003, Fournier *et al.* 2003) controls not only the radiation regime within the canopy, but also thermal and hydric conditions (Fournier *et al*. 2003), e.g. leaf area index (LAI) has a strong influence on forest transpiration (Whitehead & Jarvis 1981). Also is net primary production of forests, in most cases, closely correlated to LAI (e.g. Sullivan *et al*. 1996, Beadle 1997, Battaglia *et al.* 1998, Asner *et al*. 2003).

But not much is known about spatial variation in LAI of tropical forests on a regional or landscape scale. The major factors influencing LAI are assumed to be elevation (or temperature), water availability, soil fertility and topography, but comprehensive studies in forest stands across environmental gradients have mostly focused on temperate biomes (e.g. Bolstad *et al.* 2000, Leuschner *et al.* 2006, Meier & Leuschner 2008), and only a few studies analysed changes in the LAI of tropical forests along gradients in altitude and soil chemistry (Kitayama & Aiba 2002, Takyu *et al*. 2003, Moser *et al*. 2007).

There is a trade-off between competing for light and competing for nutrients (Tilman 1988). In several North American broad-leaved and coniferous forests, leaf area and nutrient availability have been found to be tightly linked (Gower *et al.* 1992). A tight soil fertility/leaf area relation was also found in several fertilization and liming experiments in temperate and tropical forests which resulted in substantial increases of LAI within a few years (e.g. Albrektson *et al.* 1977, Harrington *et al.* 2001). This supports the general assumption that nitrogen-poor forest soils favour carbon allocation to roots with the result that less carbon may be available for building new foliage (Ryan *et al.* 1997).

1.3.4 DIFFUSE TRANSMITTANCE OF PHOTOSYNTHETIC ACTIVE RADIATION

Photosynthetically active radiation (PAR) is a factor which is important for plant growth and development (Szeiez 1974). Equally important is its quantification in order to determine evapotranspiration and dry matter production potential of plants.

The light environment of forest plants in the understorey of tropical lowland and lower-montane rainforests is strictly energy-limited (Kinerson 1973, Holmes 1981, Barkman 1992, Curran *et al.* 1999). In the understorey of forests, solar radiation levels are typically low, and photosynthetically active radiation is generally a limiting resource for plants (Pearcy 1990, Chazdon & Pearcy 1991). How much radiation is available for forest floor herbs and tree seedlings, is dependent on the flux density of incident radiation, canopy PAR transmissivity, and day length, and thus may vary considerably with latitude, altitude, and forest type.

Altitude influences the below-canopy radiation regime of tropical forests by changes in incident radiation and in canopy structure along the slope. In tropical mountains with a moist climate, incident radiation generally tends to decrease with altitude to the height of the condensation level where cloudiness is highest, and thereafter increases again towards the mountain peaks (Hastenrath 1991, Bendix *et al.* 2008).

Diffuse transmittance of PAR (DT PAR) in the understorey of forests is also determined by daily and seasonal shifts in solar angle, weather, and the geometry of canopy openings as they change with time (Reifsnyder *et al.* 1971, Reifsnyder 1989). That seasonal variation in diffuse transmittance of PAR results primarily from shifts in the solar angle relative to canopy openings and secondarily from variation in diffuse transmittance of PAR levels outside the canopy (e.g. cloudiness), though seasonal shifts in solar angle are less drastic around the equator and therefore seasonal changes of diffuse transmittance of PAR as well.

1.4 OBJECTIVES AND HYPOTHESES

The emphasis of the present work was the quantification of soil chemical properties along an altitudinal gradient from tropical lowland to montane forests with a focus on plant-available macronutrients and their effect on forest structure (above-ground biomass (AGB), basal area (BA), liana abundance and liana basal area), leaf area index and DT PAR) as well as productivity (AGB growth and BA increment).

We conducted a landscape-scale study on the spatial variation of soil properties, forest structure and forest growth in a matrix of 80 stands of old-growth tropical moist forests on the eastern slopes of the Andes in Ecuador. The area represents an altitudinal transect of

undisturbed forest from lowlands (500 m) to montane elevation (2000 m) in the eastern equatorial Andes, providing a suitable setting for analysing the effects of altitude on soil properties and forest stand structure and also to analyse the effects of soil properties alone on forest structure and forest growth.

We phrased the following hypotheses based on the existing literature in the context of this study and tested them:

    (i)   The availability of phosphorus (P) is low in lowland forest soils, but increases with elevation, while the availability of nitrogen (N) is relatively high in the lowlands but decreases upslope.

There is substantial evidence, mostly from foliar nutrient analyses, that tree growth in many tropical lowland forests is primarily limited by P, while plant-available N seems to be relatively abundant. According to the conceptual model of pedogenesis and nutrient availability of Walker & Syers (1976), N supply should be poor in young soils and N fixation from the atmosphere should be an important process, whereas P should become progressively unavailable during pedogenesis.

    (ii)   With progressive humus accumulation on top of the soil, increasing amounts of Ca, Mg and K are stored toward higher elevations and are partially available to plants.

The increased accumulation of organic matter with increasing elevation is common in tropical montane forests and is probably caused by increased duration of water logging and lower temperatures inhibiting the decomposition of organic matter. This soil organic matter may contain most of the nutrients available for plants (Cuevas & Medina 1986, Grubb 1995, Kauffman *et al.* 1998).

    (iii)   Soil nutrients, especially phosphorus, have a positive effect on above-ground productivity.

The effects of soil chemical properties on AGB are still poorly understood and contrasting patterns have been reported (Malhi *et al.* 2006, Keeling & Phillips 2007). One goal of this study was to dilate the level of knowledge on this subject.

    (iv)   Liana density and basal area decrease with elevation.

Especially an increase of radiation intensity seems to trigger liana densities in tropical forests (Schnitzer *et al.* 2000), therefore higher elevation forests with their stunted tree height and decreasing LAI should enhance liana growth.

    (v)   Stand structural properties are more influential for liana abundance than are edaphic factors.

Phillips *et al.* (2005) reported that availability of suitable host trees might be much more important than soil conditions for the success of liana, while Macía *et al.* (2007) found environmental factors, including soil properties, to explain only 10% of the floristic differences in liana composition between various tropical forest sites in Bolivia.

(vi)   Leaf area index (LAI) decreases, and percent diffuse transmittance of PAR (DT PAR) increases with elevation.

Reductions of LAI in forests worldwide with elevation were reported in several studies. Because canopy radiance transmissivity typically shows a negative relationship to canopy leaf area, we assumed an increase of DT PAR to accompany the decrease in LAI with elevation.

(vii)   The forest floor of tropical lowland forests is exposed, on average, to lower photon flux densities than tropical montane forests and also temperate forests.

This assumption is based on hypothesis (iv) due to the expected higher LAI and therefore lower DT PAR at lowland compared to montane forests.

(viii)   Tree species diversity and stem density both have a positive effect on LAI and a negative one on DT PAR.

Species richness, through plant composition, may have greater effects on light exploitation, therefore creating a denser forest canopy and reducing the DT PAR on the forest ground.

1.5 STUDY AREA

We choose the Sumaco Biosphere Reserve (SBR) and its close proximity in the province of Napo, NE-Ecuador, to conduct our study. This reserve was established in the year 1994 and was declared a biosphere reserve by the UNESCO in the year 2000. It has nowadays a total area of 931.215 ha, with a core zone of highest conservation priority of more than 200.000 ha. It is situated on the eastern slopes of the Andes and the adjacent foothills and includes the Sumaco volcano (3732 m a.s.l., the highest peak of the SBR). Following the most recent vegetation classification for Ecuador (Palacios *et al.* 1999), the studied forests at 500 m can be classified as evergreen lowland forests, the stands at 1000 m as evergreen premontane forests, and the upper elevation forests (1500 and 2000 m) as evergreen lower montane forests. The area represents the last existing altitudinal transect of undisturbed vegetation from lowlands (400 m a.s.l.) to páramo (3700 m) in the eastern equatorial Andes and harbours probably more than 5000 (Barthlott *et al.* 2005) or even 6000 plant species (Neill & Palacios 1997).

Overall, we installed 80 permanent plots (20 m x 20 m size) at four different altitudinal levels (20 plots per level at 500, 1000, 1500, and 2000 m) to establish a transect covering 1500 m altitudinal distance. The study plots are situated at eleven sites, which belong to nine different localities (Fig. 1.1).

On seven of this eleven study sites a study on liana abundance and distribution was conducted covering all four elevation levels (10 plots per level), having ten plots at the Jatun Sacha study site at 500 m elevation and five plots at each of the study sites Hakuna Matata and Cordillera Galeras (both 1000 m), Cordillera Galeras and Sumaco Volcano (both 1500 m), and Sumaco Volcano and Cordillera Guacamayos (both 2000 m).
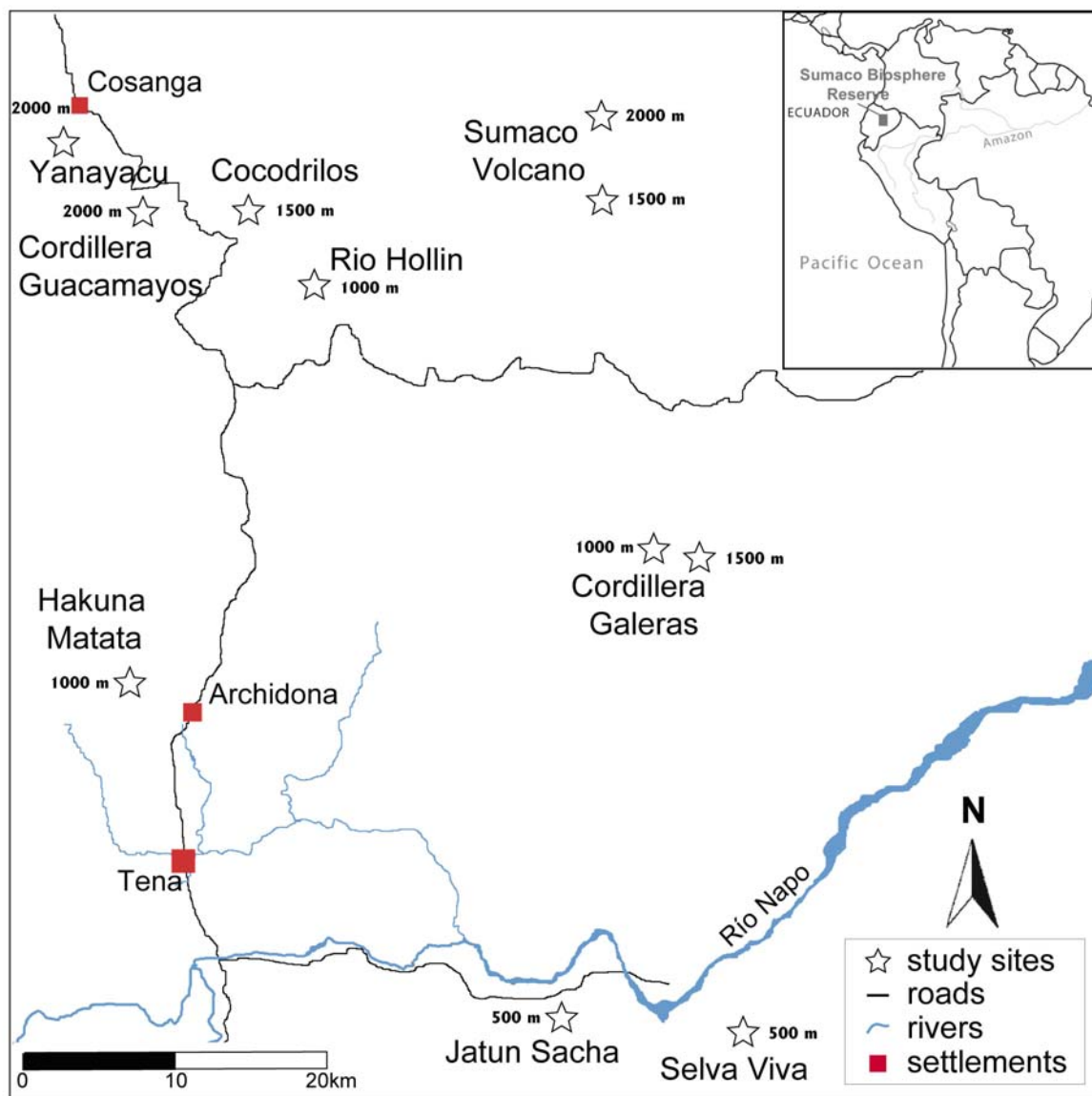

Fig. 1.1. Map of the eleven study sites with their altitudinal level [m a.s.l.] in the area of the Sumaco Biosphere Reserve in Eastern Ecuador.

All sites were selected with the aim to cover forest stands which are representative for the respective elevation. For plot installation, only areas without any kind of visible human or natural disturbance within mature forest stands were selected in order to study a matrix of old-growth stands along elevational and topographic gradients.

At each site plots were distributed to different topographic conditions to cover the range of ecological conditions. Plot size is small enough to keep environmental factors and forest structure homogeneous within the plots. Our plots are independent sampling units each containing a random sample of 16–45 stems exceeding 10 cm of diameter at breast height (dbh) from 6–30 different tree species.

Exact data on the annual precipitation of the study sites are lacking, but rainfall in the whole area is likely to exceed 2500 mm year^{-1}. The Sumaco volcano and the Cordillera Guacamayos probably receive more than 4000 mm year^{-1} and throughout the area, monthly precipitation usually never drops below 100 mm (Neill & Jørgensen 1999). The mean annual temperature decreases from approximately 22.9°C at 415 m (Jatun Sacha biological station) to 14.3°C at 2015 m (Sumaco volcano) (own unpublished data, see Fig. 1.2).
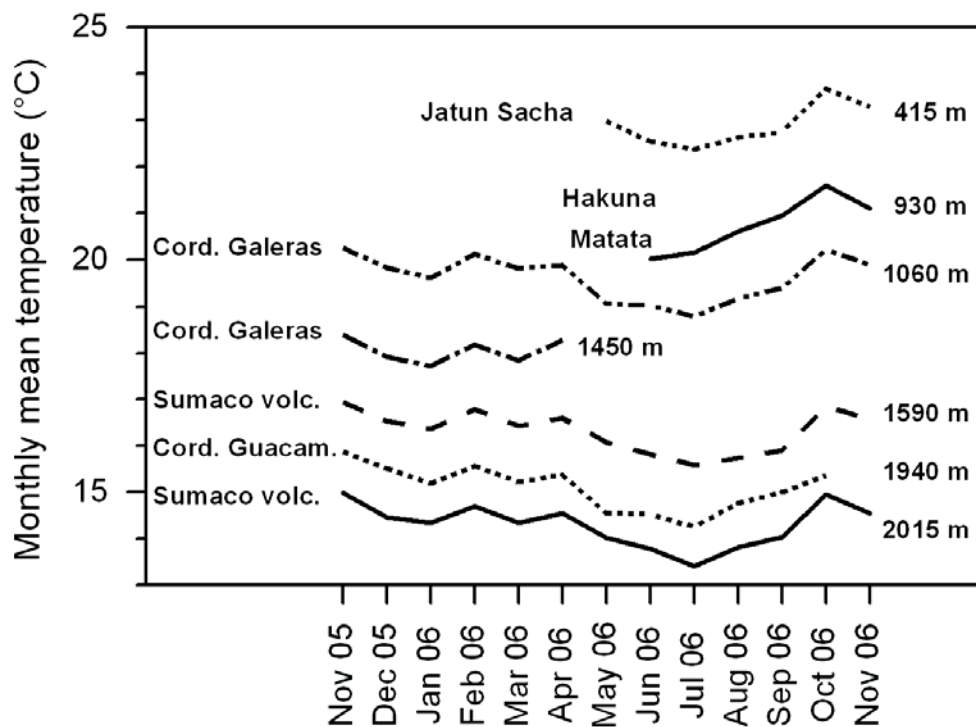

Fig. 1.2. The monthly mean temperatures [°C] of seven of our eleven study sites (with site name and elevation of the site) in the area of the Sumaco Biosphere Reserve. Temperature was measured at 2 m above the ground with HOBO PRO-Loggers (Onset Corp., USA).

The geology is very diverse in the area. Most of the region is dominated by parent rocks from the Cretaceous, mainly limestone, however, at Volcano Sumaco (basalt) and at Hakuna Matata (granite), volcanic and intrusive rocks are present, respectively. Slates are found at Cordillera Guacamayos (Sauer 1971). Though soils are very heterogeneous in our study area, gerric Ferralsols are the dominant soils at our study sites at 500 m and 1000 m and Cambisols are the preponderant soils at our study sites at 1500 m and 2000 m.

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CHAPTER

2

VARIABILITY OF INDICES OF MACRONUTRIENT AVAILABILITY IN SOILS AT DIFFERENT SPATIAL SCALES ALONG AN ELEVATION TRANSECT IN TROPICAL MOIST FORESTS (NE ECUADOR)

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2.1 ABSTRACT

The availability of key plant nutrients may change with elevation in tropical mountains due to altitudinal gradients in temperature and moisture which affect pedogenesis and nutrient cycling. In a transect from upper lowland to montane forests in NE Ecuador, we tested the hypotheses that (1) the availability of P is low in low-elevation forests, but increases upslope, while the availability of N is relatively high at low elevations but decreases with elevation, and (2) increasing amounts of calcium, magnesium and potassium are stored on top of the soil with progressive humus accumulation toward higher elevations, likely to improve nutrient availability. In each 20 plots at 500, 1000, 1500 and 2000 m a.s.l., we measured about 20 soil chemical parameters in undisturbed natural forests (80 plots in total) including *in situ* N net mineralization and nitrification rate (N_{NM} and N_{NI}, buried bag method), plant-available phosphorus (P_a, resin-bag method), and salt-exchangeable calcium, potassium and magnesium concentrations (Ca_{ex}, K_{ex}, Mg_{ex}) in the organic and mineral topsoils.

N_{NM} and N_{NI}, and the Ca_{ex}, K_{ex} and Mg_{ex} concentrations were much more variable at the plot level than across the four elevations, while P_a varied equally at small and large spatial scales and showed a large increase with elevation, supporting the first hypothesis. Net release of inorganic N in the course of nitrogen mineralization occurred at all elevations mostly as nitrate. While mass-related N_{NM} and N_{NI} rates and also organic matter C/N ratio in the topsoil remained invariant along the slope, N_{NM} and N_{NI} rates per ground area decreased by about 40% from 500 to 2000 m due to a lowered bulk density of the topsoil at higher elevations. The organic layers play a key role not only for N and P supply, but also as a storage of exchangeable Ca, Mg and K. Ca_{ex}, Mg_{ex} and K_{ex} increased with elevation per ground area and also per humus mass, supporting the second hypothesis.

KEYWORDS: Exchangeable cations, humus accumulation, nitrogen mineralization, nutrient limitation, plant-available phosphorus, tropical montane forest

ABBREVIATIONS:

N_{NM} - net N mineralization rate, N_{NI} - net nitrification rate, P_a - plant-available phosphorus

2.2 INTRODUCTION

A decrease of tree height with increasing elevation is probably the most obvious characteristic of tropical forests when climbing from the mountain foot to the summits. However, alterations in tree structure are often associated with, and may partly be caused by, distinct changes in soil properties and humus morphology from lowland to upper montane forests (Bruijnzeel & Proctor, 1995 Schawe *et al.* 2007, Wilcke *et al.* 2008). There is a vital debate as to whether the elevational temperature decrease, or other factors such as increases in precipitation, soil moisture, soil acidity, litter phenol content, or in the extent of nutrient limitation of plant growth, are key factors causing the progressive accumulation of organic matter on top of the soil along tropical mountain slopes (Grubb 1977, Tanner 1981, Jordan & Herreira 1981, Vitousek 1984, Vitousek & Sanford 1986, Schuur 2001, Schawe *et al.* 2007, Benner *et al.* 2010). Already Jenny (1980) proposed that a decreasing decomposition rate with increasing elevation is the direct cause of humus accumulation at higher altitudes.

Lower decomposition rates are linked to reduced nutrient mineralization and element cycling rates per unit soil organic matter and thus may induce nutrient shortage at higher elevations. On the other hand, increasing amounts of organic matter stored on top of the soil lead to larger nutrient stocks in the topsoil (Edwards & Grubb 1977, Marrs *et al.* 1988, Grieve *et al.* 1990) with the potential to provide additional rooting space and nutrient sources. Various authors have pointed out that nutrients released from the organic layer play an important role for plant nutrition in tropical montane forests (Grubb 1977, Edwards & Grubb 1977, 1982, Edwards 1982, Cuevas & Medina 1986, 1988, Grubb 1995, Kauffman *et al.* 1998).

There is substantial evidence, mostly from foliar nutrient analyses, that tree growth in many tropical lowland forests is primarily limited by phosphorus (P), while plant-available nitrogen (N) seems to be relatively abundant. According to the conceptual model of pedogenesis and nutrient availability of Walker & Syers (1976), N supply should be poor in young soils and N fixation from the atmosphere an important process, whereas P should become progressively unavailable during pedogenesis. Similar to calcium (Ca), magnesium (Mg) and potassium (K), P is supplied to the soil solution by weathering of parent material, and it is often present in plant-available form in very low concentrations in old, highly weathered soils (Grubb 1977, Edwards & Grubb 1977, 1982, Edwards 1982), where sorption plays an important role (Walker & Syers 1976, Vitousek 1984). Tropical montane forests most often grow on younger or rejuvenated soils where N thus may be short in supply while P limitation of

growth should be of lower importance than in lowland forests which typically grow on older soils. Nutrient addition experiments in tropical montane forests (Jamaica: Tanner *et al.* 1990, Hawaii: Harrington *et al.* 2001, Colombia: Cavelier *et al.* 2000, Venezuela: Tanner *et al.* 1992) in fact provided evidence that these forests are predominantly N-limited.

Transect studies across tropical mountain slopes may provide valuable information on elevational changes in nutrient availability and altitudinal shifts in the type of nutrient limitation of plant growth if a sufficiently large number of plots is investigated (e.g. Grieve *et al.* 1990, Bruijnzeel *et al.* 1993, Schawe *et al.* 2007, Wilcke *et al.* 2008). In this study, we searched for altitudinal effects on plant nutrient availability in tropical upper lowland (500 m) to montane forests (2000 m) with a focus on the five quantitatively most important plant nutrient elements, N, P, Ca, Mg and K. We tested the hypotheses that (i) the availability of P is low in low-elevation forest soils, but increases with elevation, while the availability of N is relatively high at low elevations but decreases upslope, and (ii) with progressive humus accumulation on top of the soil, increasing amounts of Ca, Mg and K are stored in the organic layers toward higher elevations that may improve nutrient availability. Because spatial heterogeneity of soils may be a critical confounding factor of altitudinal transect studies, we investigated a large number of forest plots (80 in total) and started with an investigation of the small- and regional-scale variability of soil properties at four elevations (each 20 plots at 500, 1000, 1500 and 2000 m elevation). We put a special emphasis on the measurement of plant-available fractions of the five nutrient elements, i.e. *in situ* measurement of N net mineralization rate, plant-available P, and salt-exchangeable Ca, Mg and K concentrations at the cation exchangers. As a study area, we choose a moist forest region in NE Ecuador which represents the last remaining continuous forest block extending from the foothills to the summits of the east equatorial Andes.

2.3 METHODS

2.3.1 STUDY AREA

The study was conducted in the Sumaco Biosphere Reserve (SBR) and its close proximity in the province of Napo, NE Ecuador, immediately at the equator. The reserve was established in 2000 and is situated on the eastern slopes of the Andes and their adjacent foothills and includes the Sumaco volcano. The area represents the last remaining altitudinal transect of undisturbed vegetation from the upper lowlands (400 m a.s.l.) to the páramo (3700 m) in the eastern equatorial Andes, a biodiversity hotspot which harbours probably more than

6000 plant species (Neill & Palacios 1997). The 80 study plots were allocated to four elevation levels (500, 1000, 1500, and 2000 m) representing an altitudinal transect of 1500 m elevational distance.

The climate varies from moist, hot tropical in the eastern lowland regions to moist, warm subtropical in the higher western reaches. Exact data on annual precipitation in the study region is lacking, but rainfall is likely to exceed 2500 mm year^{-1} in most parts of the area. The Sumaco volcano and the Cordillera Guacamayos most likely receive more than 4000 mm yr^{-1}. Throughout the area, precipitation usually never drops below 100 mm month^{-1} (Neill & Jørgensen 1999). Mean annual temperature decreases from approximately 22.9°C at 415 m (Jatun Sacha biological station) to 14.3°C at 2015 m (Sumaco volcano) (own unpublished data).

The eastern slopes of the Ecuadorian Andes (Oriente) consist of two distinct physiogeographic zones, the Oriente basin and the Sub-Andean Zone. In the Oriente, quaternary clastic sediments include a variety of deposits, from lavas and pyroclastics of various grain sizes to colluvial/alluvial materials (piedmont fans) and alluvial fills. The topographically more diverse sub-Andean zone consists of foothills rising to elevations of up to 2000 m, deeply dissected by east-flowing rivers. As a consequence of high rainfall and relatively high temperatures, rates of rock weathering are generally high. The Sub-Andean Zone borders the Cordillera Real and is a back-arc fold-thrust belt tectonically associated with the Andes (Baldock 1982).

The geology is variable in the area but not well studied. In most of the region, parent rocks from the Cretaceous dominate, mainly limestone. However, at Volcano Sumaco (basalt) and at Hakuna Matata (granite), volcanic and intrusive rocks, respectively, are present. Slates are found at Cordillera Guacamayos (Sauer 1971).

The soils show a considerable heterogeneity throughout the study region. Most of the excavated profiles at 500 and 1000 m were classified as Geric Ferralsols according to the World Reference Base for Soil Resources (IUSS Working Group WRB. 2006), while we found a preponderance of Cambisols at the upper study sites (1500 and 2000 m).

Following the most recent vegetation classification for Ecuador (Palacios *et al.* 1999), the studied forests at 500 m can be classified as evergreen lowland forests, the stands at 1000 m as evergreen premontane forests, and the upper elevation forests (1500 and 2000 m) as evergreen lower montane forests.

At each of the four elevation levels (500, 1000, 1500 and 2000 m), three study sites (at 500 m, 2) were selected which each included 5 to 12 study plots resulting in 20 plots per elevation level and 80 plots in total.

2.3.2 SOIL ANALYSIS

We installed 80 plots of 20 m x 20 m size at the four different altitudinal levels and marked them permanently. The 80 plots are grouped at 11 sites being 6 to > 70 km distant to each other. Each site had a size of about 2 km x 2 km and harboured forest stands representative for the respective elevation. Typically, each site of 4 km^2 size represented the small-scale topographic and pedologic variability in the region. For plot selection, only areas without any kind of visible human or natural disturbance were selected in mature forest stands in order to study a matrix of old-growth stands along elevational and small-scale topographic gradients. The 5 to 12 plots per site were selected at distances to each other of several hundred m (minimum distance, 100 m).

For characterizing important soil chemical properties in the 80 stands, four soil samples were collected in every plot in the period April to June 2007. We divided the study plots into four equally-sized quadrates of 10 m x 10 m. In the centre of each quadrate, a soil core of 5 cm diameter and 20-25 cm length was taken. This core was separated into two sections, the organic layer and the top 10 cm of the mineral soil. The organic layer consists of a mixture of the organic L, F and H horizons; the boundary between the organic H and the mineral soil Ah horizon was set at about 30% organic matter content using morphological criteria of the substratum for estimating organic matter content. The upper mineral soil consisted of A- and/or B-horizons with less than 30% of organic matter content.

The soil samples were stored in polyethylene bags in a refrigerator (5°C) until transported by air freight to Germany where the analyses were carried out. The fresh soil samples were analyzed for pH_{H2O} and pH_{KCl} (1N KCl) with a glass electrode according to Jackson (1958); the soil, water ratio was 1:2.5 for the mineral soil and 1:10 for the organic layer soil.

The total concentrations of C and N were determined with a C/N elemental analyzer (Vario EL III, elementar, Hanau, Germany) in the ground and dried (70°C, 48 h) soil. The concentrations of salt-extractable cations in the organic layer and in the 0 - 0.1 m horizon of the mineral soil were determined by percolating 2.5 g of air-dried soil with 100 ml 0.2 N $BaCl_2$ solution for 4 h (Bower & Wilcox 1965). The solution concentrations of exchangeable potassium (K_{ex}), magnesium (Mg_{ex}), calcium (Ca_{ex}) and aluminum (Al_{ex}) were analyzed by atomic absorption spectroscopy (Vario 6, Analytic Jena, Germany). The concentration of

hydrogen ions at the cation exchangers of the soil was calculated from the observed pH change during the percolation process.

As an estimate of plant-available phosphorus (P_a), P was extracted by resin bags (Dowex 1 x 8-50), which were placed for 16 h in a solution of 1 g soil material suspended in 30 ml of water (Sibbesen 1977, Bowman & Cole 1978). P was then re-exchanged by NaCl and NaOH solutions and analysed colorimetrically after blue-dyeing (Murphy & Riley 1962). The total P concentration of the organic layer dry mass was determined photometrically with a staining procedure (p-yellow) after digestion of the sample with 65% HNO_3 at 195°C.

2.3.3 NET N MINERALIZATION AND NITRIFICATION RATES

Between March and April 2008, eight topsoil samples (soil cores of 5 cm diameter and 10 cm length consisting of both organic layer and mineral soil material) were collected in every plot (each two in the center of the four 10 m x 10 m quadrates) to determine net N cycling rates. One soil core per quadrate was extracted in the field immediately (see procedure below) for determination of initial concentrations of ammonium and nitrate. Part of the soil from the first core was also used for gravimetric determination of actual water content (105°C, 48 h, dry weight basis) and soil bulk density. The second soil core was placed in a closed polyethylene bag, reburied in the soil at exactly the same spot were it was taken to incubate the material *in situ* for 8 days and thereafter extracted in the field in the same way as described below. The polyethylene bags permitted a certain exchange of gases but inhibited the passage of water.

Before and after incubation, the NH_4^+-N and NO_3^--N concentrations of the samples were determined by extracting about 90 g of a sample in 300 ml of a 0.5 molar K_2SO_4 solution. The extracts were shaken thoroughly for 2 h, allowed to equilibrate for another 2 h, and filtered through Whatman no. 2 filter paper (Whatman International, Maidstone, Kent, UK). The filter paper was rinsed beforehand with about 50 ml blank 0.5 M potassium sulfite solution. We added 1 ml chloroform to each filtrate for retarding microbial growth (Robertson 1984). All extracts were frozen directly after the filtration (Arnold *et al.* 2008), transferred to Germany by plane and analyzed. In all buried soil samples, there was no appreciable loss of water during the incubation period.

The concentrations of NH_4^+ and NO_3^- were measured colorimetrically by continuous flow injection (Cenco/Skalar Instuments, Breda, Netherlands) in which NH_4^+ is quantified using the Berthelot reaction method (Skalar Method 155-000) and NO_3^- is determined using the copper-cadmium reduction method (Skalar Method 461-000). Daily N net mineralization rate

(N_{NM}) per soil dry mass was calculated by subtracting the initial concentration of NH_4^+ plus NO_3^- from that after incubation divided by the days of incubation. Net nitrification rate (N_{NI}) was calculated as the difference between initial and final NO_3^- concentration. Positive N-figures indicate gain from the soil, negative ones N consumption or immobilization of N by biotic or abiotic processes in the soil. Stand-related N net mineralization and net nitrification rates were calculated by multiplying the mass-specific N_{NM}- and N_{NI}-rates with the bulk density of the soil and the depth (10 cm) of the respective soil sample, thus yielding soil volume- and ground area-related net release rates (unit, mol N ha^{-1} d^{-1}). The results of the soil analyses are presented either in the Figures 2.2 to 2.4 or in Table 2.2.

2.3.4 DATA ANALYSIS

Linear regression analyses were applied to identify significant relationships between elevation as independent variable and soil chemical parameters. All regressions were calculated using Xact software (version 8.0; SciLab, Hamburg, Germany). To test for significant differences in nutrient concentrations among the plots of different elevations, non-parametric analyses of variance (Kruskal-Wallis test), combined subsequently with two-sample tests (Wilcoxon U test) and three-factorial analyses of variance for unbalanced data sets (General Linear Models) were conducted using SAS software (version SAS 9.1 for Windows; SAS Institute, Cary, North Carolina, USA). $P < 0.05$ was used as the significance level throughout the study.

2.4 RESULTS

2.4.1 SPATIAL HETEROGENEITY OF SOIL PROPERTIES

By analyzing soil samples from 320 different locations (80 plots with each 4 sampling locations), we were able to characterize the about 20 investigated soil properties in terms of their heterogeneity at different spatial scales. Most soil chemical parameters showed the largest variability at the within-plot level, i.e. over distances of not more than 10 m (Table 2.1), while the parameters varied less between different plots, sites (at a given elevation), and between the four elevations (e.g. pH, C/N ratio, exchangeable cation concentrations, and N net mineralization/nitrification rates). Only a minority of properties varied primarily across elevations while being less variable on a regional and local scale (e.g. depth of organic layer and N_t concentration). Plant-available P was the only parameter revealing similar variances at

the within-plot, within-site, between-site and across-elevation levels, while total P showed largest variation at the within-site (between-plot) and within-plot levels (Table 2.1).

Table 2.1. Percental contribution of four different sources of variation to the total variation (= 100 %) of various soil chemical parameters in the 80-plot sample according to a variance components analysis (mixed model, all effects random). The relative importance of the components of variation was estimated with the routine REML, calculated with the statistical program R (version 2.8.1, Crawley 2007). The data set consisted of 4 elevation levels (500, 1000, 1500 and 2000 m), 3 study sites per elevation (500 m: 2), 5-12 plots per study site, and 4 sampling locations (N_{NM} and N_{NI}: 8) per plot.

Parameter	Within-plot variation	Within-site variation (between-plot variation)	Between-site variation (at a given elevation)	Variation due to elevation differences
Depth of organic layer	19.9	16.5	5.7	57.9
Organic layer				
pH_{KCl}	30.3	28.4	16.8	24.5
N_t	16.3	5.4	11.1	67.2
C/N-ratio	48.5	31.7	19.8	0.0
K_{ex}	32.1	32.5	2.1	33.3
Mg_{ex}	48.6	21.5	20.8	9.1
Ca_{ex}	34.1	28.8	28.9	8.2
Al_{ex}	56.9	15.1	28.0	0.0
P_a	20.1	27.1	26.7	26.1
P_t	37.1	43.9	19.0	0.0
Mineral soil (0 - 0.1 m)				
pH_{KCl}	40.6	19.2	11.7	28.5
N_t	23.0	11.9	21.3	43.8
C/N-ratio	24.1	18.4	22.5	35.0
$K_{ex.}$	72.4	13.6	5.8	8.2
$Mg_{ex.}$	60.5	28.5	4.6	6.4
$Ca_{ex.}$	42.5	43.4	14.1	0.0
$Al_{ex.}$	72.3	12.7	15.0	0.0
P_a	33.9	28.3	23.7	14.1
Topsoil horizon (organic layer and part of uppermost mineral soil)				
N mineralization rate (N_{NM})	65.4	24.0	5.2	5.4
N nitrification rate (N_{NI})	54.2	30.5	10.6	4.7

2.4.2 SOIL ORGANIC MATTER AND SOIL ACIDITY

The mean depth of the organic layer (L, F, H horizons) on top of the mineral soil increased about fourfold from 0.16 m in the plots at 500 m to 0.63 m at 1500 m a.s.l. and remained constant higher up on the slope (Table 2.2). A significant altitudinal trend was visible despite the considerable spatial heterogeneity of organic layer properties at a given altitude.

Table 2.2. Means ($\pm$ 1 SE, n = 20) of various soil properties of the organic layer and the mineral topsoil (0-0.1 m) at 500, 1000, 1500 and 2000 m elevation in the Sumaco Biosphere Reserve transect. K_{ex}, Mg_{ex}, Ca_{ex}, Al_{ex} - $BaCl_2$-exchangeable concentrations of K, Mg, Ca and Al, P_a - available P fraction according to the resin-bag method, P_t - total P. Mean Ca/Al ratio was calculated by averaging over the 20 plot means of Ca/Al ratio per elevation level. Different small letters indicate significant differences between the elevations.

	Elevation (m)			
Parameter	**500**	**1000**	**1500**	**2000**
	Organic layer			
Depth of organic layers [m]	0.016 ± 0.021^a	0.024 ± 0.031^a	0.063 ± 0.047^b	0.053 ± 0.032^b
Soil bulk density [Mg m^{-3}]	1.13 ± 0.04^a	0.63 ± 0.03^b	0.47 ± 0.02^b	0.57 ± 0.1^b
pH$_{KCl}$	4.66 ± 0.56^a	5.28 ± 0.65^a	3.86 ± 0.46^b	4.69 ± 0.57^a
K_{ex} [µmol g^{-1}]	6.69 ± 0.57^a	12.95 ± 0.70^b	13.05 ± 1.28^b	20.77 ± 2.31^c
Mg_{ex} [µmol g^{-1}]	32.47 ± 3.28^a	47.39 ± 2.52^{ab}	36.06 ± 3.26^a	54.05 ± 5.39^b
Ca_{ex} [µmol g^{-1}]	136.07 ± 12.18^a	275.38 ± 39.22^b	146.13 ± 20.78^a	250.15 ± 22.18^b
Al_{ex} [µmol g^{-1}]	18.91 ± 3.34^a	62.59 ± 17.78^{ab}	73.64 ± 9.06^b	50.76 ± 8.26^{ab}
Ca_{ex}/Al_{ex} ratio [mol mol^{-1}]	9.68 ± 1.93^{ab}	17.10 ± 8.72^b	3.76 ± 1.22^a	6.00 ± 1.24^a
	Mineral soil (0–0.1 m)			
pH$_{(KCl)}$	4.08 ± 0.42^a	4.47 ± 0.54^b	4.44 ± 0.46^{bc}	4.51 ± 0.47^c
K_{ex} [µmol g^{-1}]	1.72 ± 0.17^a	2.54 ± 0.16^b	1.64 ± 0.15^a	1.86 ± 0.20^a
Mg_{ex} [µmol g^{-1}]	5.70 ± 0.53^{ab}	7.56 ± 0.85^a	4.51 ± 0.56^b	4.73 ± 0.70^b
Ca_{ex} [µmol g^{-1}]	14.22 ± 2.08^a	41.28 ± 11.97^a	21.96 ± 4.10^a	30.35 ± 7.45^a
Al_{ex} [µmol g^{-1}]	44.85 ± 5.29^a	57.20 ± 7.76^a	44.33 ± 3.55^a	40.48 ± 5.70^a
Ca_{ex}/Al_{ex} ratio [mol mol^{-1}]	0.63 ± 0.24^a	2.23 ± 1.32^a	0.54 ± 0.12^a	1.23 ± 0.32^a

The acidity of the organic layer showed a large between-plot variability with plot pH (KCl) means ranging from 2.8 (at 1500 m) to 6.2 (at 1000 m), while the pH (KCl) of the mineral soil was much more uniform among the plots (3.9 – 5.3). The large majority of plots were

characterized by moderate to high soil acidities with pH (KCl) < 5. The pH (KCl) of the organic layers decreased significantly with elevation ($r^2 = 0.06$, p = 0.02), while that of the mineral soil increased ($r^2 = 0.36$, p < 0.001). Organic layer depth was positively correlated with the pH (KCl) of the mineral soil ($r^2 = 0.34$, p < 0.001).

2.4.3 AVAILABILITY OF CA, K, MG AND AL

The concentration of salt-exchangeable K in the organic layer ranged from 2.6 to 48 µmol g^{-1} (plot means). Despite a large within- and between-site variability, the K_{ex} concentration in the organic layer was positively correlated with elevation ($r^2 = 0.38$, p < 0.001). In contrast, the K_{ex} concentration in the mineral soil did not depend on elevation, and was about 10 times lower than that in the organic layer. Similarly variable were the exchangeable Mg concentrations of the organic layer (plot means from 10.9 to 135 µmol g^{-1}) and of the mineral soil (0.8 to 18.5 µmol g^{-1}). The Mg_{ex} concentration of the organic layer was positively correlated with elevation and also with the pH (KCl) ($r^2 = 0.12$, p < 0.001; $r^2 = 0.15$, p < 0.001, respectively), while the Mg_{ex} concentration of the mineral soil showed no correlation neither with elevation nor with pH (KCl). The plot means of the salt-exchangeable Ca concentration in the organic layer varied between 45 and 687 µmol g^{-1} and those of Ca_{ex} of the mineral soil between 4.2 and 238 µmol g^{-1}. Ca_{ex} of the organic layer showed a significant, but not very tight, correlation with elevation ($r^2 = 0.04$, p = 0.03), while Ca_{ex} of the mineral soil was independent from elevation. Both variables were positively correlated with pH (KCl) ($r^2 = 0.43$, p < 0.001; $r^2 = 0.25$, p < 0.001, respectively).

The exchangeable aluminium concentration in the organic layers was below the detection limit in various plots at 500, 1000 and 2000 m elevation, but reached plot means as high as 286 µmol g^{-1} in other stands. In the organic layer, the Al_{ex} means were positively correlated with elevation ($r^2 = 0.08$, p = 0.005). The Al_{ex} concentration of the mineral topsoil ranged from 4.4 µmol g^{-1} (lowest plot mean) to 179 µmol g^{-1} and was not correlated with elevation. Unlike K_{ex} and Mg_{ex} of the mineral soil, which were positively correlated with Ca_{ex} ($r^2 = 0.08$, p = 0.005; $r^2 = 0.35$, p < 0.001, respectively), Al_{ex} was negatively correlated with Ca_{ex} of the mineral soil ($r^2 = 0.05$, p = 0.02).

2.4.4 PHOSPHORUS AVAILABILITY

Plant-available phosphorus (P_a), estimated by the resin-bag exchange method, showed a very large variability among the plots at all four elevation levels. In general, the P_a concentrations were much higher (about 6 times) in the organic layer than in the upper

mineral soil (0 – 0.1 m, Figs 2.2 A and B). In the former, P_a plot means varied between 0.03 and 23.3 µmol P_a g^{-1}, in the latter, P_a minima were below the detection limit of our method, while maxima reached 4.86 µmol g^{-1}.
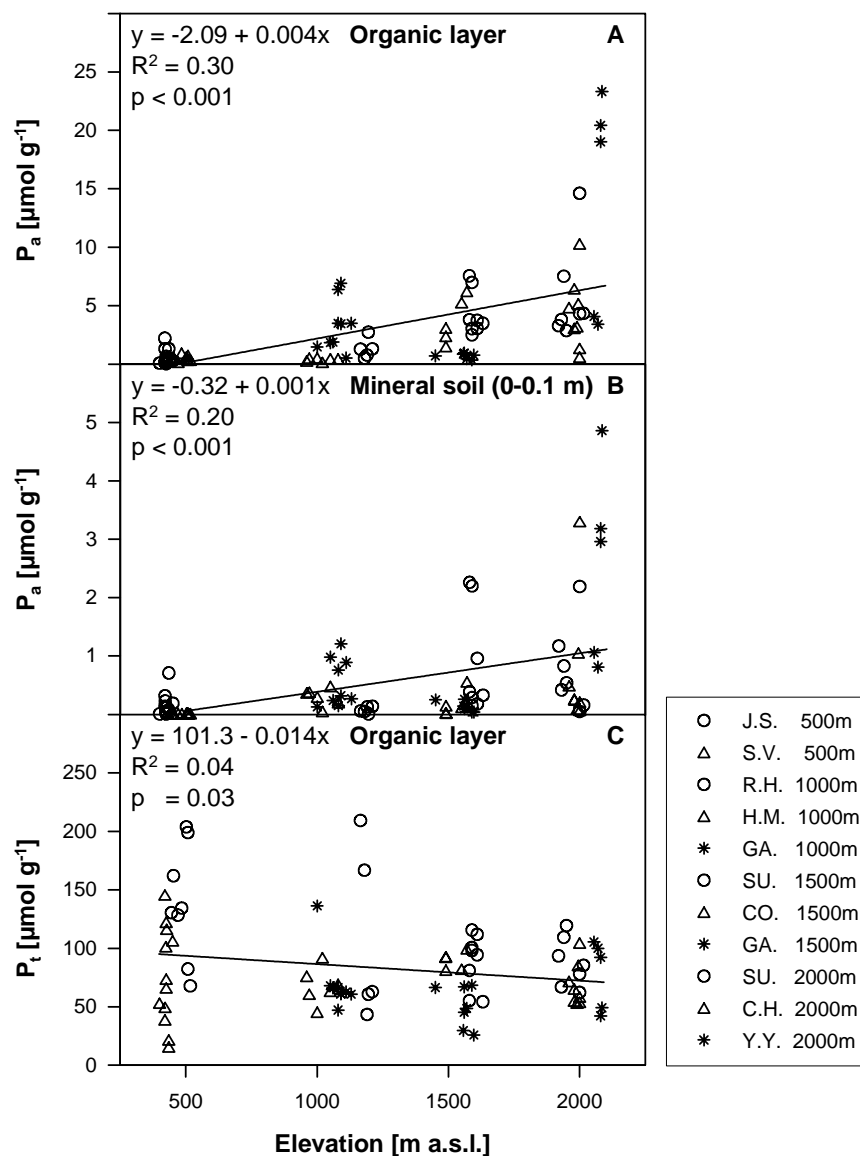

Fig. 2.2. Soil phosphorus concentrations in the 80 study plots as a function of elevation (m above sea level). (A) concentration of plant available P (P_a, resin-bag-method) in the organic layer; (B) concentration of P_a in the upper mineral soil layer (0-0.1 m), (C) total P concentration (P_t) in the organic layer. Given are the means of the 20 plots per elevation level; the location of the plots at the each 3 (500 m: 2) study sites is indicated by different symbols. Abbreviations: Jatun Sacha (J.S.), Selva Viva (S.V.), Rio Hollin (R.H.), Hakuna Matata (H.M.), Cordillera Galleras (GA.), Sumaco (SU.), Cocodrillos (CO.), Cordillera Galleras (GA.), Sumaco (SU.), Cordillera Huacamayos (C.H.), Yanayacu (Y.Y.).

Despite this high spatial variability, P_a in the organic layer and in the mineral soil tended to increase with elevation more than tenfold, with the difference between the elevation levels being significant for the 1500 to 2000 m transition (Figs 2.2 A and B). This altitudinal trend persisted even if certain very high P_a values of the Yanayacu plots at 2000 m were excluded as outliers from the analysis. Both the P_a concentrations of the organic layer and of the mineral soil showed a positive correlation with pH (KCl) ($r^2 = 0.06$, p = 0.01; $r^2 = 0.07$, p = 0.009, respectively). The concentration of total P (P_t) was only measured in the organic layer and ranged from 15.7 to 209 µmol g^{-1} revealing a weak negative correlation with elevation (Fig 2.2 C) while not being related to pH (KCl). The between-plot variability of P_t was high at 500 m (13fold difference between maximum and minimum) but declined with increasing elevation (3fold difference at 2000 m).

2.4.5 N CONCENTRATIONS AND N MINERALIZATION RATE

The nitrogen concentration in the organic material of the L, F, H layers increased from 0.58 mmol g^{-1} at 500 m to 1.59 mmol g^{-1} at 2000 m a.s.l. with lowest and highest plot means of 0.4 and 1.9 mmol g^{-1} (Fig. 2.3 C). In contrast, no elevational trend in the organic layer C/N ratio was detected (14.7 - 15.7 mol mol^{-1} as means of the elevation levels, Fig. 2.3 A). The total nitrogen (N_t) concentration of the mineral topsoil increased from 0.20 to 0.52 mmol g^{-1} from 500 to 1000 m elevation but remained constant higher upslope (minima and maxima along the transect, 0.1 and 0.9 mmol g^{-1}, Fig. 2.3 D). With elevation level means of 10.2 to 13.1 mol mol^{-1}, the C/N ratio of the mineral soil was lower than that of the organic layer, and it significantly increased from 500 to 1500 m, but dropped again toward the 2000 m level (Fig. 2.3 B).

The experiments with *in situ*-incubation of topsoil samples revealed a negative net ammonium release rate in 40 of the 80 plots, i.e. an immobilisation of NH_4^+ at a maximum rate of 2.6 µg N g^{-1} d^{-1}. Highest NH_4^+ release rates reached 2.2 µg N g^{-1} d^{-1} at the plot level. Rates of NO_3^- release (net nitrification rate) varied between 0.01 µg g^{-1} d^{-1} and 4.79 µg g^{-1} d^{-1} as plot-level means, while N mineralization rate (i.e. the sum of net NH_4^+ and NO_3^- release) ranged between large negative values (up to -2.34 µg N g^{-1} d^{-1}) at plots with intensive ammonium immobilisation to 5.08 µg N g^{-1} d^{-1} in soils with rapid ammonification and subsequent nitrification. The relative proportion of NO_3^- release of the total of mineral N released exceeded 80 % in all plots and typically ranged between 95 and 100 %.
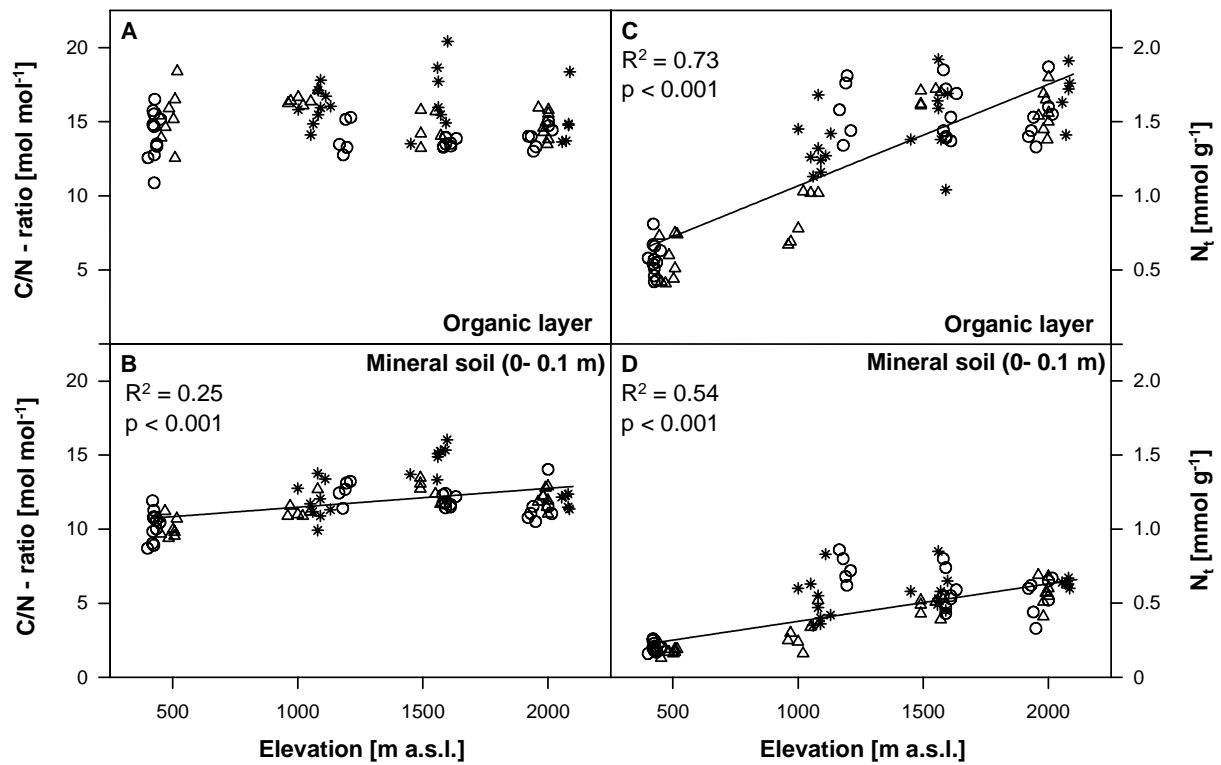
Fig. 2.3. C/N ratio and total nitrogen concentration of the soil in the 80 study plots as a function of elevation. (A) C/N ratio of the organic layer and (B) of the mineral topsoil (0 - 0.1 m), (C) total nitrogen concentration of the organic layer and (D) of the mineral soil. For symbols of the different study sites see Fig. 2.2.

N_t and C/N ratio of the mineral soil were positively correlated with pH (KCl) ($r^2 = 0.23$, p < 0.001; $r^2 = 0.05$, p = 0.03, respectively), while N_t of the organic layer was negatively related to pH (KCl) ($r^2 = 0.10$, p = 0.002).

The dry mass-based net release rate of mineral N in the uppermost 10 cm of the soil was independent of elevation (Figs 2.4 A and C). Only when N release is expressed per soil volume and ground area (termed net N mineralization and net nitrification; unit, kg N ha^{-1} d^{-1}), net mineralization and nitrification rate decreased with altitude (Figs 2.4 B and D). This altitude effect was caused by a significant increase in organic layer depth, associated with a decrease in the bulk density of the topsoil, in upslope direction. Both net mineralization and net nitrification were positively correlated with soil bulk density ($r^2 = 0.19$, p < 0.001 and $r^2 = 0.18$, p < 0.01, respectively) and also with soil moisture ($r^2 = 0.16$, p < 0.001 and $r^2 = 0.14$, p < 0.01, respectively).

In an attempt to compare the availabilities of N and P along the slope, we calculated different nutrient ratios (Figs 2.5 A - D). While the N_t/P_t-ratio of the organic layer increased with elevation ($r^2 = 0.25$, p < 0.001), the N_t/P_a-ratio (resin bag method) of both the organic

layer and the mineral topsoil decreased exponentially with altitude ($r^2 = 0.12$, p = 0.001 and r^2 = 0.06, p = 0.01, respectively). By relating N mineralization or nitrification rate (N_{NM} or N_{NI}) to available phosphorus P_a, we obtained N_{NM}/P_a and N_{NI}/P_a ratios which showed similarly exponential decreases with altitude ($r^2 = 0.24$, p = 0.001; $r^2 = 0.30$, p < 0.001) as did the N_t/P_a ratios.
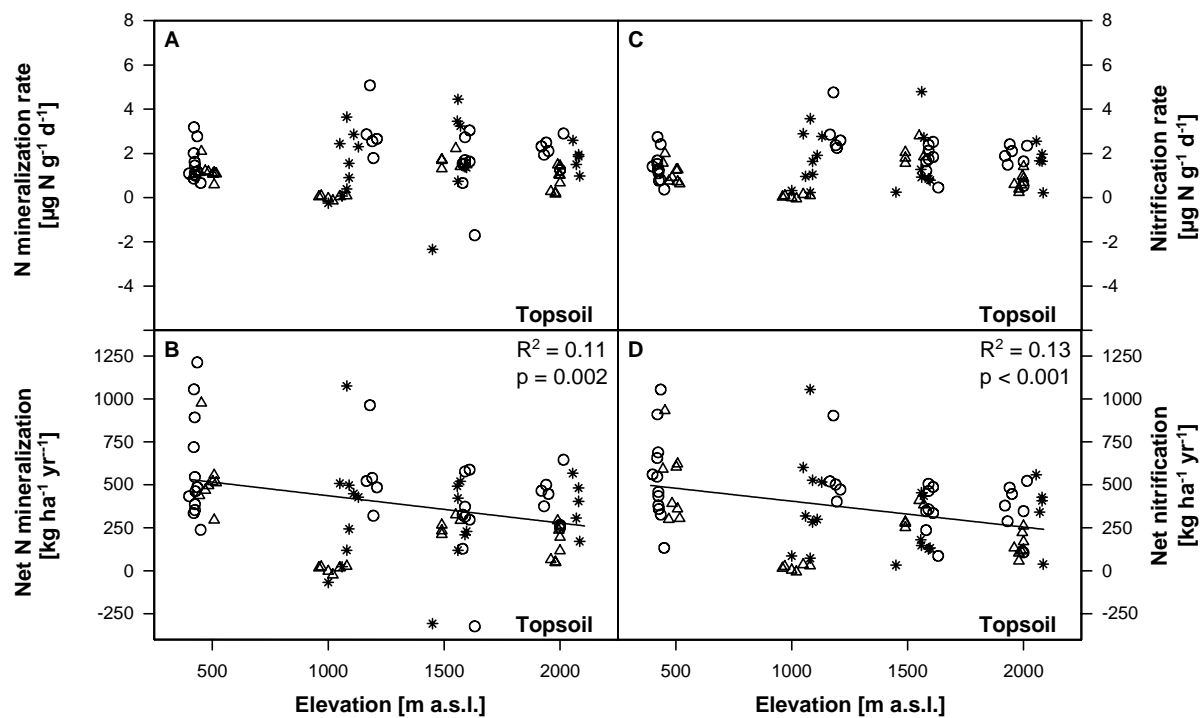

Fig. 2.4. Net mineralization of N in the 80 plots as a function of elevation either expressed per soil mass and day (A, mineralization rate), or extrapolated to a full year and related to ground area (B, net N mineralization). Net release of nitrate either expressed per soil mass and day (C, nitrification rate), or extrapolated to a full year and related to ground area (D, net nitrification). For symbols of the different study sites see Fig. 2.2. The topsoil (0.1 m) consists of the organic layer and part of the mineral soil.

2.5 DISCUSSION

2.5.1 TOPOGRAPHIC VS. ALTITUDINAL VARIATION IN NUTRIENT AVAILABILITY

Our analysis of the heterogeneity of soil chemistry at different spatial scales revealed that several soil properties in tropical mountain forests are highly variable at the plot level over distances of a few m, which makes it difficult to detect differences between plots, regions and also between elevation levels for these variables. Large altitudinal distances and/or a large number of plots investigated would be needed in these cases. The reasons for a high small-

scale spatial variability in organic layer C/N ratio, N net mineralization rate, pH and other variables may be diverse, but should include the high tree species richness of the study region with different species probably differing in their effect on soil properties, and a variable topography with ridges, slopes and valley bottoms differing in pedogenesis. On the other hand, organic layer depth and N_t concentration were found to be soil properties with a large altitudinal variation but a remarkable uniformity at the plot and sites levels in our study. This may indicate that humus accumulation and N storage in the soil are less influenced by species identity or topography, but are to a large extent under the control of temperature and rainfall, factors most closely related to elevation. With 20 plots per elevation level, that covered a variety of topographic situations, our sample was large enough to allow for the detection of significant elevational changes in a number of soil chemical properties including several parameters of N and P availability.

2.5.2 ELEVATIONAL CHANGE IN N SUPPLY AND SOIL N CONCENTRATION

From our results, a number of safe conclusions on N availability for trees in the 80-plot sample can be drawn, N net mineralization rate and nitrification rate in the topsoil did not show a significant decrease with elevation between 500 and 2000 m when N release is expressed per soil dry mass. This finding seems to contradict the assumption that soil N availability should decrease with elevation but increase with pedogenetic development in tropical forest soils (e.g. Vitousek & Sanford 1986, Marrs *et al.* 1988, Riley & Vitousek 1995, Tanner *et al.* 1998), both effects resulting in a higher N supply in lowland than in mountain forest soils. This prediction is supported by frequent reports about decreasing foliar and litter N contents with elevation in tropical mountain forests (e.g. Tanner *et al.* 1998, Moser *et al.* 2008). Lowered temperatures may be one factor underlying elevational decreases in N transformation rates because a bulk of evidence shows that N mineralization slows down in cooler environments (e.g. Meentemeyer 1977, Sveinbjörnsson *et al.* 1995, Timoney 1995, Sveinbjörnsson 2000). On the other hand, Marrs *et al.* (1988) suggested that temperature is unlikely to be a major constraint of soil N transformation in tropical montane forests because soils from higher altitudes, when incubated in the lowland at 100 m elevation, did not reveal neither higher N mineralization nor nitrification rates. This could indicate that, at least in certain mountain transects, the microbial communities at the different elevations are well adapted in their metabolic rate to the local thermal regime. In these cases, other factors, including increasing foliar phenol contents or the more frequent occurrence of hypoxia in the soil, may limit N mineralization at high elevations. Thus, temperature could be secondary to

substrate quality or other physical and chemical soil conditions in determining mineralization rate in mountain transects. The results of Kitayama *et al.* (1998) obtained in two elevation transects on different geological substrates in Sabah (Malaysia) indeed seem to indicate that temperature determines the fraction of N being mineralized only if soil organic matter quality as indicated by the C/N ratio remains sufficiently constant along the slope. In our transect, invariant net N release rates per soil mass with elevation were associated with a remarkably constant C/N ratio in the organic layer and the mineral topsoil from 500 to 2000 m. Thus, the rather uniform substrate quality on larger spatial scales could be a possible reason for the constancy of mineralization rate across the elevations, because the turnover rate of N is largely dependent on C availability for microbial demand (Hart *et al.* 1994, Corre *et al.* 2007, Sotta *et al.* 2008).

However, there are diverging observations on altitudinal change in soil organic matter C/N ratio in tropical mountains. For example, Arnold *et al.* (2008) and Proctor *et al.* (1988) reported more or less constant C/N ratios in NW Ecuadorian and Malaysian mountain transects, similar to our data, while Moser *et al.* (2008) found a pronounced increase of topsoil C/N ratio with elevation in a south Ecuadorian transect. This points to an important influence of bedrock type on soil N content and its altitudinal variation. In Central and Northern Ecuador, many summits are volcanoes that develop Andosols with relative high nitrogen concentrations when aged, while they are infrequent in S Ecuador.

However, when N_{NM} and N_{NI} rates are related to soil volume and ground area (per m^2 and 0 - 0.1 m depth) to give stand-related N supply rates, both net N mineralization and net nitrification significantly decreased (by about 40%) between 500 and 2000 m in our transect, despite the lacking elevation effect on mass-related mineralization rate. This is mostly a consequence of the fact that the humus content of the topsoil increased toward higher elevations in this transect, thereby reducing soil bulk density and lowering volume-related mineral N release rates. On the other hand, the depth of the organic layer typically increases with elevation in tropical mountain transects which could compensate for reductions in volume-related N mineralization. In fact, Leuschner *et al.* (2007) and Moser *et al.* (2008) found a more than 3fold increase in fine root biomass along a transect from 1000 to 3000 m in S Ecuador, which was associated with a large increase in organic layer depth offering more rooting space. Yet, rooting was found to be very shallow in high elevation forests (Soethe *et al.* 2006) which may reduce the importance of lower organic layer horizons as an additional nutrient source. Thus, it is likely that increasing rooting space in growing organic layers may

compensate partly, but not completely, for a reduction in volume-related N-mineralization with increasing elevation as it was observed here.

Most nitrogen set free during soil N transformation processes was released in the form of NO_3^- in our study region despite rather high soil acidity (pH (KCl) 3.6 - 4.5). Thus, acid-tolerant nitrifiers, which oxidize NH_4^+ or organic N compounds to nitrate, must be abundant in these tropical mountain soils. N-transformation studies in acid soils of temperate forests revealed that nitrification is mostly conducted by fungi, and not chemolithoautotrophic prokaryotes, at pH values below about 4.5 (Lang & Jagnow 2006). High nitrifier activity in tropical montane forests was similarly found by Rhoades & Coleman (1999) in two other montane forests in Ecuador.

Mean rates of N net mineralization in our Ecuadorian study sites were in the middle of the range of data measured in tropical rainforests, and slightly exceeded rates reported for temperate and boreal forests (Robertson 1984, Marrs *et al.* 1988). Our daily rates are close to other values reported for tropical forests with moderately fertile soils (1-3 µg N g^{-1} d^{-1}), while lower mineralization rates were observed in forests on oxisols, ultisols or other less fertile substrates, and also in some montane forests (0.1–1 µg N g^{-1} d^{-1}, Lamb 1980, Robertson 1984, Chandler 1985, Vitousek & Denslow 1986, Vitousek & Sanford 1986, Matson *et al.* 1987, Marrs *et al.* 1988, Montagnini & Buschbauer 1989). Relatively high N_{NM} rates in the montane soils of the Sumaco region correspond with relatively low soil C/N ratios.

Ammonification and nitrification are key processes of mineral N supply which characterize N availability for plants roots better than N concentrations or N-related element ratios of soil or humus material, because the latter are the consequence of various plant physiological processes including N uptake and loss and plant growth rate. We measured the net release of NH_4^+ and NO_3^- in the 80 forest plots over periods of 8 days in order to characterize the elevational and topographic variation in N supply rate from a plant perspective. This approach may yield data on mineral N net release under partly standardized field conditions, thus enabling a comparison of sites. However, the absolute amount of nitrogen compounds being available for plant uptake cannot be deduced from this approach because our investigation covered only a short time period and ignored putative seasonal variation in N transformation processes, making it difficult to extrapolate to a full year. Furthermore, the study focused on nitrate and ammonium but neglected organic N compounds that might be available for uptake by mycorrhizal fungi and plant roots as well (Hodge *et al.* 2001). Finally, we cannot exclude that the buried bag method induces certain errors by increasing N mineralization rate due to alteration of soil structure in the bags (Raison *et al.* 1987).

2.5.3 ELEVATIONAL INCREASE IN P AVAILABILITY

The availability of phosphorus to plants depends on a variety of geochemical and biological factors, several of them being difficult to measure under field conditions. Furthermore, a fully agreed analytical procedure to quantify plant-available P in forest soils does not yet exist. We used two approaches to obtain estimates of plant-available P in the topsoil horizons of the 80 forest stands of our transect. Total P in the organic layer was determined for quantifying the pool of P bound in fresh litter and humus material on top of the mineral soil. Part of this pool, especially that bound in the easily-degradable humus fraction, may be readily available as inorganic P after fungal or microbial mineralization, while P bound in recalcitrant organic molecules may resist biological degradation for much longer time (Walker & Syers 1976). A second approach used resin bags as anion exchangers to quantify the amount of inorganic P in a soil sample by applying a standardized procedure. Most likely, this technique measures soil solution P and part of the non-specifically adsorbed P, thereby approaching the plant-available fraction, while tightly bound P (precipitated and occluded fractions) will not be removed by the anion exchangers (Irion 1978, Uehara & Gillman 1981). Clearly, additional P fractions may be available to plants as well that are not measured by this technique, notably organic and inorganic P mobilized by external phosphatises and other rhizosphere processes.

Our data show for both investigated horizons a more than tenfold increase in plant-available (resin-bag exchangeable) P concentration (P_a) from 500 to 2000 m elevation, which is the largest change with elevation detected for any of the soil chemical parameters investigated in this study. Inorganic P is supplied to the P_a fraction by desorption processes, in acidic soils mostly from iron and aluminium oxide minerals, P release through organic matter mineralization, and mineral weathering (Walker & Syers 1976, Irion 1978, Uehara & Gillman 1981). Uptake by plants and microbes and, to a lesser extent, leaching with percolating water are processes which deplete the P_a pool. Since none of these processes was measured directly, we can only speculate about the causes of the remarkable increase in P_a concentrations with altitude. P_a supply through mineral weathering may increase with elevation because erosion tends to rejuvenate the soils of inclined sites in montane elevation, thereby increasing the amount of weatherable P-containing minerals in the upper soil profile, but the effect of weathering on P_a supply is presumably small. In contrast, many tropical lowland soils are dominated by aluminium and iron oxide minerals but are poor in minerals that can release P through weathering (Sanchez 1976, Högberg 1986). The roughly six-fold higher P_a concentration in the organic layer as compared to the mineral soil points to a key role of geochemical adsorption and precipitation processes in reducing the P_a pool in these soils,

because P-adsorbing Fe- and Al-oxides are much more abundant in the mineral soil than in the organic layers. Another possible explanation is mineralization of organic substances as a significant P source filling up the P_a pool in the organic layers. However, P mineralization alone does not explain the observed increase of P_a with elevation because the mass-specific mineralization rate should decrease with elevation due to much more unfavourable C/P ratios, rather than increase as it was observed for P_a. We speculate that organic anions released through decomposition in the organic layer may play an important role in reducing the adsorption of P to Al- and Fe-oxides. Production of organic anions (such as citric acid) by plant roots or fungi could further reduce P sorption (Hue 1991, Gerke & Meyer 1995). An upslope decrease in the intensity of P immobilization through microbial uptake is another possible cause underlying the increase of P_a concentrations with elevation since soil biological activity and associated soil respiration were found to decrease with elevation in South Ecuadorian mountain forests (Iost *et al.* 2008). In contrast, decreasing P uptake by tree roots is less likely because Leuschner *et al.* (2007) and Moser *et al.* (2008) found a large increase in tree fine root biomass in the organic layer with elevation in S Ecuadorian mountain forests indicating that the P demand of high-elevation forests cannot be that much smaller than at lower elevations, so that the uptake reduction could explain the tenfold increase in P_a with elevation. Whether elevational changes in the mycorrhiza associations of the trees influence P uptake and hence soluble P concentrations in the soil solution, remains an open question.

Our data show a significant decrease in the total-P concentration of the organic layers from 500 to 2000 m elevation, which consequently was associated with a large increase in the organic matter C/P_t ratio (from 39 mol mol^{-1} at 500 m to >1500 mol mol^{-1} at 2000 m, data not shown). Due to a large increase in organic layer thickness (and mass), the pool of organic P nevertheless increased with elevation in our transect. Larger C/P ratios at higher elevation indicate that the mass-specific P-mineralization rate most likely is lower in montane than in upper lowland soils, while the total amount of P released through mineralization in the topsoil may remain constant, or even increase, with increasing elevation due to the large increase in humus mass in upslope direction.

All three measured P fractions (P_t in the organic layers, P_a in the organic layer and in the mineral topsoil) showed a large variation among the plots of the same elevation, reflecting the high spatial heterogeneity of P concentrations often observed in forest soils. In addition, resin bag-extractable P occurred at about 6-fold higher concentrations in the organic layer than in the mineral topsoil immediately below, indicating large vertical gradients in P availability in

the soil and emphasizing the role of organic matter as the most important P source in these soils.

2.5.4 ELEVATIONAL CHANGE IN N VS. P AVAILABILITY

In this transect, we found only weak evidence in support of the hypothesis that N limitation of plant growth tends to increase with elevation (Grubb 1977, Edwards & Grubb 1977, Edwards 1982). Using N mineralization rate as a measure of N availability to plants, our data showed a higher N net mineralization per stand area at 500 m than at 1000, 1500 or 2000 m at least in the topsoil, but the mass-specific N_{NM} and N_{NI} rates did not decrease. Furthermore, the C/N ratio showed no decrease with elevation, while total N concentration in the topsoil even increased. Moreover, with mean daily N mineralization rates in the range of 1.5 - 1.6 µg N g^{-1} d^{-1}, the montane forests (1500 - 2000 m) of NE Ecuador were supplied with similar mineral N amounts as have been found in moderately fertile tropical lowland forest soils.
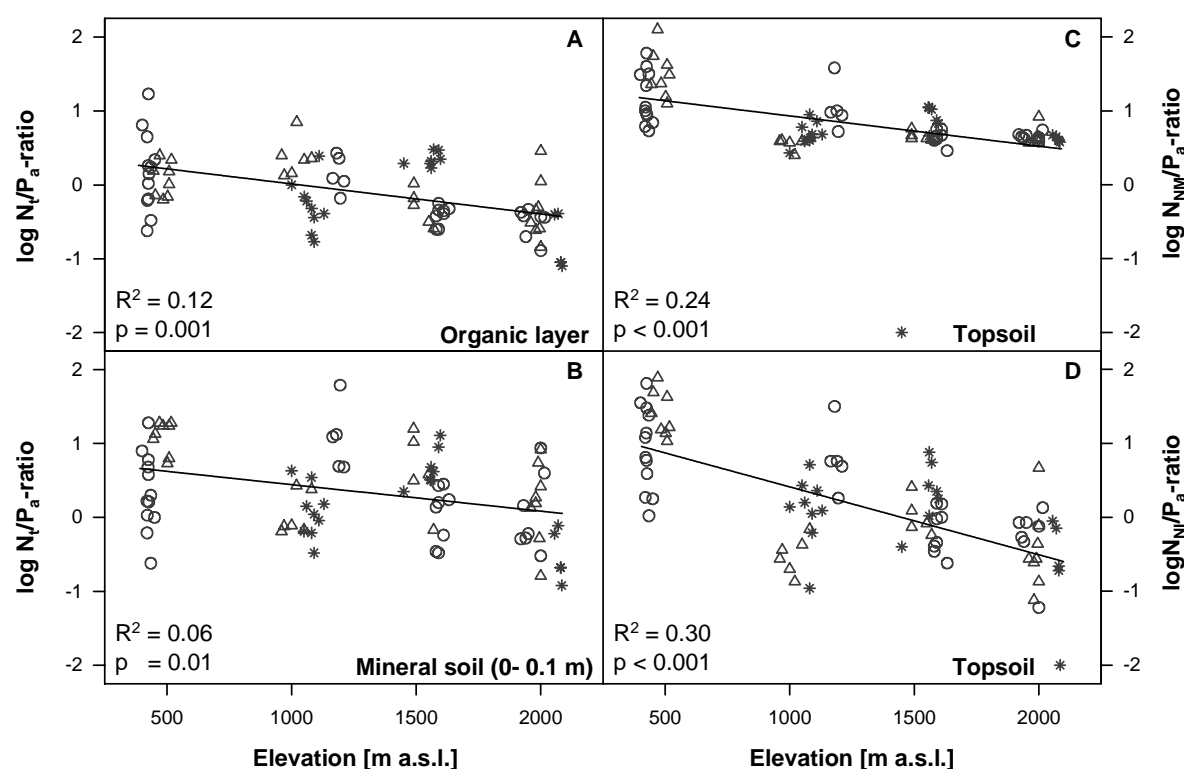
Fig. 2.5. Ratio (log-transformed) of total nitrogen to plant-available phosphorus of the organic layer (A) or the mineral soil (0 - 0.1 m) (B), and ratio (log-transformed) of N mineralization rate (N_{NM}, C) or nitrification rate (N_{NI}, D) to plant-available phosphorus of the topsoil (mixture of organic layer and mineral soil horizon, 0-0.1 m) (n=80). The r^2 and p values refer to the original non-linear relationships before log-transformation. To avoid division by zero, 0.01 was added to all P_a values in the data of Fig. 2.5 B.

In any case, from the soil C/N ratio it appears that N limitation of tree growth in the Sumaco montane forests, if being relevant, is probably less severe than in other tropical mountain forests, where elevational gradients in N supply may be different.

The situation seems to be different for P where our data provided strong evidence for a marked decrease in the severity of P shortage with increasing elevation, thus supporting the second part of the first hypothesis. When relating the availabilities of N and P to each other in a quotient of N_{NM}, P_a (or N_{NI}, P_a), we found an exponential 30-fold decrease in the N/P ratio from 500 to 2000 m elevation (Fig. 2.5). This is strong support for a decreasing importance of P limitation over N limitation with increasing elevation, irrespective of the overall significance of nutrient limitation of tree growth in these forests. Fertilization experiments at different elevations are needed to test for growth implications of this shift in N/P availability.

2.5.5 SOIL ACIDITY AND THE AVAILABILITY OF CA, MG AND K

All soils were moderately acid with a slight elevational decrease in acidity in the mineral topsoil but not in the organic layer. About 55 to 70% of the cations bound to the cation exchangers in the mineral topsoil were aluminium, followed in decreasing abundance by Ca, Mg and K. Similar results were obtained, for example, by Wilcke *et al.* (2001) in a transect study in South Ecuador. Significant altitudinal trends in the abundance of salt-exchangeable cations in the mineral soil did not exist (except for slightly smaller Mg_{ex} concentrations at 1500 and 2000 m). In the organic layer, much more Ca, K and Mg were bound to cation exchangers on a mass basis than in the mineral soil which underlines the importance of the organic layer not only for N and P supply, but also with respect to the supply of basic (non-hydrolyzing) cations (see also Kauffman *et al.* 1998, Wilcke *et al.* 2002, Wilcke *et al.* 2008). The Ca_{ex}, Mg_{ex} and K_{ex} pools in the organic layer increased with elevation due to the large increase in organic matter accumulation on top of the soil. The proportion of Al_{ex} of the cation pool was much smaller in the organic layer than in the mineral soil, typically being <20% in the latter. Therefore, the Ca/Al ratio at the exchangers, which is thought to be influential for tree root growth (Sverdrup *et al.* 1992), was >1 in the organic layer and hence much more favourable than in the mineral soil where it generally was <1. Ca/Al ratios <0.2, as were observed in certain highly acidic temperate forest soils, were found in the upper mineral soil of 12 of the 80 plots studied, with one of the eleven study sites (Selva Viva at 500 m elevation) having a mean Ca/Al-ratio in the mineral soil <0.2 (0.13 ± 0.03).

2.5.6 CONCLUSIONS

This study in 80 forest plots extending from upper lowland (500 m) to montane elevation (2000 m) on the eastern slopes of the equatorial humid Andes revealed, independently from elevation, a considerable variability of soil chemical properties on the plot level (20 m x 20 m), the site level (about 2 km x 2 km) and the regional level (about 50 km x 50 km), reflecting the local heterogeneity in topography and geology in the Sumaco elevation transect. The plant nutrition-related parameter with highest spatial variability was plant-available P (P_a), while N net mineralization and exchangeable Ca, Mg and K concentrations showed intermediate, and N_t concentration and C/N ratio of the organic layer rather low variabilities at a given elevation. Despite the spatial heterogeneity, we found a significant and large increase with elevation in P_a concentrations in the organic layer and the mineral topsoil, supporting the hypothesis that P limitation, if it plays a role, should decrease with elevation. Net release of inorganic N in the course of nitrogen mineralization occurred at all elevations mostly as nitrate and showed a higher mineral N supply per stand area at 500 m than at higher elevations in the topsoil, while mass-related N_{NM} remained invariant along the slope, corresponding to a constant C/N ratio with elevation and an increasing N_t concentration in the organic layer. It appears that N availability decreases only slightly, if at all, with elevation in this transect, which may contrast with other tropical mountains. The organic layer is playing not only a key role for N and P supply, but also as a storage of exchangeable Ca, Mg and K which increases with elevation.

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CHAPTER

3

EFFECTS OF SOIL CHEMISTRY ON TROPICAL FOREST BIOMASS AND PRODUCTIVITY AT DIFFERENT ELEVATIONS IN THE EQUATORIAL ANDES

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PAPER SUBMITTED TO OECOLOGIA

3.1 ABSTRACT

The dependence of aboveground biomass and productivity on soil fertility in tropical forests is not fully understood since previous studies yielded contrasting results. Here we quantify aboveground biomass (AGB) and wood productivity, and the impact of soil chemistry on these parameters in mature tropical forest stands of the equatorial Andes in Ecuador. In 80 plots (à 0.04 ha) at four elevation levels (500, 1000, 1500 and 2000 m a.s.l., total sample area = 3.2 ha) we measured more than 20 soil chemical parameters and inventoried all trees $\geq$ 10 cm dbh and determined stem diameter growth with dendrometer tapes in 32 plots.

Tree basal area reached the highest values at 1500 and 2000 m, whereas AGB (estimated using allometric equations) and productivity measures did not vary with elevation; across all plots, basal area averaged 47.2 $\pm$ 1.9 m^2 ha^{-1}, AGB 336 $\pm$ 17 Mg ha^{-1}, and coarse wood productivity 1.6 $\pm$ 0.2% yr^{-1} (means $\pm$ SE).

Tree coarse wood growth covaried strongest with plant-available P and exchangeable Mg in the soil organic layers. These two elements most likely control tree productivity at both lowland and lower montane elevations. Stand basal area and AGB, which are influenced by both productivity and tree longevity, covaried primarily with the exchangeable concentrations of Mg, Ca and K in the organic layers. The availability of N had a surprisingly small influence on forest biomass and productivity across the studied forest types, thereby contradicting the hypothesis of increasing N limitation of tree growth with elevation in tropical mountains.

Further investigations should consider additional soil physical and chemical parameters, notably soil moisture, which were not addressed by our study. Our results indicate that wood biomass and productivity of equatorial Andean forests are influenced by more than one nutrient species, and that N does not play a key role.

KEYWORDS: aboveground biomass, Ecuador, soil nutrients, tree growth, wood production

3.2 INTRODUCTION

In tropical mountains, tree height and tree growth rates typically decrease with increasing altitude (e.g. Leigh 1975, Bruijnzeel & Veneklaas 1998), but the underlying causes have not yet been fully understood. A multitude of possible explanations have been proposed focusing either on climatic factors (temperature, drought periods, reduced radiation, persistent leaf wetness, high wind speeds, and others) or on edaphic properties of high-elevation sites (soil water logging, elevated soil acidity in combination with putative Al toxicity, shortage of N or other nutrients, recalcitrant litter with slow decomposition, and others (see Grubb 1977, Bruijnzeel & Veneklaas 1998, Cavelier 1996, Hafkenscheid 2000, Wilcke *et al.* 2008). The role of soil chemistry for the structure and growth of tropical forests at variable elevation was most often investigated from a nutrient limitation perspective testing the hypothesis that tree growth in lowland forests is primarily limited by phosphorus, while nitrogen limitation is thought to be characteristic for tropical montane forests (e.g. Vitousek 1984, Tanner *et al.* 1998). However, other soil properties such as soil organic matter content and decomposition rate have been found to change with elevation as well (Cavelier 1996, Marrs *et al.* 1988, Schrumpf *et al.* 2001), which possibly may also affect tree stature and growth along mountain slopes. Yet, it has been found difficult to disentangle climatic and edaphic effects on the response of tree stature and growth at different elevations because soil chemical properties themselves are largely influenced by climate, namely temperature and rainfall.

The relationship between soil chemical properties (or soil fertility) and forest biomass has been investigated in more detail in several recent studies in tropical lowland forests which produced conflicting results. Laurance *et al.* (1999) and DeWalt & Chave (2004) found a higher aboveground biomass in forests on nutrient-rich entisols than in forests on nutrient-poor oxisols, probably reflecting reduced nutrient limitation of tree growth on the richer soils.

In contrast, Schaik & Mirmanto (1985) and DeWalt & Chave (2004) reported lower biomass in forests on P-rich lowland soils because tree individuals turned over faster in the stand. Other authors found no relationship between soil nutrients and aboveground biomass in tropical forests (e.g. Ashton & Hall 1992) which may indicate that soil chemistry plays an only secondary role for the structure of tropical forests while climatic influences dominate. A better understanding of how forest biomass and tree growth are covarying with soil nutrient availability is needed to reach at more adequate estimates of C stocks in, and C sequestration by, tropical forests than they are available today (Paoli *et al.* 2008).

This study investigates the variability of soil chemical properties, aboveground forest structure and tree growth in a matrix of 80 forest plots on the eastern slopes of the Ecuadorian Andes with the aims (i) to quantify effects of soil variation on stand structure, aboveground live biomass (AGB) and stem diameter growth and (ii) to identify those soil chemical properties with largest influence on the forest vegetation. Our extensive plot matrix reflected not only the small-scale (plot level and topographic) variation in soil properties and forest vegetation in a characteristic landscape patch of the equatorial Andes (20 plots per elevation) but it represented the altitudinal variation as well (four elevation levels, from lowland forest to lower montane forest). We put a special emphasis on measuring the plant-available fractions of five key plant nutrient elements (N, P, Ca, Mg, K); further, we investigated not only aboveground biomass as a static variable, but stem increment as a productivity parameter as well.

3.3 METHODS

3.3.1 STUDY AREA, PLOT SELECTION AND STAND STRUCTURAL ANALYSES

Eighty rainforest plots in the province of Napo, NE Ecuador, were selected for the joint study of soil chemistry, forest structure and aboveground productivity. The study region consists of the Sumaco Biosphere Reserve (SBR) and its direct neigborhood on the eastern slopes of the equatorial Andes stretching from the foothills in the Amazonian lowlands at about 250 m a.s.l. to the páramo at 3700 m; the study region includes the Sumaco volcano. The area is still harbouring large areas of intact forest from lowland to upper montane forests with a very species-rich flora (probably more than 6000 plant species, Neill & Palacios 1997).

The climate in the region is humid to perhumid with mean annual rainfall exceeding 2500 mm throughout the area; monthly precipitation usually never drops below 100 mm (Neill & Jørgensen 1999). Even higher rainfall (> 4000 mm yr^{-1}) is assumed to occur on Sumaco volcano and the Cordillera Guacamayos. Own temperature measurements in the study period indicate that mean annual temperature decreases from approximately 22.9°C at 415 m (Jatun Sacha) to 14.3°C at 2015 m (Sumaco volcano).

The geology and soils show a considerable heterogeneity throughout the study region covering two distinct physiogeographic regions, the Oriente basin in the Amazon lowlands and the Sub-Andean Zone. The former, quaternary clastic sediments include a variety of deposits, from lavas and pyroclastics of various grain sizes to colluvial/alluvial materials (piedmont fans) and alluvial fills. The Sub-Andean zone is topographically more diverse and

consists of foothills rising to elevations of up to 2000 m and deeply dissected east-flowing rivers. The Sub-Andean zone borders the Cordillera Real and is a back-arc fold-thrust belt tectonically associated with the Andes (Baldock 1982). In most of the area, parent rocks of the Cretaceous dominate, mainly limestone. However, basalt is present at Sumaco volcano and granite at Hakuna Matata; slates are found at Cordillera Guacamayos (Sauer 1971). In general, the geology is variable in the study region but not well explored.

Tweny-five soil pits (4-8 per elevation level) were excavated close to the study plots. Most of the profiles at the 500 and 1000 m elevation level were classified as Geric Ferralsols according to the World Reference Base for Soil Resources (IUSS working group WRB 2006), while Cambisols were dominant at 1500 and 2000 m elevation.

Based on the most recent vegetation classification for Ecuador (Palacios *et al.* 1999), the species-rich forest stands can be classified as evergreen lowland forests at 500 m, evergreen premontane forests at 1000 m, and as evergreen lower montane forests at 1500 and 2000 m.

Table 3.1. The 11 study sites at four elevation levels (Elev.) with elevation range covered, number of study plots (plots equipped with dendrometers in brackets), mean number of stems (dbh $\geq$ 5 cm), stand basal area (SBA) (dbh $\geq$ 10 cm) [m^2 400m^{-2}], mean number of tree species (No. of TS) (dbh $\geq$ 5 cm) [per 400m^{-2}] and rarefied tree species density (Rarefied TS) (N =28 trees per 400 m^2) per plot (means $\pm$ 1 SE). The conservation status of the study sites is indicated by PR (private reserve), NP (national park) and ER (ecological reserve).

Elev. (m)	Study site	Elevation range (m)	No. plots	No. of stems (n 400 m^{-2})	SBA	No. of TS	Rarefied TS
500	Jatun Sacha (PR)	400 - 450	12 (4)	55.5 ± 2.4	1.5 ± 0.1	40.5 ± 2.6	22.8 ± 0.5
	Selva Viva (PR)	445 - 520	8 (3)	66.4 ± 3.5	1.8 ± 0.2	49.4 ± 3.2	24.2 ± 0.5
1000	Hakuna Matata (PR)	960 - 1080	6 (2)	72.3 ± 5.0	1.8 ± 0.1	43.3 ± 4.3	22.2 ± 0.9
	Galeras (NP)	1050 - 1130	9 (3)	50.9 ± 2.9	2.0 ± 0.2	35.2 ± 2.9	21.5 ± 1.0
	Rio Hollín (PR)	1165 - 1200	5 (3)	75.8 ± 4.2	2.0 ± 0.3	28.6 ± 1.8	15.3 ± 0.9
1500	Galeras (NP)	1450 - 1600	7 (3)	76.4 ± 6.6	1.7 ± 0.1	40.1 ± 2.5	20.2 ± 0.8
	Cocodrilos (NP)	1490 - 1570	5 (3)	47.6 ± 3.7	2.2 ± 0.1	28.1 ± 1.2	20.2 ± 0.7
	Sumaco (NP)	1580 - 1630	8 (3)	41.8 ± 2.1	2.2 ± 0.2	26.4 ± 0.9	19.8 ± 0.4
2000	Sumaco (NP)	1920 - 2015	7 (3)	38.3 ± 3.7	2.0 ± 0.2	22.3 ± 2.5	16.9 ± 1.3
	C. Guacamayos (ER)	1940 - 2000	8 (3)	57.7 ± 6.2	1.4 ± 0.1	29.4 ± 3.0	19.2 ± 1.3
	Yanayacu (PR)	2055 - 2085	5 (2)	41.0 ± 3.7	1.9 ± 0.2	19.0 ± 1.0	15.5 ± 0.7

Each 20 plots of 20 m x 20 m size were selected at four elevation levels (500, 1000, 1500 and 2000 m) in order to include the typical topographic variation in soil types and related forest vegetation at a given elevation. Four different elevations were investigated for covering the variation in soils and vegetation caused by altitude. We studied 80 plots in total with a cumulative forest area of 3.2 ha. The study plots were selected at 11 sites belonging to nine different localities (see also Table 3.1 for further information on the study sites) that were 6 to 70 km distant to each other. Each site with a size of about 5 km^2 covered a variety of forest stands that were representative for the respective elevation with its variable topography and geology. Only mature stands without any kind of visible human or natural disturbance were selected as study plots in order to investigate a matrix of old-growth stands along elevational and small-scale topographic gradients. Larger canopy gaps did not exist on the plots. The mean distance between the 5 to 12 plots of a site (see Table 3.1) varied between 100 m and 1.8 km. Thus, all plots represented independent sampling units each containing a random sample of 16-45 stems $\geq$ 10 cm of diameter at breast height (dbh). The plot size (400 m^2) was small enough to keep environmental factors and forest structure sufficiently homogenous within the stand.

In every plot, we recorded all stems of living trees with a dbh $\geq$ 5 cm. The diameter of all trees (including palms) $\geq$ 10 cm was measured and the basal area calculated. Stem density was recorded per 400 m^2 ground area for all stems $\geq$ 5 and $\geq$10 cm dbh. For species determination, we collected voucher specimens of all unknown species; duplicates were deposited in the herbaria QCA, QCNE and GOET. Detailed information on the tree species composition of the plots is given in Homeier et al. (in prep.).

3.3.2 CALCULATION OF ABOVEGROUND BIOMASS AND MEASUREMENT OF STEM INCREMENT

In 32 of the 80 plots, all stems with a dbh $\geq$ 10 cm (n = 1016) were equipped with dendrometer tapes (type D1, UMS GmbH, Munich, Germany) that were monitored consecutively for stem diameter growth. Increment measurements were conducted in two to four plots per study site (33-60% of the plots of a site). The tapes were always mounted at 1.3 m height on the stem; on stems with buttresses or irregular bark surfaces, the measuring point was moved upwards to a height where measurement was possible. The tapes were read about 3 months after installation and subsequently at least once per following six-month-period; thus, for most of the plots, two or three (or even more) half-year-readings during the measuring period November 2005 – May 2008 are existing. Changes in dbh were determined to the nearest 0.1 mm. Annual diameter increment was calculated by relating the diameter

difference between the first and last reading to a full year. Annual cumulative basal area increment per plot was obtained by adding the basal area increments of all trees of a plot. Trees that died during the measuring period were excluded from the calculation (see Clark *et al.* 2001b).

For calculating aboveground live woody biomass (AGB) we applied the allometric equation of Chave *et al.* (2005), that was derived for tropical moist forests, with stem diameter and wood specific gravity as parameters. We considered wood specific gravity because this variable may have a profound influence on aboveground biomass of tropical forests (Baker *et al.* 2004). Wood density data for the tree species was obtained from Chave *et al.* (2006) or, if information for a species was missing, mean densities for genera and families were used. For trees that could not be identified or are still in the process of identification (i.e. for 4.9% of all stems), we used the mean wood density of the respective plot.

We used two different approaches to calculate aboveground biomass and stem growth rates at the plot level. The first approach ignored the inclination of the plot terrain and calculated with an uncorrected ground area of 400 m^2 (following de Castilho *et al.* 2006), while the second approach considered plot inclination and corrected the actual plot area by dividing plot length by cos α with α being the inclination angle. We present only the uncorrected data of the first approach because the second approach with inclination correction yielded only slightly different correlations and gave the same significant relationships as the first one.

3.3.3 SOIL CHEMICAL ANALYSES

In order to characterize the study plots in terms of their soil chemistry and nutrient availability, we conducted a set of analyses in all 80 plots with a focus on N supply, plant-available P, Ca, Mg and K, and soil acidity. The analytical methods are described in detail in Unger *et al.* (submitted). Briefly, we extracted each four soil samples per plot in the period April to June 2007. The plots were divided into four equally-sized quadrates of 10 m x 10 m size and the samples were taken in the centre of each quadrate using a soil corer of 5 cm diameter and 25 cm length. The soil core was split into two sub-samples (organic layer material, upper 10 cm of mineral soil). The organic layer included the L, F, and H horizons of variable depth; the transition from the organic H horizon to the mineral soil Ah horizon was arbitrarily set at about 30 % organic matter content using morphological criteria of the substratum for estimating organic matter content. The upper mineral soil consisted of A- and B-horizons with much lower organic matter content than the organic layers themselves. In the laboratory at the University of Göttingen, the following parameters were measured: total

carbon and nitrogen (gaschromatography), plant-available phosphorus (resin-bag method; Dowex 1 x 8-50), salt-exchangeable K, Mg, Ca, Al (NH_4Cl percolation with subsequent element analysis by atomic absorption spectroscopy), soil pH (in water and KCl), and N net mineralization and nitrification rate (buried bag method with 8-d in situ-incubation and subsequent colorimetric NH_4^+ and NO_3^- determination by continuous flow analysis).

3.3.4 STATISTICAL ANALYSES

The relationship between the more than 20 investigated soil parameters and stand structural and productivity variables was investigated by simple linear regression analysis and by partial correlation analysis to control for the effect of elevation.

Principal components analysis (PCA) was applied to identify major axes of soil variation in the 80-plot sample and to reduce the number of soil variables in the regression analyses. This was done separately for the organic layers, the upper mineral soil, and the 'topsoil horizon', the latter being a combined soil layer consisting of the organic L, F, H layers and the uppermost part of the mineral soil. The topsoil horizon was investigated in all those cases were larger samples were required for analysis (e.g. N mineralization measurements). All PCA axes explaining together at least 70% of the variance of the data set were used as independent variables in subsequent multiple regression analyses with backward variable elimination to test whether the PCA-derived eigenvectors were significant predictors for the stand structure and productivity variables. The obtained axes were found to be independent from each other and existed in a smaller number than the original soil variables. Thus, using the PCA axes in regression analyses ensured that multiple regressions did not suffer from multi-collinearity and they minimized the chance of spurious associations (Legendre & Legendre 1998). All calculations were conducted with Statistica 8.0 (StatSoft Inc., Tulsa, OK, USA).

3.4 RESULTS

3.4.1 TOPOGRAPHIC AND ELEVATIONAL VARIATION IN FOREST STRUCTURE AND ABOVEGROUND PRODUCTIVITY

The number of tree stems with a dbh $\geq$ 5 cm varied between 28 and 110 per 400 m^2 in the 80 studied plots (700 to 2750 ha^{-1}) and seemed to increase slightly from 500 to 1000 elevation to decrease again higher upslope (Fig. 3.2A). If only the stems $\geq$ 10 cm dbh are considered, the variation among the plots was less, revealing a maximum at 1000 m (mean density: 864

stems ha^{-1}). The contribution of larger-diameter stems (dbh $\geq$ 30 cm) to all stems of a plot ranged between 15 and 23% at all 4 elevation levels with no altitudinal trend visible (Fig. 3.4A). Stand basal area (dbh $\geq$ 10 cm) slightly increased from 500 m (40.8 $\pm$ 2.8 m^2 ha^{-1}) to 1500 m (50.5 $\pm$ 2.6 m^2 ha^{-1}) and remained stable higher upslope (Fig. 3.2B). The plot means of wood specific gravity showed a slight but significant decrease from the 500 m level (0.58 $\pm$ 0.01 g cm^{-3}) to the 2000 m level (0.54 $\pm$ 0.01 g cm^{-3}, Fig. 3.2C). Aboveground tree biomass (dbh $\geq$ 10 cm) as calculated from dbh and wood specific gravity revealed a considerable scatter among the each 20 plots at the 4 elevation levels (< 100 to > 900 Mg dry mass ha^{-1}) with no elevational trend visible between 500 and 2000 m (Fig. 3.2D). The AGB means of an elevation level ranged between 306 Mg ha^{-1} at 500 m and 371 Mg ha^{-1} at 1000 m.
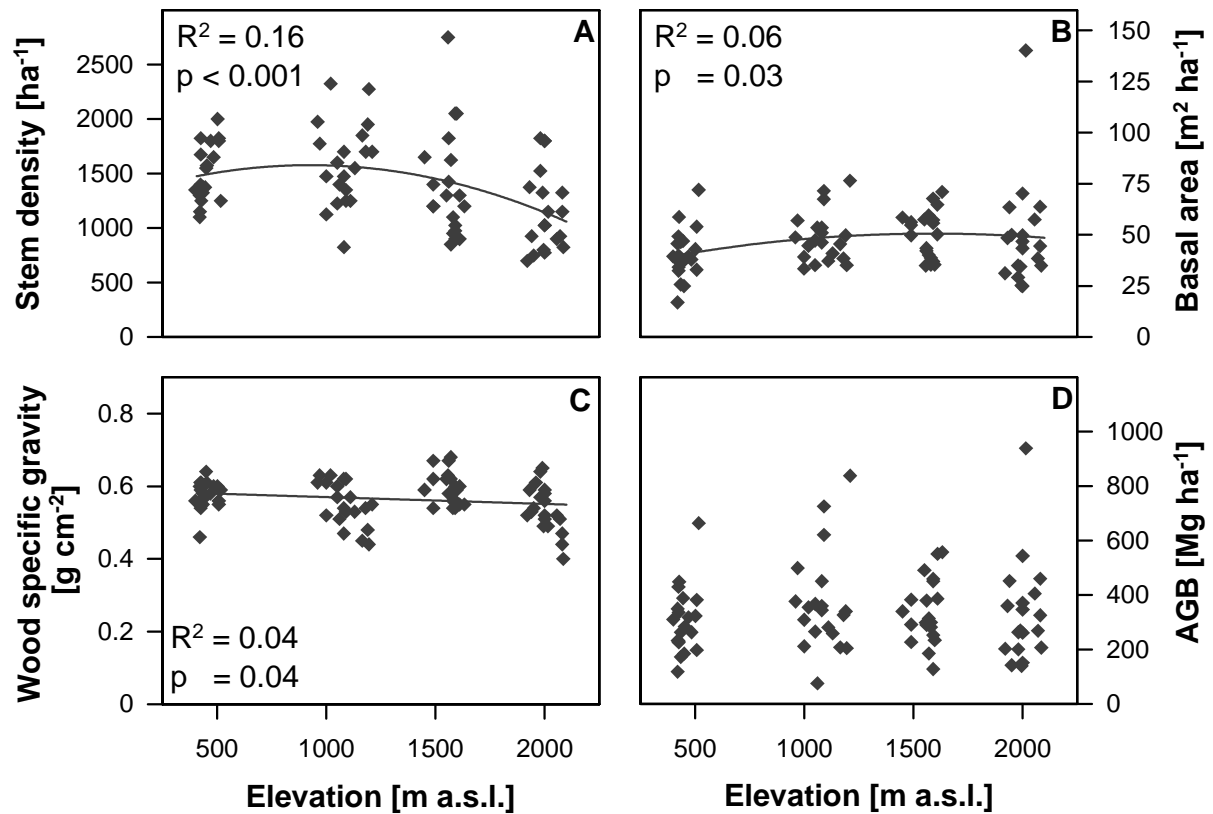
Fig. 3.2. Stem density (A), basal area (B), wood specific gravity (C), and above-ground biomass (AGB) (D) of the 80 study plots as a function of elevation. All stems with a dbh $\geq$5 cm were considered.

Our data revealed no marked elevational trend in the relative contribution of large or small dbh classes to the stand totals of basal area or AGB (Figs. 3.4C and 3.4E). Neither the plot-level means of stem diameter increment nor the plot totals of basal area increment showed significant changes with elevation (Figs. 3.3A and 3.3B). However, both growth parameters

revealed a large among-plot variation at a given elevation (coefficient of variation for 7-9 plots: 31-56% for both parameters). Similarly, the increment of coarse wood biomass (stems and branches) per year varied greatly among the stands (1.2 to 7.6 Mg dry mass ha^{-1} yr^{-1}) with no significant elevational trend existing (Fig. 3.3C).
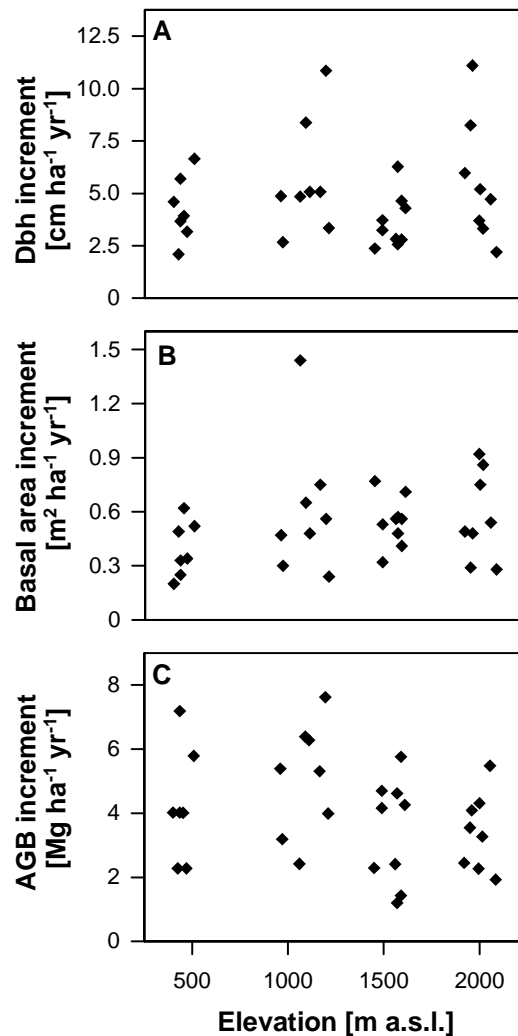
Fig. 3.3. Dbh increment (A), basal area (BA) increment (B), and above-ground biomass (AGB) increment (C) of 32 study plots as a function of elevation. All stems with a dbh ≥5 cm were considered.

As for the biomass components, we found no elevational change in the relative contribution of small- and large diameter trees to the stand total of coarse wood increment (Figs. 3.4B, 3.4D and 3.4F).

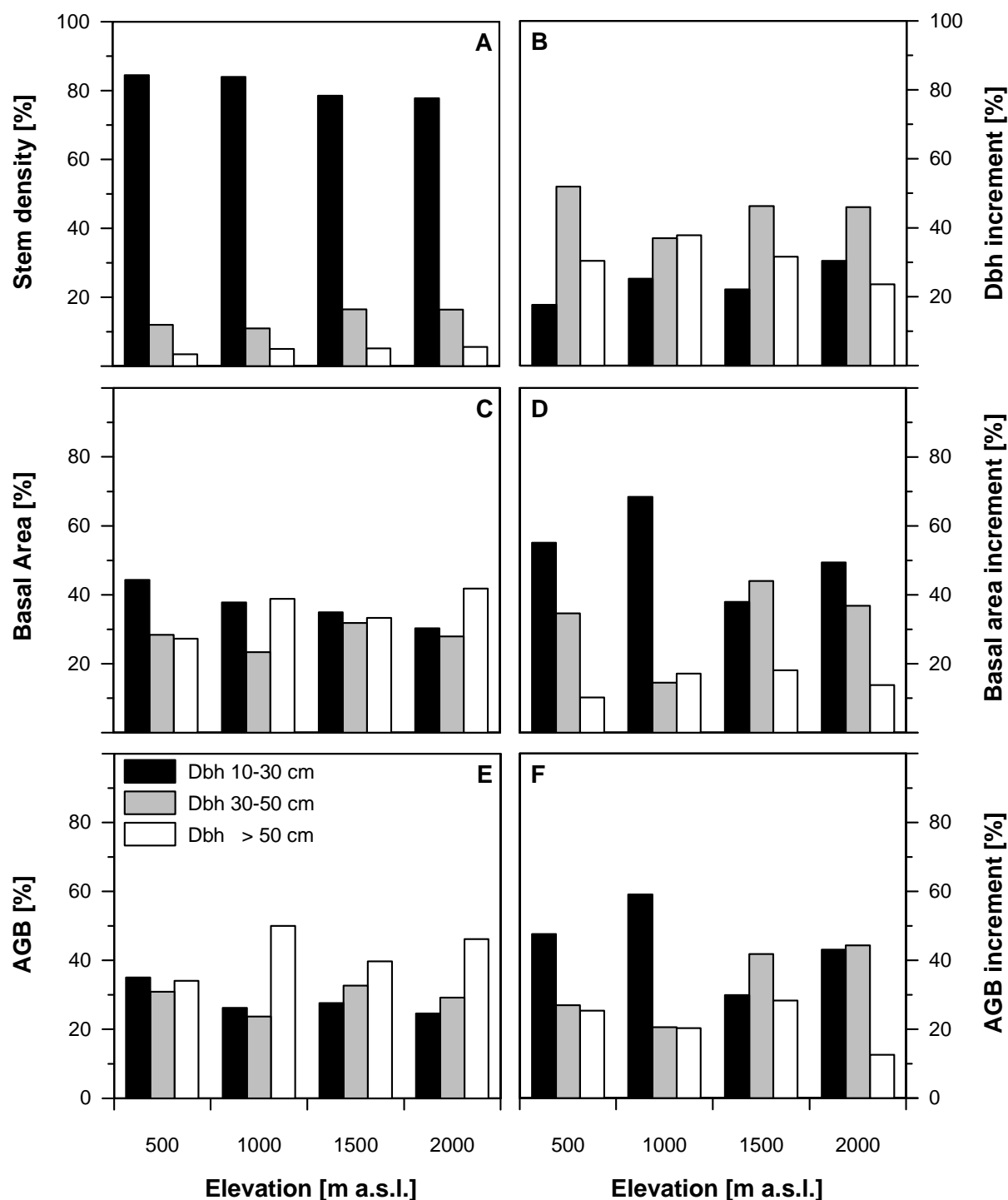**Fig. 3.4.** Percental contribution of three different dbh classes of trees (10-30 cm, 30-50 cm, > 50 cm) to the stand totals of stem density (A), dbh increment (B), basal area (C), basal area increment (D), above-ground biomass (AGB) (E) and AGB increment (F) [in %] at the four elevation levels (n = 80 plots for A, C and E; n = 32 for B, D and F).

Table 3.2. Means ($\pm$ 1 SE) of various soil properties of the organic L, F, H layers and the mineral topsoil (0-10 cm) in the each 20 plots at 500, 1000, 1500 and 2000 m elevation in the SBR transect. N_t - total nitrogen, K_{ex}, Mg_{ex}, Ca_{ex}, Al_{ex} - NH$_4$Cl-exchangeable concentrations of K, Mg, Ca and Al, P_a - available P fraction according to the resin-bag method, P_t - total P. Different small letters indicate significant differences between the elevations. The N mineralization measurements were conducted in 10 cm deep cores of the topsoil horizon consisting of the organic L, F, H layers of variable depth plus the underlying mineral topsoil. The mean of Ca/Al ratio was calculated by averaging over the 20 plot means of Ca/Al ratio per elevation. [a] - extrapolated to a full year.

	Elevation (m)			
Parameter	**500**	**1000**	**1500**	**2000**
Organic L, F, H layers				
Depth organic layer [cm]	1.58 ± 0.21 [a]	2.39 ± 0.31 [a]	6.34 ± 0.47 [b]	5.34 ± 0.32 [b]
pH$_{KCl}$	4.66 ± 0.56 [a]	5,28 ± 0.65 [a]	3.86 ± 0.46 [b]	4.69 ± 0.57 [a]
N_t [mmol g^{-1}]	0.58 ± 0.03 [a]	1.26 ± 0.07 [b]	1.57 ± 0.05 [c]	1.59 ± 0.04 [c]
C/N ratio [mol mol^{-1}]	14.68 ± 0.39 [a]	15.67 ± 0.31 [a]	14.95 ± 0.44 [a]	14.66 ± 0.27 [a]
K_{ex} [µmol g^{-1}]	6.69 ± 0.57 [a]	12.95 ± 0.70 [b]	13.05 ± 1.28 [b]	20.77 ± 2.31 [c]
Mg_{ex} [µmol g^{-1}]	32.47 ± 3.28 [a]	47.39 ± 2.52 [ab]	36.06 ± 3.26 [a]	54.05 ± 5.39 [b]
Ca_{ex} [µmol g^{-1}]	136.07 ± 12.18 [a]	275.38 ± 39.22 [b]	146.13 ± 20.78 [a]	250.15 ± 22.18 [b]
Al_{ex} [µmol g^{-1}]	18.91 ± 3.34 [a]	62.59 ± 17.78 [ab]	73.64 ± 9.06 [b]	50.76 ± 8.26 [ab]
Ca_{ex}/Al_{ex} ratio [mol mol^{-1}]	9.68 ± 1.93 [ab]	17.10 ± 8.72 [b]	3.76 ± 1.22 [a]	6.00 ± 1.24 [a]
P_a [µmol g^{-1}]	0.59 ± 0.12 [a]	1.91 ± 0.44 [a]	2.88 ± 0.49 [a]	7.29 ± 1.49 [b]
P_t [µmol g^{-1}]	100.94 ± 12.05 [a]	78.98 ± 9.53 [a]	75.55 ± 5.84 [a]	77.5 ± 5.13 [a]
Mineral soil (0–10 cm)				
pH$_{(KCl)}$	4.08 ± 0.42 [a]	4.47 ± 0.54 [b]	4.44 ± 0.46 [bc]	4.51 ± 0.47 [c]
N_t [mmol g^{-1}]	0.20 ± 0.01 [a]	0.51 ± 0.05 [b]	0.56 ± 0.03 [b]	0.58 ± 0.02 [b]
C/N ratio [mol mol^{-1}]	10.24 ± 0.19 [a]	11.92 ± 0.23 [b]	13.11 ± 0.33 [c]	11.85 ± 0.19 [b]
K_{ex} [µmol g^{-1}]	1.72 ± 0.17 [a]	2.54 ± 0.16 [b]	1.64 ± 0.15 [a]	1.86 ± 0.20 [a]
Mg_{ex} [µmol g^{-1}]	5.70 ± 0.53 [ab]	7.56 ± 0.85 [a]	4.51 ± 0.56 [b]	4.73 ± 0.70 [b]
Ca_{ex} [µmol g^{-1}]	14.22 ± 2.08 [a]	41.28 ± 11.97 [a]	21.96 ± 4.10 [a]	30.35 ± 7.45 [a]
Al_{ex} [µmol g^{-1}]	44.85 ± 5.29 [a]	57.20 ± 7.76 [a]	44.33 ± 3.55 [a]	40.48 ± 5.70 [a]
Ca_{ex}/Al_{ex} ratio [mol mol^{-1}]	0.63 ± 0.24 [a]	2.23 ± 1.32 [a]	0.54 ± 0.12 [a]	1.23 ± 0.32 [a]
P_a [µmol g^{-1}]	0.10 ± 0.04 [a]	0.36 ± 0.08 [a]	0.43 ± 0.15 [a]	1.20 ± 0.31 [b]
Topsoil horizon				
N net mineraliz. rate [nmol N g^{-1} d^{-1}]	100 ± 11 [a]	105 ± 24 [a]	115 ± 25 [a]	107 ± 12 [a]
N net mineraliz. [kg N ha^{-1} yr^{-1}][a]	572.61±59.29 [a]	310.91±73.08 [b]	266.98±53.53 [b]	311.02±38.36 [b]
Net nitrification rate [nmol N g^{-1} d^{-1}]	94 ± 9 [a]	110 ± 23 [a]	128 ± 16 [a]	96 ± 12 [a]
Net nitrification [kg N ha^{-1} yr^{-1}][a]	534.40±52.70 [a]	335.85±68.39 [ab]	298.99±32.19 [b]	280.06±36.40 [b]

3.4.2 TOPOGRAPHIC AND ELEVATIONAL VARIATION IN SOIL CHEMICAL PROPERTIES

Most of the 23 investigated soil chemical and morphological properties showed a moderate to high variability among the 20 plots per elevation level (Table 3.2). Significant increases with elevation between 500 and 2000 m were detected for the thickness of the organic layers ($r^2 = 0.48$, $p < 0.001$), and the organic layer concentrations of total nitrogen (N_t; $r^2 = 0.73$, $p < 0.001$), plant-available phosphorous (P_a, resin-bag method; $r^2 = 0.30$, $p < 0.001$) and exchangeable K ($r^2 = 0.38$, $p < 0.001$), Mg ($r^2 = 0.12$, $p < 0.001$), Ca ($r^2 = 0.04$, $p < 0.04$) and Al ($r^2 = 0.08$, $p < 0.005$), while the C/N ratio of the organic L, F, H layers remained invariant across elevation. In the mineral topsoil (0-10 cm horizon), significant elevational increases were detected for the C ($r^2 = 0.48$), N_t ($r^2 = 0.54$) and P_a concentrations ($r^2 = 0.20$) (in all cases: $p < 0.001$), while the exchangeable cation concentrations showed no clear elevational trend. No significant trends with elevation were also found for the dry mass-related net release rates of NH_4^+, NO_3^- and the associated N net mineralization rate (Table 3.2).

The PCA on the variation in soil chemical properties among the 80 plots identified three major axes in runs conducted separately for the organic layers (axes OL1 to OL3) and the mineral top soil (axes MB1 to MB3). In the analyses conducted in the combined topsoil horizon (organic layers plus part of mineral soil), two major axes were detected (axes TS1 and TS2). These axes explained more than 70 % of the total variance in all three analyses. The most characteristic soil chemical properties according to their loading on the 8 axes are listed in Table 3.3 separately for the three soil compartments investigated.

3.4.3 RELATIONSHIPS BETWEEN SOIL CHEMISTRY AND FOREST STRUCTURE AND PRODUCTIVITY

We applied a three-level approach for analysing the dependence of forest structure and tree growth on soil chemistry: first, by conducting one-factorial linear regressions of soil chemical parameters on stand structure and growth parameters, second by controlling for elevation, using partial correlation analyses (Table 3.4), and third by identifying significant influential edaphic factors, aggregated with PCA, through a backward multiple regression analysis (Table 3.5).

The regression analyses indicated that increment of stem diameter and basal area on the plot level were both positively correlated with the exchangeable concentrations of Ca in the organic layers; further, dbh increment was correlated with Mg_{ex} and plant-available P.

Table 3.3. Results of principal components analyses (PCA) on the importance of soil chemical and morphological parameters (see Table 3.2) conducted separately for the organic layer horizons, the mineral topsoil, and a combined topsoil horizon in 80 forest stands of NE Ecuador. Given are the eight principal components (eigenvectors) identified in the three groups of variables and the related factor loadings. The most characteristic variables (according to their loading) of each PCA axis are printed in bold.

Eigenvectors			
Organic L, F, H layer variables	**OL 1**	**OL 2**	**OL3**
Percent of variance explained	39.7	23.4	13.5
pH$_{KCl}$	- 0.132	**- 0.903**	0.133
C$_t$	**-0.816**	0.503	0.070
N$_t$	**- 0.765**	0.532	0.161
C/N-ratio	- 0.352	0.014	**- 0.739**
K$_{ex}$	**- 0.885**	- 0.027	0.001
Mg$_{ex}$	**- 0.818**	- 0.360	0.052
Ca$_{ex}$	**- 0.646**	- 0.562	0.152
Al$_{ex}$	- 0.022	**0.718**	0.419
P$_a$	**- 0.769**	- 0.103	0.334
P$_t$	0.346	- 0.122	**0.667**
Mineral soil (0-10 cm) variables	**MB 1**	**MB 2**	**MB 3**
Percent of variance explained	33.9	23.6	16.5
pH$_{KCl}$	0.563	- 0.189	**0.629**
C$_t$	**0.970**	0.109	- 0.108
N$_t$	**0.962**	0.010	- 0.038
C/N-ratio	**0.739**	0.328	- 0.202
K$_{ex}$	0.158	- 0.545	- 0.676
Mg$_{ex}$	- 0.138	**- 0.817**	- 0.341
Ca$_{ex}$	0.243	**- 0.848**	0.150
Al$_{ex}$	0.263	0.340	**- 0.591**
P$_a$	0.388	- 0.414	0.293
Topsoil variables	**TS 1**	**TS 2**	
Percent of variance explained	42.7	32.7	
Depth of organic layers	- 0.365	**0.813**	
Soil bulk density	0.427	**-0.792**	
N net mineralization rate	**- 0.940**	- 0.336	
Net ammonification rate	- 0.456	- 0.467	
Net nitrification rate	**- 0.852**	- 0.123	

Table 3.4. Results of simple and multiple regression analyses on the influence of 22 soil parameters (source) on 5 stand structural and productivity variables determined in 80 (or 31) plots at all four elevations levels (see Table 3.1). Given are the Pearson correlation coefficients for the simple regression analysis (one independent variable; left side of crossbar) and the multiple regression analysis (two independent variables: soil parameter and elevation; right side of crossbar) together with the significance levels (*: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$). Significant relationships are printed in bold. N = 80 for the structural data, and n = 31 for the productivity data. For units of source variables see Table 3.2.

Source	BA	AGB (Mg ha^{-1})	Dbh inc. (cm yr^{-1})	BA inc. (m^2 ha^{-1} yr^{-1})	AGB inc. (Mg ha^{-1} yr^{-1})
Organic L, F, H layers					
Depth organic layer	0.05/-0.12	-0.08/-0.16	-0.03/-0.28	0.06/**-0.32***	**-0.31***/-0.24
pH$_{KCl}$	-0.12/-0.03	-0.07/-0.03	0.21/0.05	0.03/0.12	0.17/0.13
N$_t$	**0.22***/0.08	0.08/0.07	0.21/**0.56***	0.26/-0.09	0.05/**0.39***
C/N ratio	-0.01/0.03	0.14/0.17	-0.01/0	0/0.01	-0.03/-0.04
K$_{ex.}$	**0.29**/0.33****	**0.21***/**0.33****	0.23/0.13	0.21/0.18	-0.05/0.10
Mg$_{ex.}$	0.17/**0.21***	0.13/**0.21***	**0.36***/**0.48***	0.27/**0.40***	0.29/**0.37***
Ca$_{ex.}$	**0.21***/**0.21***	0.14/0.16	**0.42**/0.39***	**0.35***/0.18	0.21/0.29
Al$_{ex.}$	0.14/0.09	0.09/0.08	-0.14/-0.01	-0.03/0.02	0.04/0.07
P$_a$	0.12/0.08	0.05/0.09	**0.35***/**0.48***	0.27/**0.66****	0.15/**0.37***
P$_t$	0.07/0.11	-0.01/0	0.01/0.06	0.17/-0.09	-0.01/0.02
Mineral soil (0 – 10 cm)					
pH$_{KCl}$	0.12/0	-0.06/-0.12	0.20/0.17	0.08/**-0.33***	-0.07/0.10
N$_t$	0.17/0.03	0.12/0.12	0.08/0.11	0.23/-0.07	0.04/0.24
C/N ratio	0.02/-0.11	0.04/0	-0.20/-0.30	0.08/-0.13	-0.16/-0.09
K$_{ex.}$	0.18/**0.19***	**0.28**/0.28****	-0.17/-0.20	0.11/0.16	-0.09/-0.08
Mg$_{ex.}$	0.04/0.12	0.13/0.18	-0.03/0.06	0.10/-0.02	0.06/0.03
Ca$_{ex.}$	0.04/0.07	0.01/0.05	0.14/0.12	**0.35***/0.07	-0.02/0.04
Al$_{ex.}$	0.01/0.03	0.10/0.11	-0.01/0.08	-0.03/**0.31***	0.18/0.16
P$_a$	-0.02/-0.08	-0.02/0.01	0.14/0.08	0.11/**0.46****	0.14/0.25
Topsoil horizon (organic layers and part of uppermost mineral soil)					
Soil bulk density	-0.10/0.10	-0.02/0.04	0.05/0.04	-0.11/**0.37***	0.15/0
N mineralization rate	0.05/0.02	0.07/0.06	-0.05/0.06	-0.17/-0.08	0.12/0.15
N ammonificat. rate	-0.15/-0.15	-0.02/-0.01	-0.03/-0.02	-0.26/0.02	0.11/0.10
N nitrification rate	0.15/0.12	0.09/0.07	-0.06/0.08	-0.06/-0.12	0.08/0.14

The partial correlation revealed P_a, Mg_{ex} and N_t concentrations of the organic layers to be the only soil factors influencing coarse wood biomass growth (Table 3.4).

K_{ex}, Mg_{ex}, Ca_{ex}, P_a and N_t of the organic layers were identified by the PCA analysis as being most characteristic for the OL1 axis (organic layers run, Table 3.3); this axis significantly influenced basal area, AGB and tree dbh increment (Table 3.5).

Table 3.5. Results of backward multiple regression analyses on the effects of the eight axes (24 variables) listed in Table 4.4 on 7 stand structural and productivity variables determined in 80 (or 31) plots at all four elevation levels. Presented are the final models with only the variables with a significant influence ($p \leq 0.05$) on the dependent variable included.

Dependent variable	Model r^2	Independent variable (PCA axis)	Parameter estimate	Standard error	t-value	p-value
Stem density	0.35	OL 2	113.62	30.12	14.23	< 0.001
		MB 1	-88.47	26.37	11.25	0.001
		MB 3	-147.45	31.58	21.80	< 0.001
Basal area	0.09	OL 1	-2.84	1.02	7.73	0.007
AGB	0.11	OL 1	-21.53	9.41	5.24	0.025
		MB 3	-32.27	13.82	5.45	0.022
D.b.h. increment	0.13	OL 1	-0.02	0.01	4.40	0.045
Basal area increment		no variable with significant influence				
AGB increment		no variable with significant influence				

3.5 DISCUSSION

3.5.1 VARIATION IN FOREST ABOVEGROUND STRUCTURE

Our investigations in 80 forest plots revealed a much larger scatter of the stem density and AGB data across the studied topographic, edaphic and elevation gradients than of the basal area data. We calculated AGB means of 306, 371, 340 and 328 Mg ha^{-1} for the 500, 1000, 1500 and 2000 m elevation level using dbh and wood density data of the species. Because we

avoided larger canopy gaps during plot selection, our AGB calculation most likely overestimates forest-wide aboveground biomass. This is reflected in a comparison of our mean AGB value of the 80 plots (336 Mg ha^{-1}) with Neotropical lowland forests which reach AGB values from 200 to 360 Mg ha^{-1}, with the highest values (320 to 360 Mg ha^{-1}) reported from Central Amazonian forests (de Castilho *et al* 2006, DeWalt *et al.* 2004, Baker *et al.* 2004, Laurance *et al.* 1999, Malhi *et al.* 2006), and is also evident from the relatively high stand basal area in our sample relative to average values between 25 and 35 m^2 ha^{-1} reported from two large data sets from Amazonian old-growth forests (Baker *et al.* 2004, Malhi *et al.* 2006). According to the analysis of Keeling & Philips (2007), the tropical forests of the world typically do not have AGBs higher than 350 Mg ha^{-1}; a notable exception are South-east Asian dipterocarp forests reaching AGB values of more than 450 Mg ha-1 (e.g. Slik *et al.* 2010: Borneo).

In contrast to several other transect studies in tropical mountains (e.g. Weaver & Murphy 1990, Raich *et al.* 1997, Aiba & Kitayama 1999, Moser *et al.* 2008), we found no significant altitudinal trend in AGB between 500 and 2000 m elevation in NE Ecuador. Despite a significant reduction in stem density, stand basal area slightly increased between 500 and 2000 m in our transect (from about 40 to 50 m^2 ha^{-1}), thereby compensating for the negative effect of lowered tree height on AGB along the slope. A missing elevation effect on AGB was recently also reported by Culmsee *et al.* (in press) for an altitudinal transect in pre-montane to upper montane forests on Sulawesi, where members of Fagaceae and southern hemispheric conifers with high biomasses play a significant role at higher elevations. A corresponding phylogeographic explanation cannot be given for the NE Ecuadorian transect. Furthermore, the distribution of tree individuals to different diameter classes did not vary with elevation which makes altitudinal shifts in demographic patterns unlikely.

3.5.2 VARIATION IN STEM GROWTH

Comparative productivity measurements in many tropical forest plots have only rarely been conducted because of the considerable labour effort required. We measured stem diameter increment in a total of 32 plots with more than 1000 trees and expressed the growth as aboveground wood mass increment (stem and branch wood) in order to obtain a rough short-term measure of aboveground productivity in forest stands existing under contrasting topographic, edaphic and elevation conditions. Clearly, coarse wood increment is only one component of the aboveground biomass production of trees, besides the production of new leaves, flowers and fruits and the growth of small-diameter twigs. These components may

contribute with more than 50% to aboveground productivity in tropical forests (Clark *et al.* 2001a), but they could not be measured in our study. Thus, our coarse wood production data may allow to compare the carbon sequestration in 'slow' C pools such as wood biomass, but they may give only a rough picture of the variation in aboveground primary production across the stands.

Due to the small size of our plots (400 m^2) and the relatively short dendrometer monitoring intervals, we ignored tree mortality in our productivity calculations (following Clark *et al.* 2001b). Further, we neglected the productivity of the understorey vegetation which typically comprises less than 3% of the forest's aboveground biomass in tropical moist forests (Brown 1997). With this approach we found a more than fivefold variation in annual wood biomass production among the 7-9 stands of an elevation level (1.2-7.6 Mg ha^{-1} yr^{-1}) which may reflect local differences in topography, soil fertility, soil moisture, stand structure and demography, or species composition. Coarse wood production of the 32 stands averaged at 4.0 Mg ha^{-1} yr^{-1}, which is in the lower range of coarse wood productivity values reported by Malhi *et al.* (2004) for Neotropical lowland forests. This it not surprising since we omitted fast-growing early-successional stands in our set of plots.

No productivity decrease was observed between 500 and 2000 m elevation despite a decline in mean air temperature by about 8.6 K. The annual AGB increment accounted for 1.6 + 0.2% of standing aboveground biomass which concurs well with the results reported by Clark *et al.* (2001a) who assumed that AGB increment should be about 1-2% of standing biomass in tropical old-growth forests.

3.5.3 RELATIONSHIPS WITH SOIL NUTRIENTS

Our study revealed significant relationships between basal area, AGB, and coarse wood growth, and several parameters characterizing soil nutrient availability. The closest correlation with tree growth was found for plant available P and exchangeable Mg (and partly Ca) in the organic layers, while the static parameters basal area and AGB were only influenced by organic layer Mg_{ex} and K_{ex},(and partly Ca_{ex}) but not by P_a. In contrast, the nutrient concentrations of the mineral topsoil were found to be much less influential. The dominant role of the nutrient status of the organic layers matches with the findings of Leuschner *et al.* (2007) and Moser *et al.* (unpubl. results) in S Ecuadorian mountain forests revealing that the highest tree fine root biomasses per soil volume occur in the organic top layers where the trees must take up a large part of the nutrients. A surprise is the negligible influence of soil N status on tree biomass and growth: neither N mineralization rate nor soil

C/N ratio were significantly correlated with any of the biomass and growth parameters. Only the N_t concentration of the organic layers correlated with basal area and growth, despite the fact that N_{min} and C/N ratio are in most cases much better measures of N availability to plants than the N_t concentration in the organic material (Ellenberg & Leuschner, in press).

Partial correlation analyses of vegetation parameters with soil fertility, after controlling for the effect of elevation (which itself may influence nutrient availability), yielded tighter correlations in most cases.

How soil nutrient availability affects the stand structure and productivity of tropical forests has been investigated in only a few studies. Our results contrast with the findings of Wilcke *et al.* (2008) in a S Ecuadorian montane forest; this study identified N_t concentration in the organic layers (together with lignin concentration) as the soil chemical variables with largest influence on tree diameter growth, while the P_t and cation concentrations of the organic layers and the mineral soil base saturation had only a small effect on stem growth.

In a Bornean lowland forest, Paoli *et al.* (2008) found significant relationships between extractable P and K in the topsoil and AGB (in particular for the tallest emergent trees), while the N_t influence was not significant. These authors investigated biomass but not growth parameters. Other authors reported contrasting results on the soil chemistry – forest biomass relationship which may have several reasons, among them regional contrasts in the spatial variability of soil fertility in the study region, or different methods used by the authors for characterizing soil nutrient availability in tropical forests, in particular the plant-availability of N and P.

The role of available P as a prominent soil factor influencing forest structure and growth in NE Ecuador (see Fig. 3.5) and W Borneo can be interpreted as support for the hypothesis that the productivity of tropical lowland forests is primarily limited by P, while N is often relatively high in supply in lowland sites (Vitousek 1984). This prediction matches with our finding that a relationship between N mineralization rate and forest biomass or growth was absent even in the low-elevation forests of our sample. However, in contrast to this hypothesis, Laurance *et al.* (1999) found a stronger co-variation by soil N than soil P with the aboveground biomass of Amazonian lowland forests. For forests at higher elevations, the hypothesis of Vitousek (1984) predicts a shift from P to N limitation of tree growth because soil biological activity and decomposition rate should be lower in the cooler climate of mountain forests, reducing N mineralization rate. In our data set, however, a significant effect of N supply rate on biomass and productivity was not detected, neither at 500 m nor at 2000 m elevation, while the dominant influence of P_a prevailed from upper lowland to montane

elevation contradicting the hypothesis. Our data match with the observation of Unger *et al.* (submitted) in the Sumaco region that mass-related N net mineralization rate does not decrease with elevation between 500 and 2000 m, and Nmin rate per stand ground area decreases only by about 40%. The variation in N supply across different elevations and topographic micro-sites seems to be smaller than the variability of available P in this part of the equatorial Andes.
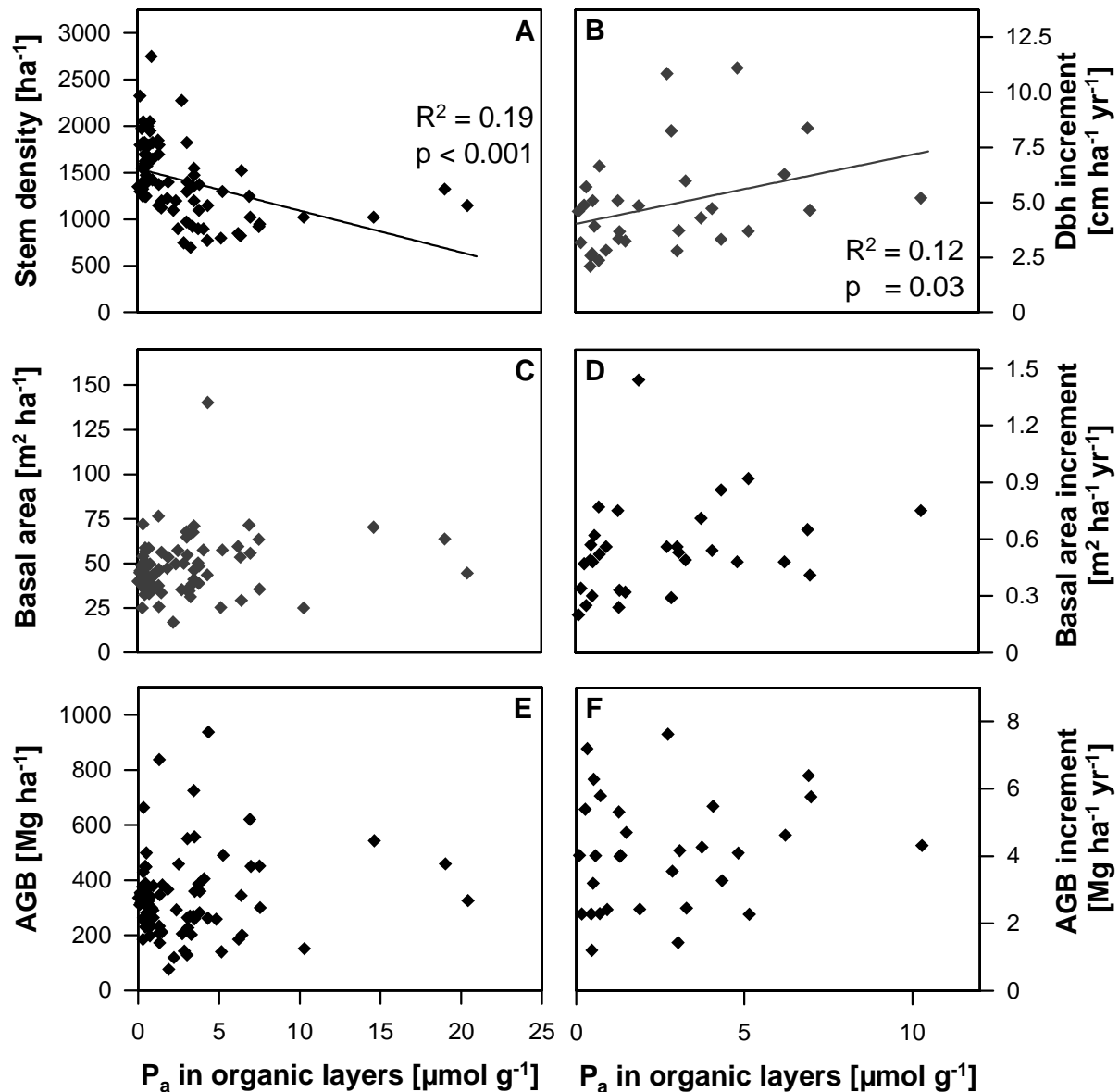

Fig. 3.5. Relationship between stem density (A), dbh increment (B), basal area (C), basal area increment (D), above-ground biomass (AGB) (E) and AGB increment (F) and the concentrations of plant-available phosphorus (P_a) in the organic L, F, H layers of the soil according to simple linear regression analyses (n = 79 for A, C and E; n = 31 for B, D and F). When elevation was included as a covariable, the P_a dependence of AGB increment was significant (see Table 3.4).

Even though our data indicate a nutrient effect on forest structure and productivity, they do not prove it. Other covarying environmental factors, notably soil moisture, could well be more influential than soil chemistry, but were not investigated. The observation of Paoli *et al.* (2008) that tallest trees are occurring on nutrient-rich alluvial soils in western Kalimantan does not necessarily reflect a nutrient effect, but could perhaps also be a consequence of a lower frequency of drought periods in the alluvial soils, thereby promoting tree height growth.

Fertilization or moisture manipulation studies, or correlative studies with a more complete set of environmental variables investigated would be needed to draw more safe conclusions on the role of soil nutrient availability for the structure and functioning of tropical forests. Because studies investigating the co-variation of biomass and productivity with both soil fertility and soil moisture are lacking so far for tropical forests, this question cannot be answered satisfactorily.

We conclude that tropical forest soils on the eastern slope of the equatorial Andes are characterized by a large spatial heterogeneity in the plant-availability of the five key nutrients, i.e. P_a, exchangeable Ca, Mg and K concentrations, and inorganic N supply rate (N_{min} and N_{nitr}). According to the analysis Unger *et al.* (submitted.), these parameters were more variable across topographic and pedologic gradients at a given elevation than across our 1500-m elevation transect. P_a and Mg_{ex} were the nutrient species that covaried strongest with tree coarse wood growth; these two elements could control tree productivity at both lowland and premontane to lower montane elevations. Stand basal area and AGB, which may be influenced by both productivity and tree longevity, covaried primarily with the exchangeable concentrations of Mg, Ca and K in the organic layers, but not by P_a. The availability of N (expressed by the in situ Nmin and Nnitr rates and the C/N ratio) had a surprisingly small influence on forest biomass and productivity, both at lowland and lower montane elevation, thereby contradicting the hypothesis of increasing N limitation of tree growth with elevation in tropical mountain forests. We raise some doubts as to whether the covariation of soil chemical and stand structural or biomass parameters may be interpreted in the direction of a causality because other important environmental factors (notably soil moisture) were not addressed by our study.

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CHAPTER

4

RELATIONSHIPS AMONG LEAF AREA INDEX, BELOW-CANOPY LIGHT AVAILABILITY AND TREE DIVERSITY ALONG A TRANSECT FROM TROPICAL LOWLAND TO MONTANE FORESTS IN NE ECUADOR

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4.1 ABSTRACT

We tested the hypotheses that, with elevation, leaf area index (LAI) decreases, and diffuse transmittance of photosynthetically active radiation (DT) increases, and that tree species diversity and stem density both have a positive effect on LAI and a negative effect on percent diffuse transmittance of PAR. 80 old-growth tropical forest stands were selected at 500, 1000, 1500 and 2000 m elevation in the Sumaco Biosphere Reserve on the eastern slope of the equatorial Andes. We measured LAI and synchronously recorded DT on the forest floor, and related the plot-level means to data on tree diversity, stem density and soil properties of the plots. LAI decreased significantly with elevation by about $1.1\ m^2\,m^{-2}$ per 1000 m altitude, reaching means of about 6.6 at 500 m and 5.2 at 2000 m a.s.l. DT increased significantly with elevation, revealing a tight negative correlation to LAI. Below canopy DT averaged 2.1% at 500 m and 4.0% at 2000 m (relative to incident radiation).

Tree species diversity and stem density had a significant positive effect on LAI and a negative effect on DT. The observed LAI decrease with elevation is a consequence of both an altitudinal decrease in stem density and a decrease in tree species diversity combined with an effect of soil fertility (C/N ratio of the upper mineral soil and plant-available P of the organic layers).

4.2 INTRODUCTION

Of all environmental factors affecting plants, light is probably the most spatially and temporally heterogeneous. The light heterogeneity in space is particularly important in tropical forests where unfavourable temperatures are less significant for plant life and light is considered to be the single-most limiting resource for plant growth (Pearcy 2007). Tree seedlings and saplings, herbaceous plants and understorey trees have been shown to be closely keyed to variation in below-canopy light availability (Denslow 1987, Strauss-Debenedetti & Bazzaz 1991). Canopy closure and the size and abundance of gaps are, therefore, important factors controlling tree regeneration, forest dynamics and forest diversity (e.g. Richards 1952, Hartshorn 1978, Hubbell 1979, Denslow 1980, Whitmore 1984, Brokaw 1987). In the absence of canopy gaps, canopy species composition can significantly influence light transmittance within and among stands (Messier & Bellefleur 1988, Canham *et al.* 1994, Kabakoff & Chazdon 1996).

How much light is penetrating through the canopy to the forest floor depends largely on the amount of canopy foliage, most often characterized as leaf area index (LAI, the one-sided cumulative leaf area of a stand per ground area). Because it is a dimensionless quantity, LAI can be measured, analysed and modelled across a range of spatial scales, from individual tree crowns to stands, whole regions or continents (Asner *et al.* 1998). The leaf area is the exchange surface between the photosynthetically active component of the vegetation and the atmosphere (Cohen *et al.* 2003, Fournier *et al.* 2003, Turner *et al.* 1999) which controls not only the radiation regime within the canopy, but also the thermal and hydric conditions (Fournier *et al.* 2003). The net primary production of forests, in most cases, is closely correlated to LAI (e.g. Beadle 1997, Asner *et al.* 2003, Battaglia *et al.* 1998, Sullivan *et al.* 1996), while canopy transmissivity typically shows a negative relationship to canopy leaf area (Zhou *et al.* 2002). Moreover, LAI has a strong influence on forest transpiration because canopy conductance for water vapour is proportional to LAI (Whitehead & Jarvis 1981).

Despite its important role in controlling canopy carbon gain and transpirative water loss, not much is known about spatial variation in LAI of tropical forests on a regional or landscape scale. It is assumed that forest LAI is influenced by elevation (or temperature), water availability, soil fertility and topography, but comprehensive studies in forest stands across environmental gradients have mostly focused on temperate biomes (e.g. Bolstad *et al.* 2000, Leuschner *et al.* 2006, Meier & Leuschner 2008). Only recently, a few studies analysed

changes in the LAI of tropical forests along gradients in altitude and soil chemistry (Kitayama & Aiba 2002, Takyu *et al*. 2003, Moser *et al*. 2007).

The possible influence of biotic factors such as tree species diversity, stem density and basal area on LAI and the below-canopy radiation regime has not been investigated in detail in tropical forests.

We conducted a landscape-scale study on the spatial variation of LAI and below-canopy light intensity in a matrix of 80 stands of old-growth tropical moist forests on the eastern slopes of the Andes in Ecuador. The area represents an altitudinal transect of undisturbed forest from lowlands to montane elevation, providing a suitable setting for analysing the effects of altitude and stand structure on LAI and canopy transmissivity. We tested the hypotheses that (i) LAI decreases, and below-canopy light intensity increases, with elevation, (ii) the forest floor of tropical lowland forests is exposed, on average, to lower photon flux densities than tropical montane forests and also temperate forests, and (iii) both tree species density and stem density positively influence LAI while having a negative effect on below-canopy light intensity. This study is part of a more comprehensive investigation on plant diversity patterns and soil fertility in the matrix of 80 forest plots in the Sumaco Biosphere Reserve of NE Ecuador (Homeier *et al.*, in prep., Unger *et al.*, subm.).

4.3 METHODS

4.3.1 STUDY AREA

The study was conducted in the Sumaco Biosphere Reserve (SBR) and its close proximity in the province of Napo, NE-Ecuador. The reserve was established in the year 2000 and is situated on the eastern slopes of the Andes and the adjacent foothills and includes the Sumaco volcano. The area represents the last existing altitudinal transect of undisturbed vegetation from lowlands (400 m a.s.l.) to páramo (3700 m) in the eastern equatorial Andes and harbours probably more than 6000 plant species (Neill & Palacios 1997).

The study sites were allocated to four elevational levels (500, 1000, 1500, and 2000 m) to establish a transect covering 1500 m altitudinal distance (Table 4.1).

Exact data on the annual precipitation of the study sites are lacking, but rainfall in the whole area is likely to exceed 2500 mm year^{-1}. The Sumaco volcano and the Cordillera Guacamayos probably receive more than 4000 mm year^{-1} and throughout the area, monthly precipitation usually never drops below 100 mm (Neill & Jørgensen 1999).

Table 4.1. The 11 study sites with their conservation status, elevation range, number of permanent plots, mean number of stems (dbh $\geq$ 5 cm), stand basal area (dbh $\geq$ 10 cm), mean number of tree species (dbh $\geq$ 5 cm) and rarefied tree species density (N =28 trees per 400 m^2) per plot [400 m^2] (means $\pm$ 1 SE). * one plot per study site was excluded from the final analysis.

Elevation level (m)	Study site	Conservation status	Elevation range (m)	No. of plots	Stem density (400 m^{-2})	Stand basal area	No. of tree species	Rarefied tree species
500	Jatun Sacha	private reserve	400-450	12	55.5±2.4	1.5±0.1	40.5±2.6	22.8±0.5
	Selva Viva	private reserve	445-520	8	66.4±3.5	1.8±0.2	49.4±3.2	24.2±0.5
1000	Hakuna Matata	private reserve	960-1080	6	72.3±5.0	1.8±0.1	43.3±4.3	22.2±0.9
	C. Galeras	national park	1050-1130	9	50.9±2.9	2.0±0.2	35.2±2.9	21.5±1.0
	Rio Hollín	private reserve	1165-1200	5	75.8±4.2	2.0±0.3	28.6±1.8	15.3±0.9
1500	C. Galeras	national park	1450-1600	7	76.4±6.6	1.7±0.1	40.1±2.5	20.2±0.8
	Cocodrilos	national park	1490-1570	5	47.6±3.7	2.2±0.1	28.1±1.2	20.2±0.7
	Sumaco	national park	1580-1630	8	41.8±2.1	2.2±0.2	26.4±0.9	19.8±0.4
2000	Sumaco	national park	1920-2015	6 (7)*	38.3±3.7	2.0±0.2	22.3±2.5	16.9±1.3
	C. Guacamayos	ecological reserve	1940-2000	7 (8)*	57.7±6.2	1.4±0.1	29.4±3.0	19.2±1.3
	Yanayacu	private reserve	2055-2085	5	41.0±3.7	1.9±0.2	19.0±1.0	15.5±0.7

The mean annual temperature decreases from approximately 22.9°C at 415 m (Jatun Sacha biological station) to 14.3°C at 2015 m (Sumaco volcano) (own unpublished data).

The geology is variable in the area. Parent rocks from the Cretaceous, mainly limestone, dominate most of the region, however, at Volcano Sumaco (basalt) and at Hakuna Matata (granite), volcanic and intrusive rocks are present, respectively. Slates are found at Cordillera Guacamayos (Sauer 1971). Though soils are very heterogeneous in our study area, gerric Ferralsols are the dominant soils at our study sites at 500 m and 1000 m and Cambisols are the preponderant soils at our study sites at 1500 m and 2000 m. Further studies of the soils and soil chemistry at our study sites (Unger *et al.*, subm.) indicate that organic matter, total nitrogen and carbon, plant-available phosphorus and extractable calcium content increase with altitude, while N mineralization and nitrification do not show an elevational trend. (see also Table 4.2).

Table 4.2. Soil chemical properties of the studied elevation levels: depth of organic layer horizon, pH_{KCl}, C/N-ratio, and plant-available P (P_a) of the organic layer and the upper mineral soil horizons (0-10 cm) (means ± 1SE). Different letters indicate significant differences.

Parameter	Elevation level			
	500 m	**1000 m**	**1500 m**	**2000 m**
Org. layer depth (cm)	1.58 ± 0.21 [a]	2.39 ± 0.31 [a]	6.34 ± 0.47 [b]	5.34 ± 0.32 [b]
	organic layer horizons			
pH_{KCl}	4.66 ± 0.56 [a]	5.28 ± 0.65 [a]	3.86 ± 0.46 [b]	4.69 ± 0.57 [a]
C/N (mol mol^{-1})	14.68 ± 0.39 [a]	15.67 ± 0.31 [a]	14.95 ± 0.44 [a]	14.66 ± 0.27 [a]
P_a (μmol g^{-1})	0.59 ± 0.12 [a]	1.91 ± 0.44 [a]	2.88 ± 0.49 [a]	7.29 ± 1.49 [b]
	upper mineral soil horizon (0-10 cm)			
pH_{KCl}	4.08 ± 0.42 [a]	4.47 ± 0.54 [b]	4.44 ± 0.46 [bc]	4.51 ± 0.47 [c]
C/N (mol mol^{-1})	10.24 ± 0.19 [a]	11.92 ± 0.23 [b]	13.11 ± 0.33 [c]	11.85 ± 0.19 [b]
P_a (μmol g^{-1})	0.10 ± 0.04 [a]	0.36 ± 0.08 [a]	0.43 ± 0.15 [a]	1.20 ± 0.31 [b]

Following the most recent vegetation classification for Ecuador (Palacios *et al.* 1999), the studied forests at 500 m can be classified as evergreen lowland forests, the stands at 1000 m as evergreen premontane forests, and the upper elevation forests (1500 and 2000 m) as evergreen lower montane forests.

4.3.2 PLOT INSTALLATION AND TREE INVENTORY

Overall, we installed 80 permanent plots (20 m x 20 m size) at the four different altitudinal levels (20 plots per level). The study plots are situated at 11 sites, which belong to nine different localities (Tab. 4.1). The sites were selected with the aim to cover forest stands which are representative for the respective elevation. For plot installation, only areas without any kind of visible human or natural disturbance within mature forest stands were selected in order to study a matrix of old-growth stands along elevational and topographic gradients.

At each site plots were distributed to different topographic conditions to cover the range of ecological conditions. Plot size is small enough to keep environmental factors and forest structure homogeneous within the plots. Our plots are independent sampling units each containing a random sample of 16–45 stems exceeding 10 cm of diameter at breast height (dbh). Mean distances between the plots at one site (calculated from geographical positions) were between 0.1 km (Hakuna Matata) and 1.8 km (Galeras 1500m). In each plot, we counted all stems of living trees with a dbh (diameter at breast height) $\geq$ 5 cm. The diameters of all trees with a dbh $\geq$ 10 cm were measured and their basal areas were calculated (trees with a dbh < 10 cm were not included in basal area calculations). For species determination, we collected voucher specimens of all unknown species with duplicates being deposited at the herbaria QCA and QCNE, Ecuador, and GOET, Germany. Tree diversity was calculated after the individual-based rarefaction method (Gotelli & Colwell 2001) as the number of species (dbh $\geq$ 5 cm) expected in a sample of 28 trees a 400 m² plot (28 being the smallest number of trees found in any one of the 80 plots).

4.3.3 LAI AND PAR MEASUREMENTS

For characterizing the leaf area index (LAI) of the stands, we conducted measurements with the LAI-2000 (LI-COR Inc., Lincoln, NE, USA) plant canopy analyzer, one of the most commonly used instruments to estimate LAI. Even though direct destructive measurements of LAI are mostly believed to be more accurate than indirect optical measurements, the LAI-2000 system has proven to provide LAI values closest to those obtained with leaf harvest methods in tropical forests (Asner *et al.* 2003, Moser *et al.* 2007).

The leaf area measurements with the LAI-2000 system were conducted in the remote mode, i.e. by synchronous readings below the canopy at 2 m height above the forest floor and in nearby open areas ("above-canopy" reading) using two systems.

All measurements were conducted during periods of overcast sky between November 2006 and April 2007. On each plot, 40 individual measurements equally arranged over the plot

were conducted. We divided the 20 m x 20 m plots into four quadrants of 10 m x 10 m size and did 10 measurements each per quadrant. The measuring points were at least 2 m distant to the subplot boundaries and more than 2 m apart from the next point. The measurements in the open were conducted in larger gaps at a distance of not more than 3 km to the plots. To avoid reductions in the sky sector seen by the LAI-2000 fish-eye lens in the open sites as may be caused by high mountains or trees at the horizon, we analysed the data from the three inner rings (0-43° from zenith), following the recommendations of Dufrêne & Breda (1995), and also for the inner ring (0-7° from zenith) only to evaluate the LAI unaffected by the partly incidence of canopy gaps in the vicinity of the plots. By masking rings selectively, we could compare relative light availability (based on gap fraction) at specific zenith angles and thus evaluate the size of canopy gaps (Nicotra *et al.* 1999). Assuming that leaf area index varies only little over time in these equatorial forests (see Rich *et al*. 1993), we ignored seasonality and conducted all LAI and radiation transmissivity measurements only once per plot.

Absolute values of incident and diffuse transmitted photosynthetically active radiation (DT) were obtained with two LI-190 sensors (LI-COR Inc., Lincoln, NE, USA), mounted on the two LAI-2000 instruments. Thus, the LAI-2000 and PPFD measurements were taken synchronously at each of the 40 measuring points per plot in the 80 plots. DT intensity was expressed in percent of the synchronously recorded PPFD in open terrain and averaged over the 40 measuring points of a plot to give a mean value of percent diffuse transmittance in the PAR range. In addition, absolute values of below-canopy PPFD (units: μmol photons $m^{-2}\,s^{-1}$) were used in the analysis.

Measuring LAI and PPFD at this height ignores the vegetation closer to the ground, which can constitute at least one foliage layer. Tropical forests vary substantially in the contribution of this low understory layer to total forest LAI (Montgomery 2004), but seedlings and young trees (< 2m height) are almost negligible concerning biomass or structure of old-growth tropical forests.

4.3.4 DATA ANALYSIS

Linear regression analyses were applied to identify significant relationships between elevation as independent variable and LAI, DT, number of stems (dbh ≥ 5cm), tree diversity, and stand basal area. All regressions were calculated using Xact software (version 8.0; SciLab, Hamburg, Germany). We calculated multiple regressions (stepwise backward variable elimination, including only variables with $p < 0.05$ in the final models) with R 2.8.1 (R Development Core Team 2008) to investigate the relationship of LAI and DT to various soil

parameters, tree basal area, stem density and tree diversity. The canopy of one plot in the Cordillera Guacamayos at 2000 m was heavily disturbed by falling trees shortly after we installed this plot. Therefore, we excluded it from all analyses. Due to the occurrence of several large trees on one plot in the Sumaco area (2000 m), the calculated basal area on this plot was extraordinarily high and most likely misleading, therefore it was also excluded and all analyses were conducted with N = 78 plots.

4.4 RESULTS

4.4.1 STEM DENSITY AND TREE SPECIES RICHNESS

The number of tree stems (dbh ≥ 5cm) per plot ranged from 28 to 110 in the sample of 78 plots considered in the analysis (Table 4.1). The number of stems per plot was 59.9 ± 10.1 (mean ± SD) at 500 m, 63.6 ± 15.1 at 1000 m, 55.4 ± 19.5 at 1500 m and 46.2 ± 15.3 at 2000 m a.s.l. being highest at intermediate elevation (1000 m) and lowest at 2000 m. Stem density showed a significant negative correlation with elevation, but this relation was not tight ($r^2 = 0.09$, $p = 0.004$). In contrast, stand basal area showed no significant elevational trend (mean over the whole transect: 1.8 ± 0.5 m² 400 m^{-2}, Table 4.1). On a one hectar basis, we measured mean basal areas of 40.8 ± 12.3 m² ha^{-1} at 500 m, 48.6 ± 12.1 m² ha^{-1} at 1000 m, 50.5 ± 11.4 m² ha^{-1} at 1500 m, and 44.0 ± 13.5 m² ha^{-1} at 2000 m.

The total number of tree species recorded in all 80 plots (total area: 3.2 ha) was greater than 640 (Homeier *et al*. in prep.). At lower elevations (500 and 1000 m), the most important tree families were Myristicaceae, Moraceae and Euphorbiaceae, whereas Lauraceae and Rubiaceae dominated in terms of species and stem numbers at higher elevations (1500 and 2000 m). The mean number of tree species per plot showed a significant decrease with elevation from 43.4 ± 9.7 at 500 m to 36.1 ± 9.9 at 1000 m, 30.8 ± 7.3 at 1500 m and 23.8 ± 8.0 at 2000 m ($r^2 = 0.41$, $p \leq 0.001$, rarefied tree species $r^2 = 0.38$, $p \leq 0.00$, respectively; see also Table 4.1).

4.4.2 LAI AND DT

Leaf area index significantly decreased with elevation by about 1.1 m^2 m^{-2} per 1000 m from about 6.6 (500 m) to 5.2 at 2000 m (Fig. 4.2). Highest plot-level LAI means were recorded with 8.0 at 1000 m (Hakuna Matata), lowest with 4.2 at 1500 m (Sumaco). The zenith LAI measurements showed a similar trend with elevation ($r^2 = 0.37$, $p \leq 0.001$), correlation was weaker, though.
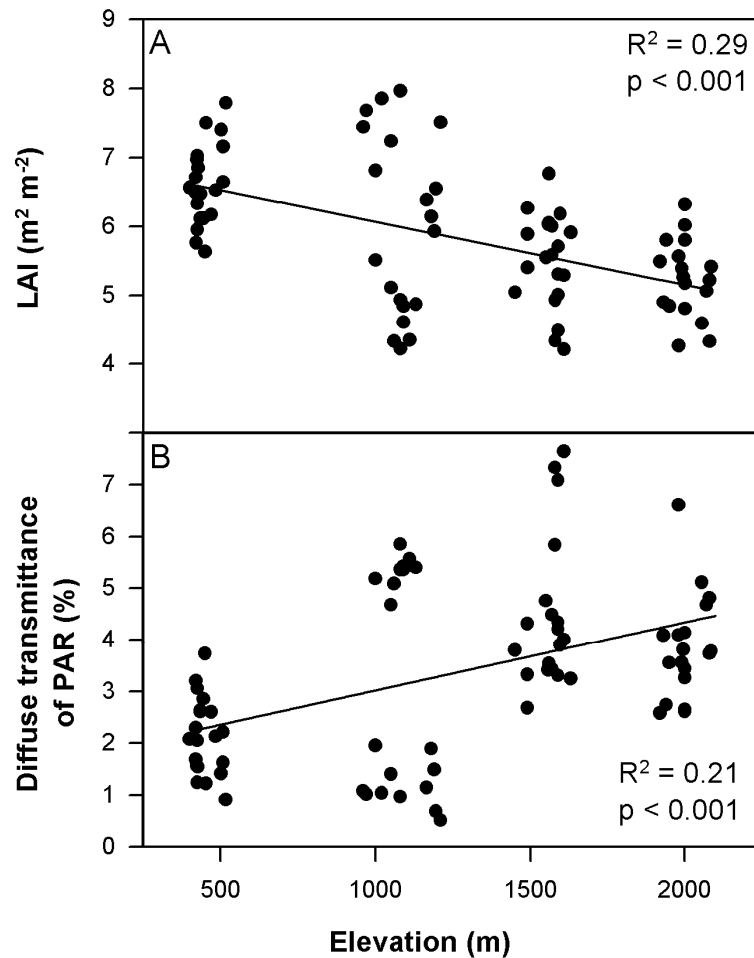
Fig. 4.2. Altitudinal change of (A) LAI and of (B) percent diffuse transmittance of PAR (DT) in the 78-plot sample. DT is given in percent of synchronously measured incident flux density. N = 40 LAI and DT measurements per plot with 20 plots per elevation level (only 18 at 2000 m) were carried out under overcast sky between 10 a.m. and 2 p.m.

The coefficient of variation (based on plot means) of LAI increased with altitude from 11.7% at 500 m to 18.7% at 2000 m (Fig. 4.3). DT generally increased with elevation, revealing an opposite trend as was found for LAI (Fig. 4.2). The lowest plot-level mean of DT was recorded at 1000 m elevation (Rio Hollin, mean = 0.5% of incident radiation), while the highest value was found at 1500 m (Sumaco, mean = 7.6%). In the 20 plots per elevation level, the median of DT varied from 1 to 4% at 500 m, but from 3 to 6.5% at 1500 m. The frequency distribution diagrams of the individual DT values reveal a left-skewed distribution at all four elevations, but more flattened curves with greater abundance of higher DT values at 1500 and 2000 m as compared to the lower elevations (Fig. 4.3B). Synchronous measurements of DT (quantum sensors) and of LAI (LAI-2000 canopy analyzer) gave a tight negative correlation of the two variables ($r^2 = 0.81$, $p \leq 0.001$, Fig. 4.4).
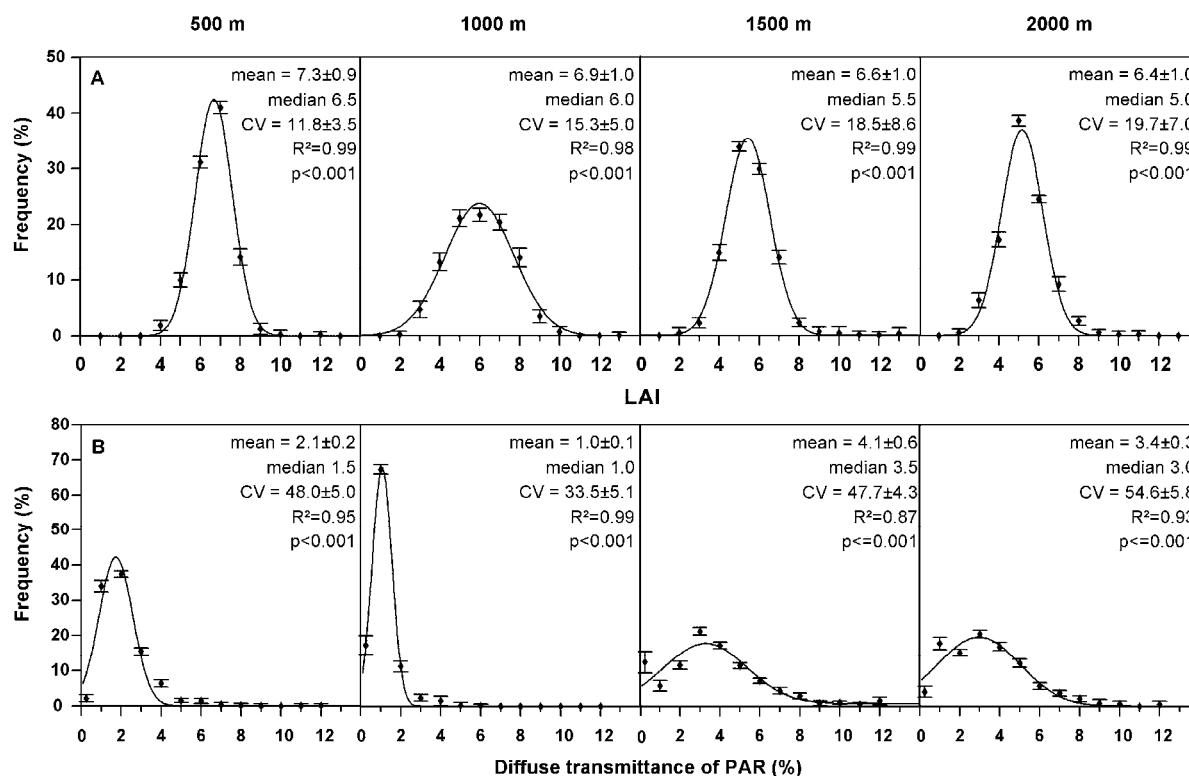
Fig. 4.3. Frequency distribution diagrams for LAI (A) and percent diffuse transmittance of PAR (B) in stands at 500, 1000, 1500 or 2000 m elevation as derived from each 40 measurements per plot in a total of 20 plots per elevation (18 at 2000 m) conducted with the LAI-2000 canopy analyzer or LI-190 quantum sensor (flux density in % of incident radiation). CV = coefficient of variation in % of mean for the 40 individual measurements per plot.
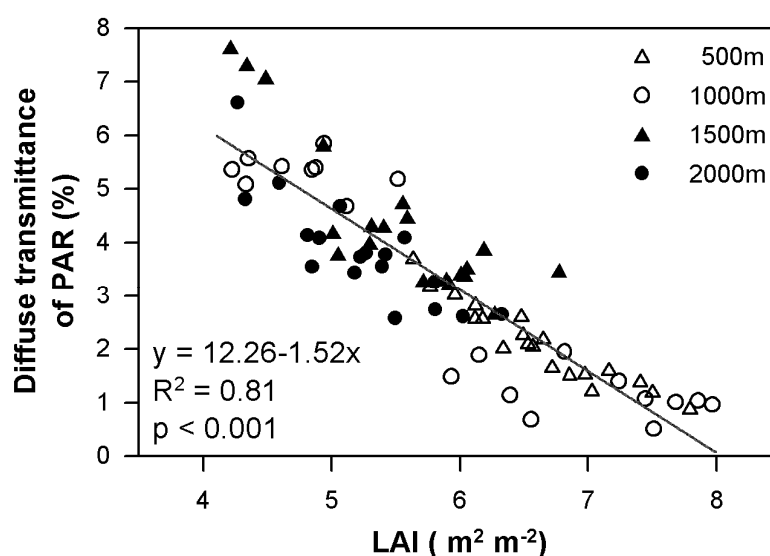

Fig. 4.4. Relationship between synchronously measured LAI (LAI-2000 canopy analyzer measurements) and percent diffuse transmittance of PAR (quantum sensor measurements) in the 78 plots. Measurements were taken under overcast sky between 10 a.m. and 2 p.m.

We observed a significant increase of LAI with stem density across the 78-plot sample ($r^2 = 0.26$, $p \leq 0.001$), while DT decreased ($r^2 = 0.19$, $p \leq 0.001$, Fig. 4.5). Tree diversity affected both parameters in the same way (LAI: $r^2 = 0.16$, $p \leq 0.001$; DT: $r^2 = 0.04$, $p \leq 0.001$) (Fig. 4.6), whereas stand basal area had no significant influence, neither on LAI nor on DT.
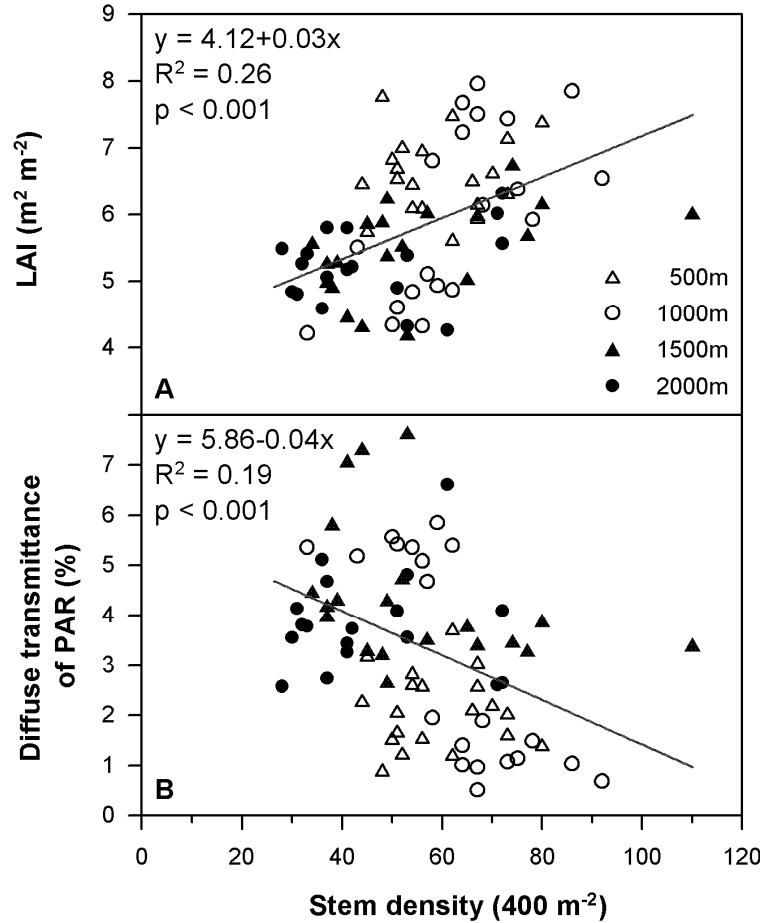

Fig. 4.5. LAI (A) and percent diffuse transmittance of PAR (B) as a function of stem density per plot in the 78 plots (all stems ≥ 5 cm dbh considered).

In addition, we found effects of the plant-available P of the organic layer (LAI: negative; $r^2 = 0.21$, $p < 0.001$; DT: positive; $r^2 = 0.13$, $p < 0.001$) and of the mineral soil C/N ratio (LAI: negative; $r^2 = 0.03$, $p = 0.05$; DT: positive; $r^2 = 0.06$, $p = 0.03$) on LAI and DT, however, the latter relationships were not very tight.

Measurements of PPFD at 2 m above the forest floor showed a significant increase with altitude (Table 4.3). The lowest value of a stand was observed at 1000 m altitude (1.4 ± 0.1 μmol m^{-2} s^{-1}, mean $\pm$ SE) the highest stand mean at 2000 m (67.7 ± 3.6 μmol m^{-2} s^{-1}). The final models of the multiple regression analyses for both LAI and DT yielded the source variables stem density and C/N ratio of the mineral soil as influential parameters, additionally plant-available P of the organic layer was found to influence LAI significantly (Table 4.4).

Table 4.3. Means (± 1SE) of photosynthetic photon flux density (PPFD) at 2m above the forest floor at four different elevations.

Elevation [m]	PPFD [µmol m-2 s-1]
500	11.57 ± 1.46
1000	7.85 ± 0.58
1500	19.33 ± 2.22
2000	35.49 ± 4.48

In addition, the dependence of LAI and DT was analysed on stand structural properties separately for the four elevations, thereby excluding the effect of altitude (data not shown). While the significance of the relationships was generally lower in these sub-samples due to the reduced number of degrees of freedom, some differences between the four elevation levels became evident. While stem density was identified as the only structural variable significantly affecting LAI and DT at the medium elevation levels of 1000 m and 1500 m, it was stand basal area at 500 m. Rarefied tree species density was the only structural variable that influenced LAI and DT significantly at 2000 m elevation.

Table 4.4. Results of multiple regression analyses on the dependence of LAI and DT on various environmental and biotic factors. The following variables were tested: organic layer depth, stem density, stand basal area, tree species diversity, plant-available soil phosphorus concentration, soil C/N-ratio and pH of the organic layer and the upper mineral soil (0-10 cm). Only the significant factors ($p < 0.05$) were included in the final models.

Dependent variable	Model R^2 (adjusted)	Source variable	Parameter estimate	R^2	p
LAI	0.35	Stem density	0.026	0.21	<0.001
		P_a (organic layer)	-0.059	0.12	0.012
		C/N ratio (mineral soil)	-0.182	0.05	0.004
DT	0.27	Stem density	-0.051	0.20	<0.001
		C/N ratio (mineral soil)	0.394	0.09	<0.001

4.5 DISCUSSION

With average leaf area indices between 5.2 and 6.6 at lowland to lower montane elevation (500 to 2000 m), our LAI estimates are somewhat higher than the global means determined by Asner *et al.* (2003) for tropical evergreen forests (4.8-4.9). Our values from NE Ecuador are also higher than values obtained with LAI-2000 measurements in three premontane to lower montane rainforests in South Ecuador (5.1 at 1050 m., 4.6 at 1540 m and 3.9 at 1890 m a.s.l., Moser *et al.* 2007) and in mountain forests in Sabah, Borneo (5.6 at 700 m, Kitayama & Aiba 2002). The comparatively low LAI values in the South Ecuadorian forests may in part result from less tall trees growing on rather steep slopes and relatively poor soils in this region (Homeier *et al.* 2010).
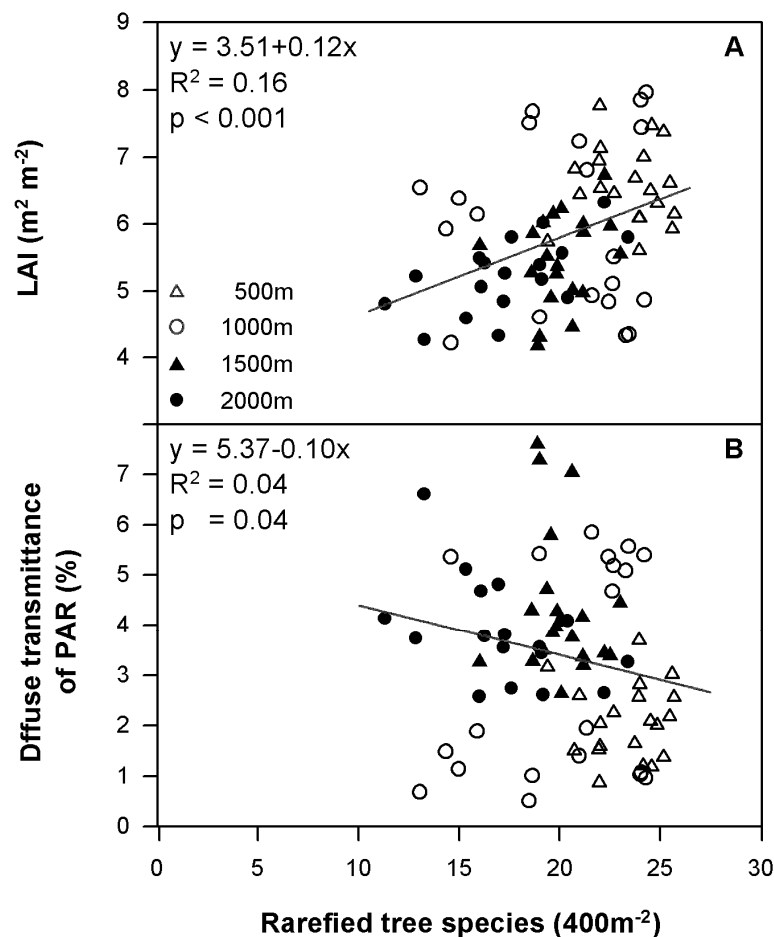
Fig. 4.6. LAI (A) and percent diffuse transmittance of PAR (B) as a function of tree diversity (rarefied trees per N = 28 trees) in the 78 plots (all stems ≥ 5 cm dbh considered).

We observed an altitudinal decrease of LAI by about 1.1 m^2 m^{-2} per km along the slope of the eastern Andes between 500 and 2000 m a.s.l. Similarly, Moser *et al.* (2007) found a leaf area decrease by 40-60% between 1000 and 3000 m elevation in South Ecuador; they concluded from a pan-tropical data review that the LAI of tropical moist forests on average decreases by 1 m^2 m^{-2} per 1000 m altitude. According to their data, this reduction should mostly be a consequence of the altitudinal decrease in tree height and an associated reduction in the number of canopy layers.

The light environment of forest plants in the understorey of tropical lowland and lower-montane rainforests is strictly energy-limited. How much radiation is available for forest floor herbs and tree seedlings, is dependent on the flux density of incident radiation, canopy PAR transmissivity, and day length, and thus may vary considerably with latitude, altitude, and forest type. Altitude influences the below-canopy radiation regime of tropical forests by changes in incident radiation and in canopy structure along the slope. In tropical mountains with a moist climate, incident radiation generally tends to decrease with altitude to the height of the condensation level where cloudiness is highest, and thereafter increases again towards the mountain peaks (Hastenrath 1991). On the eastern slopes of the equatorial Andes, the level of highest cloud frequency throughout the year is typically located at about 3000 m elevation (Bendix *et al.* 2008). In the absence of radiation data for the Sumaco transect, we thus assume for our study region, that average incident radiation most likely decreases from 500 to 2000 m due to increasing cloudiness. However, this putative decrease in incident radiation is fully compensated by an elevational increase in diffuse transmittance of PAR from about 2% at 500 m to ca. 4% at 2000 m resulting from the LAI decrease by 1.1 m² m^{-2} in our transect. In fact, we measured average below-canopy PPFD rates under overcast sky (time interval 10 a.m. to 2. p.m.) that increased from 8-12 µmol m^{-2} s^{-1} at 500 and 1000 m to >35 µmol m^{-2} s^{-1} at 2000 m, despite a general increase in cloudiness with elevation. A tendency from closed to more open canopies with more gaps is also reflected by the within-plot coefficients of variation for LAI, which increase along the slope. The decreasing zenith LAI values with elevation are affirming this tendency. Moreover, diffuse transmittance of PAR values >5% are much more abundant at 1500 and 2000 m than at 500 and 1000 m. Thus, tree seedlings and saplings and also forest floor herbaceous plants are exposed to deeper shade in lowland forests than higher upslope in the montane forests of the Eastern Andes. This should have consequences for the survivorship of tree seedlings and the abundance of herbaceous plants in the forest communities along the slope. From his studies in lowland forests, Leigh (1999) concludes that mature forests in both the tropics and the temperate zone with leaf area

indices around 7 are characterized by about 1% of incident radiation reaching the forest floor. In our study, forests with LAI of about 7 reached a slightly higher DT of about $1.4 \pm 0.7\%$. With average DT in the range of 2.0 to 2.7%, the studied forests at 500 to 1000 m elevation compare well to two neotropical lowland forests investigated by Johnson & Atwood (1970, Puerto Rico) and Rich *et al.* (1993, Costa Rica), while two paleotropical lowland forests were somewhat darker (NE Australia: Björkman & Ludlow 1972, Malaysia: Yoda 1974, about 0.4% of canopy PAR transmissivity).

Gas exchange measurements revealed that extremely shade-tolerant ground herbs of tropical forests reach light compensation of photosynthesis already at PPFD rates of 0.5 to 1.0 μmol $m^{-2} s^{-1}$ (Björkman *et al.* 1972, Mulkey 1986) and may survive at irradiance levels of 2-4 μmol $m^{-2} s^{-1}$, which equals about 0.3-0.6% of incident radiation under overcast sky. In the darkest stand of our study, we measured a mean below-canopy PPFD under overcast sky of 1.4 μmol $m^{-2} s^{-1}$, which seems to be close to this physiological limit of shade tolerance. However, the long-term average of forest floor irradiance may be substantially higher because our measurements did not include the penetration of direct sunlight through the canopy during irregularly occurring light flecks. Moreover, the large majority of our stands showed higher below-canopy PPFD rates which in a few cases at higher elevation exceeded 50 μmol $m^{-2} s^{-1}$. With a range of plot-level means of DT from 0.5 to 7.7%, the forest stands of our transect are slightly darker at the forest floor than a range of temperate broad-leaved forests in the lowlands of Central Europe at their maximum leaf area development (Ellenberg & Leuschner in press), where plot-level means reach minima of about 1% in certain beech (*Fagus sylvatica L.*) stands, but are often higher in oak, birch or pine forests where 8% are often exceeded (Hagemeier 2002). We conclude that extremely dense tropical forest canopies can reduce PAR transmissivity to the forest floor to a greater extent than it has been observed in most of the species-poor temperate forests. This discrepancy is valid, however, only in lowland forests while tropical lower montane and mid-montane forests typically have smaller leaf area indices. Thus, their PAR transmissivities are as high as, or even higher than, those of temperate lowland forests.

4.5.1 EFFECTS OF SOIL FERTILITY, TREE DIVERSITY AND STAND STRUCTURE ON LAI AND CANOPY TRANSMISSIVITY

We found a significant increase in LAI with increasing stem density in our sample of 78 plots. A similar stem density effect on stand leaf area was reported by Leuschner *et al.* (2006) for a sample of 23 closed, mature beech stands in Germany. In the Ecuadorian forests, an

increasing stem density was also associated with a decrease in percent diffuse transmittance of PAR. Several factors may be responsible for the stem density effect on leaf area and transmissivity. First, a higher number of stems increase the surface area of woody axes in the canopy, thereby enlarging the plant surface area index which is quantified by optical measurement and is often assigned to equal LAI. Second, more stems can support more epiphytes and more lianas which contribute to radiation interception in the canopy. Clearly, this explanation may not apply to temperate forests which lack vascular epiphytes.

Our data also reveal a significant positive relationship between tree diversity and leaf area index with LAI being on average by about 1.3 m^2 m^{-2} higher in a stand with 50 species per 400 m² than in a stand with only 20 species. This result might represent evidence in support of a positive diversity-productivity relationship in these tropical forests. Canopy carbon gain is a function of the amount of radiation absorbed by the stand leaf area with absorbed radiation being the difference between incident radiation and transmitted plus reflected radiation. Assuming that canopy reflectivity is less variable across the stands than is absorptivity, a decreasing PAR transmissivity would then be indicative of a higher radiation absorption and thus higher productivity of the stands with larger leaf area indices. As with stem density, the apparent species diversity effect on LAI may have several reasons: First, the complementary use of canopy space by the foliage of different tree species could increase stand leaf area and canopy absorptivity, and would represent a true diversity effect. On the other hand, a sampling effect (species with large leaf areas are more likely to be included in species-rich than in species-poor stands), might also explain the observed diversity-leaf area relationship. The significant effect of tree species diversity (but not of stem density) on LAI disappeared when soil fertility indicators such as nitrogen and phosphorus content of the upper mineral soil (0-10 cm) or the organic layer horizons were included in the multiple regression analysis. This indicates for our study region that the LAI increase (or decrease of canopy transmittance, respectively) is caused by the combined effects of stem density and putative soil fertility effects (mineral soil C/N ratio and organic layer plant-available P concentration) on LAI. The effect of tree diversity on LAI and DT remains speculative because of the close correlation of tree diversity with stem density and the multitude of changes of various abiotic and biotic factors, also influencing LAI and DT.

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CHAPTER

5

FACTORS CONTROLLING THE ABUNDANCE OF LIANAS ALONG AN ALTITUDINAL TRANSECT OF TROPICAL FORESTS IN ECUADOR

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5.1 ABSTRACT

In the light of putatively increasing liana abundances in present-day tropical forests and a persistent lack of understanding of liana abundance patterns and the responsible factors, we attempt to identify the key factors controlling liana abundance along an altitudinal transect in NE Ecuador. At four elevational levels (500, 1000, 1500, and 2000 m), each represented by 10 plots of 400 m^2, the abundance and diameters of all lianas (dbh $\geq$ 1 cm) and trees (dbh $\geq$ 10 cm) were recorded in old-growth forest stands in the Sumaco Biosphere Reserve (SBR). Results were analysed with available data on soil chemical properties and canopy structure.

The mean density of lianas and liana basal area did not differ significantly between the elevational levels; however, the mean liana diameter decreased with increasing elevation. Liana density, basal area and abundance per tree individual were strongly correlated with host tree diameter.

The most important determinants of liana abundance in the SBR were structural stand properties (tree basal area and mean tree dbh), but soil nitrogen availability (indicated by C/N ratio) was also found to have some influence. The notably high variation in liana abundance among different old-growth forest stands mainly reflects differences in stand structure between the studied mature forests, whereas the effect of elevation seems to be of less importance.

5.2 INTRODUCTION

Lianas, or woody vines, are structural parasites, relying on support by other plants. They can significantly influence forest ecology and ecosystem function (Schnitzer & Bongers 2002), and have been found to influence important forest dynamic processes, e.g. by reducing the growth of adult trees (Clark & Clark 1990) and lowering seedling recruitment and growth (Pérez-Salicrup 2001). Furthermore, lianas may increase tree mortality (Phillips *et al.* 2005) and alter gap-phase regeneration (Schnitzer *et al.* 2000).

Lianas are an important structural component of most tropical forests (Schnitzer & Bongers 2002). Typically, they comprise between 15% and 45% of the woody individuals and species in tropical forests (Gentry 1991, Pérez-Salicrup *et al.* 2001, Schnitzer 2005) and contribute up to 40% of forest leaf area and leaf productivity (Hegarty & Caballé 1991).

Recent investigations have shown that the abundance of lianas in tropical forests may increase with global climate change, probably promoted by a higher atmospheric CO_2 concentration (Phillips *et al.* 2002, Wright *et al.* 2004). Lianas as disturbance-adapted life forms (Hegarty & Caballé 1991) are profiting to some degree from increasing forest disturbance by humans. When lianas become more abundant they can reduce the amount of carbon sequestered by a forest stand if the leaf area of highly productive trees is reduced due to liana shading (Schnitzer & Bongers 2002).

Several factors have been suggested to influence the abundance, species richness and distribution of lianas in tropical forests. Tree fall dynamics together with host tree identity and abundance may be important factors determining the composition of liana communities (Ibarra-Manríquez & Martínez-Ramos 2002). Liana density tends to increase in disturbed forests (Hegarty & Caballé 1991) because of elevated radiation intensities (Schnitzer *et al.* 2000). Consequently, lianas are more abundant in seasonal dry forests, where light intensity is high underneath the seasonally deciduous canopy (Gentry 1991). Furthermore, in eastern Amazonia the biomass of lianas was, in contrast to tree biomass, three times higher in low than in high stature forests (Gerwing & Farias 2000).

Lianas have been suggested to be less abundant and to have lower biomass on nutrient poor than on more fertile soils (DeWalt *et al.* 2006, Gentry 1991, Laurance *et al.* 2001, Putz & Chai 1987). Macía *et al.* (2007) reported that environmental factors, including soil properties, explained just 10% of the floristic differences in liana composition between various sites in Madidi National Park in Bolivia. Recent studies have shown that the success of lianas may depend more on the availability of suitable host trees than on soil conditions (Phillips *et al.*

2005). Liana density may even be unrelated to soil fertility or to other soil gradients in Neotropical forests (van der Heijden & Phillips 2008).

Despite increasing attention from researchers, the ecology of lianas is in many respects still poorly understood. Particularly limited is our knowledge about altitudinal patterns of liana abundance and growth. However, in certain African (Balfour & Bond 1993) and Asian tropical forests (Parthasarathy *et al.* 2004), a decrease of liana abundance with elevation was reported. Comparable information is missing for Neotropical forests.

Understanding liana distribution patterns and the factors controlling them is essential to reach at more reliable predictions of future changes in liana abundance due to alterations in climate and in disturbance regimes of tropical forests.

In the present paper, we explore the patterns of liana abundance and the distribution of liana diameters and basal areas along an altitudinal transect from 500 to 2000 m in old-growth forest stands in NE Ecuador. Study objectives were to analyse the change in liana density, liana basal area and stem diameter distribution with increasing elevation from tropical lowland to lower montane forest. We tested the hypotheses that (i) liana density and basal area decrease with elevation and (ii) stand structural properties are more influential for liana abundance than are edaphic factors.

5.3 METHODS

5.3.1 STUDY AREA

The study was conducted in the Sumaco Biosphere Reserve (SBR) and its close proximity in the province of Napo, NE Ecuador. The reserve was founded in the year 2000 and is situated on the eastern slopes of the Andes and the adjacent foothills, including the Sumaco volcano. The area represents the last existing altitudinal transect of undisturbed vegetation from lowlands (400m) to páramo (3700 m) in the eastern equatorial Andes and harbours probably more than 6000 plant species (Neill & Palacios, 1997).

There is no exact rainfall data for the study sites, but total annual rainfall in the study area exceeds 2500 mm and Sumaco volcano and Cordillera Guacamayos probably receive more than 4000 mm year^{-1}; throughout the region, monthly precipitation usually never drops below 100 mm (Neill & Jørgensen, 1999).

Following the system of Palacios *et al.* (1999), the forests at 500 m (Jatun Sacha) can be classified as evergreen lowland forests, the stands at 1000 m (Cordillera Galeras and Hakuna

Matata) as evergreen premontane forests and the uppermost stands (1500 and 2000 m) as evergreen lower montane forests.

We selected seven study sites which differ in their geology. Parent rocks from the Cretaceous (mostly limestone) are widespread. However, at Sumaco volcano (basalt) and at Hakuna Matata (granite), volcanic and intrusive rocks, respectively, occur. Furthermore, slates are found at Cordillera Guacamayos (Sauer 1971).

Of the seven studied forest sites, those on Sumaco volcano and Cordillera Galeras are part of the Sumaco-Napo-Galeras National Park. The other locations are located in private reserves (Hakuna Matata and Jatun Sacha) or in the Antisana Ecological Reserve (Cordillera Guacamayos).

5.3.2 PLOT SELECTION AND DATA COLLECTION

The seven study sites were located at four elevation levels (500, 1000, 1500, and 2000 m) forming an elevational transect from 500 to 2000 m. The sites were selected according to the presence of sizeable tracts of intact forest representative for the elevation. Five (in Jatun Sacha: ten) permanent plots of 400 m^2 (20 m x 20 m) per study site were installed, resulting in 10 plots per elevation level. Plot positions deviated not more than 100 min elevation from the predetermined levels. Only areas without any kind of visible human or natural disturbance within closed mature forest stands were chosen in order to study liana abundance patterns unrelated to forest disturbance.

At each site the plots were selected at contrasting topographic conditions to cover a broad range of ecological conditions. Plot size was small enough to keep environmental factors and forest structure homogeneous within the plots. The plots represent independent sampling units, each containing a random sample of 16–45 stems exceeding 10 cm diameter at breast height (dbh). Mean distances between the plots at a given site (calculated from geographical positions) were between 0.1 km (Hakuna Matata) and 1.8 km (Galeras 1500 m).

The inventory of lianas was carried out in 2006, largely following the protocol given by Gerwing *et al.* (2006). Lianas were here defined as plants that germinated in the ground but that are ultimately dependent on other plants for structural support. All liana stems (ramets) $\geq$ 1 cm in dbh that originated in one of the investigated plots were inventoried and the dbh was measured with a calliper at 1.3 m above the ground. The tree mainly supporting a liana was recorded as its host tree. The diameters of all trees (dbh $\geq$ 10 cm) inside the plots were measured at 1.3 m above the ground.

5.3.3 INVESTIGATION OF STAND STRUCTURAL AND SOIL PARAMETERS

The canopy cover of each plot was estimated from 16 spherical densiometer (Lemon 1957) readings per plot. Furthermore, the leaf area index (LAI) was measured by means of two LI-COR LAI-2000 canopy analyzers (LI-COR, Inc., Lincoln, NE, USA) at 2 m above the ground. Measurements were carried out simultaneously under overcast sky at an open site close to the study plot (''above canopy'' values) and at 40 points systematically distributed within the plot.

Soil chemical parameters (pH(KCl), C/N ratio, exchangeable concentrations of Mg, K, Ca, Al, and plant available P) were investigated in the upper 10 cm of the mineral soil from four soil samples per plot (for detailed methods see Unger *et al.*, submitted for publication). Results are reported in Table 5.1.

5.3.4 DATA ANALYSIS

The absolute numbers and diameters of lianas and trees of each plot were used to calculate densities, total basal areas per plot, mean diameters, and the proportion of infested trees for each plot, study site and elevation level. Significances of the differences between the study sites and among the elevation levels were tested using ANOVA (with post hoc Tukey HSD-test) or Kruskal-Wallis-ANOVA (with subsequent Wilcoxon-U-test) depending on whether the data set was normally distributed or not. These analyses were conducted with SAS software (SAS Institute Inc., Cary, North Carolina, USA). Size class distribution tables were produced for each elevational level by pooling all plots. These tables were used to analyse the distribution of lianas by size classes and to evaluate the association between liana diameter distribution and the elevational levels at which they were found.

Regression models for the dependence of liana numbers and liana basal areas per tree on the diameter of the host trees were calculated. For this, the host trees were pooled in seven diameter size classes. Subsequently, the mean liana number and basal area per tree as well as the proportion of trees infested with lianas were analysed for their dependence on the diameter class midpoint of the host trees. In order to identify those factors controlling liana abundance on the plot level we applied partial and multiple regression models. Pearson correlations were performed using Xact 8 software (Scilab GmbH, Hamburg, Germany), whereas stepwise multiple regressions were calculated with R 2.8.1 (R Development Core Team 2008) using backward variable elimination (only parameters with $p \leq 0.05$ were left in the models).

Table 5.1. Slope and Chemical soil properties (pH, exchangeable concentrations of K, Mg, Ca and Al, concentrations of plant-available P and C/N ratios) of the mineral soil (upper 10 cm) of the seven study sites (means and SEs of 5 plots per study site and 10 plots at Jatun Sacha are given).

Study site / elevation level	Slope [°]	pH (KCl)	K [µmol g^{-1}]	Mg [µmol g^{-1}]	Ca [µmol g^{-1}]	Al [µmol g^{-1}]	P$_a$ [µmol g^{-1}]	C/N
Jatun Sacha (500m)	13.3 ± 3.5	4.1 ± 0.0	2.0 ± 0.2	6.1 ± 0.6	20 ± 2	36 ± 5	0.16 ± 0.06	10.2 ± 0.3
Hakuna Matata (1000 m)	24.0 ± 4.0	4.1 ± 0.1	3.0 ± 0.3	9.6 ± 1.9	18 ± 2	50 ± 5	0.30 ± 0.06	11.5 ± 0.3
Cord. Galeras (1000 m)	20.5 ± 5.2	4.3 ± 0.1	2.4 ± 0.1	7.5 ± 1.3	69 ± 24	45 ± 9	0.55 ± 0.14	11.9 ± 0.4
Cord. Galeras (1500 m)	14.0 ± 2.3	4.2 ± 0.1	1.8 ± 0.2	4.3 ± 0.7	17 ± 3	55 ± 7	0.14 ± 0.03	14.8 ± 0.4
Sumaco volcano (1500 m)	11.5 ± 2.2	4.4 ± 0.0	1.9 ± 0.2	6.0 ± 0.7	33 ± 8	39 ± 3	0.85 ± 0.32	11.9 ± 0.1
Sumaco volcano (2000 m)	9.5 ± 4.2	4.5 ± 0.0	2.0 ± 0.5	5.2 ± 1.4	31 ± 9	24 ± 6	0.77 ± 0.28	11.5 ± 0.5
Cord. Guacamayos (2000 m)	37.0 ± 3.2	4.5 ± 0.0	1.7 ± 0.2	3.9 ± 0.7	16 ± 1	35 ± 7	0.72 ± 0.39	12.1 ± 0.2

Table 5.2. Parameters characterizing the stand structure of the seven study sites (5 plots per site and 10 at Jatun Sacha; upper section of table) and of the four elevation levels (10 plots per elevation; lower section). Means (± 1 SE) are given. Different superscripted letters indicate significant differences (ANOVA, Tukey HSD test) between the levels.

Study site / elevation level	Trees with dbh ≥ 10 cm [400m⁻²]	Mean tree dbh [cm]	Tree basal area [m² 400m⁻²]	Canopy cover [%]	LAI [m² m⁻²]	Trees infested by lianas [%]
Jatun Sacha (500m)	31.1 ± 2.6	20.8 ± 0.7	1.37 ± 0.17	91.1 ± 0.7	6.3 ± 0.2	51.8±1.9
Hakuna Matata (1000 m)	38.0 ± 1.4	21.6 ± 0.8	1.80 ± 0.15	88.5 ± 0.8	7.4 ± 0.2	52.7±1.8
Cord. Galeras (1000 m)	30.2 ± 1.2	23.2 ± 1.6	2.17 ± 0.27	88.4 ± 0.9	4.6 ± 0.1	45.2±6.7
Cord. Galeras (1500 m)	37.0 ± 2.3	22.1 ± 0.8	1.76 ± 0.16	88.4 ± 0.6	6.0 ± 0.3	40.2±5.5
Sumaco volcano (1500 m)	22.8 ± 1.4	25.7 ± 2.0	1.98 ± 0.23	87.8 ± 0.5	5.1 ± 0.2	75.1±7.7
Sumaco volcano (2000 m)	22.2 ± 3.0	27.9 ± 2.8	2.84 ± 0.74	87.5 ± 0.9	5.1 ± 0,3	82.1±3.2
Cord. Guacamayos (2000 m)	28.4 ±1.2	21.4 ± 0.8	1.30 ± 0.16	89.8 ± 1.5	5.3 ± 0.4	51.8±4.1
500 m	31.1 ± 2.6[ab]	20.8 ± 0.7[a]	1.37 ± 0.17[a]	91.1 ± 0.7[a]	6.3 ± 0.2[a]	51.8[a]
1000 m	34.1 ± 1.6[a]	22.3 ± 0.8[ab]	1.98 ± 0.16[a]	88.4 ± 0.6[b]	6.0 ± 0.5[ab]	48.9[a]
1500 m	29.9 ± 2.7[ab]	23.5 ± 0.9[b]	1.87 ± 0.14[a]	88.1 ± 0.4[b]	5.5 ± 0.2[ab]	57.7[a]
2000 m	25.3 ± 1.9[b]	24.2 ± 1.3[b]	2.07 ± 0.44[a]	88.7 ± 0.9[b]	5.2 ± 0.2[b]	67.0[a]

A canonical correspondence analysis (CCA) was carried out with Canoco (version 4.5, ter Braak & Smilauer 2002) to analyse the relationships between liana abundance (liana density, liana basal area), forest structure (tree density, mean tree dbh, tree basal area, canopy cover, LAI) and environmental parameters. We used the automatic forward selection procedure to get the best set of non-redundant environmental variables for predicting liana abundance and forest structure.

5.4 RESULTS

5.4.1 ABUNDANCE OF LIANAS AND TREES

In total, 2243 lianas were counted in the 40 plots with a cumulative stand area of 1.6 ha (1403 ha^{-1}). The density of lianas was highest at 2000 m, where 795 lianas were found on an area of 4000 m^2, equivalent to a liana density of 1988 ha^{-1}. Liana density showed no change with altitude, reaching lowest values at 500 m (Fig. 5.2a Kruskal–Wallis test: $p = 0.03$ for study sites and $p = 0.29$ for elevation levels). The plots located on Sumaco volcano (1500 and 2000 m) harboured the highest numbers of lianas (Fig. 5.2a) with a peak value in liana density of 2810 ha^{-1} at 2000 m (mean of 5 plots extrapolated to 1 ha). This is twice as high as the average liana density in the whole study area. The liana density of the other six study sites was much lower and ranged between 875 and 1500 ha^{-1} with significant differences existing only between Hakuna Matata and Cordillera Galeras (1500 m).

In contrast, mean liana dbh decreased with increasing altitude (Fig. 5.2b, study sites: $p < 0.01$, elevation levels: $p < 0.01$), whereas liana basal area per plot did not show any consistent pattern with elevation (Fig. 5.2c, study sites: $p = 0.29$, elevation levels: $p = 0.35$). The liana basal area per plot was highest at the sites in Jatun Sacha, Hakuna Matata and on Sumaco volcano (2000 m) with values above 0.75 m^2 ha^{-1}. The density of trees decreased slightly with increasing altitude while mean tree dbh increased and plot basal area showed no significant trend (Table 5.2). Due to the higher absolute number of lianas at higher elevations, the proportion of trees infested with at least one liana was highest at 2000 m (67.0%) and lowest at 1000 m (48.9%) even though the differences were not significant. When averaged over all plots of our study, 54.1% of the trees were infested by at least one liana. The number of lianas per diameter class rapidly decreased with increasing liana dbh at all four elevation levels (Fig. 5.3).
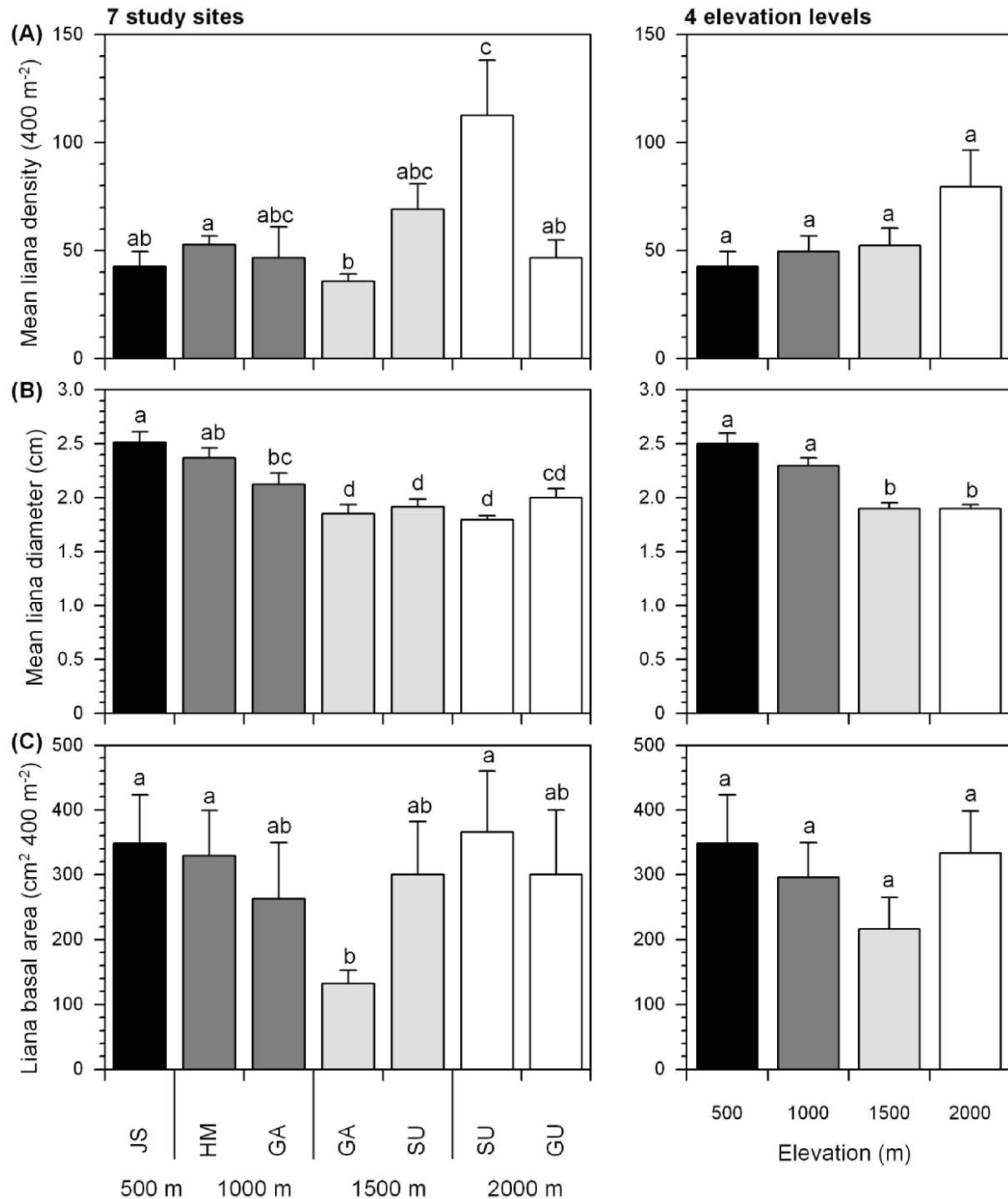
Fig. 5.2. Density (A),mean diameter (B) and cumulative basal area (C) of lianas for the seven study sites (left section of figure) and at the four elevation levels (right section). At each study site, 5 plots (400 m² each) were sampled with the exception of JS, where 10 plots were inventoried. Given are means (±1 SE). Different letters indicate significant differences (Wilcoxon-U-test) between the study sites or between the elevation levels. Study sites are Jatun Sacha (JS), Hakuna Matata (HM), Cordillera Galeras (GA), Sumaco volcano (SU) and Cordillera Guacamayos (GU).
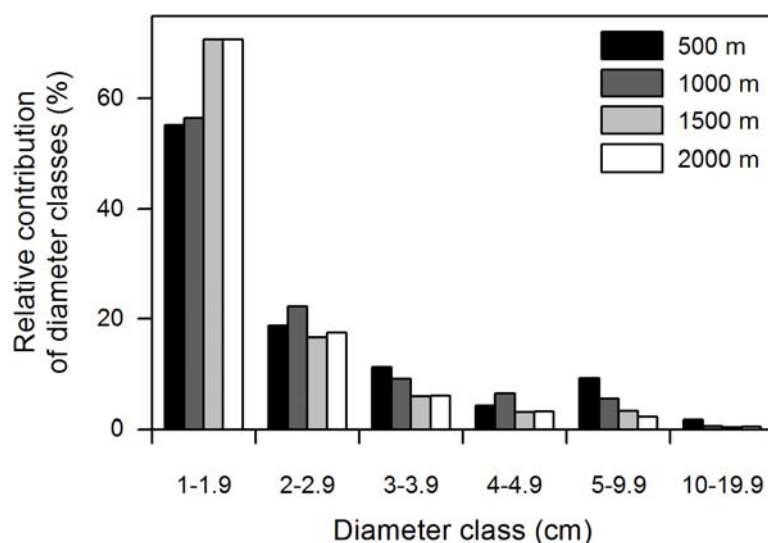
Fig. 5.3. Diameter class distribution of all lianas (dbh ≥ 1 cm) from 40 plots (total area: 1.6 ha) at four elevations in the Sumaco Biosphere Reserve (each 10 plots per elevation level, cumulative area per elevation level: 0.4 ha).

By far the highest number of lianas had a diameter smaller than 2 cm (>50% at all elevation levels). In general, thick lianas with diameters >5 cm were more common at lower elevations (500 and 1000 m), while thin lianas (<2 cm) occurred at higher densities at upper elevations (1500 and 2000 m).

5.4.2 LIANA ABUNDANCE AND SITE CONDITIONS

In order to identify the factors controlling the abundance of lianas along the altitudinal transect and between the different study sites, several regression models were run. We found a positive relationship between host tree dbh and infestation rate (Fig. 5.4a), and exponential increases of the mean number of lianas per tree, and the mean liana basal area per tree and host tree dbh (Fig. 5.4b and c).

Individual regression models calculated for all sampled environmental factors identified plot tree basal area, mean tree dbh, elevation, and exchangeable Ca and Al concentrations of the soil as explaining factors for the variability of liana density (Table 5.3). The liana basal area, in contrast, could only be explained by canopy cover.

Fig. 5.4. Relationships between (A) proportion of infested trees, (B) number of lianas and (C) liana basal area and the diameter of the host tree (midpoint of diameter class) for all trees between 10 and 80 cm of dbh at the 40 study plots (total area: 1.6 ha). Given are means (±1 SE).

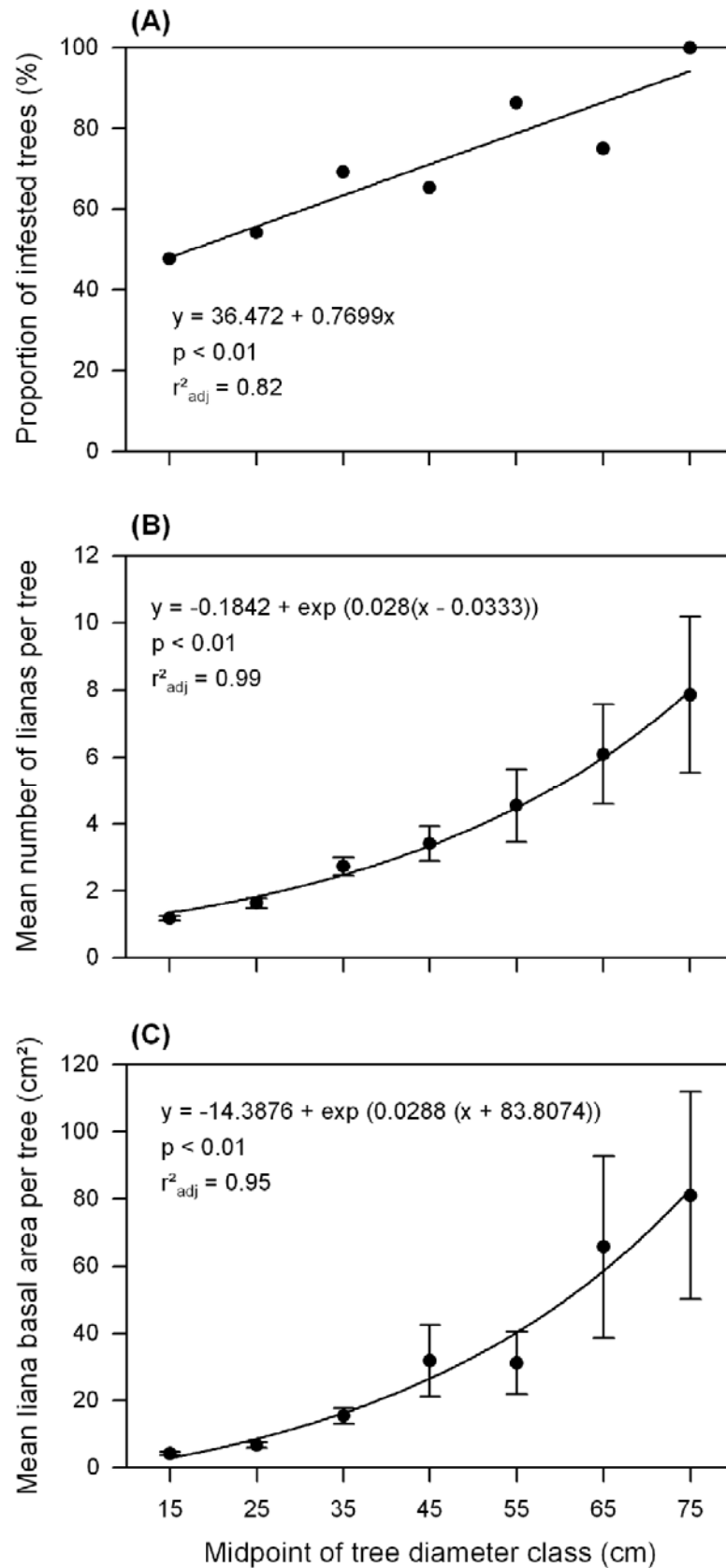**Table 5.3.** Pearson correlation coefficients for the relationships between the density and the cumulative basal area of lianas and 14 parameters characterizing site conditions (Tab. 5.1) and stand structure (see Tab. 5.2) of the 40 studied plots (p-value in parentheses). Significant correlations (* p<0.05) are printed in bold ().

Parameter	Liana density	Liana basal area
	r	r
Number of trees (dbh ≥ 10cm)	-0.21 (0.20)	0.02 (0.90)
Tree basal area (dbh ≥ 10cm)	**0.72** (<0.001)	0.28 (0.08)
Mean tree dbh (cm)	**0.65** (<0.001)	0.26 (0.10)
Canopy cover (%)	-0.01 (0.99)	**0.33** (0.04)
LAI (m^2 m^{-2})	-0,24 (0.38)	0.15 (0.24)
Elevation (m)	**0.36** (0.02)	-0.09 (0.59)
Slope	-0.22 (0.18)	-0.05 (0.74)
pH (KCl)	0.21 (0.18)	-0.03 (0.88)
K (μmol g^{-1})	0.17 (0.29)	0.07 (0.67)
Mg [μmol g^{-1}]	0.16 (0.33)	0.12 (0.46)
Ca (μmol g^{-1})	**0.35** (0.03)	0.13 (0.44)
Al (μmol g^{-1})	**-0.38** (0.02)	-0.12 (0.47)
P_a (μmol g^{-1})	0.23 (0.15)	0.01 (0.95)
C/N	-0.15 (0.36)	-0.28 (0.08)

Results of a multiple regression analysis on the factors controlling liana abundance and basal area are shown in Table 5.4. Tree basal area, soil C/N ratio, and elevation had a significant effect on the liana density per plot explaining 62% of the observed variability. Twenty-three percent of the variability of the basal area of lianas per plot could be explained by the parameters canopy cover and mean tree diameter.

The CCA-biplot illustrates the relationships between liana abundance and environmental variables (Fig. 5.5). The first two axes of the CCA together explained 29.4% of the variance in liana abundance and forest structure data, indicating that there are other environmental factors such as climate, which may strongly influence these parameters. Elevation had the highest correlation with axis 1 (r = 0.46), while C/N ratio showed the highest correlation with axis 2 (r = 0.48).

Table 5.4. Results of multiple regression analyses on the effects of the 13 variables listed in Table 5.2 on the number and basal area of lianas in the 40 studied forest plots. Presented are the final models which included only those variables (3 and 2, respectively) with a significant influence ($p \leq 0.05$) on the dependent variable.

Dependent variable	Model r^2 (adjusted)	Independent variable	Parameter estimate	Standard error	Partial regression coefficient	p-value
Liana density	0.59	C/N	-7.29	2.54	0.05	0.007
		elevation	0.02	0.01	0.12	0.009
		tree basal area	27.14	4.65	0.45	< 0.001
Liana basal area	0.19	canopy cover	36.68	13.02	0.14	0.008
		mean tree dbh	22.50	9.13	0.10	0.019

5.5 DISCUSSION

The mean liana density recorded in our study (1402 ha^{-1}, dbh $\geq$ 1 cm) is within the range of density values reported for other tropical forests. For example, a comparison of four Neotropical lowland forests (La Selva, Costa Rica; Barro Colorado Island, Panama; Cocha Cashu, Peru and KM41, Brazil) revealed average liana densities of 704 stems (dbh $\geq$ 1 cm) ha^{-1} (DeWalt & Chave 2004). In Yasuní National Park in Ecuador, Burnham (2002) sampled on average 1812 lianas (dbh $\geq$ 1 cm) ha^{-1} in a total of twelve 0.2 ha plots, Mascaro *et al.* (2004) found an overall density of 816 lianas (dbh $\geq$ 1 cm) ha^{-1} on nine 864 m^2 plots in Costa Rica and in Southeast Mexico, an average of 2092 liana stems (dbh $\geq$ 1 cm) ha^{-1} was reported (Ibarra-Manríquez & Martínez-Ramos 2002).

On the other hand, the variation in liana density among plots in our study was very high compared to other investigations in tropical forests (minimum: 895 ha^{-1} at Cordillera Galeras, 1500 m; maximum: 2810 ha^{-1} at Sumaco volcano, 2000 m) (e.g. DeWalt & Chave 2004, Parthasarathy *et al.* 2004). This may result from the relatively large number of plots investigated (40) and the considerable environmental heterogeneity covered. This broad data

set forms a sound platform for an investigation of the factors controlling liana abundance on the landscape level.

Several authors postulated a decrease in liana density and basal area with elevation in tropical mountains (Balfour & Bond 1993, Putz & Chai 1987, Parthasarathy *et al.* 2004) which is not confirmed by our data from Ecuador. In the SBR, liana density was not decreasing with elevation and liana basal area remained constant between 500 and 2000 m, as well; the highest liana density was found at the uppermost elevation. In general, the differences in liana density and basal area (be they significant or not) were smaller among the elevation levels than among the different study sites. Thus, other factors besides elevation seem to be important in controlling liana abundance in the SBR.
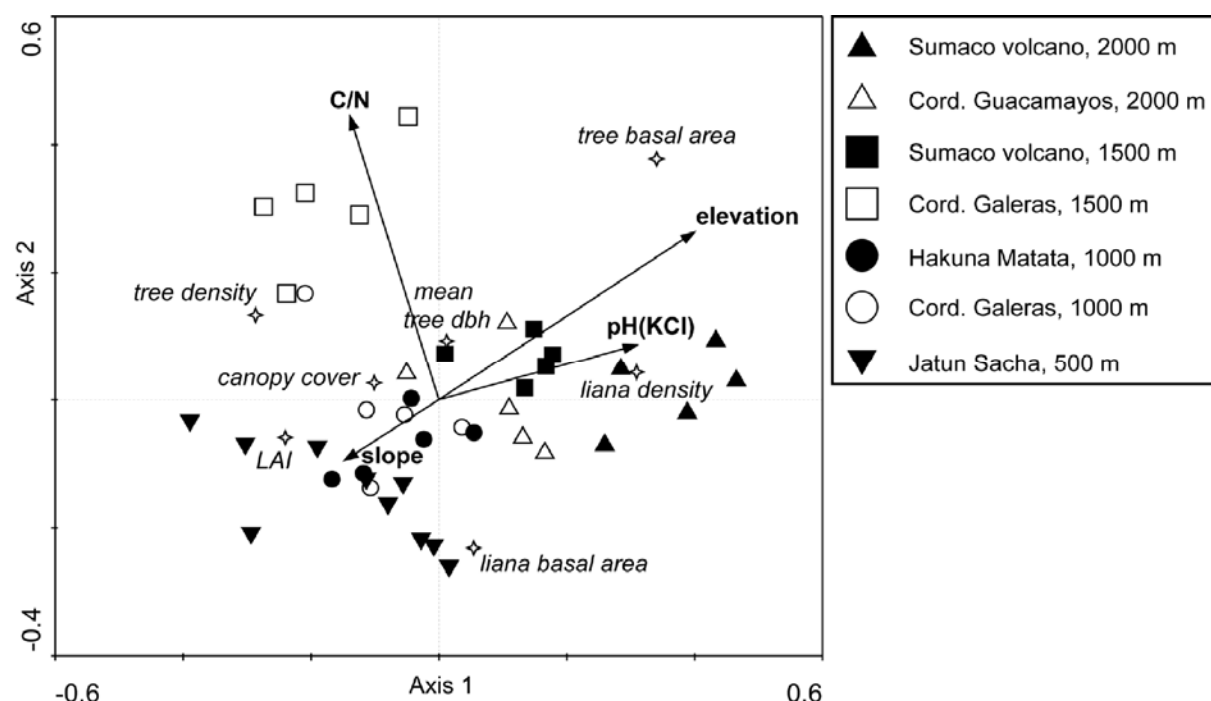
Fig. 5.5. Ordination based on canonical correspondence analysis (CCA) relating liana abundance and forest structure (stars) of the plots at the seven study sites (different signatures, see legend) to environmental variables (arrows).We included the following environmental variables: elevation, slope, pH, C/N ratio, exchangeable concentrations of Mg, K, Ca, Al and plant available P. The variables C/N ratio, elevation, pH and LAI were selected as the best predictors for liana abundance and forest structure (automatic forward selection procedure, Canoco software). The first two axes of the CCA together explain 29.4% of the variance in liana abundance and forest structure data.

Fifty-four percent of the investigated trees were infested with at least one liana. As for liana density, this result is very similar to data obtained in other investigations in Neotropical forests. For tropical wet forests in Costa Rica, Clark & Clark (1990) calculated that approximately 50% of the trees (dbh ≥ 10 cm) had lianas in their crowns. Pérez-Salicrup & de Meijere (2005) found 63% of the studied trees at Los Tuxtlas (Mexico) carrying at least one liana; in Yasuní (Ecuador) more than 60% of the studied trees were hosts of lianas (Nabe-Nielsen 2001)and Malizia & Grau (2006) reported 65% of the trees infested in a subtropical montane forest in north-western Argentina.

In our study, liana infestation rate did not differ significantly between the four elevation levels, but showed significant differences between the various study sites. Thus, similar to liana density and basal area, stand structural attributes, soil properties or other factors must be more decisive for infestation rate than is elevation (or temperature).

The search for the factors controlling liana abundance revealed a highly significant influence of host tree dimensions, in particular diameter at breast height. Plotting the number of lianas per tree against tree dbh (with the trees pooled in seven dbh classes) revealed a highly significant positive relationship with an exponential increase. The coefficients of determination for the dependence of liana basal area and the proportion of infested trees on dbh were also high. Thicker trees are older and have had more time to accumulate lianas. In addition, a larger diameter is usually related to a more favourable canopy position in terms of light capture (Malizia & Grau 2006). Lianas cannot choose their host tree, but the probability of reaching greater stem diameters and approaching maturity is undoubtedly higher on bigger trees.

In a subtropical wet forest in Puerto Rico, larger trees tended to have a higher percentage of crown infestation by lianas as well (Rice *et al.* 2004). A similar pattern was found in a subtropical montane forest in north-western Argentina by Malizia & Grau (2006) and in a lowland forest in Ecuador by Nabe-Nielsen (2001). In a southern Peruvian rainforest, Phillips *et al.* (2005) observed that especially large lianas (dbh ≥ 10 cm) depended on large trees to support them and to provide access to high-light environments in the upper canopy.

Earlier investigations reported that lianas might be more abundant and have a higher biomass on more fertile soils (DeWalt *et al.* 2006, Gentry 1991, Laurance *et al.* 2001, Putz & Chai 1987). Phosphorus availability and aluminium toxicity are suggested to be among the most important soil chemical properties controlling vegetation patterns in tropical lowland forests (Sollins 1998). In our study, we obtained some support for a relationship between soil chemistry and liana abundance because soil C/N ratio explained a significant share of

variation in liana abundance. Correlation analysis showed a possible negative effect of exchangeable aluminium and a positive one of exchangeable calcium on liana densities. In contrast to our results and the above cited studies, Phillips *et al.* (2005) found that soil parameters explained just a small part of the variation observed in liana abundance in a southern Peruvian rainforest. Similarly, DeWalt & Chave (2004) and van der Heijden & Phillips (2008) found that liana density is unrelated to soil fertility or to other soil-related gradients.

Multiple regression analyses indicated tree basal area to be the main factor controlling liana densities in our plots. This highlights the importance of thick old trees with long continuity for lianas. Together with mean tree dbh, canopy cover was identified as an influential factor for liana basal area, revealing an increase of liana basal area with cover. We assume that the positive relationship is a consequence of the fact that optical techniques for measuring canopy cover do not distinguish between tree and liana foliage with the result that canopy closure increases with liana density. Thus, a denser canopy is rather a consequence and not the cause of a higher liana basal area.

The identification of mean tree diameter as an influential factor in the multiple regression model corresponds with the close relationship between liana basal area and tree diameter shown for the complete set of studied trees, although there was no significant correlation to liana basal area (Table 5.3).

Our results show that forest structural attributes such as tree diameter and tree basal area are more influential for liana abundance, basal area and diameter distribution patterns than are soil parameters. Certain other recent studies reached similar conclusions. Balfour & Bond (1993), Phillips *et al.* (2005) and van der Heijden & Phillips (2008) postulated that the success of lianas might depend more on the availability of suitable host trees than on soil conditions.

The lack of liana species identification may partly limit the interpretation of our results, because more general conclusions drawn for the liana community as a whole may not be applicable to individual liana taxa which are known to show a rather diverse response to environmental variables (e.g. Burnham 2002, Mascaro *et al.* 2004, Parthasarathy *et al.* 2004).

In conclusion, we found neither a decrease of liana density nor of liana basal area with elevation and thus we have to reject our first hypothesis. The most important determinants of liana abundance in the SBR are structural stand properties (tree basal area and mean tree dbh), but nitrogen availability (indicated by C/N ratio) was also found to have some influence, thus

our second hypothesis was confirmed. The notably high variation in liana abundance among different old-growth forest stands mainly seems to reflect differences in stand structure.

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SYNTHESIS

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6.1 SUMMARY OF THE PRESENT FINDINGS AND DISCUSSION

In this chapter the main results of this study are represented and are assessed and discussed with the hypotheses, given in the first chapter in mind, taking also into account the already existing knowledge on these subjects.

For facilitating the overview of the general soil data, the site means of the main soil parameters of the organic layer horizons, the upper mineral soil and the topsoil are listed in Table 6.1 and Table 6.2.

One of the main topics of this study was to test the hypothesis whether the availability of phosphorus is low in lowland tropical forests but increases with elevation, while the availability of nitrogen is relatively high but decreases with elevation, possibly constituting in a switch of phosphorus to nitrogen limitation for the plants along the Andean slope.

All measured P fractions (plant-available P of the organic layer horizons and the upper mineral soil, and total P content of the organic layer horizons) showed a large variation among plots of the same elevation, reflecting the high spatial heterogeneity of P concentrations often observed in forest soils. But plant-available P was the only parameter revealing similar variances on a local (within-plot and within-site variation), a regional (between site variation) and a landscape scale (between elevation variation). P_a concentrations showed a more than ten-fold increase from 500 to 2000 m in both horizons, which is the largest change with elevation detected in any of the soil chemical parameters investigated in this study. In addition, resin-bag extractable P occurred at about six-fold higher concentrations in the organic layers than in the mineral topsoil immediately below, indicating large vertical gradients in P availability in the soil and emphasizing the role of organic matter as the most important P source for plants. Though the content of total P declined with elevation, the accompanied large increase in organic layer thickness (and mass) resulted in an overall increase of the organic P pool with elevation.

The large and significant increase in P_a concentrations in the organic layers and the mineral topsoil with elevation is, despite its spatial heterogeneity, supporting the hypothesis that P availability increases and therefore P limitation, if it occurs, decreases with elevation. The reasons for this increase in phosphorus with elevation remains speculative, less proceeded pedogenetic development in tropical forest soils along our altitudinal transect, an increased P mineralization, a decreased P immobilization through microbial uptake or an elevational change in the mycorrhiza associations of the trees influencing the P uptake and hence the soluble P concentrations in the soil solution are possible explanations therefore.

Table 6.1: The 11 study sites with their mean elevation [m a.s.l.], depth of organic layer horizons (o.l.h.) [cm], pH$_{KCl}$, C/N-ratio [mol mol^{-1}], total nitrogen (N$_t$) [mmol g^{-1}], content of exchangeable potassium (K$_{ex.}$), magnesium (Mg$_{ex.}$), calcium (Ca$_{ex.}$) and aluminum (Al$_{ex.}$) [µmol g^{-1}], plant-available phosphorus (P$_a$) and total phosphorus content (P$_t$) [µmol g^{-1}] of the organic layer L, F and H horizons (site means ± 1SE).

Study site	Elevation	Depth o.l.h.	pH$_{KCl}$	C/N-ratio	N$_t$	K$_{ex.}$	Mg$_{ex.}$	Ca$_{ex.}$	Al$_{ex.}$	P$_a$	P$_t$
Jatun Sacha	426 ± 5	2.0 ± 0.3	4.5 ± 0.1	14.2 ± 0.5	0.6 ± 0.0	6.0 ± 0.6	26.9 ± 2.2	148.4 ± 13.8	14.0 ± 3.4	0.6 ± 0.2	75.9 ± 12.2
Selva Viva	486 ± 12	0.9 ± 0.1	4.2 ± 0.1	15.4 ± 0.6	0.6 ± 0.0	7.8 ± 1.1	40.9 ± 6.7	117.6 ± 21.8	26.2 ± 6.0	0.5 ± 0.1	138.6 ± 17.3
Hakuna Matata	1013 ± 21	1.6 ± 0.2	4.5 ± 0.1	16.6 ± 0.1	0.9 ± 0.1	12.3 ± 1.3	49.0 ± 4.5	181.5 ± 23.0	28.7 ± 5.0	0.4 ± 0.1	67.7 ± 6.4
Rio Hollin	1188 ± 8	3.6 ± 0.4	3.8 ± 0.1	14.0 ± 0.5	1.6 ± 0.1	12.6 ± 1.2	40.6 ± 3.8	184.2 ± 11.2	155.4 ± 43.5	1.3 ± 0.4	108.7 ± 33.3
Galeras 1000m	1077 ± 17	2.2 ± 0.5	4.8 ± 0.2	16.0 ± 0.4	1.3 ± 0.1	13.6 ± 1.2	50.1 ± 4.1	388.6 ± 70.3	33.6 ± 18.3	3.3 ± 0.7	70.0 ± 8.5
Galeras 1500m	1555 ± 22	7.9 ± 1.0	3.3 ± 0.1	16.7 ± 0.9	1.5 ± 0.1	14.4 ± 3.0	25.3 ± 4.9	68.3 ± 16.6	71.0 ± 18.3	0.7 ± 0.1	50.2 ± 6.8
Cocodrillos	1518 ± 17	5.8 ± 0.6	3.6 ± 0.1	14.7 ± 0.5	1.7 ± 0.0	11.5 ± 1.8	31.3 ± 3.9	111.3 ± 21.5	102.7 ± 13.1	3.7 ± 0.9	89.6 ± 3.5
Sumaco 1500m	1598 ± 8	5.3 ± 0.4	3.9 ± 0.1	13.6 ± 0.1	1.6 ± 0.1	12.8 ± 1.7	48.4 ± 3.3	236.1 ± 21.5	57.8 ± 11.5	4.3 ± 0.7	88.9 ± 8.3
Sumaco 2000m	1965 ± 17	5.8 ± 0.6	4.4 ± 0.1	13.6 ± 0.1	1.5 ± 0.1	23.4 ± 4.0	52.2 ± 5.0	276.4 ± 30.7	27.1 ± 10.6	5.8 ± 1.6	87.9 ± 8.0
C. Guacamayos	1988 ± 6	5.0 ± 0.4	4.2 ± 0.1	14.1 ± 0.3	1.6 ± 0.1	16.0 ± 1.7	41.1 ± 3.9	181.5 ± 19.6	49.2 ± 13.4	4.4 ± 1.1	68.3 ± 6.5
Yanayacu	2074 ± 5	5.2 ± 0.7	4.4 ± 0.3	15.1 ± 0.9	1.7 ± 0.1	24.7 ± 6.6	77.5 ± 15.9	323.2 ± 53.3	86.5 ± 6.3	3.9 ± 0.8	14.0 ± 4.3

Soil parameters of the organic layer horizons

Table 6.2: The 11 study sites with their pH_{KCl}, C/N-ratio [mol mol^{-1}], total nitrogen (N_t) [mmol g^{-1}], content of exchangeable potassium ($K_{ex.}$), magnesium ($Mg_{ex.}$), calcium ($Ca_{ex.}$) and aluminum ($Al_{ex.}$) [µmol g^{-1}] and plant-available phosphorus (P_a) content [µmol g^{-1}] of the upper mineral soil (0 – 0.1 m), and N mineralization rate ($N_{min.}$-rate) [µg N g^{-1} d^{-1}], Net N mineralization (Net N min.) [kg ha^{-1} yr^{-1}], N nitrification rate ($N_{nitr.}$-rate) [µg N g^{-1} d^{-1}] and Net nitrification (Net nitr.) [kg ha^{-1} yr^{-1}] of the topsoil (0 – 0.1 m, a mixture of organic layer horizons and upper mineral soil horizons). (site means ± 1SE).

Study site	Soil parameters of the upper mineral layer (0 – 0.1 m)								Soil parameters of the topsoil (0 – 0.1 m)			
	pH_{KCl}	C/N-ratio	N_t	$K_{ex.}$	$Mg_{ex.}$	$Ca_{ex.}$	$Al_{ex.}$	P_a	$N_{min.}$-rate	Net N min.	$N_{nitr.}$-rate	Net nitr.
Jatun Sacha	4.1 ± 0.0	10.3 ± 0.3	0.2 ± 0.0	2.0 ± 0.2	6.1 ± 0.5	19.6 ± 2.3	35.9 ± 4.7	0.2 ± 0.1	1.5 ± 0.2	593 ± 89	1.4 ± 0.2	543 ± 74
Selva Viva	4.1 ± 0.0	10.2 ± 0.2	0.2 ± 0.0	1.2 ± 0.2	5.1 ± 1.1	6.1 ± 0.7	58.2 ± 9.7	0.1 ± 0.0	1.2 ± 0.2	541 ± 69	1.2 ± 0.2	522 ± 77
Hakuna Matata	4.1 ± 0.1	11.5 ± 0.3	0.3 ± 0.0	3.0 ± 0.3	9.6 ± 1.9	17.9 ± 1.6	49.9 ± 4.5	0.3 ± 0.1	0.1 ± 0.0	18 ± 8	0.1 ± 0.0	26 ± 7
Rio Hollin	4.4 ± 0.0	12.6 ± 0.3	0.7 ± 0.0	2.3 ± 0.4	5.2 ± 0.5	19.8 ± 3.5	87.4 ± 23.1	0.1 ± 0.0	3.0 ± 0.6	566 ± 107	3.0 ± 0.5	560 ± 88
Galeras 1000m	4.3 ± 0.1	11.9 ± 0.4	0.5 ± 0.0	2.4 ± 0.1	7.5 ± 1.2	68.8 ± 24.1	45.3 ± 8.7	0.5 ± 0.1	1.5 ± 0.4	364 ± 114	1.7 ± 0.4	418 ± 101
Galeras 1500m	4.2 ± 0.1	14.8 ± 0.4	0.6 ± 0.1	1.8 ± 0.2	4.3 ± 0.7	16.9 ± 2.8	54.8 ± 7.2	0.1 ± 0.0	1.8 ± 0.8	241 ± 117	1.6 ± 0.6	216 ± 66
Cocodrillos	4.6 ± 0.0	12.8 ± 0.3	0.5 ± 0.0	0.9 ± 0.2	2.4 ± 1.3	10.9 ± 3.6	39.0 ± 7.0	0.2 ± 0.1	1.7 ± 0.2	275 ± 21	2.1 ± 0.2	329 ± 32
Sumaco 1500m	4.4 ± 0.0	11.9 ± 0.1	0.5 ± 0.1	1.9 ± 0.2	6.0 ± 0.7	33.2 ± 8.5	38.6 ± 2.9	0.8 ± 0.3	1.4 ± 0.5	285 ± 102	1.7 ± 0.2	353 ± 50
Sumaco 2000m	4.5 ± 0.0	11.5 ± 0.4	0.6 ± 0.1	2.0 ± 0.5	5.2 ± 1.4	30.7 ± 9.4	23.6 ± 5.7	0.8 ± 0.3	2.0 ± 0.2	422 ± 52	1.8 ± 0.2	368 ± 53
C. Guacamayos	4.5 ± 0.0	12.1 ± 0.2	0.6 ± 0.0	1.7 ± 0.2	3.9 ± 0.7	16.0 ± 1.5	35.4 ± 6.7	0.7 ± 0.4	0.9 ± 0.2	167 ± 36	0.8 ± 0.1	157 ± 24
Yanayacu	4.4 ± 0.1	11.9 ± 0.2	0.6 ± 0.0	1.9 ± 0.3	5.4 ± 1.9	52.9 ± 25.5	72.3 ± 7.8	2.6 ± 0.7	1.8 ± 0.3	386 ± 69	1.6 ± 0.4	355 ± 86

Compared to a large variety of studies in tropical forests and especially tropical cloud forests (Zinck 1986, Marrs *et al.* 1988, Grieve *et al.* 1990, Kitayama 1992, Payton 1993, Bruijnzeel & Proctor 1995, Kitayama *et al.* 1998, Rhoades & Coleman 1999, Hertel *et al.* 2008), were the phosphorus content varied between 1-3 μg g^{-1} (Costa Rica, 100 m, Marrs *et al.* 1988, Borneo, 800 m, Kitayama *et al.* 1998, Venezuela, 1580 m, Zinck 1986, Argentina, 750 – 1050 m, Hertel *et al.* 2008) up to 78 μg g^{-1} (Indonesia, 2100 m, Payton 1993), we found very high values of extractable phosphorus concentrations in the organic layer horizons (ranging from means of 18 μg g^{-1} at 500 m to 226 μg g^{-1} at 2000 m), but very low phosphorus concentrations in the upper mineral soil (with means of 3 μg g^{-1} at 500 m and 13 μg g^{-1} at 2000 m). But the method of plant-available phosphorus extraction varies between the different studies, making it difficult to compare these values.

As for nitrogen, total N of the organic layer and the upper mineral soil horizons was measured and also the net release of NH_4^+ and NO_3^- in the topsoil to quantify elevational and topographic variation in N supply from a plant perspective. The total nitrogen concentration of the organic layers and the uppermost mineral soil horizon also increased significantly from 500 to 2000 m in the Ecuador transect, and the total N concentrations of the organic layer horizons but also of the upper mineral soil were remarkably uniform at local range (within plot and within site variation), indicating that N storage in the soil is less influenced by species composition or topography, rather than being controlled by factors linked to elevation like temperature and rainfall. In all plots more than 80% of the total mineral N released in our samples was set free as NO_3^-, indicating the important role of nitrifiers in the N transformation in both lowland and montane forests. The higher N_t concentrations had no effect on N mineralization, though, because N mineralization rate and nitrification rate in the topsoil, when expressed per soil dry mass, remained almost constant within this altitudinal transect. When N mineralization and nitrification rate were expressed per soil volume, however, both net N mineralization and net nitrification significantly decreased (by about 40%) along the elevation transect, due to the increasing humus content and the thereby reduced soil bulk density of the topsoil toward higher elevations. So only if rates of N supply are expressed by volume, the data seem to support the assumption of a decreasing N supply.

N concentrations and cycling rates on a mass basis are larger in organic layers than in mineral soils of tropical forests (Livingston *et al.* 1988, Vitousek & Matson 1988, Wilcke *et al.* 2002), and nitrogen content in our study area declined significantly with soil depth by a factor varying from 1.5 to 6. Total concentration of nitrogen in the organic layer was in the comparable range of other tropical forest soil studies (Steinhardt 1979, Edwards 1982, Marss

et al. 1988, Hafkenscheid 2000, Wilcke *et al.* 2002). Both carbon content and concentration of total nitrogen of the organic layers and also of the upper mineral soil increased with elevation. This increase of total nitrogen content in parallel with total carbon content in the soils with elevation was also found by Bruijnzeel & Proctor (1995).

A number of incubation-based measurements of N mineralization and nitrification have been carried out within tropical forests, including lowland forests (Robertson 1984, Chandler 1985, Vitousek & Denslow 1986, Matson *et al.* 1987), subtropical rainforests (Pfadenhauer 1979, Lamb 1980, Chandler & Goosem 1982, Ramakrishnan & Saxena 1984, Saxena & Ramakrishnan 1986), tropical savannas (Bernhard-Reversat 1982) and montane tropical forests (Tanner 1977, Balakrishnan & Mueller-Dombois 1983, Vitousek *et al.* 1983, Arnold *et al.* 2008). In general, these studies show that N mineralization and nitrification are substantially more rapid in most lowland tropical forests than in most temperate or boreal forests (Ellenberg 1977, Corre *et al.* 2007), results consistent with the large amounts of N circulated annually within most lowland tropical forests (Proctor 1984, Vitousek 1984, Vitousek & Sanford 1986). But timing, temperature, soil-water content, and mode of incubation all differ among tropical studies; incubations have been carried out in the field, under controlled conditions in the laboratory, and after size or density fractionation of soils (Sollins *et al.* 1984), complicating direct comparisons.

With the exception of one study site, Hakuna Matata at 1000 m elevation, the N mineralization and nitrification rates measured in this study were generally above the range reported for forests with oxisols, ultisols or other less fertile soils, and also some montane forests (0.1-1 μg N g^{-1} d^{-1}, Lamb 1980, Robertson 1984, Chandler 1985, Vitousek & Denslow 1986, Vitousek & Sanford 1986, Matson *et al.* 1987, Marrs *et al.* 1988, Rhoades & Coleman 1999), and in the range that has been reported for tropical forests with moderately fertile soils (1-3 μg N g^{-1} d^{-1}) (Robertson 1984, Marrs *et al.* 1988). The data of the net N mineralization and nitrification, though, are in the upper range of the findings of Ellenberg (1977), lower than the findings of Pfadenhauer (1979), Hafkenscheid (2000) or Wilcke *et al.* (2002) and considerably lower than the very high net N mineralization found by Vitousek & Denslow (1986) in La Selva, Costa Rica (> 800 kg ha^{-1} yr^{-1}).

The results of this study are contradicting the assumption that soil N availability should decrease with elevation and increase with pedogenetic development in tropical forest soil. In summary hypotheses (i) had to be partly rebuted. A low availability of P in lowland forest soils and its increase with elevation could be confirmed, but the availability of N did not show

an opposing trend to P, in the contrary, N storage and availability were low in the lowland forest soils and also increased with elevation.

All cations showed very high within-plot and within-site variation in the upper mineral soil and also in the organic layer horizons, and none of the cation contents of the upper mineral soil were correlated with elevation, being consistent with the findings of Grieve *et al.* (1990), while all cation contents of the organic layer horizons significantly increased with rising elevation.

About 50 to 70% of the cations bound exchangeably to the cation exchangers in the upper mineral soil were aluminum, followed in decreasing abundance by Ca, Mg and K, while in the organic layers about 50 to 70% of the cations were calcium, followed in decreasing abundance by Al, Mg and K. Calcium as an element closely related to the carbonate buffering system in the soil had also the highest range of all analysed cations. While Al content was much higher in the mineral soil compared to the organic layers, much more Ca, K and Mg were bound to cation exchangers on a mass basis in the organic layer horizons than in the mineral soil, which additionally underlines the importance of the organic L, F and H horizons not only for N and P supply, but also for plant nutrition of basic (non-hydrolyzing) cations.

Landon (1991) stated that at a Ca/Mg-ratio above five in the soil availability of magnesium is aggravated, while a Ca/Mg-ratio below three indicates a decreased absorbing capacity of calcium for the plants. Taking the Ca/Mg-ratio into account, there is an indication for a possible calcium limitation at 1500 m elevation, while the study sites at 500, 1000 and 2000 m of elevation are more likely to predominantly lack magnesium. Variation of calcium, magnesium and Ca/Mg-ratio is huge however, and at all altitudes plots with a mean Ca/Mg-ratio below three were found.

Though on a third of our plots we found a hint for Mg limitation in the organic layer horizons, in summary we can state, that combined with the large increase in organic matter accumulation on top of the soil, the exchangeable Ca, Mg and K pools in the organic layers increased immensely with elevation. The organic layer horizons were moderately to highly acidic with pH_{KCl} values ranging from 2.8 to 5.9 in the whole study area and did not show an elevational trend, therefore plant availability of cations was not impaired by soil acidity with increasing elevation, confirming hypotheses (ii), stating that with progressive humus accumulation on top of the soil, increasing amounts of Ca, Mg and K are stored toward higher elevations and are partially available to plants. Compared to lowland tropical forest sites in the Amazonia basin our study sites were moderately nutrient-rich (Marrs *et al.* 1988, Tuomisto *et al.* 2003, Baillie *et al.* 2006, John *et al.* 2007) and also exceeded by far the

nutrient contents of the soils of the montane tropical forests in southern Ecuador (Wilcke *et al.* 2008).

Another important aim of this study was to quantify possible effects of soil fertility on stand structure, above-ground biomass and above-ground productivity parameters like stem diameter growth and to identify those soil chemical properties which have the largest influence on these parameters. A summary of the main data of forest stand structure, tree diversity and productivity is given in Table 6.3. Hypothesis (iii) stated that soil nutrients, especially phosphorus, have a positive effect on above-ground productivity.

With above-ground biomass means between 306 Mg ha^{-1} at 500 m and 371 Mg ha^{-1} at 1000 m elevation and an overall mean of 336 Mg ha^{-1} (see also Table 6.3 for site means of forest structure, tree diversity and productivity data) our calculations for AGB were comparable with the highest values for AGB reported in the Central Amazonian forests (Laurance *et al.* 1999, De Walt *et al.* 2004, Baker *et al.* 2004, de Castilho *et al.* 2006, Malhi *et al.* 2006), owing these results mainly to our study design, were only plots without any sign of natural or human disturbance were chosen and canopy gaps on our plots were avoided, therefore most likely overestimating the forest-wide AGB when calculated on a hectare basis. The majority of global tropical sites do not exceed aboveground biomass levels of 350 Mg ha^{-1} (Keeling & Phillips 2007), but there are a few exceptions of exceptional high biomass levels, like the findings of Kitayama & Aiba (2002) at Mount Kinabalu on Borneo, Malaysia (437-554 Mg ha^{-1}) and of various tropical forests in south eastern Asia which are rich of the angiosperm trees of the Dipterocarpaceae family with an AGB exceeding 450 Mg ha^{-1} (e.g. Hoshizaki *et al.* 2004, Slik *et al.* 2010).

A significant reduction in stem density with rising elevation was found, but the stand basal area slightly increased along our elevational transect, so in contrast to several other transect studies in tropical mountain forests a significant trend in AGB between 500 and 2000 m elevation in the study area could not be detected.

The above-ground biomass increment measured on 32 of our total of 80 plots varied by more than a factor of six (1.2 – 7.6 Mg ha^{-1} yr^{-1}) and showed a decline with elevation from 5.1 ± 0.6 Mg ha^{-1} yr^{-1} at 1000 m elevation to 3.4 ± 0.4 Mg ha^{-1} yr^{-1} at 1500 and 2000 m elevation, but this trend was not significant, though. Compared with other tropical forests and the global means (8.8 Mg ha-1 yr-1, Clark *et al.* 2001) our findings on AGB increment are very low.

Table 6.3: The 11 study sites with their number of stems (dbh $\geq$ 5 cm), number of tree species (dbh $\geq$ 5 cm), rarefied tree species (for N = 28 trees per 400 m²), LAI [m² m⁻²] and diffuse transmittance of photosynthetic active radiation (DT PAR) [% of incident radiation] per plot (400 m²), and tree basal area (BA) (dbh $\geq$ 10 cm) [m² ha⁻¹], tree above-ground biomass (AGB) (dbh $\geq$ 10 cm) [m² ha⁻¹], tree above-ground biomass (AGB) [Mg ha⁻¹], Basal area increment (BA inc.) [m² ha⁻¹ yr⁻¹] and AGB increment (AGB inc.) [Mg ha⁻¹ yr⁻¹] [per plot (means ± 1 SE).

Study sites	Forest stand structure and diversity [per plot (400 m²)]					Forest stand structure and productivity [per ha⁻¹]			
	No. stems	No. tree species	Rarefied tree species	LAI	DT PAR	BA	AGB	BA inc.	AGB inc.
Jatun Sacha	55.5 ± 2.4	40.5 ± 2.6	22.8 ± 0.5	6.4 ± 0.1	2.3 ± 0.2	37.6 ± 3.4	275.3 ± 29.4	0.3 ± 0.1	4.4 ± 1.0
Selva Viva	66.4 ± 3.5	49.4 ± 3.2	24.2 ± 0.5	6.9 ± 0.2	1.9 ± 0.2	45.5 ± 4.4	352.7 ± 49.5	0.5 ± 0.1	4.0 ± 1.0
Hakuna Matata	72.3 ± 5.0	43.3 ± 4.3	22.2 ± 0.9	7.5 ± 0.2	1.2 ± 0.2	46.0 ± 3.2	376.0 ± 35.4	0.4 ± 0.1	4.3 ± 1.1
Rio Hollín	75.8 ± 4.2	28.6 ± 1.8	15.3 ± 0.9	6.5 ± 0.3	1.1 ± 0.3	49.1 ± 7.3	383.5 ± 117.0	0.5 ± 0.1	5.6 ± 1.1
Galeras 1000m	50.9 ± 2.9	35.2 ± 2.9	21.5 ± 1.0	4.8 ± 0.1	5.3 ± 0.1	50.1 ± 4.3	360.5 ± 66.7	0.9 ± 0.3	5.0 ± 1.3
Galeras 1500m	76.4 ± 6.6	40.1 ± 2.5	20.2 ± 0.8	6.0 ± 0.2	3.6 ± 0.1	41.7 ± 3.1	301.6 ± 18.7	0.6 ± 0.1	2.0 ± 0.4
Cocodrilos	47.6 ± 3.7	28.1 ± 1.2	20.2 ± 0.7	5.7 ± 0.2	3.9 ± 0.4	55.6 ± 1.6	315.7 ± 55.0	0.4 ± 0.1	4.5 ± 0.2
Sumaco 1500m	41.8 ± 2.1	26.4 ± 0.9	19.8 ± 0.4	4.9 ± 0.2	5.5 ± 0.6	55.1 ± 4.6	389.2 ± 51.8	0.6 ± 0.2	3.8 ± 1.3
Sumaco 2000m	38.3 ± 3.7	22.3 ± 2.5	16.9 ± 1.3	5.0 ± 0.2	3.4 ± 0.2	63.9 ± 13.6	414.2 ± 102.1	0.5 ± 0.2	3.1 ± 0.3
C. Guacamayos	57.7 ± 6.2	29.4 ± 3.0	19.2 ± 1.3	5.5 ± 0.3	3.8 ± 0.5	35.1 ± 3.7	250.2 ± 29.5	0.7 ± 0.1	3.6 ± 0.6
Yanayacu	41.0 ± 3.7	19.0 ± 1.0	15.5 ± 0.7	4.9 ± 0.2	4.4 ± 0.3	47.9 ± 5.5	333.2 ± 45.4	0.4 ± 0.1	3.7 ± 1.8

The major reason for the low plant growth results is the lack of the fine litter production on our sites. Referring to Clark *et al.* (2001), the found above-ground biomass increment would be 1.72 times the coarse wood production, when fine litter production would be included in the calculations, and it would increase by a factor of 1.93, if also the in situ consumption of plant biomass by herbivores would be included in these calculations (Malhi *et al.* 2004).

But even when taking these values into account, the measured above-ground biomass production would summon up to 6.9 or 7.7 Mg ha^{-1} yr^{-1}, respectively, and are still considerably lower than the global means. Since we included only old-growth forest plots without any major disturbances and gaps we therefore omitted fast-growing early-successional stands in our study area, excluding the areas with a far higher productivity rate in our study design.

AGB increment accounted for $1.6 \pm 0.2\%$ of total AGB which concurs well with the results of Clark *et al*. (2001), who assumed that, in old-growth tropical forests, AGB increment should range between 1-2 % of standing AGB, though AGB and forest productivity were not correlated on our study sites, supporting the findings of Malhi *et al.* (2004).

The high heterogeneity of soil nutrient contents, forest structure and growth parameters of tropical forests worldwide are concealing clear effects of soil nutrients on forest structure. Gathering the various soil parameters into groups as a result of a principal component analysis and using these functional groups as parameters in a multiple regression analyses improved our insight of the effects of soil parameters on forest structure slightly. We could find a significant effect of the main soil nutrients total nitrogen, plant-available phosphorus and also the exchangeable cation contents of K, Mg and Ca of the organic layer horizons on basal area and also AGB, but the effect remained weak, though.

On the other hand, plant-available phosphorus and the exchangeable magnesium content of the organic layer horizons had a significant positive effect on all above-ground increment parameters, after exclusion of the elevation effect. Thus, it appears from the partial correlation that especially the above-ground biomass increment in our forest stands is influenced by soil nutrients especially in the organic layer horizons including plant-available phosphorus and salt-exchangeable magnesium.

Our results show the high heterogeneity of soil nutrient content, forest stature and also increment parameters of the tropical forest stands already on a very small scale as plot-size of 400 m², which makes general conclusions so difficult. Still, of all analyzed soil parameters of our study plant-available phosphorus was identified in partial correlations to have the strongest effect on coarse wood productivity, dbh. increment and basal area increment.

Therefore we suggest that plant-available phosphorus content especially in the organic layer horizons but also in the upper mineral soil is a primary driver of above-ground biomass increment throughout our study area, confirming hypothesis (iii).

The mean liana density was 1402 lianas ha^{-1} (with dbh ≥ 1 cm), ranging in between the lower values of 704 lianas ha^{-1} of various neotropical lowland forests (DeWalt & Chave 2004) and 816 lianas ha^{-1} of tropical forest plots in Costa Rica (Mascaro *et al.* 2004) and the higher values of 1812 lianas ha^{-1} of forest plots in Ecuador of Burnham (2002) or 2092 lianas ha^{-1} found in forests of Southeast Mexico (Ibarra-Manríquez & Martínez-Ramos 2002). The variation of liana density among plots was very high, though (ranging in between 895 lianas ha^{-1} at 1500 m elevation and 2810 lianas ha^{-1} at 2000 m elevation), but a clear trend of liana abundance with elevation could not be found. Over all, 54% of the investigated trees were infested by at least one liana with a dbh ≥ 1 cm, being in the range for liana infestation of other tropical wet forests in Costa Rica (Clark & Clark 1990), Ecuador (Nabe-Nielsen 2001), Mexico (Pérez-Salicrup & de Meijere 2005) or Argentina (Malizia & Grau 2006). Liana infestation rate showed a significant difference between the various study sites but no significant trend between the four elevation levels, therefore hypothesis (iv), stating that liana density and basal area would decrease with elevation, had to be neglected.

The factor controlling liana density the most in this study was tree basal area of the infested trees. Also mean tree dbh and canopy cover were identified as the most influential factors for liana basal area. The canopy cover increases with an increasing liana basal area, but this canopy cover increase is a consequence of the optical methods used in this study for measuring the canopy cover, which do not distinguish between tree and liana foliage. Thus, the denser canopy cover is rather a consequence than the cause of higher liana basal area.

Also a support for the influence of soil chemical properties on liana abundance was found, because soil nitrogen availability explained a significant share of variation in liana abundance. Also a possible negative effect of exchangeable aluminum and a positive effect of exchangeable calcium of the upper mineral soil on liana density was detected, supporting the findings of Gentry (1991), Laurance *et al.* (2001) or DeWalt *et al.* (2006), but disagreeing with the findings of DeWalt & Chave (2004) or van der Heijden & Phillips (2008), who could not find any relationship between soil fertility or other soil related gradients and liana density. So hypothesis (v), stating that stand structural properties are more influential for liana abundance than are edaphic factors, was confirmed.

Preceding studies on forest structure found a decrease of tree height with increasing elevation and along with it a coherent decrease of LAI. Therefore we postulated the

hypothesis (vi) that LAI decreases with elevation and that the diffuse transmittance of the photosynthetic active radiation (DT PAR, in percent of the incident radiation) increases with elevation. The DT PAR is dependent besides flux density of incident radiation and day length of the canopy PAR transmissivity, which is typically negatively linked to canopy leaf area, and thus forest structure and canopy density.

The LAI [$m^2 m^{-2}$] decreased constantly from 6.6 ± 0.1 (elevation means ± 1 SE) at 500 m to 6.2 ± 0.3 at 1000 m, 5.5 ± 0.2 at 1500 m to 5.2 ± 0.1 at 2000 m, which added up to an observed altitudinal decrease of LAI by about 1.1 $m^2 m^{-2} km^{-1}$ along the slope of the eastern Andes between 500 and 2000 m a.s.l., and these findings were astonishingly similar to the findings of Moser *et al.* (2007) in tropical forests in southern Ecuador, who found a decrease of LAI by 1 $m^2 m^{-2}$ per 1000 m altitude. On the other hand, the diffuse transmittance of PAR constantly increased from $2.1 \pm 0.2\%$ at 500 m to $4.4 \pm 0.3\%$ at 1500 m and decreased hereafter to $3.8 \pm 0.2\%$ at 2000 m again, resulting in an overall significant increase with elevation. Both parameters, LAI and DT PAR, were also tightly connected with each other, as we also found a highly significant negative linear correlation ($r^2 = 0.79$, $p \leq 0.001$) between LAI and DT PAR. Working hypotheses (vi) was therefore confirmed in our study.

The cloudiness generally increases with elevation till the height of the condensation level is reached (e.g. condensation level is reached at about 3000 m elevation at montane tropical forests in southern Ecuador (Bendix *et al.* 2008)), and is attended by a decrease of incident radiation (Hastenrath 1991, Bendix *et al.* 2008). But this general decrease of incident radiation along our altitudinal transect was more than just compensated by the decreasing LAI and therefore increasing DT PAR. The measured average photon flux densities of PAR increased from 11.6 $\mu mol\ m^{-2}\ s^{-1}$ at 500 m to 35.5 $\mu mol\ m^{-2}\ s^{-1}$ at 2000 m. Thus, the forest floor of montane tropical forests received more photosynthetic active radiation than lowland forest floors, not just in means of DT PAR, but also in actual photon flux density. With plot level means from 0.5 to 1.0% of DT PAR at study sites like Hakuna Matata and Rio Hollin (both at 1000 m elevation level) we found forest stands with a slightly darker forest floor than a range of temperate broad-leaved forests in the lowlands of Central Europe (Ellenberg & Leuschner, in press), herewith confirming also hypothesis (vii).

We conclude that extremely dense tropical forest canopies can reduce PAR transmissivity to the forest floor to a greater extent than it has been observed in most of the species-poor temperate forests. This is only true for lowland forests, though, while tropical lower montane and mid-montane forests typically have smaller leaf area indices. Thus, their PAR transmissivities are as high as, or even higher than, those of temperate lowland forests.

We also investigated hypothesis (viii), stating, that tree species density and stem density both have a positive effect on LAI and a negative one on DT PAR, as species richness, through plant composition, may have greater effects on light exploitation, therefore creating a denser forest canopy and reducing the DT PAR on the forest ground.

We found a significant increase in LAI with increasing stem density in our sample along the altitudinal gradient, a relationship which also persisted in the smaller 20-plot samples at 1000 and 1500 m elevation, indicating an effect of stem density on LAI independent of the elevational effect. The increasing stem density was also associated with a decrease in percent DT PAR. Several factors may be responsible for the stem density effect on leaf area and canopy transmissivity. First, a higher number of stems increase the surface area of woody axes in the canopy, thereby enlarging the plant surface area index which is quantified by optical measurement and is often assigned to equal LAI. Second, more stems can support more epiphytes and more lianas which contribute to radiation interception in the canopy.

The reasons for the apparent species diversity effect on LAI might be the complementary use of canopy space by the foliage of different tree species, increasing possibly stand leaf area and canopy absorptivity, representing a true diversity effect. On the other hand, a sampling effect (species with large leaf areas are more likely to be included in species-rich than in species-poor stands), or indirect third-party effects (through higher stem densities, which increase plant surface area index, or through higher epiphyte biomass) might also explain the observed diversity-leaf area relationship. However, separate analyses in sub-samples with defined stem density revealed a positive effect on LAI independently from stem density, confirming not only the stem density effect on LAI but also supporting the tree species diversity effect on LAI and DT PAR of hypothesis (viii).

6.2 FINAL CONCLUSIONS

A main goal of this study was to test the hypothesis that N limitation of plant growth tends to increase with elevation in tropical forests, while P limitation decreases (Grubb 1977, Edwards & Grubb 1977, Edwards 1982). In summary hypothesis (i) had to be partly rebuted. We could confirm a low availability of P in lowland forest soils and its increase with elevation, but the availability of N did not show an opposing trend to P, in the contrary N availability was low in the lowland forest soils and also increased with elevation, this trend being supported by an increase of total nitrogen content in the organic layer horizons and also

in the upper mineral soil as well by the constant N mineralization and nitrification rates (expressed on soil dry mass).

The concentrations of exchangeable Ca, Mg and K in the organic layer horizons increased significantly with elevation, and this rise of cation concentrations was also accompanied by an increasing accumulation in organic matter. Within our entire study area the acidity of the organic layer horizons were moderately to high, but an elevational trend of soil acidity was not found and an impaired plant availability of the exchangeable cations with elevation is therefore unlikely. Hypothesis (ii) was confirmed, the pools of plant-available Ca, Mg and K are increasing with elevation.

Another aim was to clarify, which of the soil fertility parameters have the most effect on both forest structure as well as forest productivity parameters (hypothesis (iii)). This was especially difficult because most of the soil parameters and also the forest vegetation parameters are strongly influenced by elevation, respectively temperature and precipitation which are closely linked to elevation. Also the high heterogeneity of soil nutrient contents, forest structure and growth parameters within our study sites are concealing clear effects of soil nutrients on forest structure and even impeded our statistical analyses.

Still, a weak effect of the following soil parameters total nitrogen, plant-available phosphorus and also the exchangeable cation contents of K, Mg and Ca of the organic layer horizons were found on forest structure parameters like basal area and also AGB. While the productivity parameters in form of diameter at breast height (dbh.), basal area and also AGB increment were all positively affected by plant-available phosphorus and the exchangeable magnesium content of the organic layer horizons, after the effect of elevation was excluded.

Hypothesis (iii) was therefore confirmed. The results of simple and partial correlation analyses encourage the conclusion that of all soil elements especially the phosphorus content in the organic layer horizons but also in the upper mineral soil is the soil mineral with the biggest positive effect on above-ground biomass productivity. Plant-available N (expressed by the in situ N mineralization and nitrification rates and the C/N-ratio) had a surprisingly small influence on forest biomass and productivity, both at lowland and lower montane elevation, thereby also contradicting the part of hypothesis (i) of increasing N limitation of tree growth with elevation in tropical mountain forests.

For the liana studies, the liana basal area per plot varied in between the four elevation levels but did not show a significant trend with elevation, while the mean liana diameter decreased significantly with elevation, and the mean liana density increased slightly with elevation, but did not show any significant trend with elevation neither. Hypothesis (iv) was therefore

rejected. The most important determinants for liana abundance in the Sumaco Biosphere Reserve were structural stand properties like host tree basal area and mean tree dbh, though soil chemical properties like nitrogen availability seem to have some influence on liana abundance as well, so hypothesis (v) was confirmed, stand structural properties are more influential for liana abundance than are edaphic factors.

LAI significantly decreased and DT PAR increased with elevation, and both parameters were tightly linked to each other, hypothesis (vi) was therefore confirmed.

In the lowland tropical forests of our study area we found the highest mean leaf area indices and also the lowest photon flux densities (at more than a third of all lowland tropical forest plots at 500 and 1000 m elevation we measured photon flux densities below 5 μmol m^{-2} s^{-1}). Some plot level means of DT PAR at these altitudes were also below the range of temperate broad-leaved forests of Central Europe, and therefore hypothesis (vii) was confirmed.

Finally, hypothesis (viii) was affirmed. An increase of LAI with an increasing number of stems per plot seems only logical and was also affirmed in our studies, the effect of tree species diversity on LAI and DT PAR proved much more complicated to determine, because species diversity is always closely linked to stem density as well. By finding the LAI being significantly higher in a stand with 50 species per plot than in a stand with only 20 species, we found evidence in support of a positive diversity-productivity relationship in these tropical forests, confirming the stem density effect on LAI and supporting the effect of tree species diversity on LAI and DT PAR.

6.3 RESUMEN

Un objetivo principal de este estudio fue probar la hipótesis de que la limitación del elemento N en el crecimiento de las plantas tiende a aumentar con la altitud en los bosques tropicales, mientras que la limitación de P disminuye (Grubb 1977, Grubb & Edwards 1977, Edwards, 1982). En resumen, la hipótesis (i) tuvo que ser parcialmente rechazada. Se podría confirmar una baja disponibilidad de P en los suelos de los bosques de tierras bajas y su aumento con la altitud, pero la disponibilidad de N no mostró una tendencia opuesta a la de P. Es así que, la disponibilidad de N fue baja en los suelos de los bosques de tierras bajas y también aumentó con la elevación, esta tendencia está respaldada por un aumento del contenido total de Nitrógeno en los horizontes de capa orgánica y en el suelo mineral superior, así como también por la mineralización de N constante y las tasas de nitrificación (expresada en la masa seca del suelo).

Las concentraciones intercambiables de Ca, Mg y K en los horizontes de capa orgánica aumentaron considerablemente con la altitud, y este aumento de las concentraciones de cationes estuvo también acompañado por una creciente acumulación de materia orgánica. En toda nuestra área de estudio, la acidez de los horizontes de capa orgánica es de moderada a alta, pero no se encontró una tendencia altitudinal de la acidez del suelo, por lo tanto es poco probable un deterioro en la disponibilidad de los cationes intercambiables por las plantas con la altitud. La hipótesis (ii) fue confirmada, las concentraciones disponibles de Ca, Mg y K de las plantas aumentan con la altitud.

Otro objetivo fue aclarar cuál de los parámetros de fertilidad del suelo tienen mayor efecto, tanto en la estructura del bosque, como en los parámetros de productividad del bosque (hipótesis (iii)). Esto fue especialmente difícil debido a que la mayoría de los parámetros del suelo y de la vegetación de los bosques están fuertemente influenciadas por la altitud, temperatura y precipitación, las cuales están estrechamente vinculadas a la elevación. Además, la gran heterogeneidad del contenido de nutrientes del suelo, la estructura del bosque y los parámetros de crecimiento dentro de nuestros sitios de estudio están ocultando los claros efectos de los nutrientes del suelo sobre la estructura de los bosques, e incluso están impidiendo nuestros análisis estadísticos.

Sin embargo, un efecto limitado de los siguientes parámetros del suelo como el Nitrógeno total, la disponibilidad de Fósforo para la planta y el contenido de cationes intercambiables de K, Mg y Ca de los horizontes de capa orgánica, se encuentran en los parámetros de la estructura del bosque como área basal y AGB. Mientras que, los parámetros de la productividad constituidos por diámetro a la altura del pecho (dap), área basal y el incremento AGB fueron llevados a cabo positivamente por la disponibilidad de Fósforo de la planta y el contenido de Magnesio intercambiable de los horizontes de capa orgánica, después de que el efecto de la altitud fue excluido.

La Hipótesis (iii) fue confirmada. Los resultados de los análisis de correlación simple y parcial llevan a la conclusión de que de todos los elementos del suelo, especialmente el contenido de Fósforo, están presentes en los horizontes de capa orgánica y también en el suelo mineral superior con el mayor efecto positivo sobre la productividad de la biomasa por encima del suelo. La cantidad de N disponible para la planta (expresada por la mineralización de N *in situ*, las tasas de nitrificación y la relación de C/N) tuvo una influencia sorprendentemente pequeña sobre la biomasa forestal y la productividad en tierras bajas y bosques montanos de menor altitud. Con esto también se contradice parte de la hipótesis (i),

es decir, el aumento de la limitación de N en el crecimiento de los árboles con el incremento de la altitud en los bosques tropicales de montaña.

En cuanto al estudio de los bejucos, el área basal de las lianas por parcela varió entre los cuatro niveles altitudinales, pero no mostraron una tendencia significativa con la elevación. En tanto que con la altitud, la media del diámetro de las lianas disminuyó y la densidad media de las lianas aumentó ligeramente. A pesar de ello, no muestran ninguna tendencia significativa con la elevación en ningun caso. La Hipótesis (iv) fue rechazada. Los determinantes más importantes de la abundancia de las lianas en la Reserva de Biosfera Sumaco fueron las propiedades estructurales tales como el área basal de los árboles hospederos y la media basal de árboles (dap). Aunque las propiedades químicas del suelo como la disponibilidad de Nitrógeno, parecen tener alguna influencia sobre la abundancia de las lianas. Así la hipótesis (v) fue confirmada, las propiedades estructurales son más influyentes para la abundancia de lianas que los factores edáficos.

Con el aumento de la altitud, LAI disminuyó considerablemente y el DT PAR aumentó, además ambos parámetros estuvieron estrechamente vinculados entre sí. Con lo cual la hipótesis (vi) fue confirmada.

En los bosques tropicales de tierras bajas de nuestra área de estudio encontramos los mayores índices del área media de la hoja y también las menores densidades de flujo de fotones (en más de un tercio de todas las parcelas de bosque tropical de tierras bajas a 500 y 1000 m de altitud se determinó una densidad de flujo de fotones por debajo de 5 mmol m^{-2} s^{-1}). Algunas medias del nivel de DT PAR en las parcelas en estas altitudes, también estuvieron por debajo del rango de los bosques templados de hoja ancha de Europa Central, por lo tanto la hipótesis (vii) fue confirmada.

Por último, la hipótesis (viii) fue reafirmada. Un aumento de la LAI con un creciente número de tallos por parcela, parece ser lógico y se afirmó también en nuestros estudios. El efecto de la diversidad de especies de los árboles sobre la LAI y el DT PAR fue mucho más complicado de determinar, debido a que la diversidad de especies siempre está estrechamente vinculada a la densidad de los troncos. Al ser la LAI significativamente mayor en un grupo con 50 especies por parcela que en un grupo con sólo 20 especies, encontramos pruebas que apoyan una relación positiva entre la diversidad y la productividad en estos bosques tropicales. Con este hecho se confirma no sólo el efecto de la densidad del tallo sobre la LAI sino también el efecto de la diversidad de especies de árboles sobre la LAI y el DT PAR.

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CHAPTER

7

APPENDIX

Appendix 1. The 11 Study sites with the GPS-position and exact elevation (measured in the centre of each plot) of their plots and the indication, which of the plots were used for further measurements of stem growth (Trees with dendrometers), and equipped with data loggers for Air Temperature and Humidity (at 1.5 m above the ground) and/or Soil Temperature measurements (below the organic litter layer).

Study site: Jatun Sacha					**Elevation level 500 m**
Plot No.	**GPS-Position** **(plot centre)**	**Elevation** **[m a.s.l.]**	**Stem growth** **data** **(Dendrometers)**	**Air Temp. &** **Humidty** **data**	**Soil** **Temperature** **data**
1	S1° 04 99.6 W77° 36 43.2	425	✓	✓	✓
2	S1° 04 03.7 W77° 37 00.0	400	✓	✓	✓
3	S1° 05 20.7 W77° 36 82.9	425	none	none	none
4	S1° 04 21.5 W77° 36 93.4	435	✓	✓	✓
5	S1° 04 74.7 W77° 36 42.6	435	✓	✓	✓
6	S1° 04 72.3 W77° 36 38.2	420	none	none	none
7	S1° 04 39.8 W77° 36 72.0	421	none	none	none
8	S1° 04 76.1 W77° 36 51.4	427	none	none	none
9	S1° 04 79.4 W77° 36 51.3	424	none	none	none
10	S1° 04 96.4 W77° 36 42.8	425	none	none	none
11	S1° 05 07.2 W77° 36 22.9	450	none	none	none
12	S1° 05 14.5 W77° 36 23.7	420	none	none	none

Study site: Selva Viva					**Elevation level 500 m**
Plot No.	**GPS-Position** **(plot centre)**	**Elevation** **[m a.s.l.]**	**Stem growth** **data** **(Dendrometers)**	**Air Temp. &** **Humidty** **data**	**Soil** **Temperature** **data**
13	S1° 03 94.8 W77° 31 22.0	502	none	none	none
14	S1° 03 96.7 W77° 31 28.0	508	none	none	none
15	S1° 03 96.0 W77° 31 28.2	508	✓	✓	✓
16	S1° 05 45.8 W77° 30 52.5	517	none	none	none
17	S1° 05 41.3 W77° 30 59.0	453	✓	none	none
18	S1° 05 40.0 W77° 30 62.7	445	none	none	none
19	S1° 05 28.2 W77° 30 84.5	470	✓	none	none
20	S1° 05 16.7 W77° 30 95.1	484	none	none	none

Study site: Hakuna Matata					Elevation level 1000 m	
Plot No.	GPS-Position (plot centre)	Elevation [m a.s.l.]	Stem growth data (Dendrometers)	Air Temp. & Humidty data	Soil Temperature data	
21	S0° 53 87.4 W77° 50 67.4	970	✓	✓	✓	
22	S0° 53 87.2 W77° 50 67.2	960	✓	✓	✓	
23	S0° 53 49.2 W77° 50 40.2	1000	none	none	none	
24	S0° 53 81.4 W77° 50 74.2	1050	none	none	none	
25	S0° 53 48.4 W77° 50 41.2	1020	none	none	none	
26	S0° 53 48.7 W77° 50 46.7	1080	none	none	none	

Study site: Rio Hollin					Elevation level 1000 m	
Plot No.	GPS-Position (plot centre)	Elevation [m a.s.l.]	Stem growth data (Dendrometers)	Air Temp. & Humidty data	Soil Temperature data	
27	S0° 40 55.1 W77° 44 90.2	1190	none	none	none	
28	S0° 40 53.8 W77° 44 88.5	1195	✓	none	none	
29	S0° 40 54.4 W77° 44 83.5	1210	✓	none	none	
30	S0° 40 82.2 W77° 44 82.5	1165	✓	✓	✓	
31	S0° 40 79.6 W77° 44 89.5	1180	none	none	none	

Study site: Galeras					Elevation level 1000 m	
Plot No.	GPS-Position (plot centre)	Elevation [m a.s.l.]	Stem growth data (Dendrometers)	Air Temp. & Humidty data	Soil Temperature data	
32	S0° 49 76.1 W77° 34 03.2	1090	✓	✓	✓	
33	S0° 49 79.3 W77° 34 05.9	1080	none	none	none	
34	S0° 48 86.3 W77° 34 65.8	1060	✓	✓	✓	
35	S0° 48 92.3 W77° 34 62.6	1090	none	none	none	
36	S0° 50 27.4 W77° 33 62.3	1110	✓	none	none	
37	S0° 48 79.9 W77° 34 66.9	1050	none	none	none	
38	S0° 49 76.6 W77° 34 07.3	1000	none	none	none	
39	S0° 50 26.9 W77° 33 62.6	1130	none	none	none	
40	S0° 48 92.0 W77° 34 60.1	1080	none	none	none	

Study site: Galeras					Elevation level 1500 m	
Plot No.	GPS-Position (plot centre)	Elevation [m a.s.l.]	Stem growth data (Dendrometers)	Air Temp. & Humidty data	Soil Temperature data
41	S0° 49 70.5 W77° 32 55.5	1450	✓	✓	✓
42	S0° 49 66.5 W77° 32 34.9	1560	✓	✓	✓
43	S0° 49 75.0 W77° 32 26.1	1597	none	none	none
44	S0° 49 75.8 W77° 32 21.4	1557	none	none	none
45	S0° 49 76.8 W77° 32 13.9	1570	✓	none	none
46	S0° 49 77.6 W77° 32 17.4	1560	none	none	none
47	S0° 49 75.4 W77° 32 30.8	1590	none	none	none

Study site: Cocodrillos					Elevation level 1500 m	
Plot No.	GPS-Position (plot centre)	Elevation [m a.s.l.]	Stem growth data (Dendrometers)	Air Temp. & Humidty data	Soil Temperature data
48	S0° 38 38.6 W77° 47 09.1	1550	none	none	none
49	S0° 38 32.9 W77° 46 93.7	1490	✓	✓	✓
50	S0° 38 16.7 W77° 46 54.4	1490	none	none	none
51	S0° 38 16.3 W77° 46 55.3	1490	✓	✓	none
52	S0° 38 17.9 W77° 47 08.9	1570	✓	none	none

Study site: Sumaco					Elevation level 1500 m	
Plot No.	GPS-Position (plot centre)	Elevation [m a.s.l.]	Stem growth data (Dendrometers)	Air Temp. & Humidty data	Soil Temperature data
53	S0° 37 15.0 W77° 35 75.7	1580	none	none	none
54	S0° 37 14.0 W77° 35 80.3	1590	✓	✓	✓
55	S0° 37 69.8 W77° 35 22.4	1610	✓	✓	✓
56	S0° 37 68.8 W77° 35 25.2	1610	none	none	none
57	S0° 38 12.0 W77° 35 21.5	1590	✓	none	none
58	S0° 38 98.4 W77° 35 20.5	1590	none	none	none
59	S0° 37 14.5 W77° 35 78.0	1580	none	none	none
60	S0° 37 71.9 W77° 35 21.1	1600	none	none	none

Study site: Sumaco					**Elevation level 2000 m**
Plot No.	**GPS-Position** (plot centre)	**Elevation** [m a.s.l.]	**Stem growth data** (Dendrometers)	**Air Temp. & Humidty data**	**Soil Temperature data**
61	S0° 35 48.1 W77° 35 26.3	1920	✓	✓	✓
62	S0° 35 47.9 W77° 35 26.5	1940	none	none	none
63	S0° 35 39.8 W77° 35 31.0	1950	✓	none	none
64	S0° 38 01.8 W77° 35 44.6	2015	✓	✓	✓
65	S0° 35 10.1 W77° 35 43.3	2000	none	none	none
66	S0° 35 31.1 W77° 35 16.0	1931	none	none	none
67	S0° 35 06.0 W77° 35 43.9	2000	none	none	none

Study site: Cordillera Guacamayos					**Elevation level 2000 m**
Plot No.	**GPS-Position** (plot centre)	**Elevation** [m a.s.l.]	**Stem growth data** (Dendrometers)	**Air Temp. & Humidty data**	**Soil Temperature data**
68	S0° 38 29.5 W77° 50 39.6	2000	✓	✓	✓
69	S0° 38 55.1 W77° 50 21.4	1940	✓	✓	✓
70	S0° 38 19.6 W77° 50 38.4	1995	✓	✓	✓
71	S0° 38 37.9 W77° 50 35.4	1990	none	none	none
72	S0° 38 19.3 W77° 50 23.8	1980	none	none	none
73	S0° 38 42.0 W77° 50 34.2	1980	none	none	none
74	S0° 38 19.4 W77° 50 38.4	2000	none	none	none
75	S0° 38 19.6 W77° 50 38.6	2000	none	none	none

Study site: Yanayacu					**Elevation level 2000 m**
Plot No.	**GPS-Position** (plot centre)	**Elevation** [m a.s.l.]	**Stem growth data** (Dendrometers)	**Air Temp. & Humidty data**	**Soil Temperature data**
76	S0° 36 14.1 W77° 53 00.1	2085	✓	✓	✓
77	S0° 36 13.1 W77° 52 73.1	2080	none	none	none
78	S0° 36 29.2 W77° 52 60.5	2055	✓	none	none
79	S0° 36 33.9 W77° 52 70.2	2070	none	none	none
80	S0° 36 08.1 W77° 53 04.6	2080	none	none	none

Appendix 2. 24 soil profiles of six study sites (four profiles per study site) (Selva Viva (500 m), Hakuna Matata and Cordillera Galeras (1000 m), Cordillera Galeras and Volcano Sumaco (1500 m) and Volcano Sumaco (2000 m)) with their physical characteristics (sand, silt and clay content) [%]. Explanation of the soil profile abbreviations: A – mineral soil horizon of the surface soil, enriched with humus, B – mineral soil horizon of the subsoil with altered mineral supply because of inclusions and/or weathering, C1 and C2 – granular soil mixed with soil from the soil horizons above, R – Bedrock, Ah – dark mineral soil horizon, rich on organic material, Al – mineral soil horizon, rich on organic material but poor on clay, Bws1 and Bws2 – B horizons of the mineral soil, enriched with sesquioxides, bleached by wetness, Bw – bleached B horizon, Ah/B, Bw/C and B/C – transitional horizons.

Physical characteristics

Selva Viva 500 m
Profile No.: III
Inclination: sloped
Soil type: geric Ferralsol

Clay
Silt
Sand

Ah
Bws1
Bws2
C

Soil profiles

Physical characteristics

Selva Viva 500 m
Profile No.: IV
Inclination: sloped
Soil type: geric Ferralsol

Clay
Silt
Sand

Ah
Bws1
Bws2
C

Soil profiles

Physical characteristics

Hakuna Matata 1000 m
Profile No.: V
Inclination: even
Soil type: geric Ferralsol

Clay
Silt
Sand

Ah
B
B/C
C

Soil profiles

165

Physical characteristics

Hakuna Matata 1000 m
Profile No.: VI
Inclination: even
Soil type: geric Ferralsol

- Clay
- Silt
- Sand
- Ah
- B
- B/C
- C

Soil profiles

Physical characteristics

Hakuna Matata 1000 m
Profile No.: VII
Inclination: sloped
Soil type: geric Ferralsol

- Clay
- Silt
- Sand
- Ah
- B
- C

Soil profiles

Physical characteristics

Hakuna Matata 1000 m
Profile No.: VIII
Inclination: sloped
Soil type: geric Ferralsol

- Clay
- Silt
- Sand
- Ah
- B
- C

Soil profiles

Physical characteristics

Soil profiles

Cord. Galeras 1000 m
Profile No.: IX
Inclination: even
Soil type: geric Ferralsol

Clay
Silt
Sand

Al
Ah
B
C

Physical characteristics

Soil profiles

Cord. Galeras 1000 m
Profile No.: X
Inclination: even
Soil type: Ferralsol

Clay
Silt
Sand

Al
Ah
Bws1
Bws2
C

Physical characteristics

Soil profiles

Cord. Galeras 1000 m
Profile No.: XI
Inclination: sloped
Soil type: geric Ferralsol

Clay
Silt
Sand

Al
Ah
Ah/B
B
C

Cord. Galeras 1000 m
Profile No.: XII
Inclination: sloped
Soil type: geric Ferralsol

Cord. Galeras 1500 m
Profile No.: XIII
Inclination: even
Soil type: ferralic Cambisol

Cord. Galeras 1500 m
Profile No.: XIV
Inclination: even
Soil type: ferralic Cambisol

Physical characteristics

Cord. Galeras 1500 m
Profile No.: XV
Inclination: sloped
Soil type: ferralic Cambisol

Clay
Silt
Sand

Al
Ah
B

Soil profiles

Physical characteristics

Cord. Galeras 1500 m
Profile No.: XVI
Inclination: sloped
Soil type: ferralic Cambisol

Clay
Silt
Sand

Al
Ah
B
C
R

Soil profiles

Physical characteristics

Sumaco 1500 m
Profile No.: XVII
Inclination: even
Soil type: Cambisol

Clay
Silt
Sand

Al
Ah
Ah/B
B
C

Soil profiles

169

Physical characteristics

Sumaco 1500 m
Profile No.: XVIII
Inclination: even
Soil type: Luvisol

Clay
Silt
Sand

Ah
Al
B
C1
C2

Soil profiles

Physical characteristics

Sumaco 1500 m
Profile No.: XIX
Inclination: sloped
Soil type: Cambisol

Clay
Silt
Sand

Al
Ah
B

Soil profiles

Physical characteristics

Sumaco 1500 m
Profile No.: XX
Inclination: sloped
Soil type: Luvisol

Clay
Silt
Sand

Ah
Al
B
C1
C2

Soil profiles

Physical characteristics

Sumaco 2000 m
Profile No.: XXI
Inclination: even
Soil type: stagnic Acrisol

Soil profiles

Physical characteristics

Sumaco 2000 m
Profile No.: XXII
Inclination: even
Soil type: stagnic Cambisol

Soil profiles

Physical characteristics

Sumaco 2000 m
Profile No.: XXIII
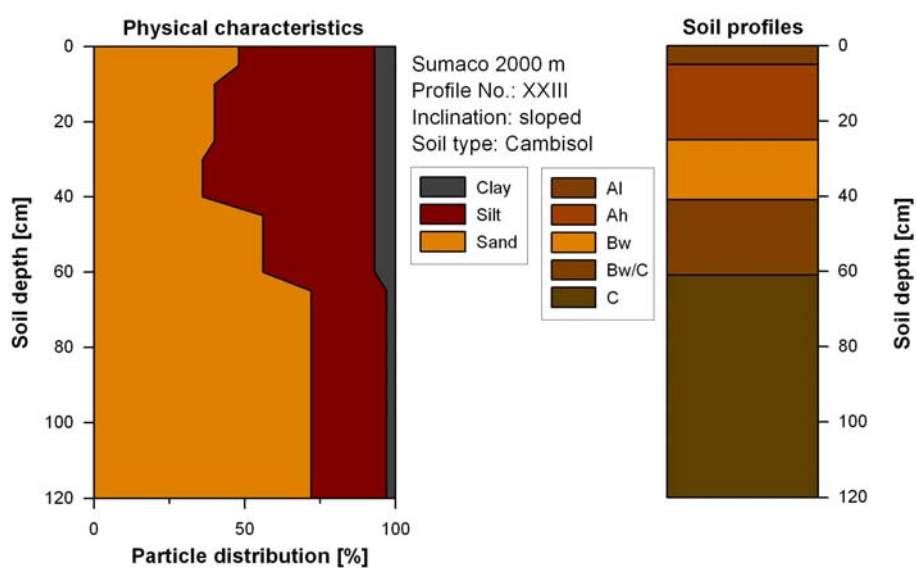Inclination: sloped
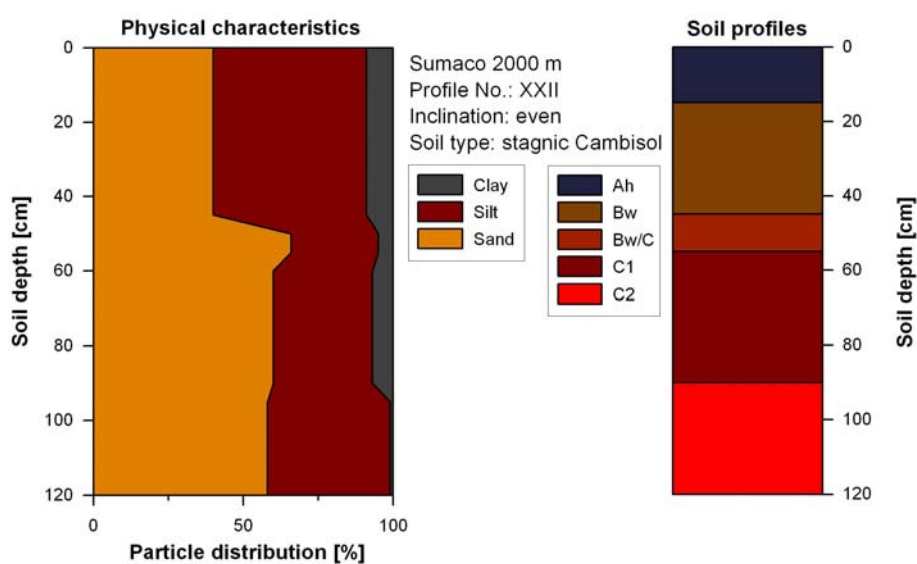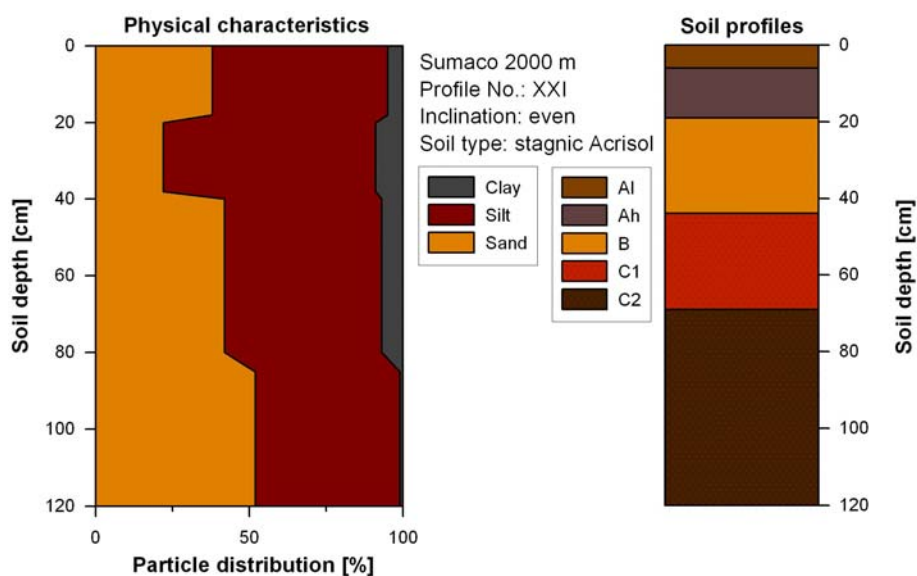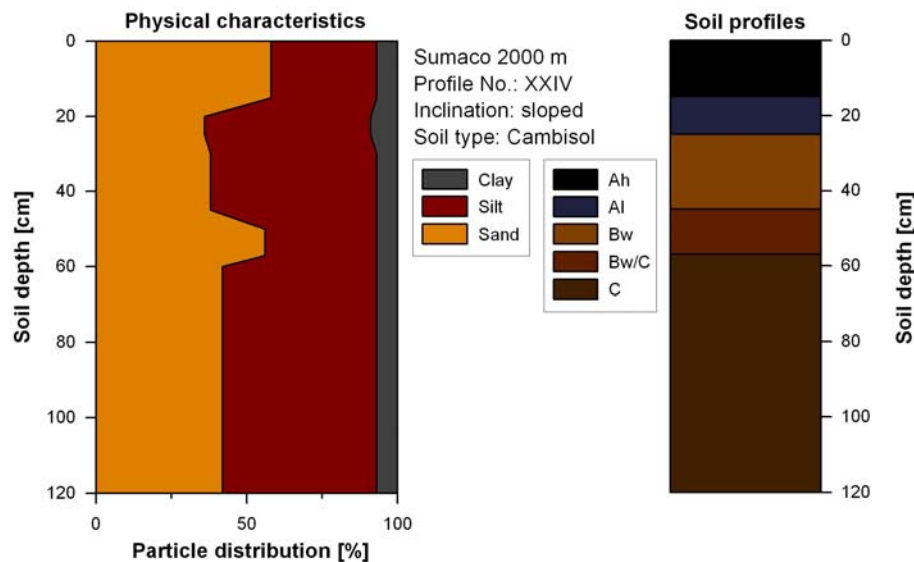Soil type: Cambisol

Soil profiles

171

Ferralic properties – The ferralic horizon is a subsurface horizon resulting from long and intense weathering, in which the clay fraction is dominated by low activity clays and the silt and sand fractions by highly resistant minerals, such as iron-, aluminum-, manganese- and titanium oxides.

Geric properties – Mineral soil material with very low cation exchange capacity (< 1.5 cmolc kg^{-1} clay).

Stagnic properties – Features in connexion with temporary saturation of soil material caused by rainfall and slow percolation.

Terms for soil groups and diagnostic properties according to IUSS Working Group WRB. 2006. Symbols for the different soil horizons are used according to Catt (1986), Driessen & Dudal (1991), Zech & Hintermaier-Erhard (2002) and/or AG Boden (2005).

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ZECH, W., HINTERMAIER-ERHARD, G. 2002. Böden der Welt. Spektrum-Verlag, Berlin.

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