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Trace gas fluxes and belowground carbon allocation in tropical montane forest soils of Southern Ecuador

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EL ERROR NUESRO ES PENSAR QUE LA NATURALEZA

ES DE NOSOTROS, CUNADO EN REALIDAD,

NOSOTROS SOMOS PARTE DE ELLA

Wrightihg at the Entrance to the Podocarpus National park in Bombuscaro

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Zusammenfassung

Tropische Wälder sind eine wichtige Quelle für die Treibhausgase Kohlendioxid (CO_2) und Distickstoffoxid (Lachgas, N_2O) und für Stickstoffmonoxid (NO), ein Ausgangsstoff bei der Bildung von Ozon, und sie sind Senken für das Treibhausgas Methan (CH_4). Die Einschätzung der Bodenspurengasflüsse und des Kohlenstoffkreislaufes tropischer Wälder ist derzeit noch überproportional stark von Arbeiten aus Tieflandwäldern bestimmt. In Bezug auf den Spurengasaustausch in tropischen Bergwäldern (TMF), steht dagegen nur eine beschränkte Menge an Daten zur Verfügung und ihr Kohlenstoffkreislauf ist nur ansatzweise erforscht, obwohl TMFs etwa 9% der tropischen Waldfläche ausmachen. In dieser Dissertation werden die Ergebnisse einer extensiven Studie über den Austausch von CO_2, N_2O, NO, and CH_4 zwischen Boden und Atmosphäre, dessen mögliche biogeochemische Einflussgrößen, sowie über die unterirdische Kohlenstoff-Allokation (TBCA) in tropischen Bergwäldern in Südecuador präsentiert. Der spezielle Fokus dieser Studie lag dabei auf dem Einfluss von Nährstofflimitierungen. Die Flüsse von CO_2, N_2O and CH_4 wurden mittels stationären geschlossenen Kammern und Gaschromatographie in drei Höhestufen entlang eines Höhengradienten von 1000 m bis 3000 m (1000 m, 2000 m, 3000 m) und entlang topographischer Gradienten (Unterhang, Mittelhang, Kamm) bestimmt. NO Flüsse wurden im Feld unter Verwendung offener dymamischer Kammern und eines LMA-3D NO_2 Analysegeräts mit Chemilumineszenzdetektion gemessen. Zusätzlich wurde die potentielle Kapazität verschiedener Bodensubstrate aus mehreren Bodentiefen CH_4 in atmosphärischen Konzentrationen aufzunehmen mittels eines Labor-Inkubationsversuchs untersucht. Die Bestimmung der Nährstoffverfügbarkeit im Boden erfolgte mit Hilfe verschiedener Extraktionmethoden und über die Interpretation diverser Indizes (C:N, C:K, C:P Verhältnisse, $\delta\,^{15}N$ Signaturen der Streu). Zur Abschätzung der unterirdischen Kohlenstoff-Allokation schließlich, wurden einjährige Messungen von Bodenatmung und oberirdischer Streuproduktion herangezogen.

In den untersuchten TMFs nahm die Mächtigkeit der organischen Auflage mit steigender Meereshöhe und vom Unterhang zum Kamm zu, während die Nährstoffverfügbarkeit in gleicher Richtung abnahm. Die oberirdische Streuproduktion erwies sich als stickstoff- (N), phosphor-

(P) und auf den meisten Flächen auch kalium- (K) limitiert. Sie war hauptsächlich and den Vorrat verfügbarer Nährstoffe in der organischen Auflage gebunden, obwohl der Mineralboden reicher an verfügbarem P und K war. Basalflächenzuwachs und oberidische Streuproduktion korrelierten positiv mit Indizes von Nährstoffverfügbarkeit (C:N Verhältnis und δ ^{15}N Signaturen der Streu), während die TBCA keine derartigen Zusammenhänge erkennen ließ. Die Abnahme der TBCA mit zunehmender Meereshöhe und vom Unterhang zu dem Kammlagen und stand vielmehr im Zusammenhang mit dem Bodenwassergehalt und der Mächtigkeit der organischen Auflage. Die Spurengasflüsse in den Böden unserer TMF Standorte waren niedriger, als die Flüsse vieler Tieflandstandorte und lagen im Allgemeinen innerhalb der bisher von tropischen Bergwäldern berichteten Spannweite. Stickoxid- und CH_4- Flüsse standen in keinem nachweisbaren Zusammenhang mit der Bodenfeuchte oder der Mächtigkeit der organischen Auflage, während die Bodenatmung mit beiden Parametern negativ korreliert war. Die Stickoxidflüsse waren positiv korreliert mit Indikatoren die die längerfristige N-verfügbarkeit widerspiegeln, wie C:N Verhältnis und δ ^{15}N Signaturen in der Streu, und mit Indikatoren der Waldprimärproduktivität, wie oberirdische Streuproduktion und Basalflächenzuwachs. Die Streuqualität hatte positiven Einfluss auf die Bodenatmung, und die Aufnahmeraten von CH_4 im Boden stiegen mit dem Gehalt an mineralischem N im Boden und dem Gesamtvorrat an P im Mineralboden, sowie mit zunehmenden CO_2 Emission. Die Ergebnise des Inkubationsversuchs zeigten eine hohe potentielle CH_4 Aufnahmekapazität in den unteren Schichten der organischen Auflagen der 2000 m und 3000 m Standorte.

Die engen Korrelationen von Nährstoffverfügbarkeit mit oberirdischer Streuproduktion und Basalflächenzuwachs können als Anzeichen einer Nährstofflimitierung der Waldprimärproduktion in den untersuchten TMFs interpretiert werden. Die dichte Durchwurzelung der organischen Auflagen und die engen Zusammenhänge zwischen der Nährstoffverfügbarkeit in der organischen Auflage und den Nährstoffkonzentrationen in der Streu deuten darauf hin, dass der Nährstoffkreislauf in den organischen Auflagen konzentriert und weitgehend vom Mineralboden entkoppelt ist. Im Gegensatz zur oberirdischen Waldprimärproduktivität war die TBCA nicht nährstofflimitiert. Die Abnahme der TBCA mit ansteigender Meereshöhe ging mit einer Zunahme der Feinwurzelbiomasse einher, was durch längere Persistenz der Wurzeln erklärt werden kann. Zusammen mit einem langsamen Abbau der

organischen Substanz, mag dies zur hohen C-Speicherung in den organischen Auflagen der TMFs beitragen.

Spurengasflüsse waren positiv mit verschiedenen Indizes von Nährstoffverfügbarkeit korreliert. Wir fanden Anzeichen dafür, dass zunehmend ungünstige Bodenbedingungen und schlechtere Streuqualität die allgemeine mikrobielle Aktivität mindern und somit Bodenatmung, Stickoxidflüsse und die Aufnahme von CH_4 verringern. Enge lineare Zusammenhänge von N-oxiden mit oberirdischer Streuproduktion und Basalflächenzuwachs zeigen, dass Stickoxidflüsse und Waldprimärproduktivität über die N-verfügbarkeit verbunden sind und eröffnen die Möglichkeit, die Waldprimärproduktivität (speziell den Basalflächenzuwachs) als Kovariable in Vorhersagemodelle für Stickoxidflüsse in N-limitierten Ökosystemen zu integrieren. CH_4 Aufnahmeraten waren positiv mit Konzentrationen von mineralischem Stickstoff im Boden korreliert, was darauf hinweist, dass CH_4 Aufnahmen in erster Linie nährstofflimitiert waren und der Mechanismus der Ammoniuminhibition als regulierender Faktor vernachlässigbar ist. Im Gegensatz zur weitverbreiteten Annahme, stellten die organischen Auflagen in den untersuchten TMFs keine reinen Gasdiffusionsbarrieren dar, sondern zeigten beträchtliche, potentielle CH_4 Aufzunahmekapazitäten und könnten damit zur Entfernung von CH_4 aus der Atmosphäre beitragen.

SUMMARY

Tropical forest soils are important sources of the greenhouse gases carbon dioxide (CO_2) and nitrous oxide (N_2O), and of nitric oxide (NO), a precursor of ozone production. They are also sinks for the greenhouse gas methane (CH_4). Estimates on soil trace gas fluxes and on carbon cycling from tropical forest soils are heavily biased towards lowland forests. Limited data is available on trace gas exchange from tropical montane forest (TMF) soils and their carbon cycle has only been marginally explored, although TMFs cover approximately 9% of the tropical forest area. This dissertation presents the results of a comprehensive study on soil CO_2, N_2O, NO, and CH_4 exchange and possible biogeochemical regulators, with a special focus on the influence of nutrient availability in TMFs of southern Ecuador. Soil CO_2, N_2O and CH_4 fluxes were determined using static closed chambers and gas chromatographic analysis at three sites along an elevation gradient from 1000 m to 3000 m (1000 m, 2000 m, 3000 m) and along topographic gradients (lower slope, midslope, ridge),. NO fluxes were measured in the field using open dynamic chambers and a LMA-3D NO_2 Analyzer with chemiluminescence detection. To determine the potential atmospheric CH_4 uptake of different soil substrates, a laboratory incubation experiment using organic layer and mineral soil samples from different soil depths was conducted. Nutrient availability was determined by applying various extraction methods and by evaluating several indices (C:N, C:K, C:P ratios, $\delta^{15}N$ signature of litterfall). Finally, total belowground carbon allocation (TBCA) was estimated from year-round soil respiration and aboveground litterfall measurements.

Soil organic layer thickness increased while nutrient availability decreased with both increasing elevation and along the topographic gradient from the lower slope to the ridges. Aboveground litter production appeared to be limited by nitrogen (N), phosphorus (P) and to a certain degree by potassium (K). It was positively related mainly to available nutrient stocks of the organic layer, although stocks of K and P were larger in the mineral soil. Tree basal area increment and aboveground litter production showed close positive correlations with indices of N availability (C:N ratio and $\delta^{15}N$ signature of litterfall), while TBCA was not correlated to nutrient availability. TBCA decreased with elevation and from the lower slope position toward the ridges and was negatively correlated to soil moisture and organic layer thickness. Soil trace

gas fluxes from the three TMF sites were lower than reported for tropical lowland sites but were generally within the range reported in other montane forest sites. Soil respiration was positively correlated with both parameters, whereas no correlations of N-oxides and CH_4 with soil moisture and organic layer thickness were found. N-oxide fluxes showed close positive correlations with long-term indices of N availability (e.g. C:N ratio, the $\delta\ ^{15}N$ signature of litterfall) and with indices of forest productivity, such as aboveground litter production and tree basal area increment. Soil respiration was positively correlated with litter quality indices. CH_4 uptake rates increased with soil mineral N content, total P content of the mineral soil and with increasing CO_2 emissions. Incubated samples from the deepest organic layers at the 2000 m and 3000 m sites revealed high potential CH_4 oxidation rates.

The close correlations of nutrient availability with aboveground litterfall and tree basal area increment is an evidence that forest productivity is nutrient limited in the investigated TMFs. Dense rooting of the organic layer and the close relationships between nutrient availability in the organic layer and nutrient concentrations in aboveground litterfall, suggest that nutrient cycling is concentrated in the organic layer and is largely decoupled from the mineral soil. In contrast to aboveground forest productivity, TBCA was not related to nutrient availability. The decline in TBCA with increasing elevation at our study site corresponded with an increase in fine root biomass which can be explained with higher root longevity. Together with slow decomposition rates in the organic layers, this may contribute to the large carbon storage in organic layers of TMF soils. Soil trace gas fluxes were correlated positively with different indices of nutrient availability. We found evidence that increasingly adverse soil conditions (low nutrient availability, high soil moisture) and lower litter quality limit microbial activity and consequently reduce soil respiration, N-oxide fluxes and CH_4 uptake capacity of the soils. The close linear correlations of N-availability with forest productivity and N-oxide fluxes show that N availability links N-oxide fluxes and forest productivity and opens the possibility to include forest productivity, especially tree basal area increment, as co-variable to predict N-oxide fluxes in nitrogen limited TMFs. The largest CH_4 uptake corresponded with high concentrations of soil mineral N indicating that atmospheric CH_4 uptake primarily nutrient-limited, and that ammonia inhibition may be neglected as regulating factor for soil CH_4 oxidation in these soils. Contrary to findings in temperate forests the organic layer did not only act as gas diffusion barriers, but showed substantial potential to oxidize atmospheric CH_4.

RESUMEN

Los bosques tropicales son fuentes importantes de gases de efecto invernadero como el dióxido de carbono (CO_2), óxido de nitrógeno (N_2O) y de monóxido de nitrógeno (NO); el cual es un precursor de la producción de ozono y además son sumideros de los gases de efecto invernadero como el metano (CH_4). Estimaciones de los flujos de gases traza y el ciclo del carbono de los suelos de los bosques tropicales están fuertemente sesgados hacia los bosques de tierras bajas. Hay escasos datos disponibles sobre el intercambio de gases de los bosques tropicales de montaña (tropical montane forest, TMF) y su ciclo del carbono ha sido explorado marginalmente, a pesar de que los TMF cubren cerca el 9% del área de los bosques tropicales. Esta tesis presenta los resultados de un extensivo estudio sobre el intercambio de CO_2, NO_2, NO y CH_4 en el suelo y sus posibles reguladores biogeoquímicos con un especial enfoque en la influencia de la disponibilidad de nutrientes en los TMF en el sur del Ecuador

En tres sitios a lo largo de la gradiente de elevación comprendida entre los 1000 hasta los 3000 ms.n.m. (1000, 2000, 3000 ms.n.m.) y a lo largo también de gradientes topográficas (baja pendiente, pendiente media y crestas de montaña), flujos de CO_2, N_2O y CH_4 en el suelo fueron determinados usando cámaras estáticas cerradas y análisis por cromatografía de gases. Los flujos de NO fueron medidos en el campo usando cámaras dinámicas abiertas y LMA-3D NO_2 analizador con detección de quimioluminiscencia. Para determinar el potencial de absorción de CH_4 atmosférico en diferentes sustratos de suelo, un experimento de incubación de laboratorio con muestras de capas orgánicas y del suelo mineral provenientes de diferentes profundidades de suelo fue llevado a cabo. La disponibilidad de nutrientes en el suelo fue determinada aplicando varios métodos de extracción y por la elevación de varios índices (C:N, C:K, C:P ratio, valor de $\delta^{15}N$ de la hojarasca). Por último la asignación de carbono subterráneo (total belowground carbon allocation, TBCA) fue estimada a partir de las mediciones de la respiración del suelo y de la hojarasca superficial durante el un año.

El espesor de la capa orgánica del suelo aumentó y la disponibilidad de nutrientes disminuyó con el aumento de la altitud y desde la posición de las bajas pendientes a las crestas en el evaluado TMF. La producción de hojarasca superficial parecía estar limitada por Nitrógeno (N), Fósforo (P) y hasta cierto punto por el Potasio (K). Se relacionó positivamente sobre todo a las

existencias disponibles de nutrientes de la capa orgánica, aunque las reservas de K y P fueron mayores en el suelo mineral. El incremento de la área basal de los arboles y la producción de hojarasca superficial mostraron estrechas correlaciones positivas con los índices de disponibilidad de N (C:N ratio y valor de δ^{15}N de la hojarasca), mientras que TBCA no se correlacionó a la disponibilidad de nutrientes. TBCA disminuyó con la altitud y desde las pendientes bajas hacia las crestas y fue más bien relacionada con la humedad del suelo y el espesor de la capa orgánica. Los flujos de gases traza de los TMF fueron menores que los reportados para los sitios de tierras bajas tropicales y en general estuvieron entre los rangos reportados para otros sitios de bosques de montaña. No he encontrado correlaciones de óxidos-N y CH_4 con la humedad del suelo y el espesor de la capa orgánica, mientras que la respiración del suelo se correlacionó positivamente con ambos parámetros. Los flujos óxidos-N mostraron estrechas correlaciones positivas con los índices de largo plazo de disponibilidad de N como C:N ratio y el valor de δ^{15}N de la hojarasca y con los índices de productividad de los bosques, como producción de hojarasca superficial y el incremento de área basal de los árboles. La respiración del suelo se correlacionó positivamente con índices de calidad de hojarasca superficial y los valores de absorción de CH_4 incrementaron con el contenido de Nitrógeno en el suelo, el contenido total de P del suelo mineral y el incremento de las emisiones de CO_2. Muestras incubadas de las partes más inferiores de las capas orgánicas de los sitios de los 2000 y 3000 ms.n.m. revelaron un alto potencial de absorción de CH_4.

Las estrechas correlaciones de la disponibilidad de nutrientes con la hojarasca superficial y el incremento del área basal de los árboles pueden ser interpretadas como una evidencia de que la productividad de los bosques es limitada en nutrientes en el investigado TMF. El denso enraizamiento de la capa orgánica y la inmediata relación entre la disponibilidad de nutrientes en la capa orgánica y la concentración de nutrientes en la hojarasca superficial sugieren que el ciclo de los nutrientes esta concentrado en la capa orgánica y en gran parte disociada del suelo mineral. En contraste a la productividad de la superficie forestal, TBCA no estaba relacionado con la disponibilidad de nutrientes. La disminución de TBCA con el incremento de la elevación en nuestro estudio correspondió con un incremento en la biomasa de raíces finas lo cual puede ser explicado con la más alta longevidad de las raíces. Junto con el lento proceso de descomposición cuantificado, en las capas orgánicas, esto puede contribuir a la retención de carbono en grandes capas orgánicas de los suelos del TMF. El flujo de gases traza en el suelo fue

correlacionado positivamente con diferentes índices de disponibilidad de nutrientes. Se han encontrado evidencias de que las condiciones del suelo cada vez más adversas y la menor calidad de la hojarasca, por lo general limitan la actividad microbiana y así reduce la respiración del suelo, los flujos de óxidos-N y la capacidad de absorción de CH_4 de los suelos. Las correlaciones lineales estrechas de los flujos de óxido de N mostraron que la disponibilidad de N vincula flujos de óxidos-N y la productividad de los bosques y abrieron así la posibilidad de incluir la productividad forestal, especialmente el incremento en el área basal de los arboles como una co-variable en las predicciones de flujos de óxidos-N en los TMF limitado de nitrógeno. La mayor absorción de CH_4 correspondió con mayores concentraciones de N en el suelo mineral que indica que la absorción de CH_4 atmosférico es principalmente limitada en nutrientes y que la inhibición amoniaco puede dejarse de lado como un factor regulador para la oxidación de CH_4 del suelo, en estos suelos de bosques tropicales de Montana. Contrariamente a la creencia común, las caspas orgánicas no solo actuaron como barreras de difusión de gases, pero mostraron considerable capacidad potencial de oxidación para CH_4 atmosférico y por lo tanto pueden contribuir a remover el CH_4 de la atmósfera.

THESIS OUTLINE

Chapter 1 gives an introduction to tropical montane forest (TMF) physiognomy and ecosystem functioning and presents a short overview over the current knowledge about trace gas fluxes from tropical forest soils. Furthermore, the objectives and hypotheses of this work are presented. At last, Chapter 1 provides general information about the study area in southern Ecuador and the methodology used for investigation. **Chapter 2** addresses the question whether forest productivity and soil nitrous- and nitric-oxide fluxes are linked through soil nitrogen availability along elevation and topographic gradients in the studied ecosystem and assays the possibility to use forest productivity as a proxy for N-oxide estimation. **Chapter 3** investigates soil methane fluxes, their biogeochemical controls and the contribution of the organic layers to atmospheric methane uptake of TMF soils. **Chapter 4** examines the influence of nutrient availability on total belowground carbon allocation along elevation and topographic gradients in TMFs. **Chapter 5** summarizes and discusses the results presented in Chapters 2 to 4 and provides suggestions for further research.

INTRODUCTION

1.1 Distribution and physiognomy of tropical montane forests

According to the definition of the Global Forest Resources Assessment 2000 (FAO 2000), tropical montane forests (TMF) are classified as forests within the tropical latitude which grow above 1000 m a.s.l. (FAO 2000). TMFs are distinguished from lowland forests mainly by their different physiognomy and flora. The transition zone from lowland to montane forests and altitudinal zonation within TMFs is compressed on small outlying mountains compared to large mountains ('Massenerhebung' effect, Richards 1952). Therefore, forests showing typical characteristics of TMFs may occur at elevations as low as 300 m in smaller mountain systems (Bubb et al. 2004). The altitudinal expansion of TMFs reaches to up to 4000 m on the Himalayan slopes of Asia and up to about 3500 m in Ethiopian highlands and the mountains of east Africa. In Central America TMFs grow up to altitudes of 3800 m (FAO 2000) and forests of the South American Andes reach altitudes of up to 4000 m (Richter 2008). Information on the land area covered by TMFs vary between 1.5 and 3.3 · 10^6 km^2, which makes up between 9 and 22% of the world's tropical forest area (Bubb et al. 2004; FAO 2000). Ascending moist tropical mountain slopes, ecofloristic zones are successively shifting from lowland rainforest over premontane forest, lower montane forest (LMF) and upper montane forest (UMF) to elfin forests (Grubb et al. 1963). Besides the shift in plant species composition, the most remarkable feature of TMFs is the gradual decrease in tree height from up to 40 m in American lowland forests and 50 - 60 m in Asian lowland forests to less than 10 m in elfin forests (Aiba & Kitayama 1999; Grubb 1977; Homeier et al. 2008; Leuschner & Moser 2008; Raich 1998). Additional typical traits include more inclined tree trunks, a tendency to smaller, thicker and harder (xeromorphic) leaves and a higher abundance of epiphytes (Ashton 2003; Bruijnzeel & Veneklaas 1998; Gradstein 2008; Grubb 1977). Similar changes in forest and leaf structure have also been found from lower slopes toward ridge positions in tropical mountains in Jamaica, Malaysia, American Samoa and Ecuador among others (Homeier et al. 2010; Takyu et al. 2002; Tanner 1977; Webb et al. 1999). To explain these differences, a variety of hypotheses has been proposed, most of which are related directly or indirectly to climate. Most prominently, lower temperatures, higher precipitation, increased cloud formation and fog occurrence as well as higher UV-B radiation and nutrient limitations have been suggested (Bruijnzeel & Veneklaas 1998; Foster 2001; Gerold 2008; Grubb 1977; Tanner et al. 1998).

1.2 Tropical montane forests ecosystem functioning

TMFs do not only differ from lowland forests in structure and flora, but also in ecosystem functioning (Bruijnzeel & Veneklaas 1998). Regarding the present study the most important ecosystem functions are forest productivity, nutrient and carbon cycling and the mitigation of trace gas fluxes. TMFs generally exhibit smaller aboveground productivity compared to tropical lowland forests, as expressed by lower litterfall rates, a decline in aboveground tree biomass and stem girth in crement and slower ecosystem nutrient-cycling (Bruijnzeel & Veneklaas 1998). Productivity of TMFs was shown to be limited by phosphorus (P), potassium (K) and, in contrast to many lowland forests, by nitrogen (N) (Tanner 1985; Tanner et al. 1998; Vitousek 1984). These findings appear to be mainly related to soil development (Walker & Syers 1976). Soils under tropical lowland forests are often highly weathered (McGroddy et al. 2008), whereas erosion on the slopes of tropical mountains often leads to shallow and younger soils (Foster 2001). Phosphorus and K are macronutrients in the soil organic matter, which are almost exclusively supplied by the soils parent material (Walker & Syers 1976). In contrast, carbon (C) and N are derived from the atmosphere and accumulate in the organic matter over time. Thus, with proceeding soil and ecosystem development, soils will become poorer in P and K, which are successively bound in unavailable forms or washed out, and will become richer in N (Hedin et al. 2009). Additional to soil development other factors may contribute to observed nutrient limitations of TMF productivity. Increasingly adverse climatic conditions (low temperatures and high soil moisture content) and lower litter quality with increasing elevation reduce microbial mineralization of organic matter (Marrs et al. 1988; Tanner 1981; Vitousek & Sanford 1986), causing nutrient accumulation in the thick organic layers that cover the mineral soil. Slower nutrient cycling and nutrient storage in organic matter are linked to efficient ecosystem nutrient use regarding N, P and K (Hedin et al. 2009; Vitousek 1984). TMFs reveal high nutrient use efficiencies in the sense that plants need less nutrients for a certain amount of C fixed, as indicated by high C:nutrient ratios in litterfall (Hedin et al. 2009; Vitousek 1984) and in terms of small nutrient leaching and gas losses.

Other important forest ecosystem functions are C sequestration and C storage. Global soil and vegetation C stocks in tropical forests account for about $1.1 *10^{12}$ Mg C (Fischlin et al. 2007) which is equivalent to 148% of the atmospheric carbon. With respect to C fluxes, TMFs are

among the least studied terrestrial ecosystems (Bruijnzeel & Veneklaas 1998; Clark 2007). Reduced microbial mineralization rates and slower C turnover, due to higher precipitation and lower litter quality in TMFs, lead to an increased storage of C on the forest floor and in the mineral soil (Hertel et al. 2003; Schuur 2001; Schuur et al. 2001). Although comparably much is known about the features of aboveground C allocation in TMFs, it is still unclear how environmental and nutrient conditions influence total belowground carbon allocation (TBCA) and if increasing TBCA might possibly compensate for the decline in aboveground biomass (Leuschner et al., 2007).

However, forest productivity, soil nutrient cycling and ecosystem C sequestration do not only change with elevation in TMF. Topography, drainage characteristics, and disturbance history cause a complex pattern of soil properties, nutrient and soil water availability, which overlays elevation gradients in montane regions. The resulting small-scale heterogeneity also affects forest ecosystem functioning, including nutrient and carbon accumulation in thick organic layers and lower aboveground tree productivity at ridge positions compared to the slopes (Homeier 2008; Homeier et al. 2010; Tanner 1977).

1.3 Soil trace gas fluxes in tropical montane forests

Soils naturally act as sources or sinks for several trace gases and thus co-regulate the global budgets of these gases (Conrad 1996). Climate relevant trace gases interacting with soils are carbon dioxide (CO_2), nitrous oxide (N_2O) and methane (CH_4), which are three of the five most important greenhouse gases (Forster et al. 2007). A fourth gas emitted by forest soils, nitric oxide (NO) plays a crucial role in regulating troposphere ozone concentrations (Crutzen 1979). Carbon dioxide is produced in soils mainly by root respiration and heterotrophic respiration of soil organisms. Nitrous oxide and NO are produced in soils largely during nitrification and denitrification processes (Davidson et al. 2000; Firestone & Davidson 1989). Finally, CH_4 is an important product of anaerobic organic matter decomposition in soils (Conrad 1996). However, soils act as net CH_4 sink under aerobic conditions and microbial oxidation in aerated upland soils is the primary biotic sink for atmospheric CH_4 (Potter et al. 1996).

Since soil trace gas production and consumption processes are related to microbial activity, the amount of gas exchange with the atmosphere is largely regulated by soil temperature, moisture, texture and aeration as well as substrate availability (Conrad 1996). According to the conceptual "hole in the pipe" model (HIP), rates of soil N cycling and N availability control the total amount of N_2O + NO production, whereas soil moisture regulates the relative importance of the two gases and the rates of gas diffusion through the soil (Firestone & Davidson 1989). Tropical soils play a major role for the mitigation of soil trace gas fluxes, since they are considered the largest natural terrestrial source of N_2O (Bouwman et al. 1995) and to account for 10 to 20% of the annual soil CH_4 consumption (Potter et al. 1996; Prather et al. 2001). Furthermore, tropical forests cycle more than 10% of the atmospheric CO_2, through photosynthesis, respiration and microbial decay (Malhi, 2005) every year. Estimates on the source and sink strengths of tropical soils regarding these trace gases are however mainly based on field studies that are heavily biased towards lowland forests. There are few data available about trace gas fluxes and their controlling factors in TMFs (Davidson et al. 2000; Ishizuka et al. 2005; Keller & Reiners 1994). Increasing precipitation and decreasing temperatures with elevation, changes of soil moisture, nutrient limitation and the accumulation of organic matter along topographic gradients in TMFs may result in conditions unfavorable for CO_2, N_2O and NO production and CH_4 uptake. Studies carried out on trace gas fluxes in TMF suggest that trace gas exchange rates from TMF soils are smaller compared to lowland forests and decline with increasing elevation (Cavelier & Penuela 1990; Holtgrieve et al. 2006; Köhler et al. 2009a; Köhler et al. 2009b; Matson & Vitousek 1987; Purbopuspito et al. 2006; Raich 1998). Although studies in temperate regions show strong topography effects on N-oxide emissions (Corre et al. 1996; Meixner & Eugster 1999), most of the studies done in TMF do not include information on topographic positions. To improve estimations and modelling of trace gas fluxes, the identification of proxies with the potential to predict trace gas fluxes is indispensable, since direct measurement of trace gas fluxes on tropical mountain slopes is challenging (Davidson et al. 2000; Ishizuka et al. 2005; Keller & Reiners 1994).

1.4 Study objectives

The aim of the present work was to investigate the soil-atmosphere trace gas exchange in tropical montane forests, and to examine if CO_2, N_2O, NO and CH_4 fluxes as well as carbon allocation patterns are linked to forest productivity through nutrient availability. The main regulation factors of trace gas fluxes and possible changes in the relationships with elevation and topography were studied. The specific objectives of this study were:

1) To investigate whether forest productivity and soil N-oxide fluxes are linked through N availability along elevational and topographic gradients in TMFs and if, consequently, forest productivity may be used as a proxy for N-oxide flux estimation.

2) To study atmospheric CH_4 exchange of tropical montane forest soils, investigate its biogeochemical controls and the contribution of organic layers to the atmospheric CH_4 uptake.

3) To examine the influence of nutrient availability on total belowground carbon allocation along elevation and topographic gradients.

With these aims I tested the following hypotheses:

1) Soil N-oxide fluxes increase with increasing N availability.

2) Forest productivity increases with increasing soil N availability

3) Forest productivity is a good proxy for N-oxide fluxes in such N-limited ecosystems.

4) CH_4 fluxes decrease with increasing N availability.

5) Soil CH_4 uptake decreases with increasing elevation and with decreasing soil diffusivity.

6) Soil organic layers do not, or only little, contribute to the uptake of atmospheric CH_4 in tropical montane forests.

7) Total belowground carbon allocation increases with decreasing nutrient availability.

1.5 Study area and experimental design

The study was carried out within or close to the Podocarpus National Park (PNP) in the Province Zamora-Chinchipe between the cities of Loja and Zamora in southern Ecuador (Figure 1.1). The PNP, founded in 1982 by the *Instituto Ecuatoriano Forestal y de Areas Naturales y Vida Silvestre* on an area of 1462.8 km², forms one of the last continuous primary forests in southern Ecuador (Calderón 2002) and stretches from 900 m to 3600 m in elevation. The location of the PNP, in the transition zone between the northern and southern Andes and between the Amazonian and the Pacific ecozones (Beck & Richter 2008) contributes to the fact, that the PNP is a biodiversity hotspot supporting about 3000 to 4000 vascular plant species and showing a high level of endemism (Madsen 1989).
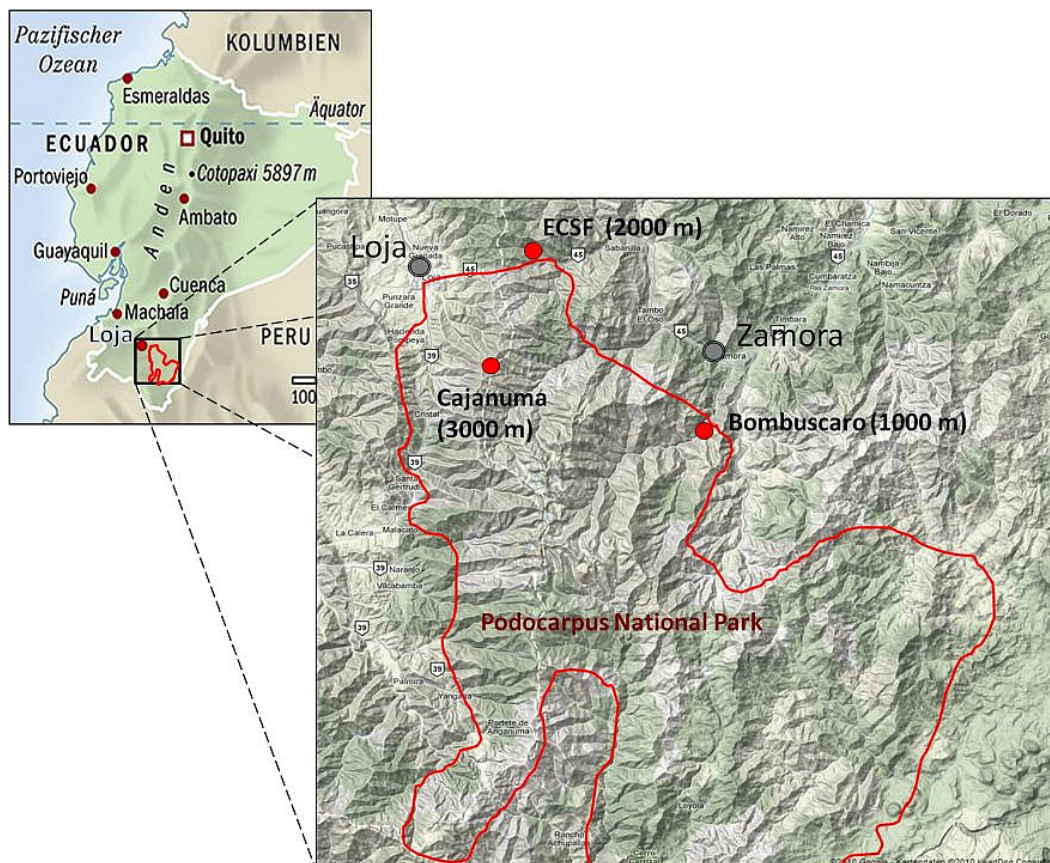
Figure 1.1: Location of the three study sites within and close to the National Park Podocarpus in southern Ecuador. Map sources: Small map: http://blog.blumenbutler.de. Large map: Google Maps 2010. Borders of the national park: Ministerio del Ambiente, Ecuador.

For this study three sites were selected along an elevation gradient from 1000 m to 3000 m within the PNP and the adjacent Reserva Biológica San Francisco: 990-1200 m a.s.l. (Bombuscaro, 04° 06' S, 78° 58' W), 1800-2100 m a.s.l. (Estaciòn Científica San Francisco, ECSF, 03° 58' S, 79° 04' W) and 2800-3000 m a.s.l. (Cajanuma, 04° 06' S, 79° 11' W) (Figure 1.1).
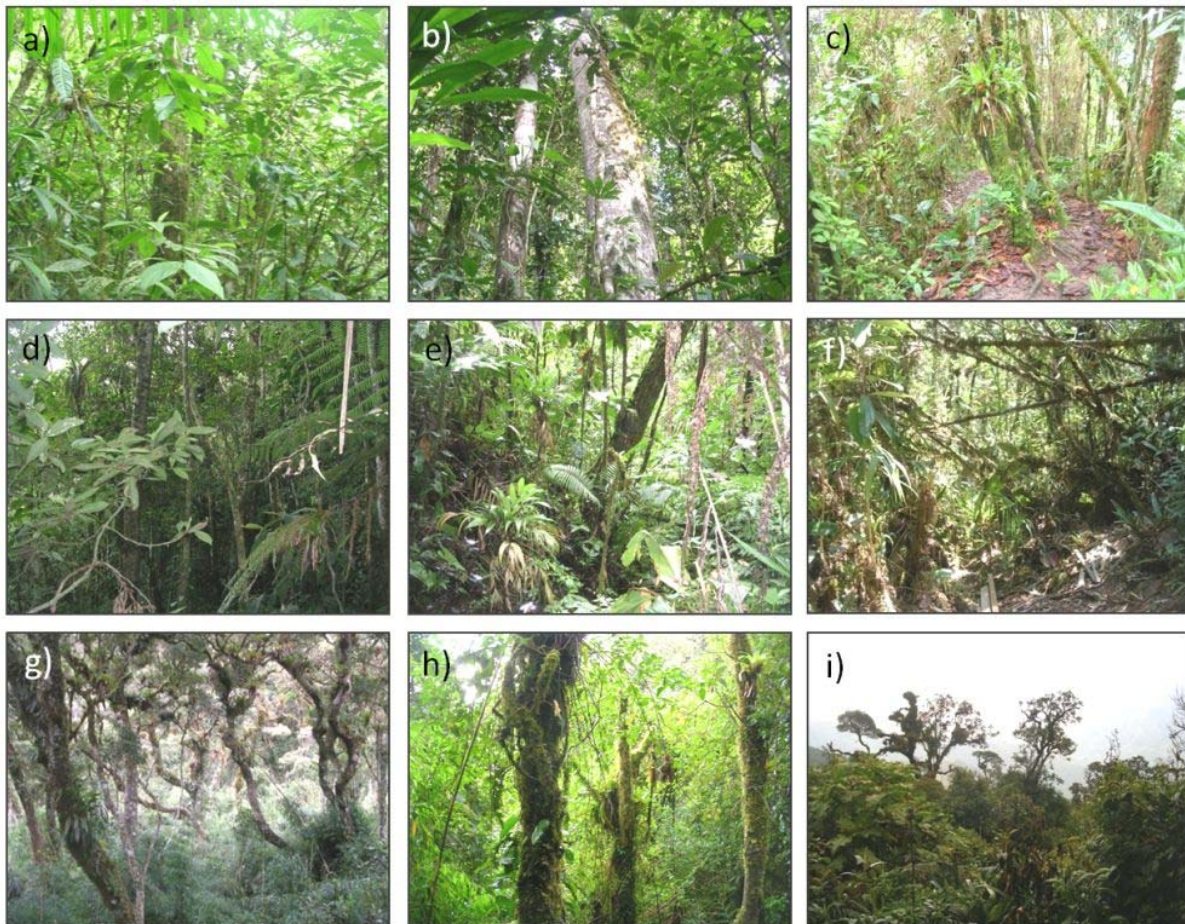
Figure 1.2: Pictures of the forests at three landscape positions along the elevation gradient: a-c) 1000 m site, d-f) 2000 m site, g-i) 3000 m site (from left to right within rows: lower slope, midslope, ridge). Photographs: Katrin Wolf

The natural vegetation is premontane forest with tree heights of 20 to 30 m at the 1000 m site (Figure 1.2 a-c), lower montane forest, with tree heights of 15 to 25 m at the 2000 m site (Figure 1.2 d-f) and upper montane forest, with tree heights of 6 to 12 m at the 3000 m site (Figure 1.2 g-i). Along with tree height, tree physiognomy changed toward reduced slenderness of stems and

smaller mean diameters. Forests are more and more characterized by higher stem densities and a decline in overall aboveground tree biomass (Homeier et al. 2010; Takyu et al. 2005). Similar changes in forest structure and plant physiognomy as with elevation occurred along topographic gradients, from lower slopes to ridge positions, within each respective elevational zones (Homeier et al. 2010). At each of the three elevations 18 plots (20 x 20 m) were installed such that they covered the three main topographic positions: lower slope, midslope and ridge. Each of the 54 plots contained four chambers for soil trace gas flux measurement and six litter traps, installed in a random design along two orthogonal transects.

1.6 Methodological outline of soil trace gas flux measurements

We measured soil fluxes of CO_2, N_2O and CH_4 using static closed chambers (Figure 1.3 a) bi-monthly over a period of one year from May 2008 until May 2009. Gas samples were analyzed using a gas chromatograph equipped with an electron capture detector (ECD) to measure CO_2 and N_2O and a flame ionization detector (FID) to determine CH_4 (Figure 1.3 b). Nitric oxide (NO) was measured in the field using open dynamic chambers and analyzed with a chemiluminescence detector, after NO oxidation to NO_2 by a chrome oxide catalyst (Figure 1.3 c).

Figure 1.3: Field and laboratory equipment for soil trace gas flux measurements. a) Chamber base for static and open dynamic chamber measurements with thermometer and hydrometer for concomitant temperature and soil moisture measurements, b) gas chromatograph with autosampler and glass vials for the measurement of CO_2, N_2O and CH_4, and c) LMA-3D NO_2 Analyzer for NO measurement with the closed chamber. Photographs: Katrin Wolf and Guntars O. Martinson.

Concomitantly to every gas sampling soil temperature, gravimetric soil moisture and the concentration of extractable ammonium (NH_4^+) and nitrate (NO_3^-) in the upper 5 cm of the soil was determined.

Furthermore, we conducted a laboratory incubation experiment to investigate potential CH_4 uptake activity of different soil substrates and the texture effect on potential CH_4 uptake at different soil depths. More detailed descriptions of the study sites and the methodologies for trace gas and auxiliary measurements, as well as for the determination soil properties and forest productivity are provided in the Material and Methods sections of the Chapters 2 to 4.

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CHAPTER

2

NITROGEN AVAILABILITY LINKS FOREST PRODUCTIVITY, SOIL NITROUS OXIDE AND NITRIC OXIDE FLUXES OF A TROPICAL MONTANE FOREST IN SOUTHERN ECUADOR

2.1 Abstract

Tropical forests are important sources of the greenhouse gas nitrous oxide (N$_2$O) and of nitric oxide (NO), a precursor of ozone. In tropical montane forests nitrogen limitation is common which affects both soil N$_2$O and NO fluxes and forest productivity. Here we present evidence that forest productivity and N-oxide (N$_2$O + NO) fluxes are linked through N availability along elevation and topographic gradients in tropical montane forests. We measured N-oxide fluxes, several indices of N availability, and forest productivity along an elevation gradient from 1000 m to 3000 m and along topographic gradients. Organic layer thickness of the soils increased and N availability decreased with increasing elevation and along the topographic gradient from the lower slope position to the ridges. Annual N$_2$O fluxes ranged from -0.53 μg(N)m^{-2}h^{-1} to 14.54 μg(N)m^{-2}h^{-1} while NO fluxes ranged from -0.02 μg(N)m^{-2}h^{-1} to 1.13 μg(N)m^{-2}h^{-1}. Both N-oxide fluxes and forest productivity increased with increasing N availability and showed close positive correlations with indices of N availability (C:N ratio and δ ^{15}N signature of litterfall). We interpret the close correlations of N-oxide fluxes with total litterfall and tree basal area increment as evidence that N availability links N-oxide fluxes and forest productivity. This opens the possibility to include forest productivity as co-variable in predictions of N-oxide fluxes in nitrogen limited tropical montane forests. Especially increment of tree basal area was a promising proxy to predict soil N-oxide fluxes in these N limited ecosystems, possibly because it better reflects long-term forest productivity than total litterfall.

2.2 Introduction

Tropical forest soils are considered the largest natural source of the greenhouse gas nitrous oxide (N$_2$O) with a source strength of 3.0 Tg N yr^{-1} (Werner et al. 2007). Additionally, they can produce considerable amounts of nitric oxide (NO), which plays a crucial role regulating troposphere ozone concentrations (Crutzen 1979). Estimates of the source strengths of N$_2$O and NO are based on field studies that are still heavily biased towards tropical lowland forests. The few studies on N$_2$O and NO fluxes carried out in tropical montane forests show that the trace gas emissions decrease with increasing elevation (Hall et al. 2004; Purbopuspito et al. 2006). Measurements of nitrogen oxide fluxes from tropical montane forests range between 0.01 and 3.75 kg (N) ha^{-1}yr^{-1} for N$_2$O (Breuer et al. 2000; Holtgrieve et al. 2006; Ishizuka et al. 2005;

Köhler et al. 2009; Purbopuspito et al. 2006) and between 0.03 and 0.4 kg (N) ha^{-1}yr^{-1} for NO, an estimate that is based on two studies only (Davidson & Kingerlee 1997). The relative wide range of N-oxide fluxes reported may reflect the complex pattern of soil properties, nutrient and soil water availability caused by topography, drainage characteristics and disturbance history that overlay elevation gradients in montane regions. Such small-scale heterogeneity potentially affects fluxes of N$_2$O and NO and forest productivity. Although studies in temperate regions show strong topography effects on N-oxide emissions (Corre et al. 1996; Meixner & Eugster 1999), most of the studies done in tropical montane forests do not include information on topographic positions.

Direct measurements of N$_2$O and NO fluxes in the field are laborious and challenging, which is why several studies have been carried out to test proxies that may have the potential to predict N-oxide fluxes (Davidson et al. 2000; Ishizuka et al. 2005; Keller & Reiners 1994). The conceptual "hole-in-the-pipe model" (HIP) explains the main controls on N$_2$O and NO fluxes. Rates of N cycling and N availability control the total amount of N$_2$O + NO produced, whereas soil moisture regulates the relative importance of the two gases by influencing the main N$_2$O and NO producing processes nitrification and denitrification through the gas diffusion rate of the soil (Davidson et al. 2000; Firestone & Davidson 1989). Some indices of N cycling rates and N availability (e.g. soil mineral N, net N mineralization and net N nitrification) are temporally and spatially highly variable, which limits the applicability of these indices, despite reports of positive correlations with N oxide fluxes (Veldkamp et al. 1999). C:N ratios and δ^{15}N signatures of litterfall are more integrative indices of the long-term N cycle (Kahmen et al. 2008; Robinson 2001) making them more promising predictors of N$_2$O and NO fluxes (Davidson et al. 2000; Purbopuspito et al. 2006).

In contrast to many lowland forests, productivity of tropical montane forests is limited by N, or nitrogen and phosphorous (P) together (Tanner et al. 1998). This appears to be mainly related to the soil development where forest productivity on young soils (common in tropical montane forests) tends to be N-limited, whereas forest productivity on heavily weathered soils (common in tropical lowland forests) tends to be P-limited (Walker & Syers 1976). Further evidence of N limitation comes from slow net and gross N mineralization rates in montane forest soils compared to lowland forest soils (Arnold et al. 2009; Marrs et al. 1988) and lower δ^{15}N

signatures of leaves and litter (Martinelli et al. 1999). The microbial processes of nitrification (responsible for NO, N_2O and NO_3^- production) and denitrification (responsible for NO, N_2O and N_2 production) discriminate against ^{15}N, thus leading to ^{15}N enrichment of soil and plant material in the ecosystem (Houlton & Bai 2009). An N-limited ecosystem, with small N losses through leaching and gas emissions therefore displays lower $\delta^{15}N$ signatures compared to ecosystems where more N is lost relative to N cycling rates (Amundson et al. 2003; Corre et al. 2010; Houlton et al. 2006). Finally, low N concentration and high C:N ratios in leaves and litter of montane forests indicate N limitation of tree growth (Tanner et al. 1998).

In summary, there is evidence that in tropical montane forests forest productivity is limited by N and that N-oxide fluxes depend on N cycling rates and N availability (Corre et al. 2010). In the present study our goal was to analyze whether forest productivity and N-oxide fluxes are linked through N availability along elevation and topographic gradients in tropical montane forests. Our hypotheses were the following: 1) N-oxide fluxes increase with increasing N availability, 2) forest productivity increases with increasing N availability in N-limited ecosystems, and 3) forest productivity shows good correlations with N-oxide fluxes in such N-limited ecosystems. We tested our hypotheses by measuring N_2O and NO fluxes, several indices of N availability, and forest productivity during one year along elevation and topographic gradients in natural tropical montane forests in southern Ecuador. Our results show that both N-oxide fluxes and forest productivity are linked through N availability and we suggest that predictions of soil N_2O + NO fluxes of N-limited ecosystems can be improved using forest productivity as a co-variable.

2.3 Material and Methods

Study Area

The study area is located in the Cordillera del Consuelo, which forms part of the eastern chain of the Andes in southern Ecuador. Three study sites were selected along an elevation gradient (Table 2.1): 990-1200 m a.s.l. (Bombuscaro, 04° 06' S, 78° 58' W, hereafter called the '1000 m site'), 1800-2100 m a.s.l. (San Francisco, 03° 58' S, 79° 04' W, hereafter called the '2000 m site') and 2800-3000 m a.s.l. (Cajanuma, 04° 06' S, 79° 11' W, hereafter called the '3000 m site'). The 1000 m site is located close to the city of Zamora, Zamora-Chinchipe

province within the Podocarpus National Park (PNP). Natural vegetation consists of "premontane rain forest" (Homeier et al. 2008) and most important tree families are Moraceae, Rubiaceae and Melastomataceae. The 2000 m site is situated between the cities of Loja and Zamora within the Reserva San Francisco (RSF), a private reserve that borders the PNP. Vegetation can be classified as "lower montane rain forest" (Homeier et al. 2008). Most important tree families of the 2000 m site are Lauraceae, Euphorbiaceae, Melastomataceae and Rubiaceae. The 3000 m site is located south of the city of Loja within the PNP. Forest is classified as "upper montane rain forest" (Homeier et al. 2008). Cunoniaceae, Clusiaceae and Melastomataceae are the most important tree families of this site. Stand height decreased with elevation and from the lower slope positions to the ridge positions within every site. The annual mean temperature decreased from 19.4 °C at the 1000 m site to 9.4 °C at the 3000 m site, annual precipitation increased from 2230 mm at 1000 m, and 1950 mm at 2000 m, to 4500 mm at 3000 m (Table 2.1) (Moser et al. 2007). Rainfall showed little seasonality (Emck 2007). For most of the study area, Paleozoic metamorphic schists and sandstones with some quartz veins form the parent material for soil development. Only at the 1000 m site soil parent material of half of the plots consists of deeply weathered granitic rock of the Jurassic Zamora granitoide formation (Litherland et al. 1994).

2.3.1   Experimental design

We installed 54 plots (20 x 20 m) at three elevation levels (1000 m, 2000 m, and 3000 m) forming an elevation transect from 1000 m to 3000 m. Eighteen plots per elevation were distributed over the topographic positions lower slope, midslope and ridge, with six replicates each. Vertical deviation of plots from the pre-determined levels was never more than 200 m. All plots were covered by mature, closed-canopy forest that is representative for the respective topographic position. Plot size was small enough to ensure homogeneity of environmental factors and forest structure. Each plot contained six litter traps and four chamber bases, which we placed in a random design along two orthogonal transects. For the calculations, we corrected plot size for inclination.

Table 2.1: Site characteristics of the topographic positions across the elevation gradient.

	1000 m			2000 m			3000 m		
	lower slope	midslope	ridge	lower slope	midslope	ridge	lower slope	midslope	ridge
Height a.s.l. (m)		990-1200			1800-2100			2800-3000	
Air temperature (°C)[a]		19.4			15.7			9.4	
Precipitation (mm yr^{-1})[a]		2230			1950			4500	
Gravimetric moisture (g g^{-1})[b]	1.0 (0.2)aA	0.9 (0.2)aA	1.8 (0.2)bA	1.7 (0.3)aB	2.1 (0.3)aB	4.3 (0.1)bB	2.1 (0.2)aB	2.9 (0.3)bC	4.5 (0.2)cB
Organic layer thickness (cm)[b]	2.5 (0.7)	2.6 (1.0)A	6.5 (1.9)A	4.0 (0.9)a	12.2 (3.1)aB	24.0 (2.9)cB	6.6 (0.7)a	14.2 (1.6)bB	22.2 (3.4)cB
Organic layer									
pH (H$_2$O)[b]	4.9 (0.5)a	4.8 (0.6)a	3.7 (0.1)b	4.6 (0.2)a	4.8 (0.5)a	3.4 (0.1)b	4.0 (0.3)	3.7 (0.1)	3.6 (0.1)
C:N[b]	18.5 (0.7)A	18.6 (1.5)A	20.5 (0.7)A	15.7 (0.8)aB	15.6 (0.6)aA	21.1 (0.7)bA	20.5 (0.8)aA	23.9 (1.4)bB	26.7 (1.3)cB
δ ^{15}N (‰)[b]	3.7 (0.5)A	2.1 (0.7)A	1.9 (0.5)	4.0 (0.3)aA	3.0 (0.2)aA	1.0 (0.4)b	1.4 (0.2)aB	0.2 (0.3)bB	0.6 (0.2)ab
Total P (mg (P) g^{-1})[b]	1.1 (0.1)	1.2 (0.1)A	0.6 (0.02)A	1.2 (0.1)a	1.1 (0.2)aA	0.5 (0.0)bAB	0.8 (0.1)aA	0.6 (0.1)abB	0.4 (0.02)bB
Mineral soil layer (Ah)									
pH (H$_2$O)[b]	5.0 (0.3)A	5.1 (0.4)A	4.2 (0.1)	4.6 (0.2)aA	4.7 (0.4)aA	3.7 (0.1)	3.7 (0.1)B	3.7 (0.0)B	3.7 (0.1)
Base Saturation (%)[b]	65.9 (19.6)aA	59.9 (18.2)aA	2.2 (0.4)b	46.3 (14.9)A	42.5 (17.3)A	3.3 (0.7)	8.2 (0.5)B	6.9 (1.3)B	8.3 (1.5)
C:N[b]	16.3 (0.6)aA	15.0 (0.7)a	21.3 (1.2)bB	13.2 (1.1)B	14.1 (1.5)	17.0 (0.8)A	14.2 (0.2)aAB	18.0 (1.1)b	22.3 (1.0)cB
δ ^{15}N (‰)[b]	5.8 (0.1)A	4.7(0.3)A	5.2 (0.1)	5.9 (0.3)A	5.1 (0.2)A	5.2 (0.2)	4.1 (0.3)B	3.4 (0.3)B	4.8 (0.6)
Total P (mg (P) g^{-1})[b]	0.7 (0.2)	0.8 (0.2)A	0.6 (0.1)A	0.5 (0.1)a	0. 7 (0.1)aA	0.2 (0.0)bB	0.3 (0.0)	0.2 (0.0)B	0.1 (0.0)B
Sand (%)	42.4 (8.6)A	46.9 (8.9)	33.0 (7.3)	26.7 (2.1)AB	25.8 (5.3)	23.9 (2.9)	21.8 (3.9)B	32.1 (6.7)	36.0 (4.8)
Silt (%)[b]	30.6 (7.5)A	35.8 (8.2)	35.6 (5.8)A	55.3 (3.0)B	53.1 (3.8)	60.9 (1.8)B	57.5 (0.3)B	49.7 (2.5)	50.0 (2.0)AB
Clay (%)[b]	26.9 (2.6)a	17.3 (2.3)b	31.5 (2.1)aA	18.1 (2.1)	21.1 (2.1)	15.2 (2.1)B	20.7 (3.6)	18.2 (4.3)	14.1 (3.3)B

[a] Moser et al. (2007)

[b] Means (± SE, n = 6) within rows followed by different letter indicate significant differences among topographic positions at each elevation (small letters) and differences among elevations at each topographic position (capital letters) (one-way ANOVA with Fisher's LSD test at $P \leq 0.05$).

2.3.2   Soil characterization

Twelve to sixteen soil profiles per elevation were dug until the underlying parent material was reached (0.5 - 1.5 m depth). We opened the profiles outside the boundaries of the plots under closed canopy and undisturbed, representative vegetation. Bulk density was determined for mineral soil using steel cores (250 cm^3) and for the organic layer by measuring the thickness and dry weight of an area of 400 cm^2 (Blake & Hartge 1986; Schlichting & Stahr. 1995). We expressed moisture content as gravimetric moisture content and as water-filled pore space (WFPS), assuming a particle density of 2.65 g cm^{-3} for mineral soil (Linn & Doran 1984) and of 1.4 g cm^{-3} for the organic layer (Breuer et al. 2002). Disturbed soil samples for chemical analysis were taken from the organic layer (as a pooled sample covering the whole depth of the organic layer) and from each mineral soil horizon. Oven-dried samples (45 ˚C for three days) were sieved and stored in plastic bags until air transport to Germany. All samples were analyzed for total carbon, nitrogen, phosphorous, total base cations and pH (H$_2$O). In addition, effective cation exchange capacity (ECEC) was measured for the mineral soil horizons. Total C and N were determined using ground samples and a CNS Elemental Analyzer (Elementar Vario EL, Hanau, Germany). Total P and total base cations were measured using Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP-AES; Spectro Analytical Instruments, Kleve, Germany) after pressure digestion in 65 % HNO$_3$ (Heinrichs et al. 1986). ECEC was determined from sieved samples by measuring cations in percolates of soils with unbuffered 1 M NH$_4$Cl using ICP-AES (König & Fortmann 1996). Base saturation was calculated as the percentage of exchangeable base cations (Na, K, Ca and, Mg) of all exchangeable cations. Soil pH was measured in a suspension of soil in H$_2$O with a 1:1 ratio for sieved mineral soil and a 1:10 ratio for material from the organic layer. Texture was determined by sedimentary fractionation of the clay fraction (25 °C, 21 h, 30 cm fall height) following the Atterberg method after wet sieving of the sand and coarse silt fraction (630 μm, 200 μm, 63 μm and, 20 μm) and after destruction of organic matter with 30 % H$_2$O$_2$ and Fe oxides with 4 % Na-Dithionite-Citrate solution (Schlichting E. 1995).

We measured δ^{15}N signatures on composite soil samples consisting of four subsamples taken with an auger within one meter distance of the chamber bases. Depending on the depth of the organic layer, we took samples from organic layer (0-10 cm depth and if present also 10-20 cm

depth) and three depths of the mineral soil (0-10 cm, 10-20 cm, 20-30 cm depth). Samples were dried at 45 ˚C for three days, sieved and stored in plastic bags until analysis in Germany. Ground samples were analyzed for $\delta^{15}N$ signature using an elemental C and N analyzer (NA1500, CE - Instruments, Rodano, Milano, Italy) and an isotope ratio mass spectrometer (Delta V Plus, Thermofisher, Bremen, Germany). The isotope signatures were expressed as $\delta^{15}N$ (‰):

$$\delta^{15}N \ (‰) = [(R_{sample}/R_{std})-1] \times 10^3 \qquad (1)$$

where $R_{sample} = {}^{15}N/{}^{14}N$ is the ratio of the sample and $R_{std} = {}^{15}N/{}^{14}N$ is the ratio of the reference (atmospheric N$_2$) (Martinelli et al. 1999).

2.3.3 Forest structure and productivity

We approximated forest productivity by annual tree basal area increment and annual total litterfall. In the study plots we made an inventory of all trees with stems ≥ 0.1 m diameter at breast height (dbh) and their basal area was calculated. After approximately one year we measured all trees again and we calculated the increment of plot basal area as the sum of the individual tree increments per plot over one year (diameter difference between first and second measurement was calculated for one year).

Total litterfall was collected monthly (bi-weekly at 1000 m) from six litter traps (60 x 60 cm) per plot. Total litterfall, including leaves, twigs, epiphytes, flowers and fruits, was dried at 60 ˚C and weighed. Total litterfall of December 2008 was collected, ground and sent to Germany for analysis. Litter samples of the six litter traps were proportionally pooled for each plot and analyzed for total C and N, total P, total base cations and $\delta^{15}N$ signatures as described above for soil samples.

2.3.4 N$_2$O and NO flux measurements

We measured N$_2$O fluxes from static closed chambers with a base area of 0.044 m^2. Six months prior to the first measurements, we installed chamber bases, inserting them approximately 0.02 m into the soil. The chamber bases were not moved until the end of the

sampling period. Chambers had a mean volume of 13 liter; lids were equipped with two Luer lock valves for sampling and pressure compensation during sampling. Gas samples were taken at 2, 14, 26, and 38 minutes following chamber closure and stored in pre-evacuated glass containers (60 ml). To assure that tubing and glass containers were evacuated and containers were filled to atmospheric pressure, pressure was checked with a manometer during sampling. Gas samples were analyzed using a gas chromatograph (Shimadzu GC-14B, Duisburg, Germany) equipped with an electron capture detector (ECD) combined with an autosampler (Loftfield et al. 1997), which was located in a laboratory near our field sites in Ecuador. We analyzed gas samples typically within 48 hours following sampling. Gas concentrations were calculated by comparing integrated peak areas of samples with four standard gases (320, 501, 1001, and 3003 ppb N_2O; Deuste Steiniger GmbH, Mühlhausen, Germany). N_2O measurements were conducted bi-monthly over a period of one year (May 2008 – May 2009).

Nitric oxide (NO) was measured in the field using open dynamic chambers, which were closed for six minutes using the same chamber bases as for N_2O sampling. Analysis of NO was conducted using a Drummond LMA-3D NO_2 Analyzer with chemiluminescence detector (Drummond Technology, Ontario, Canada). NO was analyzed following oxidation to NO_2 using a CrO_3 catalyst and reaction with a Luminol solution. As the CrO_3 catalyst is sensitive to relative humidity the gas stream was monitored with a portable relative humidity meter (GFTH 95, Greisinger electronic GmbH, Regenstauf, Germany) and the relative humidity was held below a value of 40 % by mixing the air from the chamber with make-up air that was dried using silica gel. Flow rate through the chamber was approximately 1.5 L min^{-1}. The detector was calibrated in the laboratory before field measurement using a standard gas (3000 ppb NO; Deuste Steiniger GmbH, Mühlhausen, Germany) which was diluted using make-up air to the range of concentrations measured in the field. Detector signal and time were recorded every five seconds with a CR800 Series data logger (Campbell Scientific, Utah, USA). NO measurements were carried out four times within the same year as the N_2O measurements. All gas fluxes were calculated from the linear increase of gas concentration of the chamber air over time, multiplied by the density of air and the ratio of chamber volume to soil surface area (Köhler et al. 2009). Dilution of the NO concentration in the chamber by outside air flow through the chamber is negligible during the initial linear part of the concentration increase (Bakwin et al. 1990). Zero

fluxes were included. Annual gas fluxes were calculated from the average of the monthly measurements expressed on a yearly basis.

2.3.5 Soil mineral N, net N-mineralization and net nitrification

Soil mineral N was determined on a composite soil sample, which consisted of four subsamples per plot. We collected these samples from the top 0.05 m of the surface (organic layer or mineral soil), within one meter distance of the chamber bases concomitantly to every gas sampling. In the field, part of the composite sample was added to a polyethylene bottle containing 150 ml of 0.5 molar potassium sulfate (K_2SO_4) solution. The remaining sample was stored in plastic bags for determination of gravimetric moisture content in the laboratory after drying for 24 hours at 105 °C. Extraction of soil mineral N was finished within 12 hours after field sampling. Extracts were filtered through filter papers (4 µm nominal pore size) after one hour of agitation, and frozen immediately after a drop of chloroform was added. Samples remained frozen during transport by air to Germany, where analysis was conducted. Ammonium (NH_4^+) and nitrate (NO_3^-) concentrations of the extracts were analyzed using a continuous flow injection colorimeter (Cenco/Skalar Instruments, Breda, Netherlands) (Arnold et al. 2009).

We determined net rates of soil N mineralization and nitrification once a year. To determine initial NH_4^+ and NO_3^- levels (T_0) four soil samples were taken per plot. A subsample of the composite plot sample was extracted in the field, as described above. The remaining subsample was put into a plastic bag, and inserted into the soil for a ten day incubation period ("buried bag method", (Hart et al. 1994)). After incubation, soil mineral N was extracted as described to obtain T_1 - NH_4^+ and NO_3^- concentrations. Net N mineralization and nitrification rates were calculated from the difference in mineral N concentrations between T_1 - and T_0 (Hart et al. 1994).

2.3.6 Statistical analyses

Statistical analysis was carried out on the plot mean N$_2$O and NO fluxes (average of four chambers). Using the N$_2$O flux data, we first tested the spatial independence of the six plots for each topographic position, and these plots were spatially independent based on the rank version of von Neumann's ratio test (Bartels 1982). For testing the effect of elevation and topography and of continuous variables in time series data (i.e. bi-monthly measurements of N$_2$O, NO fluxes

and soil mineral N), we applied linear mixed effects models (lme) with elevation and topographic position, or the continuous variable as fixed effects, and replicate plots nested in time as random effect. We used lme for time series data because they account for temporal correlation among observations on the same experimental unit (Piepho et al. 2004). Models describing time series data were tested for autocorrelation effects by including a first order autoregressive structure and for heteroscedasticity of residual variance by including variance functions (Bliese & Ployhart 2002). For testing the elevation and topography effects on data that were measured only once (i.e. soil characteristics, vegetation parameters and net rates of soil N transformation), we used two-way analysis of variance (ANOVA) with Fisher LSD test. For testing the influence of soil N transformation rates on N-oxide fluxes, we used the average N-oxide fluxes across a year for each plot. The average N_2O and $N_2O + NO$ fluxes were first log-transformed to correct for the non-normal distribution of the dataset. The relationships among net N mineralization, net nitrification, N_2O, NO and $N_2O + NO$ fluxes were assessed by lme, which includes different error variances of the different spatial scales of the hierarchical design (Crawley 2009) and hence showed better fit ($P < 0.05$) than the general least square model (gls). Additionally, lme models are unaffected by randomly missing data (Piepho et al. 2004). The relationships among soil characteristics, vegetation parameters and annual N-oxide fluxes were assessed by linear regression on the means of six plots for each topographic position (n = 9; 3 topographic positions of 3 elevations). Linear regression was used because lme did not improve the fit of the gls model on the 9-point database ($P < 0.60$). Means with ±1 standard error are given in the text. Effects were accepted as statistically significant if $P \leq 0.05$. Analyses were conducted using R version 2.10.1 *(R Development Core Team 2009)* and Statistica Service Pack 8 (StatSoft Inc., Tusla, USA).

2.4 Results

2.4.1 Soil characterization

Organic layer thickness increased with elevation and from the lower slope position to the ridge positions ($P < 0.001$ for elevation and topography effect). Spatial variation in organic layer thickness was high within short distances ranging from 0.00 m to 0.18 m at the 1000 m site, and

from 0.08 m to 0.55 m on the ridges of the 2000 m and 3000 m sites. Soils at lower slope positions, at midslope positions and on well drained ridge positions of the 1000 m and 2000 m sites were Eutric or Dystric Cambisols (IUSS Working Group WRB 2006) (Typic Eutropepts and Typic Dystropepts (Soil Survey Staff 1975)). Soils at the ridge position of the 1000 m site holding thicker organic layers were Humic Cambisols (Typic Humitropept). On most ridge positions of the 2000 m and 3000 m sites, water logging lead to the development of Histic Planosols and Stagnic Histosols (Typic Albaquults). At the 3000 m site, Stagnic Cambisols and Planosols (Aquic Dystropept, Typic Albaquults) dominated at the lower and midslope positions. Table 2.1 summarizes soil characteristics of the different elevations and topographic positions.

2.4.2   Forest structure and productivity

Both elevation and topography influenced dbh (P = 0.03 for elevation effect and P < 0.001 for topography effect) and stem density (P = 0.01 for elevation effect, P = 0.001 for topography effect and the interaction), whereas tree basal area only differed with topographic position (P = 0.02). Mean dbh decreased and stem density increased with increasing elevation. Along the topographic gradient, mean dbh decreased from the lower slope position to the ridges whereas stem density increased slightly (Table 2.2). Both elevation and topography affected annual total litter production and annual tree basal area increment (P < 0.001 for annual litter production, P < 0.001 for tree basal area increment and elevation and P < 0.05 for tree basal area increment and topography). Litter production and tree basal area increment were highest at the lower slope position of the 2000 m site and lowest at all positions at 3000 m (Table 2.2).

We found strong positive correlations between annual litter production and N concentrations in litterfall (P < 0.001, R^2 = 0.82) and tree basal area increment and N concentrations in litterfall (P < 0.001, R^2 = 0.83) (Figure 2.1 a, b).

Table 2.2: Forest structure, productivity and total litterfall characteristics of the topographic positions across the elevation gradient.

	1000 m			2000 m			3000 m		
	lower slope	midslope	ridge	lower slope	midslope	ridge	lower slope	midslope	ridge
Structure and productivity									
Mean dbh ($\geq$10cm)[b]	22.6 (1.4)	22.6 (1.9)A	18.7 (1.4)A	23.8 (2.6)a	19.0 (0.6)bAB	16.8 (0.6)bAB	24.0 (1.8)a	15.9 (0.3)bB	14.7 (0.7)bB
Stem density (400m²)[b]	32.8 (3.5)	36.0 (3.0)	22.6 (7.4)A	30.4 (3.6)a	45.4 (2.8)b	45.4 (3.6)bAB	34.4 (6.8)	49.3 (7.3)	56.7 (4.8)B
Basal area (m² ha⁻¹)[b]	44.8 (5.0)	57.2 (15.0)	20.3 (7.2)	48.9 (8.6)	40.4 (4.3)	29.2 (3.0)	44.8 (4.6)	28.1 (4.2)	28.6 (4.2)
Total litter production (Mg ha⁻¹yr⁻¹)[b]	7.0 (0.3)aA	8.6 (0.5)bA	6.4 (0.5)aA	9.5 (0.5)aB	9.8 (0.6)aB	7.1 (0.3)bA	4.7 (0.2)C	4.8 (0.5)C	4.5 (0.2)B
Basal area increment (m² ha⁻¹yr⁻¹)[b]	0.6 (0.1)AB	0.8 (0.2)A	0.7 (0.2)A	0.9 (0.2)aB	0.8 (0.1)aA	0.4 (0.1)bAB	0.4 (0.03)A	0.3 (0.1)B	0.3 (0.1)B
Total Litter									
N (mg g⁻¹)[b]	16.5 (0.4)A	15.9 (0.6)A	15.3 (1.2)A	21.1 (1.7)aB	19.3 (1.2)aB	13.8 (0.7)bA	12.0 (0.4)aC	9.9 (0.8)aC	7.1 (0.3)bB
N (g m⁻²)[b]	11.6 (0.8)A	13.7 (0.8)A	10.1 (1.5)A	19.7 (1.4)aB	19.2 (2.2)aB	9.7 (0.6)bA	5.7 (0.3)C	4.7 (0.5)C	3.1 (0.2)B
C:N[b]	31.7 (1.0)A	32.6 (1.4)A	35.8 (2.9)A	24.8 (2.4)aA	27.0 (2.2)aA	39.6 (2.2)bA	43.8 (1.8)aB	55.5 (5.0)bB	77.9 (3.1)cB
δ ¹⁵N (‰)[b]	1.6 (0.2)A	1.1 (0.4)A	1.2 (0.4)A	3.4 (0.4)aB	1.8 (0.3)bA	- 1.3 (0.4)cB	0.3(0.2)aC	- 1.4 (0.7)bB	- 2.6 (0.5)bC
P (mg (P) g⁻¹)[b]	0.8 (0.1)A	0.8 (0.1)A	0.7 (0.1)A	1.3 (0.1)aB	1.2 (0.2)aB	0.6 (0.0)bAB	0.6 (0.0)A	0.4 (0.0)C	0.3 (0.1)B
P (g m⁻²)[b]	0.6 (0.1)aA	0.7 (0.1)aA	0.5 (0.1)bA	1.2 (0.1)aB	1.2 (0.3)aB	0.4 (0.04)bA	0.3 (0.02)aC	0.2 (0.02)bC	0.2 (0.03)bB

[b] Means (± SE, n = 6) within rows followed by different letter indicate significant differences among topographic positions at each elevation (small letters) and differences among elevations at each topographic position (capital letters) (one-way ANOVA with Fisher's LSD test at $P \leq 0.05$).

Furthermore, several indices of N availability, e.g. C:N ratio and $\delta^{15}N$ signatures of litterfall displayed strong correlations with litter production (P < 0.01, R^2 = 0.62 for C:N ratio (Figure 2.1 a) and P = 0.02, R^2 = 0.54 for $\delta^{15}N$ signatures of litterfall) and tree basal area increment (P < 0.01, R^2 = 0.70 for C:N ratio (Figure 2.2 b) and P < 0.001, R^2 = 0.81 for $\delta^{15}N$ signatures of litterfall).
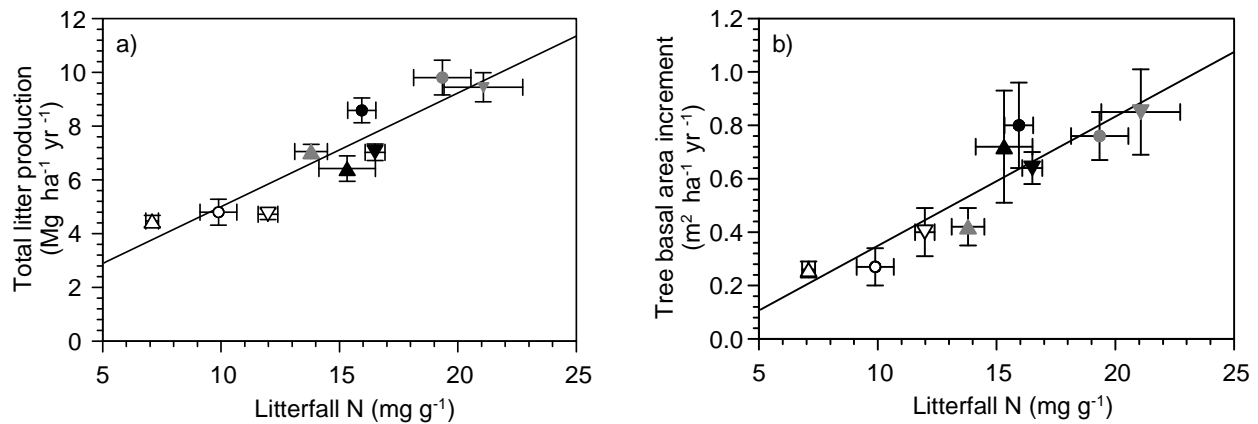
Figure 2.1: Linear regression of litterfall N and a) total litter production (Y = 0.77 + 0.42 *X, $P < 0.001$, $R^2 = 0.82$), b) tree basal area increment (Y = -0.14 + 0.05 * X, $P < 0.001$, $R^2 = 0.83$) of the topographic positions across the elevation gradient. Symbols used for data: full black, 1000 m; full grey, 2000 m; open, 3000 m; ▼ Lower slope, ● Midslope, ▲ Ridge.
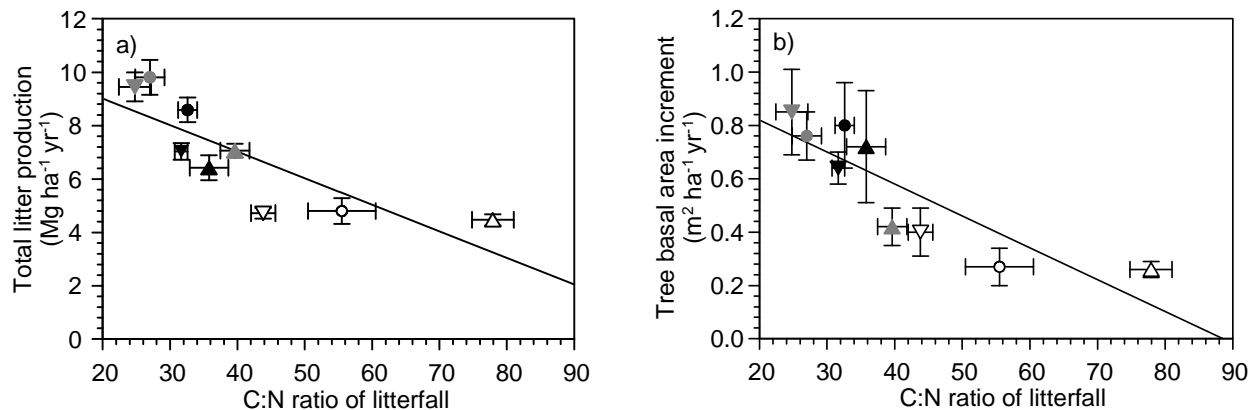
Figure 2.2: Linear regression of C:N ratio of litterfall and a) total litter production (Y = 11.0 – 0.09 * X, $P < 0.01$, $R^2 = 0.62$), b) tree basal area increment (Y = 1.06 - 0.01 * X, $P < 0.01$, $R^2 = 0.70$) of the topographic positions across the elevation gradient. Symbols used for data: full black, 1000 m; full grey, 2000 m; open, 3000 m; ▼ Lower slope, ● Midslope, ▲ Ridge.

2.4.3   N-oxide fluxes and soil moisture

Nitrous oxide fluxes did not display clear seasonality at any of the sites, probably because of the lack of a pronounced dry season. Elevation as well as topography influenced N_2O fluxes ($P < 0.001$ for elevation and topography effect) and NO fluxes ($P < 0.001$ for elevation and $P = 0.02$ for topography). N_2O and NO fluxes were highest at the lower slope positions of the 2000 m site and lowest at the 3000 m site (Table 2.3). Topography affected N_2O fluxes at 2000 m ($P < 0.001$) and NO at 3000 m ($P = 0.02$). In both cases gas fluxes decreased toward the ridge positions. Ridge positions at the 3000 m site showed negative annual N_2O fluxes and zero NO fluxes, while soils at the lower slope and midslope positions emitted N_2O and NO.

At all elevations N_2O fluxes exceeded NO fluxes. We did not calculate a N_2O/NO ratio because negative N_2O fluxes occurred and NO fluxes were close to zero. Gravimetric moisture content increased with elevation and from the lower slope positions to the ridges ($P < 0.001$ for the influence of elevation and topography effect). Throughout the sites gravimetric moisture content did not correlate with $N_2O + NO$ fluxes ($P = 0.06$, $R^2 = 0.33$) or the ratio of N_2O/ N oxide emissions ($P = 0.08$, $R^2 = 0.29$). Excluding the elevation effect, gravimetric moisture content did not influence $N_2O + NO$ fluxes within either of the sites. We did not use WFPS as index for soil moisture content, because a comparison of calculated WFPS of organic layers and mineral soil was not possible.

Table 2.3: Annual N-oxide fluxes (means ± SE) of the topographic positions across the elevation gradient in µg N m^{-2} h^{-1}

	1000 m			2000 m			3000 m		
	lower slope	midslope	ridge	lower slope	midslope	ridge	lower slope	midslope	ridge
N$_2$O[b]	1.90 (1.38)A	3.53 (1.13)	4.14 (1.56)	14.54 (2.13)aB	3.68 (1.46)b	1.15 (1.48)b	1.63 (1.14)A	1.34 (1.43)	-0.53 (0.94)
NO[b]	0.75(0.10)	1.11 (0.32)A	0.72 (0.31)A	1.11 (0.36)	1.13 (0.33)A	0.14 (0.08)B	0.19 (0.06)a	0.06 (0.04)abB	-0.02 (0.03)bB
N$_2$O + NO[b]	2.66 (1.32)A	4.63 (1.36)	4.85 (1.77)A	15.66 (2.27)aB	4.82 (1.50)b	1.28 (1.51)cB	1.82 (1.09)C	1.41 (1.46)	-0.54 (0.92)C

[b] Means (± SE, n = 6) within rows followed by different letter indicate significant differences among topographic positions at each elevation (small letters) and differences among elevations at each topographic position (capital letters) (Linear mixed effects models with Fisher's LSD test at $P \leq 0.05$).

Table 2.4: Average soil mineral N, net N mineralization and net nitrification rates (means ± SE) of the topographic positions across the elevation gradient.

		1000 m			2000 m			3000 m		
	Unit	lower slope	midslope	ridge	lower slope	midslope	ridge	lower slope	midslope	ridge
Extractable NH$_4^+$ [b]	kg (N) ha^{-1}	2.2 (0.4)A	1.8 (0.5)A	1.5 (0.5)	0.8 (0.2)B	0.9 (0.3)AB	0.9 (0.2)	0.6 (0.1)B	0.7 (0.1)B	0.8 (0.1)
Extractable NO$_3^-$ [b]	kg (N) ha^{-1}	0.4 (0.1)A	0.4 (0.1)A	0.6 (0.3)A	0.4 (0.1)aA	0.3(0.1)aA	0.04 (0.02)bB	0.0B	0.02 (0.01)B	0.03 (0.01)B
Net N mineralisation[c]	kg (N) ha^{-1} 10d^{-1}	3.6 (1.2)A	3.1 (0.9)	0.8 (0.6)AB	1.7 (0.4)B	1.4 (0.7)	1.5 (0.3)AB	0.2 (0.2)B	0.6 (0.4)	- 0.4 (0.3)B
Net nitrification[c]	kg (N) ha^{-1} 10d^{-1}	3.9 (1.5)A	1.7 (1.3)	0.4 (0.6)	0.8 (0.5)B	1.8 (0.6)	0.02 (0.3)	0.0B	0.04 (0.04)	0.0

[b] Means (± SE, n = 6) within rows followed by different letter indicate significant differences among topographic positions at each elevation (small letters) and differences among elevations at each topographic position (capital letters) (Linear mixed effects models with Fisher's LSD test at $P < 0.05$).

[c] Means (± SE, n = 6) within rows followed by different letter indicate significant differences among topographic positions at each elevation (small letters) and differences among elevations at each topographic position (capital letters) (one-way ANOVA with Fisher's LSD test at $P \leq 0.05$)

2.4.4   Indices of N availability and their control on N–oxide fluxes

Elevation affected mineral N content of the topsoil (P < 0.001 for NH_4^+ and NO_3^-). We found declining mineral N concentrations with increasing elevation. Topography did not have significant influence on mineral N content of the soil, with the exception of the 2000 m site (P < 0.001). At all sites, extractable NH_4^+ was the dominant form of mineral N and in 60 % of the extracts NO_3^- was below detection limit. At the 3000 m site, NO_3^- was below detection limit in 90 % of the extracts. Elevation had stronger influence on net N mineralization rate (P < 0.001) and net nitrification rate (P = 0.01) than topography (P = 0.05 for net N mineralization and net nitrification). Both net N mineralization and net nitrification rates were declining with increasing elevation, whereas there was no clear trend along the topographic gradient of either elevation (Table 2.4). Throughout all sites and within each site, bi-monthly measured mineral N contents did not significantly influence N_2O and NO fluxes. Net N mineralization and net nitrification rates did not affect annual means of the N_2O, NO or N_2O + NO fluxes.

Nitrogen cycling indices such as C:N ratio and $\delta\ ^{15}N$ signatures of litterfall, organic layer and upper mineral soil were affected by elevation as well as topography (P < 0.001 for elevation and topography effect on C:N ratio and $\delta\ ^{15}N$ signature of all three substrates). C:N ratios of litterfall, organic layer and upper mineral soil increased and $\delta\ ^{15}N$ signatures of litterfall and organic layer decreased along the topographic gradient form the lower slope position to the ridges at all sites (Table 2.2). Differences in these N cycling indices between topographic positions and between elevations were less pronounced in the mineral soil, indicating that $\delta\ ^{15}N$ enrichment and N cycling were restricted to the organic layer. The lower slope positions at the 2000 m site showed lowest C:N ratios and highest $\delta\ ^{15}N$ signatures of litterfall and organic layer. Negative $\delta\ ^{15}N$ signatures of litterfall occurred at the ridges of the 2000 m site and at midslope and ridge positions of the 3000 m site. Throughout the elevation gradient, we found strong correlations of N_2O + NO fluxes with C:N ratio and $\delta\ ^{15}N$ signatures of litterfall (P = 0.02, R^2 = 0.54 for C:N ratio, and P < 0.001, R^2 = 0.83 for $\delta\ ^{15}N$ signatures) (Figure 2.3 a, b) and of the organic layer (P = 0.01, R^2 = 0.57 for C:N ratio, and P = 0.01, R^2 = 0.58 for $\delta\ ^{15}N$ signatures). Ratios of C:N and $\delta\ ^{15}N$ signatures of the mineral soil did not correlate with N_2O + NO fluxes. Finally, we found strong correlations of N_2O + NO flux with proxies of forest productivity like annual litter production (P = 0.02, R^2 = 0.53) and tree basal area increment (P < 0.01, R^2 = 0.72) (Figure 2.3

c, d). Both proxies also showed strong correlations with NO fluxes ($P < 0.001$, $R^2 = 0.77$ for annual litter production, and $P = 0.01$, $R^2 = 0.65$ for tree basal area increment) and with N_2O fluxes ($P < 0.05$, $R^2 = 0.44$ for annual litter production and $P = 0.05$, $R^2 = 0.38$ for tree basal area increment).
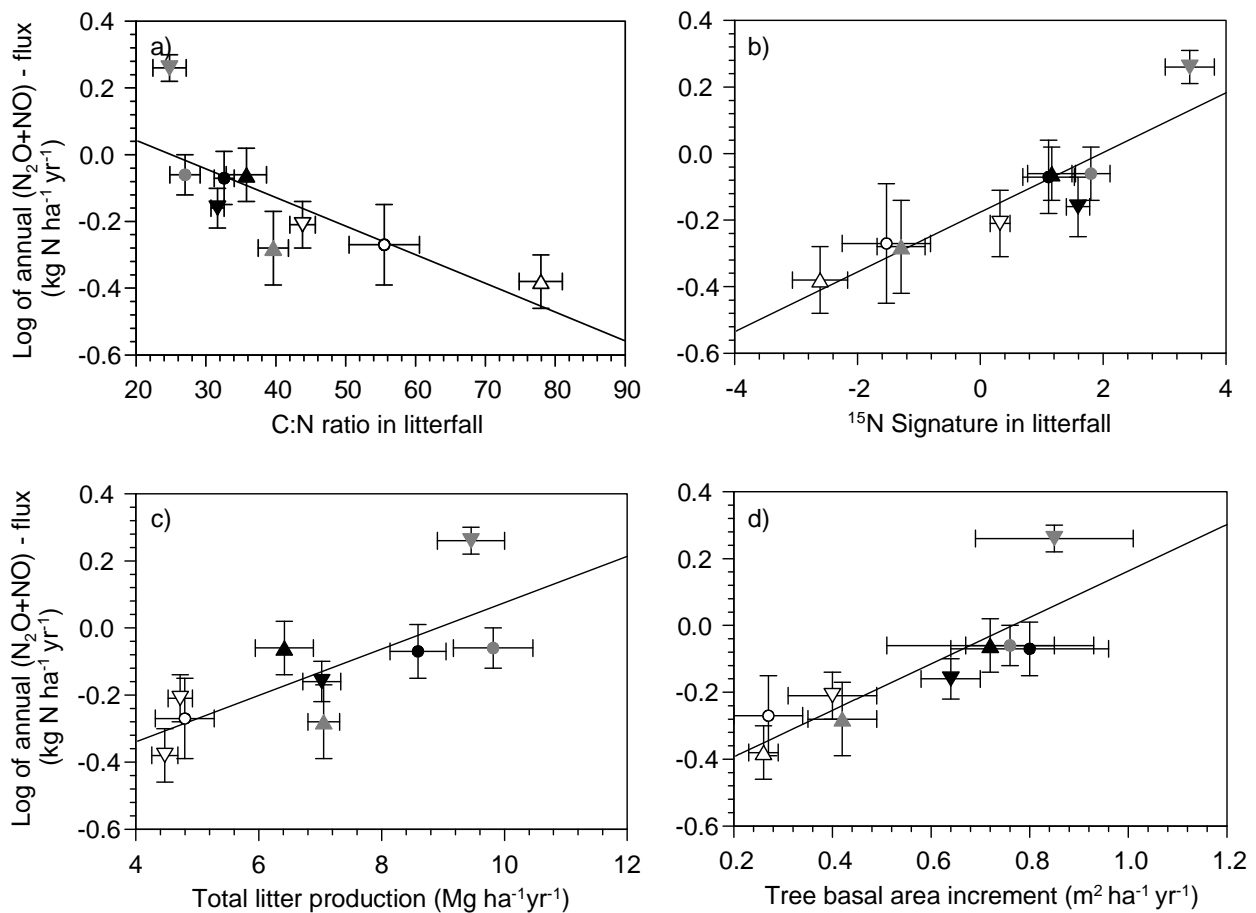
Figure 2.3: Linear regression of log-transformed annual $N_2O + NO$ fluxes and a) C:N ratio of total litterfall ($Y = 0.22 - 0.01 * X$, $P = 0.02$, $R^2 = 0.54$), b) $\delta^{15}N$ of litterfall ($Y = -0.18 + 0.09 * X$, $P < 0.001$, $R^2 = 0.83$), c) total litter production ($Y = -0.62 + 0.07 *X$, $P = 0.02$, $R^2 = 0.53$), and d) tree basal area increment ($Y = -0.53 + 0.69 * X$, $P < 0.01$, $R^2 = 0.72$) of the topographic positions across the elevation gradient. Symbols used for data: full black, 1000 m; full grey, 2000 m; open, 3000 m; ▼ Lower slope, ● Midslope, ▲ Ridge.

2.5 Discussion

2.5.1   Organic layers and nitrogen availability along elevation and topographic gradients

The increasing thickness of organic layers with increasing elevation and from lower slopes to ridge positions have been reported for other tropical montane forests (Arnold et al. 2009; Grubb 1977; Purbopuspito et al. 2006). Thick organic layers imply that considerable amounts of nitrogen are stored and not actively cycling in the ecosystem. Grubb (1977) suggested that this was one of the reasons for reduced N-availability in tropical montane forests. Thick organic layers develop if decomposition is slower than organic matter (above- and belowground litter) input. While the lower temperatures (causing slower decomposition, Table 2.1) together with an increase in root/aboveground biomass ratio (Leuschner et al. 2007) probably explains the increasing thickness of organic layers with elevation, water logging has been suggested to contribute to the slow decomposition of organic matter on the relatively flat ridge positions at 2000 m and 3000 m (Leuschner et al. 2007; Wilcke et al. 2002). Additionally, the feedback of tree vegetation to the environmental conditions at the exposed ridges in combination with the low nutrient availability probably affected species composition (Homeier et al. 2010) and reduced litter quality at the ridge positions (as shown by the high C:N ratios, Table 2.2) further reduced decomposition rates. In summary, we found evidence that a combination of climatic and hydrological conditions and the resulting plant feedbacks contributed to the observed large differences in organic layer thickness of these tropical montane forest soils.

Several lines of evidence suggest that parallel to the increasing thickness of organic layers, N availability decreased with elevation and from lower slope to ridge positions. First, net N-mineralization and net nitrification rates decreased with increasing elevation. Similar findings were reported in studies comparing tropical forests at different elevations (Arnold et al. 2009; Grubb 1977; Köhler et al. 2009; Marrs et al. 1988; Silver et al. 1994). Second, the C:N ratios of litterfall (Table 2.2) and of soil organic layers (Table 2.1) suggest decreasing N availability with elevation and from the lower slope to the ridge position. In ecosystems with low N availability nutrient use efficiency is high (Vitousek 1982) leading to high C:N ratios in plant tissue. In our study, this was evident at the ridge positions at the 2000 m site and all positions at the 3000 m site. Third, the decreasing $\delta^{15}N$ signatures of litterfall and of the organic layer with increasing

elevation and from lower slope positions to the ridges imply decreasing N availability. Signatures of $\delta^{15}N$ reflect the long-term behavior of the soil N cycle of an ecosystem. Forest ecosystems with high N availability have high $\delta^{15}N$ signatures because isotopic light N is preferentially lost from the ecosystem owing to fractionation during nitrification and denitrification, leaving ^{15}N enriched N behind (Robinson 2001). Sotta et al. (2008) showed this in the $\delta^{15}N$ signatures of litterfall and soil, which reflected the magnitude of soil N cycling rates of a lowland forest in the Brazilian Amazon. The $\delta^{15}N$ signatures of litterfall also correlated with nitrogen losses from tropical forests in Indonesia (Purbopuspito et al. 2006) and Panama (Corre et al. 2010). On volcanic ash soils in Hawaii, however, $\delta^{15}N$ signatures in mineral soil and leaves depended on soil development stage rather than elevation (Vitousek et al. 1989). At our study sites, slope processes rejuvenate soils at all elevations, leading to relatively young soils throughout the study sites. Our elevation gradient thus does not reflect a chronosequence in terms of soil age. Consequently, nitrogen availability was not controlled by soil development. Finally, at the 1000 m site most of the mineralized N was also nitrified, whereas at 3000 m net nitrification was only 3 % of net N mineralization. This suggests that microbial N immobilization increased along the elevation gradient implying increasing competition of nitrogen with increasing elevation (Arnold et al. 2009).

We can summarize that in these tropical montane forests organic layer thickness increased and N availability decreased with increasing elevation and from lower slope to ridge positions. At the 2000m site, the lower slope and midslope positions displayed a higher N availability than the 1000m site, which indicates that at this elevation the 'topography effect' was more pronounced than the 'elevation effect'. These results suggest that in these tropical montane forests thickness of organic layers and N availability can be predicted based on elevation and topographic position (Pennock & Corre 2001).

2.5.2 N availability and forest productivity

Annual litter production at our study sites was within the range reported for tropical montane forest sites (Röderstein et al. 2005; Vitousek 1984; Vitousek et al. 1995), whereas values for the lower and midslope positions of the 2000 m site were on the high end compared to other studies (Hall et al. 2004; Purbopuspito et al. 2006; Röderstein et al. 2005; Veneklaas 1991). Our finding

that forest productivity (expressed as annual litter production and tree basal area increment) decreased with increasing elevation and from the lower slope positions to the ridge positions reflects the results from earlier studies carried out in tropical montane forests (Grubb 1977; Homeier et al. 2010; Moser et al. 2007; Takyu et al. 2002; Tanner et al. 1998) and mirrors the systematic change in N availability. However, litterfall does not always change systematically with elevation in tropical mountains as shown by Clark et al. (2001) and Röderstein et al. (2005). Stem growth and basal area increment of tropical forest trees is determined by site conditions and the succession stage of the forest stand and it has been shown to vary strongly across tropical forest landscapes (Clark et al. 2001; Malhi et al. 2004). In contrast to findings from tropical forests in Brazil, where forest productivity decreased with soil development (Anderson et al. 2009; Malhi et al. 2004), soil age did not control productivity along our elevation gradient because we did not have systematic differences in soil development. Since we studied only old-growth forests, our plots contain primarily late-successional, slow-growing tree species and our basal area increment rates between 0.3 and 0.9 m² ha^{-1} yr^{-1} are probably below the forest stands' average because we omitted early-successional stands which contain many pioneer species. However, our values are in the range of basal area increment rates reported from neotropical forests (0.3 – 1.1 m² ha^{-1} yr^{-1} (Malhi et al. 2004)), with basal area growth rates of the lower and midslope positions of the 2000 m site being in the upper range, indicating the high productivity of these sites.

The correlations of forest productivity with proxies of N availability (C:N ratio and δ ^{15}N signature of litterfall) suggest that forest productivity depended on N availability and that the forest sites we studied were (co-) limited by nitrogen. This is in line with the results from other studies, that found a positive correlation between tree growth and N availability (Cavelier et al. 2000; Homeier et al. 2010; Tanner et al. 1992) in neotropical montane forests. Also nitrogen addition experiments in tropical montane forests have shown significant increases in forest productivity following nitrogen additions which indicates N limitation (e.g. Adamek et al., (2009)). This was also the case in a nutrient addition experiment conducted close to our sites (Homeier et al., unpublished data).

2.5.3   N-oxide fluxes and N availability

The N₂O fluxes in these tropical montane forests were lower than most studies published from tropical lowland forests (Köhler et al. 2009; Werner et al. 2007). They fit within the range of values reported for tropical montane forests, with a study from Hawaii reporting lower fluxes (Matson & Vitousek 1987; Riley & Vitousek 1995) and studies from Panama (Köhler et al. 2009), Indonesia (Purbopuspito et al. 2006), Australia (Breuer et al. 2000) and Hawaii (Holtgrieve et al. 2006) reporting slightly higher N₂O fluxes. The lower slope position at the 2000 m site was the only site that displayed much higher N₂O fluxes than expected. Only few studies measured NO fluxes from tropical montane forests. Their results are in the same range as our measurements at 1000 m and 2000 m elevation (Köhler et al. 2009; Purbopuspito et al. 2006); but higher than our fluxes measured above 2000 m (Purbopuspito et al. 2006).

The N₂O + NO fluxes largely followed the gradients that we detected for N availability. This was clear for the declining N₂O + NO fluxes with elevation, but was not significant for topographic position at all elevations, due to the high spatial variability between sites (Table 2.3). Other studies have also reported lower N₂O emissions and even N₂O uptake at ridge positions compared to lower slope positions (Bowden et al. 1992; Corre et al. 1996; Reiners et al. 1998). For the different proxies for N availability that we tested, we did not find good correlations of N-oxide fluxes with mineral N, net N mineralization and net nitrification rates as have been reported in a range of studies carried out in tropical ecosystems (Erickson et al. 2001; Holtgrieve et al. 2006; Keller & Reiners 1994; Matson & Vitousek 1987; Riley & Vitousek 1995). The reason is probably the high temporal and spatial variability of mineral N pools and net N mineralization and net nitrification rates (Veldkamp et al. 1999). We did however find strong correlations with more integrative indices of the long-term N cycle: C:N ratio and $\delta\ ^{15}$N signature of litterfall which has also been shown in other studies conducted in tropical ecosystems (Davidson et al. 2000; Erickson et al. 2001; Purbopuspito et al. 2006). The combined results of very low N-Oxide emissions, low N turnover rates and negative δ^{15}N signatures of plant litter at high elevations and on the ridges illustrate that slow N mineralization combined with N uptake by the vegetation probably resulted in marginal nitrification rates (often not detectable at our sites) and consequently minimal N-Oxide fluxes (Handley et al. 1999). Furthermore, at these wet sites any soil nitrate that may have been produced was probably

completely consumed by denitrification, thus reducing the expression of the isotope effect at the ecosystem scale (Houlton et al. 2006). In contrast, at the slightly drier and warmer sites, higher δ^{15}N signatures illustrate the strong discriminating effect of nitrification and denitrification caused by the high N-oxide emissions (Houlton & Bai 2009). A test of C:N ratios and δ^{15}N signatures of organic layers and mineral soil as proxies for $N_2O + NO$ fluxes, resulted in weaker correlations and supported similar findings of Purbopuspito et al. (2006) in montane forests of Indonesia.

2.5.4 Nitrogen availability as a link between forest productivity and N-oxide fluxes

The close correlation of indices of N availability with forest productivity and N-oxide fluxes we interpret as evidence that nitrogen availability controls both forest productivity and N-oxide fluxes in the studied tropical montane forests. The good correlations of indices of forest productivity with N oxides fluxes in our study (Figure 2.3 c, d) suggest that data on forest productivity have the potential to be used as predictors of $N_2O + NO$ fluxes. However, it is important to note that we can only expect close correlations between indices of forest productivity and N oxide fluxes in ecosystems that are (co)-limited in nitrogen. If nitrogen is not the limiting nutrient, forest productivity does not increase with N availability while N-oxide fluxes do. Thus, in ecosystems that are not N-limited (e.g. many tropical lowland forests), we cannot expect that forest productivity correlates with N availability and N-oxide fluxes.

Information on ecosystem productivity, especially on litter production rates is available for a wide range of ecosystems, including tropical montane forests which opens the possibility to include these data as predictors or as co-variables to improve prediction of N-oxides fluxes. However, data on litter production can be quite variable and in some studies extremely high litter production rates with large standard errors have been reported (possibly caused by animals, strong winds, etc). As a result, the close correlation of $N_2O + NO$ flux with litter production that we found in our study could not be confirmed after including data from other studies carried out in tropical montane forests (Holtgrieve et al. 2006; Purbopuspito et al. 2006; Schuur & Matson 2001). Tree basal area increment however showed a closer correlation to $N_2O + NO$ fluxes compared with litter production and is probably a better long-term measure of forest productivity compared to litter fall. In addition, tree basal increment is estimated by measuring the whole

plots and not by collecting a random sample, as is the case with litterfall. Presently the scientific community is doing considerable efforts to improve estimates of aboveground biomass and changes in aboveground biomass of tropical forests. The results of our study illustrate that in N-limited forests these improved biomass estimates may be used to improve N-oxide flux estimates as well.

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CHAPTER

3

ATMOSPHERIC METHANE UPTAKE BY TROPICAL MONTANE FOREST SOILS AND THE CONTRIBUTION OF ORGANIC LAYERS

3.1 Abstract

Microbial oxidation in aerobic soils is the primary biotic sink for atmospheric methane (CH_4), a powerful greenhouse gas. Although tropical forest soils are estimated to globally account for 10% to 20% of annual soil CH_4 consumption (15–30 Tg CH_4), limited data are available on CH_4 exchange from tropical montane forests. We present the results of an extensive study on CH_4 exchange from tropical montane forest soils along an elevation gradient (1000 m, 2000 m, 3000 m) and topographic gradients (lower slope, midslope, ridge position) in southern Ecuador. We investigated soil CH_4 exchange, possible controls, and the organic layer contribution to the atmospheric CH_4 uptake using both, field measurements and laboratory incubations. All soils were net atmospheric CH_4 sinks, with decreasing annual uptake rates from 5.9 kg CH_4-C $ha^{-1}yr^{-1}$ at 1000 m to 0.6 kg CH_4-C $ha^{-1}yr^{-1}$ at 3000 m. Topography had no effect on soil atmospheric CH_4uptake. Positive correlations between CH_4 uptake rates, mineral nitrogen and total phosphorus content of the mineral soil and with CO_2 emissions indicated that the largest CH_4 uptake corresponded with favorable conditions for microbial activity. Incubated organic layer profiles from the 2000 m and 3000 m sites revealed CH_4 uptake of up to 70 µg CH_4-C m^{-2} h^{-1} in the deeper organic layers. Our results suggest that CH_4 uptake in these tropical montane forest soils may be nutrient-limited. Contrary to the results from temperate regions -, the organic layer in tropical montane forest soils contributed considerably to the uptake of atmospheric CH_4. The study shows that all soils were net sinks of methane and that the differentiation of elevation levels is necessary for the methane balances on regional scale.

3.2 Introduction

Methane (CH_4) is a trace gas with a global warming potential 21 times greater than that of carbon dioxide (CO_2) and participates in chemical reactions producing tropospheric ozone (Forster et al. 2007; Topp & Pattey 1997). Oxidation processes are the main sink of atmospheric CH_4, with the reaction of hydroxyl-radicals (OH) in the troposphere accounting for approximately 90% of annual CH_4 removal (Prather et al. 2001). Although soils can act as sinks and sources for CH_4, microbial oxidation (methanotrophy) in aerated upland soils is the primary biotic sink for atmospheric CH_4 (Potter et al. 1996). Two forms of methanotrophic oxidation are

known in aerated soils. The first, low affinity oxidation, is only found near methane sources (e.g. in peat soils and rice paddies) and is performed by methylotrophic bacteria at CH_4 concentrations higher than $40\ \mu L\ L^{-1}$ (Conrad 1996; Le Mer & Roger 2001). The second, high affinity oxidation, occurs at atmospheric CH_4 concentrations and is responsible for atmospheric CH_4 consumption by aerated soils (Conrad 1996).

The net CH_4 exchange between soils and the atmosphere is controlled by soil physical and chemical properties that determine gas diffusivity, microbial activity and the balance between the processes of CH_4 production (methanogenesis) and uptake (methanotrophy). Gas diffusivity is considered the primary regulating factor for CH_4 consumption in soils, as the potential consumption of atmospheric CH_4 by high affinity methanotrophs generally exceeds the rate of CH_4 to diffuse from the atmosphere into the soil (Striegl 1993). Soil texture and soil moisture mainly control diffusivity in soils by regulating permeability and gas transport resistance, as CH_4 diffuses 10^4 times faster in air than in water (Dörr et al. 1993; Topp & Pattey 1997). Organic layers are considered to affect CH_4 oxidation primarily as gas diffusion barriers because they display little, if any, CH_4 oxidation capacity (Butterbach-Bahl et al. 2002; Saari et al. 1998; Steinkamp et al. 2001). The removal of the organic layer led e.g. to enhanced CH_4 uptake of temperate forest soils (Brumme & Borken 1999; Saari et al. 1998). Besides substrate availability, microbial activity in soils is regulated by temperature, where increasing temperatures lead to higher microbial activity, and nutrient availability (Conrad 1996). N availability can indirectly affect CH_4 uptake, by competition of NH_4^+ with CH_4 for methane oxidizing enzymes and the blocking of enzyme functions by products of NH_4^+ oxidation (Schnell & King 1994). Negative correlations between CH_4 uptake rates and extractable NH_4^+ or nitrification rates have been reported in tropical regions (Mosier & Delgado 1997; Veldkamp et al. 2001). Furthermore, net CH_4 fluxes in soils are the result of CH_4 production and CH_4 oxidation which are regulated by spatial and temporal variability of anaerobic and aerobic microsites in the soil. Anaerobic microsites in upland soils may occur during wet periods or due to consumption of soil oxygen because of high microbial activity (Verchot et al. 2000). An enhanced occurrence of anaerobic microsites can turn soils from net sinks for atmospheric CH_4 into net sources (Davidson et al. 2004; Keller & Reiners 1994; Keller et al. 2005).

Most tropical lowland rainforest soils are sinks for atmospheric CH_4 (Kiese et al. 2003; Kiese et al. 2008; Werner et al. 2006). Uptake of atmospheric CH_4 in aerobic tropical forest soils is estimated to account for about 28% of the global annual soil consumption (6.2Tg yr^{-1} CH_4)(Dutaur & Verchot 2007). Montane forests cover about 9% of the tropics (FRA 2000) but only few studies have been conducted on CH_4 fluxes in tropical montane forests (Delmas et al. 1992; Ishizuka et al. 2005; Kiese et al. 2008; Purbopuspito et al. 2006). The extreme variation in elevation and topographic gradients are likely to affect methane fluxes (e.g. increasing precipitation and decreasing temperatures at higher elevations, changes of soil moisture and the accumulation of organic matter in the organic layers). We are not aware of a study on the potential contribution of organic layers to oxidize methane in tropical montane forest soils even though thick organic layers frequently occur in these ecosystems (Edwards & Grubb 1977).

Here, we present the results of an extensive study on CH_4 exchange from tropical montane forests soils along an elevation gradient from 1000 m to 3000 m and along topographic gradients (lower slope, midslope, and ridge) in southern Ecuador. We tested the following hypotheses: 1) net uptake of atmospheric CH_4 decreases with increasing elevation, 2) net uptake of atmospheric CH_4 decreases with increasing organic layer thickness; 3) net uptake of atmospheric CH_4 is inhibited by high N availability and that 4) organic layers contribute not or only little to the uptake of atmospheric CH_4 in tropical montane forests soils. We investigated soil CH_4 exchange, possible biogeochemical controls, and the contribution of organic layers to the atmospheric CH_4 uptake using a combination of field measurements and laboratory incubations of mineral soil and organic layers.

3.3 Methods

3.3.1   Study area

The study was carried out along an elevation gradient from 1000 m to 3000 m within and close to Podocarpus National Park. The park is located in the Cordillera del Consuelo, which forms part of the eastern chain of the Andes in southern Ecuador. Three study sites were selected (Table 3.1): premontane rainforest, from 990 to 1200 m a.s.l. (hereafter the '1000 m site'), lower montane forest, from 1800 to 2100 m a.s.l. (hereafter the '2000 m site') and upper montane

forest, from 2800 to 3000 m a.s.l. (hereafter the '3000 m site'). At each study site (1000 m, 2000 m, 3000 m) we established 18 plots at three landscape positions: lower slope, midslope and ridge. Annual precipitation showed little seasonality (Emck 2007). For most of the study area, Paleozoic metamorphic schist and sandstones with some quartz veins form the parent material for soil development. However, at the 1000 m site, soil parent material of half of the plots consists of deeply weathered granitic rock of the Jurassic Zamora granitoide formation (Litherland et al. 1994). Organic layer thickness increased with elevation and from lower slope positions to ridge positions (Table 3.1), but displayed large spatial variation, ranging from 0 to 30 cm at the 1000 m site, and from 0.5 to 75 cm at the 2000 m and 3000 m sites. At the ridge positions of the 2000 m and 3000 m sites and to some extend at the ridges of the 1000 m site, thick organic layers led to Humic and Histic characterization of soil types. Soils at well-drained positions of the 1000 m and 2000 m sites classified as Eutric or Dystric Cambisols. Soils with hydromorphic properties (Stagnic Cambisols or Planosols) were found on the ridges of the 2000 m site and at all topographic positions of the 3000 m site (Chapter 2.4.1).

3.3.2   Experimental design

At each elevation, we established eighteen plots, six at each landscape position (lower slope, midslope and ridge positions). All plots were situated in mature, closed-canopy forest that was representative for the respective topographic position. In each plot we installed four chamber bases for gas exchange measurements in a random design along two orthogonal transects, in total 216 chambers (54 plots x four chambers per plot). Chamber bases were installed six months prior to the first measurements, inserting them approximately 0.02 m into the soil and remained in place until the end of the sampling period. Chamber lids were equipped with a Luer-Lock sampling port and a vent for pressure equilibration. Methane, soil respiration, soil moisture content, soil temperature, and soil mineral N were measured bi-monthly over a period of one year (May 2008 – May 2009).

Table 3.1: Site characteristics and soil properties of the upper mineral soil (Ah-horizon) at the topographic positions across the elevation gradient

	1000 m			2000 m			3000 m		
	Lower slope	Midslope	Ridge	Lower slope	Midslope	Ridge	Lower slope	Midslope	Ridge
Coordinates	04° 06' S, 78° 58' W			03° 58' S, 79° 04' W			04° 06' S, 79° 11' W		
Elevation a.s.l. (m)	990-1200			1800-2100			2800-3000		
Air temperature (°C)[a]	19.4			15.7			9.4		
Precipitation (mm yr^{-1})[a]	2230			1950			4500		
Organic layer thickness (cm)[b]	2.5 (0.7)	2.6 (1.0)A	6.5 (1.9)A	4.0 (0.9)a	12.2 (3.1)aB	24.0 (2.9)bB	6.6 (0.7)a	14.2 (1.6)abB	22.2 (3.4)bB
Organic layer									
pH (H_2O)[b]	4.9 (0.5)a	4.8 (0.6)a	3.7 (0.1)b	4.6 (0.2)a	4.8 (0.5)a	3.4 (0.1)b	4.0 (0.3)	3.7 (0.1)	3.6 (0.1)
C:N[b]	18.5 (0.7)A	18.6 (1.5)A	20.5 (0.7)A	15.7 (0.8)aB	15.6 (0.6)aA	21.1 (0.7)bA	20.5 (0.8)aA	23.9 (1.4)bB	26.7 (1.3)cB
Total P (mg g^{-1})[b]	1.1 (0.1)	1.2 (0.1)A	0.6 (0.02)A	1.2 (0.1)a	1.1 (0.2)aA	0.5 (0.0)bAB	0.8 (0.1)aA	0.6 (0.1)abB	0.4 (0.02)bB
Mineral soil (Ah)									
pH (H_2O)[b]	5.0 (0.3)A	5.1 (0.4)A	4.2 (0.1)	4.6 (0.2)AB	4.7 (0.4)AB	3.7 (0.1)	3.7 (0.1)B	3.7 (0.0)B	3.7 (0.1)
C:N[b]	16.3 (0.6)a	15.0 (0.7)a	21.3 (1.2)bAB	13.2 (1.1)	14.1 (1.5)	17.0 (0.8)A	14.2 (0.2)a	18.0 (1.1)ab	22.3 (1.0)bB
Total P (mg g^{-1})[b]	0.7 (0.2)	0.8 (0.2)A	0.6 (0.1)	0.5 (0.1)	0. 7 (0.1)AB	0.2 (0.0)	0.3 (0.0)	0.2 (0.0)B	0.1 (0.0)
Sand (%)	42.4 (8.6)	46.9 (8.9)	33.0 (7.3)	26.7 (2.1)	25.8 (5.3)	23.9 (2.9)	21.8 (3.9)	32.1 (6.7)	36.0 (4.8)
Silt (%)[b]	30.6 (7.5)A	35.8 (8.2)	35.6 (5.8)A	55.3 (3.0)B	53.1 (3.8)	60.9 (1.8)B	57.5 (0.3)B	49.7 (2.5)	50.0 (2.0)AB
Clay (%)[b]	26.9 (2.6)ab	17.3 (2.3)b	31.5 (2.1)aA	18.1 (2.1)	21.1 (2.1)	15.2 (2.1)B	20.7 (3.6)	18.2 (4.3)	14.1 (3.3)B

[a] Moser et al. (2007)

[b] Means (± SE, n = 6) within rows followed by different letter indicate significant differences among topographic positions at each elevation (small letters) and differences among elevations at each topographic position (capital letters) (two-way ANOVA with Tukey HSD test at $P \leq 0.05$)

3.3.3 Site characterization

Soil characteristics of the plots were determined from 41 soil profiles (0.5-1.5 m) at the beginning of the study (2008). Bulk densities of the mineral soil and the organic layers were determined according to Blake and Hartge (1986). For chemical analysis, samples from the organic layer (as a pooled sample covering the whole depth of the organic layer) and from the Ah horizon were oven-dried (45˚C for three days), sieved and stored in plastic bags until air transported to Germany. Total carbon (C_{tot}) and total nitrogen (N_{tot}) were determined using ground samples and a CNS Elemental Analyzer (Elementar Vario EL, Hanau, Germany). Total P (P_{tot}) and total base cations were measured using Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP-AES; Spectro Analytical Instruments, Kleve, Germany) after pressure digestion in 65% HNO_3. Soil pH was measured in a suspension of soil in H_2O with 1:1 and 1:10 ratio for sieved mineral soil and organic layer, respectively. Soil texture of the Ah horizon was determined by sedimentary fractionation of the clay fraction (25°C, 21 h, 30 cm fall height) following the Atterberg method after wet sieving of the sand and coarse silt fraction (630, 200, 63 and 20 µm) and destruction of organic matter with 30% H_2O_2 and Fe oxides with 4% Na-Dithionite-Citrate solution (Schlichting et al.. 1995). Soil moisture content, soil mineral N, and soil temperature were determined at the depth of 0 to 0.05 m of the surface (organic layer or mineral soil), within a one meter distance of the chamber bases concomitantly with every gas sampling. We expressed soil moisture as gravimetric moisture content. Soil mineral N (ammonia (NH_4^+) and nitrate (NO_3^-)) was determined on a composite soil sample, which consisted of four subsamples per plot. In the field, part of the composite sample was added to a polyethylene bottle containing 150 ml of 0.5 molar potassium sulfate (K_2SO_4) solution. The remaining part of each sample was stored in a plastic bag for determination of gravimetric moisture content in the laboratory after drying for 24 hours at 105°C. Extraction of soil mineral N was finished within 12 hours after field sampling to avoid shifts in NH_4^+ and NO_3^- concentrations in the soil over time (Arnold et al. 2008). Extracts were filtered through filter papers (4 µm nominal pore size) after one hour of agitation, and frozen immediately after a drop of chloroform was added to prevent further N turnover. Samples remained frozen during transportation by air to Germany, where analysis was conducted. Ammonium and NO_3^- concentrations of the extracts were analyzed using a continuous flow injection colorimeter (Cenco/Skalar Instruments, Breda, Netherlands) (Arnold et al. 2009).

3.3.4   Field measurement of net CH_4 exchange and soil respiration

We measured net exchange rates of CH_4 and CO_2 bi-monthly over a time period of one year (May 2008-May 2009). We used static closed chambers with a base area of 0.044 m^2 and a closed chamber volume of 13 liters. Gas samples were taken 2, 14, 26, and 38 minutes following chamber closure using pre-evacuated glass containers (60 ml). Pressure was checked with a manometer during sampling to assure that containers had been evacuated properly and were filled to atmospheric pressure. Gas samples were analyzed within 48 hours following sampling using a gas chromatograph (Shimadzu GC-14B, Duisburg, Germany) equipped with a flame ionization detector (FID) and an electron capture detector (ECD) combined with an autosampler (Loftfield et al. 1997). Gas concentrations were calculated by comparing integrated peak areas of samples with four standard gases (1.5, 2.0, 10 and 20 μL L^{-1} standard concentrations of CH_4; and 350, 700, 1500, 5000 μL L^{-1} standard concentrations of CO_2; Deuste Steiniger GmbH, Mühlhausen, Germany). Methane exchange rates were calculated from the linear change of CH_4 concentration in the chamber air over time, while CO_2 emissions were calculated by fitting both linear and quadratic regression models if CO_2 concentrations increased asymptotically (Wagner et al. 1997). Positive flux rates represent net emissions and negative values represent net uptake rates by soils. Based on the Akaike Information Criterion the quadratic model was found to be statistically more adequate and therefore applied in about 50% of the cases. By applying this data screening and model fitting, we minimized underestimations of CO_2 emissions that may have occurred by using linear models uncritically with static chamber flux data (Livingston et al. 2006). Annual fluxes were calculated from the average of the bi-monthly measurementsPotential uptake of atmospheric CH_4 and soil respiration at different soil depths

To determine the potential uptake of atmospheric CH_4 and soil respiration at different soil depths and to determine the influence of temperature on gas flux rates, we conducted a laboratory incubation experiment. Undisturbed samples from mineral soils and organic layers were taken from selected soil profiles using stainless steel cores (100 cm^3). We sampled 12 soil profiles of the mineral soil at the lower slope positions of the 1000 m site, where no organic layer was present. We sampled six mineral soil profiles from soils on deeply weathered granite and six from young, shallow soils over schist. The mineral soil profiles consist of samples from four different soil depths: 0-5 cm, 5-10 cm, 10-15 cm and 15-20 cm. Furthermore, we sampled 15 organic layer profiles from the ridge positions of the three elevations. The organic layers profiles

were sampled in 5-cm depth intervals from the surface to the mineral soil and include two depth of the underlying mineral soil (0-5 cm and 5-10 cm). We sampled three organic layer profiles over weathered granite at 1000 m, seven organic layer profiles at 2000 m and five organic layer profiles at 3000 m. Additionally, we took disturbed samples of each profile depth to determine gravimetric moisture content after drying for 24 hours at 105°C. The undisturbed samples were transported to the laboratory of the Technical University in Loja and were incubated the next day.

We incubated soil cores at field moisture and two different temperatures (15 °C and 25°C) under ambient air in closed glass flasks (0.4 L) with a septum sampling port. Soil cores were pre-incubated for 24 hours at the respective incubation temperature. If necessary, soil moisture was re-adjusted to the initial moisture content prior to incubation, by weighing soil cores and adding distilled water. After 90 minutes of incubation, a gas sample (10 ml) was taken from the headspace of the flask through a septum with a gas tight syringe (SEG International, Ringwood, Australia), and the concentration of CH_4 and CO_2 was measured with the gas chromatograph described above. Methane fluxes and CO_2 emissions were calculated as the difference of the gas concentration measured after the incubation of 90 minutes (T_1) and the initial concentration in fresh air before the incubation flask was closed (T_0 concentration, fresh ambient air). The gas fluxes were related to the soil core surface area (24 cm^2) and expressed as flux per square meter. After incubation, soil material was dried at 45°C, ground and analyzed for pH, C_{tot}, N_{tot}, P_{tot} and base cations as described for the soil samples above.

3.3.5 CH_4 concentration in soil air of organic layers

To determine in situ soil air CH_4 concentration at different organic layer depths, we sampled soil air in 10-cm steps from the mineral soil to the surface at the same sampling points at 2000 m and 3000 m selected for the incubation experiment. We measured 3 profiles per sampling point using a steel tube (1.8", 60-80 cm, Alltech, Unterhaching) and pre-evacuated glass containers (20 ml), after evacuating the tubing with a syringe. Gas concentrations were measured using the gas chromatograph described above. Measurements were carried out during a relatively dry period (October- November 2010) and during a wet period (February -March 2011).

3.3.6   Statistical analyses

Statistical analysis of data from the field measurements was carried out on the plot mean of trace gas fluxes (average of four chambers). Linear mixed effects models (LME) were applied to test the effect of:

1) elevation and topography on time series data (i.e. bi-monthly measurements of trace gas fluxes, soil moisture and soil mineral N), with elevation and topographic position as fixed effects, and replicate plots nested in time as a random effect;

2) continuous variables (soil moisture and soil mineral N) on temporal variance of the gas fluxes, with the continuous variable as fixed effect and replicate plots nested in time as a random factor;

3) continuous variables on the spatial variability of annual gas fluxes, including topographic positions nested into the elevations as spatial random factor;

4) temperature and soil texture on trace gas fluxes of the incubated samples, with profile depth as a random factor.

5) wet and dry season, soil depth and elevation on CH_4 soil air concentrations, including the hierarchical sampling structure as a spatial random factor.

We used LME for time series data because they account for temporal correlation among observations on the same experimental unit (Piepho et al. 2004) and we used LME to test spatial correlations to account for the hierarchical study design by including different error variances of the different spatial scales (Crawley 2009). Linear mixed effects models were tested for autocorrelation effects by including a first order autoregressive structure and for heteroscedasticity of residual variance by including variance functions (Bliese & Ployhart 2002). Model residuals were tested for normal distribution and data was transformed if necessary. For testing the elevation and topography effects on data that were measured once (i.e. soil characteristics) we used two-way analysis of variance (ANOVA). The relationships among soil characteristics and annual trace gas fluxes were assessed by linear regression on the means of six plots for each topographic position (n = 9; 3 topographic positions of 3 elevations). The effects of soil depth on trace gas fluxes were tested using one–way ANOVA. For multiple comparison

after LME and ANOVA Tukey HSD test was applied. Correlations of trace gas fluxes from the incubated samples with continuous variables (i.e. carbon concentrations) were examined using generalized least square models (GLS) on the elevation mean of each profile depth. GLS models were tested for autocorrelation effects of profile depth by including a spherical correlation structure. Means with ±1 standard error are given in the text. Effects were accepted as statistically significant if $P \leq 0.05$. Analyses were conducted using R version 2.10.1 (R Development Core Team 2009) and STATISTICA Service Pack 8 (StatSoft Inc., Tusla, USA).

3.4 Results

3.4.1   Soil net CH_4 fluxes along elevation and topographic gradients

Atmospheric CH_4 uptake of the soil decreased with increasing elevation ($P < 0.001$), whereas topography did not affect atmospheric CH_4 uptake. Soil net CH_4 fluxes did not display a clear seasonality () and soils of all elevations and topographic positions were net sinks for atmospheric CH_4 with annual mean uptake rates ranging from 0.6 ± 1.2 kg CH_4-C ha^{-1} yr^{-1} at 3000 m to 5.9 ± 1.0 kg CH_4-C ha^{-1} yr^{-1} at 1000 m (Figure 3.1). Positive CH_4 fluxes (emissions) occurred in 5.3% of all measurements and increased with elevation from 2.1% at 1000 m and 5.2% at 2000 m to 8.9% at 3000 m. Variability of fluxes was highest at the lower slope position at 3000 m where 22% of CH_4 fluxes measured were positive. We found no effect of different soil parent material (granite vs. schist) on net atmospheric CH_4 uptake rates ($P = 0.40$) (Table 3.3). To determine the effect of elevation and slope position on soil moisture in the top 0.05 m of the soil we separated results from the organic layer and the mineral soil. Gravimetric moisture content of mineral soils without organic layer, which were only found at the 1000 m site, was lowest at the midslope position and highest at the ridges ($P = 0.003$). Gravimetric soil moisture in the top 0.05 m of the organic layers increased with elevation ($P < 0.001$) and from the lower slope positions to the ridges at 2000 m and 3000 m ($P < 0.001$, Table 3.3). We did not detect a relationship between bi-monthly measured net CH_4 flux rates and soil moisture across elevations and topographic positions, neither in mineral soil nor in the organic layer. In addition, we found no significant correlation between the annual CH_4 uptake and the mean soil moisture content (data not shown).
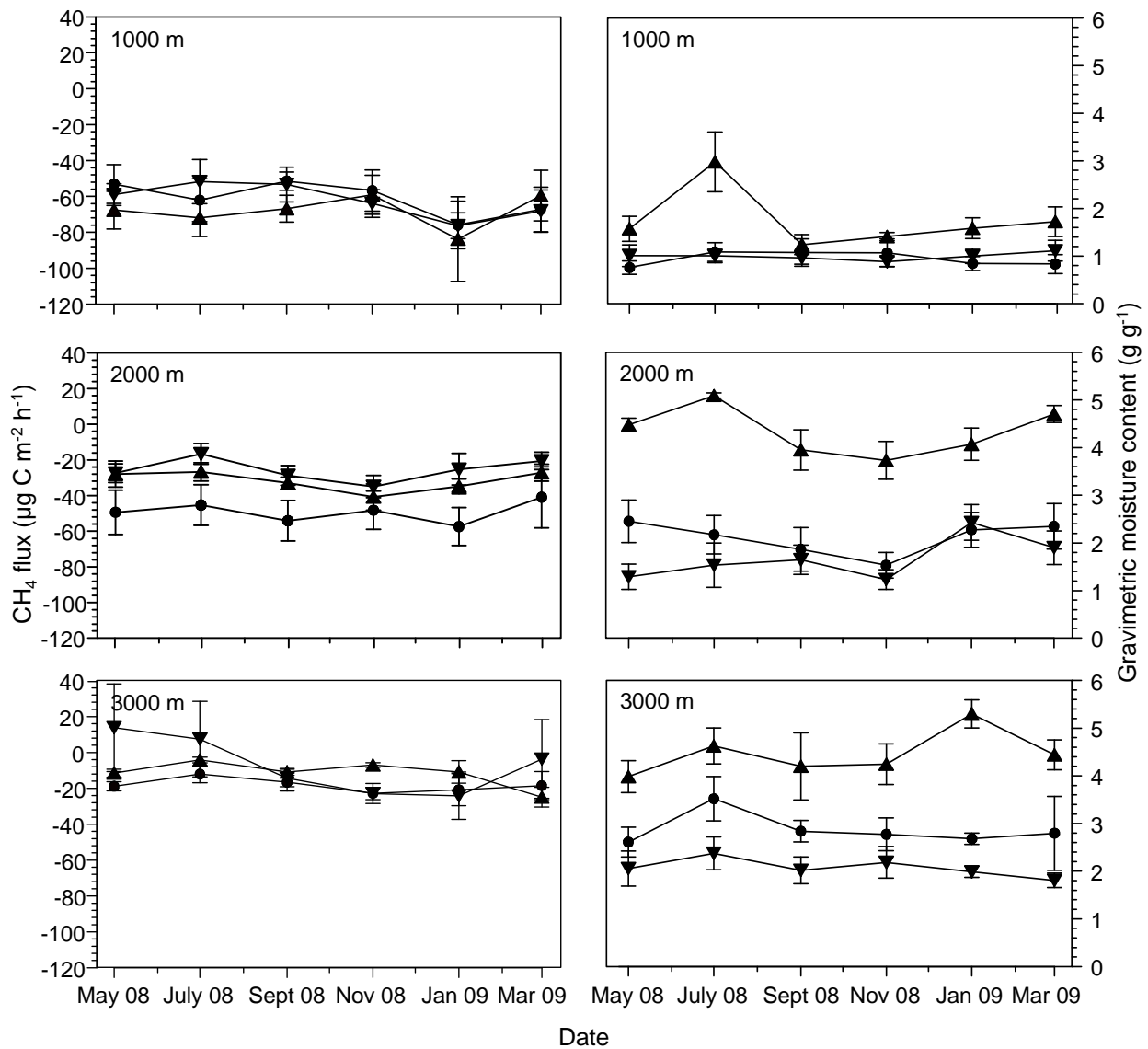
Figure 3.1: Annual course of soil net CH$_4$ exchange rates and gravimetric soil moisture (means ± SE, n = 6) of the three topographic positions (▼ Lower slope, ⬤ Midslope, ▲ Ridge) across the elevation gradient (1000 m, 2000 m, 3000 m). Negative values represent CH$_4$ uptake rates.

Table 3.2: Mean annual soil CH_4 and CO_2 fluxes (means ± SE) and parallel measured parameters of the top soil (0-5 cm) at the topographic positions across the elevation gradient.

	1000 m			2000 m			3000 m		
	Lower slope	Midslope	Ridge	Lower slope	Midslope	Ridge	Lower slope	Midslope	Ridge
CH_4 (kg C ha^{-1} yr^{-1}) [a]	-5.5 (0.7)A	-5.4 (0.9)A	-5.9 (1.0)A	-2.3 (0.3)B	-4.3 (0.9)A	-2.7 (0.3)B	-0.6 (1.2)B	-1.6 (0.4)B	-1.0 (0.1)C
CO_2 (Mg C ha^{-1} yr^{-1}) [a]	10.3 (0.8)A	10.3 (0.1)A	9.8 (0.9)A	8. 8 (0.4)A	7.6 (0.6)B	6.7 (0.7)B	6.4 (0.4)B	5. 7 (0.7)B	3.7 (0.5)C
Soil parameters in 0-5cm									
Gravimetric moisture mineral soil (g g^{-1})	0.1 (0.2)a	0.6 (0.1)a	1.7 (0.03)b	NA	NA	NA	NA	NA	NA
Gravimetric moisture organic layer (g g^{-1})	NA	1.7 (NA)	1.8 (0.3)A	1.8 (0.3)aB	2.1 (0.3)a	4.3 (0.1)bB	2.1 (0.2)a	2.9 (0.3)a	4.5 (0.3)bB
NH_4^+ (kg N ha^{-1}) [a,b]	2.2 (0.4)A	1.8 (0.5)	1.5 (0.5)	0.8 (0.2)B	0.9 (0.3)	0.9 (0.2)	0.6 (0.1)aB	0.7 (0.1)a	0.8 (0.1)b
NO_3^- (kg N ha^{-1}) [a,b]	0.4 (0.1)A	0.4 (0.1)A	0.6 (0.3)A	0.4 (0.1)aA	0.3(0.1)aA	0.04 (0.02)bB	0.0B	0.02 (0.01)B	0.03 (0.01)B

[a] Means (± SE, n = 6) within rows followed by different letter indicate significant differences among topographic positions at each elevation (small letters) and differences among elevations at each topographic position (capital letters) (Linear mixed effects models with Tukey HSD test at $P \leq 0.05$).

[b] Parameters from organic layers or mineral soil

NA: No data available, NA for standard errors if the mean belongs to one repetition

Table 3.3: Soil characteristics and annual flux rates of CH₄ and CO₂ (means ± SE) of soils from two substrates of the topographic positions at 1000 m.

	Lower slope		Midslope		Ridge	
	Schist	Granite	Schist	Granite	Schist	Granite
Sand (%)[ac]	24.2 (2.4)a	60.7 (5.3)b	27.4 (1.4)a	66.3 (3.9)b	16.7 (1.7)a	49.2 (0.9)b
Silt (%)[ac]	47.1 (3.8)a	14.2 (0.04)b	54.0 (1.0)a	17. 7 (1.7)b	48.1 (1.0)a	23.1 (3.5)b
Clay (%)[ac]	28.7 (1.5)	25.1 (5.3)	18.6 (2.2)a	16.1 (4.4)a	35.2 (0.7)a	27.8 (2.6)b
pH (H_2O) [ac]	5.4 (0.2)	4.5 (0.4)	5.9 (0.3)a	4.3 (0.3)b	3.9 (0.1)a	4.5 (0.1)b
C:N [ac]	16.3 (0.6)	16.4 (1.2)	14.5 (1.5)	15.6 (0.2)	19.0 (0.9)a	23.7 (0.8)b
Total P (mg g^{-1}) [ac]	1.1 (0.1)a	0.3 (0.02)b	1.4 (0.2)a	0.3 (0.1)b	0.8 (0.04)a	0.4 (0.1)b
NH_4^+ (kg N ha^{-1})[bd]	2.8 (0.6)	1.5 (0.2)	1.0 (0.4)	2.7 (0.3)	2.7 (0.2)	0.4 (0.1)
NO_3^- (kg N ha^{-1}) [bd]	0.4 (0.2)	0.3 (0.03)	0.2 (0.04)	0.5 (0.2)	1.1 (0.3)a	0.01 (0.01)b
CH₄ (kg C ha^{-1} yr^{-1}) [b]	-5.0 (0.7)	-6.0 (1.4)	-5.1 (1.3)	-5.6 (1.5)	-8.0 (0.5)a	-3.8 (0.8)b
CO₂ (Mg C ha-1 yr-1) b	10.1 (0.3)	10.4 (1.6)	8.7 (0.3)	11.8 (2.7)	11.4 (0.5)	8.3 (1.2)

[a] Means (± SE, n = 3) within rows followed by different letter indicate significant differences among the substrates (small letters) (one-way ANOVA at $P \leq 0.05$).

[b] Means (± SE, n = 3) within rows followed by different letter indicate significant differences among the substrates (small letters) (Linear mixed effects models for time series data at $P \leq 0.05$).

[c] Parameters were taken from the Ah horizon

d Parameters were taken from the top 5 cm of the soil (including mineral soil or organic layer)

Atmospheric CH_4 uptake of the soil increased with increasing soil temperature along the elevation gradient ($P < 0.001$, $R^2 = 0.89$), NO_3^- content ($P < 0.001$, $R^2 = 0.72$) and NH_4^+ content ($P < 0.002$, $R^2 = 0.72$) of the top 0.05 m (mineral soil or organic layer) and with increasing $P_{(tot)}$ ($P < 0.001$, $R^2 = 0.66$) and pH value of the upper mineral soil ($P = 0.02$, $R^2 = 0.51$). Smaller scale soil temperature changes within the elevation levels, organic layer thickness, P_{tot}, C:N ratios and the pH value of the organic layer did not affect atmospheric CH_4 uptake. Annual CO_2 emissions and annual CH_4 uptake by soils with and without organic layers were correlated positively across all elevations ($P < 0.01$, $R^2 = 0.66$, Figure 3.2 a). When considering only gas fluxes from the soils covered by an organic layer, this correlation was even stronger ($P = 0.02$, $R^2 = 0.74$), while the correlation in mineral soils without organic layer was not significant ($P = 0.13$, $R^2 = 0.13$).
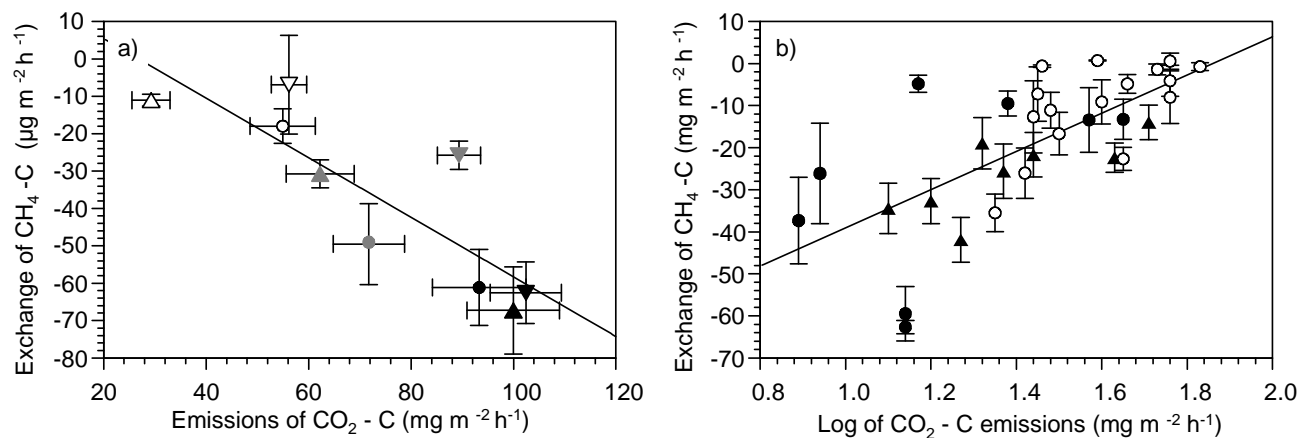
Figure 3.2: Relation between soil CO_2 emission rates and soil CH_4 uptake rates (means ± SE) for a) flux rates measured in the field at different topographic positions (▼ Lower slope, ● Midslope, ▲ Ridge) across the elevation gradient (black: 1000 m; full grey: 2000 m; open: 3000 m) (y = -21.38 + 0.80 * x, n = 9 *P* = 0.005, $R^2 = 0.66$), and for b) undisturbed, field-moist soil samples at different depths of the organic material (open symbols) and the mineral soil (black symbols), incubated at 25°C in the laboratory (y = -84.49 + 45.42 * x, n = 32, *P* < 0.001, $R^2 = 0.45$). Symbols used: black circles, mineral soil with overlying organic layer, black triangles, mineral soil without overlying organic layer; open circles, organic layer samples.

3.4.2 Potential uptake of atmospheric CH_4 at different soil depths

All incubated, undisturbed samples from the mineral soil profiles (profiles of the 1000 m site, which had no organic layer) were net sinks for atmospheric methane (Figure 3.3). Methane uptake rates ranged from 3.5 to 60.5 μg CH_4-C m^{-2} h^{-1} with the highest uptake rate of atmospheric CH_4 at a soil depth of 5–10 cm (P = 0.05). The incubated mineral soil profiles from the coarse textured granite substrate displayed a higher potential uptake of atmospheric CH_4 than the profiles from the fine textured schist substrate (P < 0.001) (Figure 3.3).
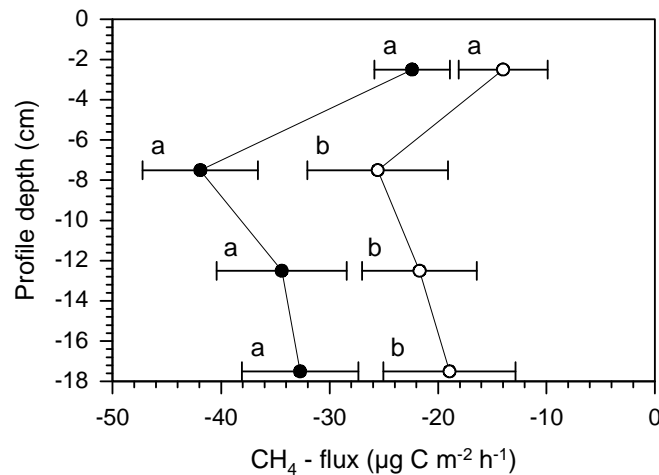
Figure 3.3: Mean CH_4 uptake rates of undisturbed field moist-soil samples at different depths of the mineral soil profiles, which had no organic layer in schist (open symbols) and granite (black symbols) material at 1000 m, incubated at 25°C in the laboratory. Means (± SE, n = 6) within one depth followed by different letter indicate significant differences among the substrates (Kruskal-Wallis-Test at $P \leq 0.05$).

Incubated organic layer samples generally acted as sinks for atmospheric CH_4, except for the samples from the top 5 cm, which contained mainly roots and fresh plant residues and emitted CH_4 in 65% of the cases (Figure 3.4). The incubated organic material from the 1000 m site showed a potential CH_4 uptake ranging from -0.2 to -29.7 μg CH_4-C m^{-2} h^{-1}. The potential CH_4 uptake in the organic material from 2000 m ranged from +3.1 (emission!) to -55.8 μg CH_4-C m^{-2} h^{-1} and from +12.9 to -54.5 μg CH_4-C m^{-2} h^{-1} in the organic material from 3000 m. Potential CH_4 uptake of atmospheric CH_4 in the mineral soil underlying the organic layers was higher at 1000 m than at 2000 m or 3000 m (P < 0.01), with uptake rates ranging from 7.5 to 70.0 μg CH_4-

C m^{-2} h^{-1} at 1000 m, from 0.8 to 24.4 µg CH$_4$-C m^{-2} h^{-1} at 2000 m and from -3.4 to 33.4 µg CH$_4$-C m^{-2} h^{-1} at 3000 m.
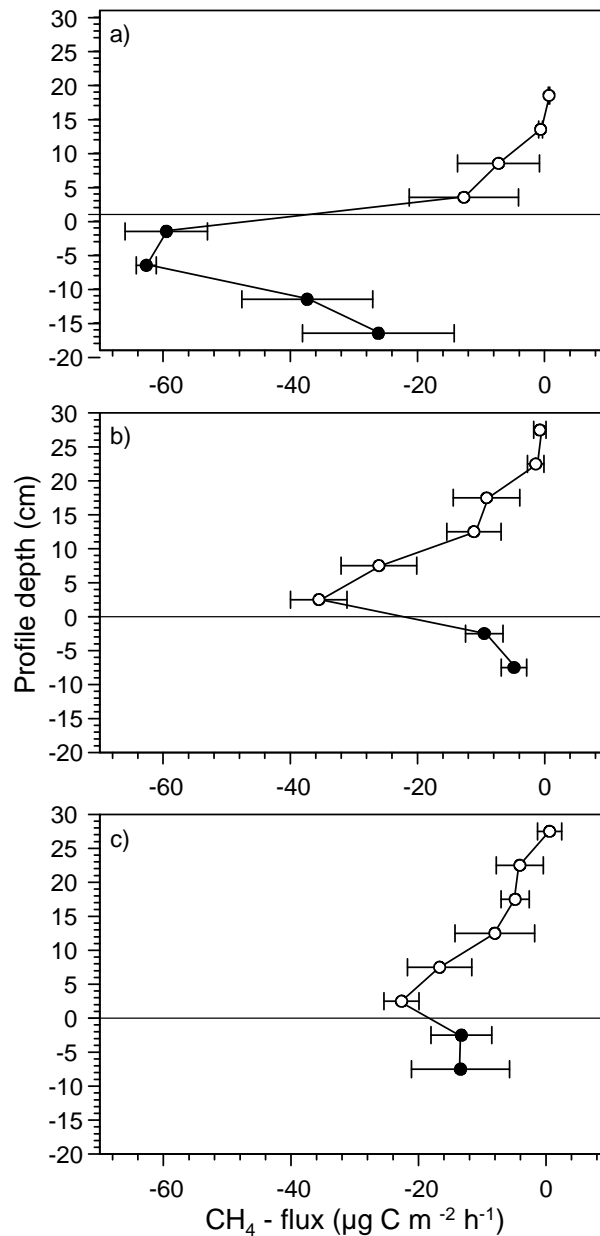
Figure 3.4: Mean CH$_4$ fluxes (± SE) of undisturbed, field-moist soil samples from different depths of the organic layer (open symbols) and the mineral soil (black symbols) incubated at 25°C in the laboratory. The samples were taken from a) the 1000 m site (n = 3), b) the 2000 m site (n = 7) and c) the 3000 m site (n = 5).

We found a clear stratification of the potential atmospheric CH_4 uptake rates within the sampled organic layer profiles. The CH_4 uptake rates in the organic layer profiles from all elevations increased with increasing profile depth (P < 0.00, Figure 3.4). At the 1000 m site, potential CH_4 uptake of the underlying mineral soil was higher than the organic material (P ≤ 0.05, Figure 3.4 a). At the 2000 m and the 3000 m sites potential atmospheric CH_4 uptake was largest at the deepest organic layer overlying the mineral soil (Figure 3.4 b, c). Organic layer thickness did not affect the potential atmospheric CH_4 uptake of the underlying mineral soil.

Carbon dioxide emissions from the incubated mineral soil and organic layer profiles were largest in the top soil samples, ranging from 31.1 to 68.2 mg CO_2-C m^{-2} h^{-1} in the mineral soil and from 28.9 to 140.9 mg CO_2-C m^{-2} h^{-1} in the organic layer. Soil respiration decreased with soil depth of all profiles (data not shown). Temperature manipulation affected soil respiration from samples of the organic layer from all elevations (P < 0.001), whereas it did not affect soil respiration of the mineral soil samples (P = 0.2). A temperature increase from 15 to 25°C resulted in a doubling of the CO_2 emissions rates from samples of the organic layer as shown by the doubling of the slope of the regression function (Figure 3.5 a). Temperature manipulation did neither affect CH_4 uptake rates of samples from the organic layer profiles during the incubation Figure 3.5 b), nor did it affect the CH_4 uptake rates of the mineral soil profiles (data not shown).
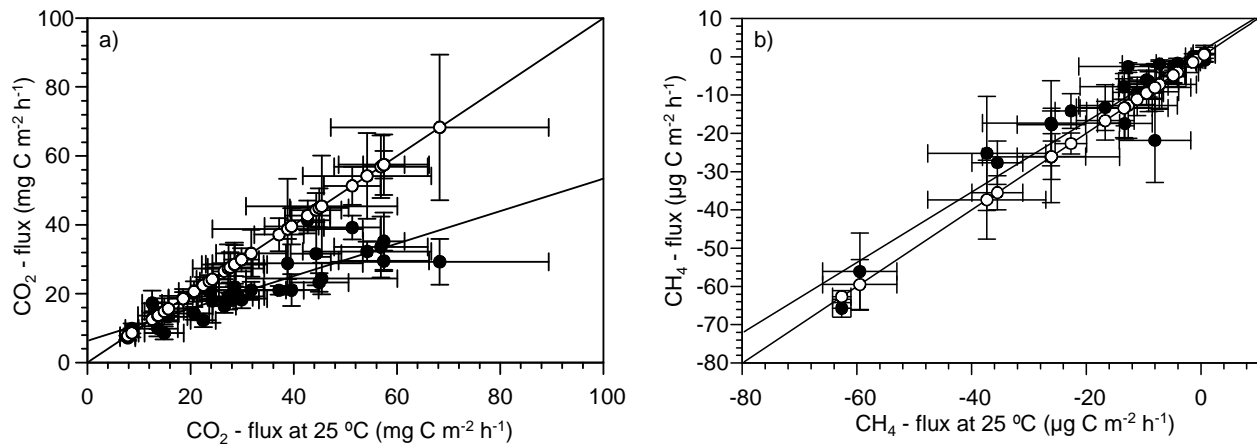
Figure 3.5: Relation between mean (± SE) trace gas fluxes of undisturbed, field-moist samples of the mean organic layer profile from each elevation incubated at 25°C (open symbols) and 15°C (black symbols) for a) CO_2 fluxes (y = 7.0 + 0.4 * x, n = 16, _P_ = 0.006, _R^2_ = 0.74) and b) CH_4 fluxes (y = - 0.6 + 0.7 * x, n = 16, _P_ = 0.01, _R^2_ = 0.67).

Throughout the elevations, potential CH_4 uptake of the incubated mineral soil profiles and organic layer profiles increased with decreasing basal respiration ($P < 0.001$, $R^2 = 0.45$, Figure 3.2 b). Throughout the elevation gradient, potential atmospheric CH_4 uptake of the incubated organic material did not correlate with total carbon content, cation concentration, gravimetric moisture content, or pH-values. However, potential CH_4 uptake of organic material from the 1000 m site correlated positively with P_{tot} content of the organic material ($P = 0.03$, $R^2 = 0.90$). In contrast, potential CH_4 uptake of organic material of the 2000 m site increased with decreasing total carbon content ($P = 0.04$; $R^2 = 0.62$), calcium (Ca^{2+}, $P = 0.01$; $R^2 = 0.78$) and magnesium (Mg^{2+}, $P = 0.01$; $R^2 = 0.78$) concentrations and pH-values ($P < 0.01$; $R^2 = 0.91$) of the organic material.

3.4.3 CH_4 concentrations in the soil air of organic layers

Methane concentration in the soil air decreased with soil depth ($P < 0.0001$ for both elevations), both during wet and dry periods, with lowest CH_4 concentrations above the mineral soil (Figure 3.6). Methane concentrations were higher during the dry period measurements compared to the wet period measurements ($P < 0.0001$ for both elevations) (Figure 3.6). Elevation did not affect CH_4 concentration in the soil air of the organic layers neither during the

wet nor during the dry period. CH_4 concentration in soil air was always lower than the atmospheric concentration and there was no evidence of in situ net production of CH_4 within the soil profile.
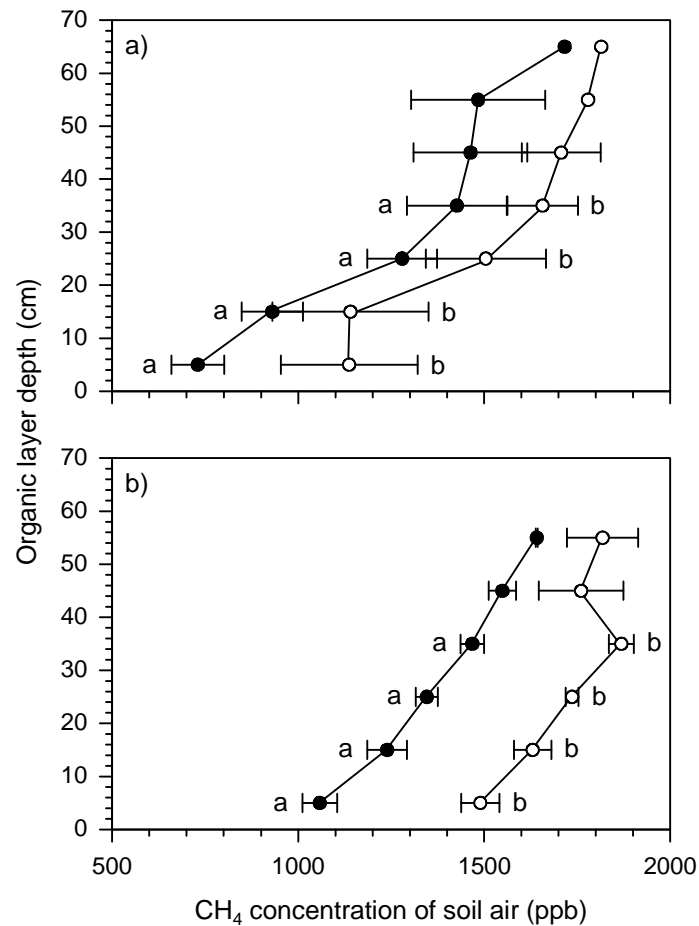
Figure 3.6: Mean soil air CH_4 concentrations (± SE) at different depths of the organic layer during a wet period (black symbols) and a dry period (open symbols), from the a) 2000 m site and b) the 3000 m site

3.5 Discussion

3.5.1   Net exchange of CH_4 under field conditions

Annual CH_4 uptake rates under field conditions at the 2000 m and 3000 m sites were comparable to those reported for tropical montane forest soils at comparable elevation in Indonesia (1.5 and 3.3 kg CH_4-C ha^{-1} yr^{-1}) (Ishizuka et al. 2005; Purbopuspito et al. 2006). Annual CH_4 fluxes at the 1000 m site were larger than previously reported for other premontane forests in Africa (Delmas et al. 1992), Australia (Kiese et al. 2008), Indonesia (Purbopuspito et al. 2006) and China (Werner et al. 2006) and were also larger than those reported from lowland forests in Costa Rica (Keller & Reiners 1994; Reiners et al. 1998) and Brazil (Keller et al. 2005). Instead the 5.4 to 5.9 kg CH_4-C ha^{-1} yr^{-1} CH_4 uptake rates at our 1000 m site were comparable to CH_4 fluxes from temperate beech forests (Butterbach-Bahl & Papen 2002b) and temperate spruce forest ecosystems (Steinkamp et al. 2001).

Both the increased incidence of net CH_4 emission rates with increasing elevation and a general decrease in CH_4 uptake rates resulted in decreased annual net CH_4 uptake with elevation. This trend was mirrored by the maximum CH_4 uptake rates measured for the incubated soil samples and by the less pronounced decline of soil air CH_4 concentrations in the organic layers at the drier 3000 m site. The lack of influence of topography on CH_4 uptake that we detected supports results from forest sites in Costa Rica where no differences in CH_4 uptake between topographic positions was detected (Reiners et al. 1998). Furthermore we found no evidence that seasonal water-logging turned net methane-oxidizing tropical forest soils into net CH_4 sources as reported for seasonal lowland rain forests in Brazil (Davidson et al. 2004; Verchot et al. 2000). Seasonal variation in soil water condition in our study area was rather limited because of the largely non-seasonal climate.

3.5.2 CH_4 fluxes and their controls

In contrast to the general idea that soil moisture content is an important driver for CH_4 fluxes (Butterbach-Bahl 2004; Curry 2007; Davidson et al. 2004; Keller & Reiners 1994), neither temporal nor spatial variability of net CH_4 exchange could be explained by it. We believe that there are several reasons in our study for this lack of correlation between soil moisture content

and net exchange of atmospheric CH_4. First, the absence of a pronounced dry season and the resulting minimal variations in soil moisture content hamper the quantification of seasonal soil moisture effects. A similar justification was used to explain the lack of correlation between CH_4 flux and soil moisture in Indonesia (Purbopuspito et al. 2006; Veldkamp et al. 2008). Second, we measured soil moisture content in the top 5 cm of the soil only, whereas the main CH_4 uptake activity was located in different depths of the organic layer and mineral soil. Finally, it is unlikely that moisture contents in the highly porous, coarse material of the upper organic layer are high enough to restrict CH_4 diffusion into the soil. Evidence for this is provided by the relatively slow decline of in situ soil air CH_4 concentrations, especially at the 3000 m site. Our incubation of mineral soil from different geological substrates corroborates findings that coarser soil texture leads to larger potential atmospheric CH_4 uptake as a result of higher gas diffusivity (Dörr et al. 1993; Saari et al. 1997). However, this texture effect did not explain the spatial variability of atmospheric CH_4 uptake observed in our field measurements. We found no evidence that landscape differentiation using the geological substrate or soil texture would improve estimates of soil CH_4 uptake in this region. This finding contrasts with studies in temperate forest ecosystems where soil texture was identified as a main control of soil uptake of atmospheric CH_4 (Saari et al. 1997).

We found no indication that ammonium inhibition of methanotrophic bacteria was a control mechanism for CH_4 uptake (Brumme et al. 2005; Guckland et al. 2009). On the contrary, we detected positive correlations between soil mineral N content and annual CH_4 uptake which suggests that methanotrophic activity may have been N limited. This finding supports the findings of other studies carried out in several ecosystems that show a lower oxidation activity due to nitrogen limitation (Brodelier et al. 2004). Furthermore, positive correlations with P_{tot} content, pH-value of the Ah horizon and field CO_2 emissions suggest that higher CH_4 uptake occurred at those locations where conditions were generally more favorable for microbial activity.

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3.5.4 Stratification of potential uptake of atmospheric CH_4 in mineral soil and organic layers

The detected stratification of atmospheric CH_4 uptake in the incubated mineral soil profiles, with highest potential CH_4 uptake at a soil depth of 5-10 cm confirms findings of studies from temperate and subarctic forest soils (Schnell & King 1994). The subsurface location of maximum CH_4 oxidation is probably due to edaphic factors in the surface layer, that are suboptimal or

inhibitory for the growth of CH_4 oxidizing bacteria, e.g. high NH_4^+ concentrations and the occurrence of anaerobic microsites. The negative relationship between CO_2 production and atmospheric CH_4 consumption of our incubated soil samples, may be the result of CH_4 inhibition by NH_4^+ released due to rapid N-mineralization of organic matter. We can, however, not exclude that this is an artifact of our incubation, as under field conditions an accumulation of NH_4^+ would normally not happen due to plant uptake (see also Arnold, 2008). In addition to inhibition by accumulated NH_4^+, stratification of potential CH_4 uptake may also be due to the sensitivity of microorganisms to temperature and soil moisture changes, which are more pronounced in the upper organic layer than in the deeper organic layer or in the Ah horizon (Butterbach-Bahl & Papen 2002). Finally, we also found some evidence that anaerobic microsites were created, due to high microbial activity in the uppermost organic layers leading to low methanotrophic activity.

The results of the laboratory incubations of the organic layer samples at the 1000 m site appear to endorse the widely accepted idea that organic layers consume little, if any, atmospheric CH_4 and that most of the CH_4 uptake capacity is located in the upper mineral soil (Conrad 1996). However, the results from our incubations of the 2000 m and 3000 m organic layers revealed substantial capacity to oxidize atmospheric CH_4, with highest methanotrophic activity located in the lowest organic layers right above the mineral soil, which contained mainly strongly decomposed and humified organic matter. As the CH_4 concentrations measured in the soil air were below atmospheric, we conclude that this methanotrophic activity was of the high affinity type.

3.5.5   Conclusions

Although we found as expected a decrease in CH_4 uptake rates with increasing elevation, the widely accepted control mechanisms gas diffusivity, NH_4^+ inhibition and the creation of anaerobic microsites could not or only partly explain variations in atmospheric CH_4 uptake of these tropical montane forest soils. In contrast we found some unexpected factors controlling net methane fluxes. Net methane uptake occurred mainly under conditions that are generally favorable for microbial activity, and we found indications that it was N limited instead of inhibited by NH_4^+. Finally, we showed that in the thick organic layers substantial high affinity methane oxidation occurred which can influence the CH_4 budget of tropical montane forest soils.

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CHAPTER

4

SOIL NUTRIENT AVAILABILITY AND BELOWGROUND CARBON ALLOCATION OF TROPICAL MONTANE FORESTS IN SOUTHERN ECUADOR

4.1 Abstract

Although total belowground carbon allocation (TBCA) accounts for a considerable fraction of carbon assimilated by forest ecosystems, large uncertainties remain about how environmental conditions control the rate of TBCA and the ratio between TBCA and aboveground carbon allocation. The carbon cycle of tropical montane forests has marginally been explored even though montane forests cover about 9% of the tropical forest area and provide a great opportunity to study TBCA along nutrient, soil moisture and temperature gradients. Here we investigate the influence of nutrient availability and elevation on TBCA in tropical montane forests in southern Ecuador. We estimated TBCA from year-round soil respiration and aboveground litterfall measurements along an elevation gradient from 1000 m to 3000 m and from lower slope to ridge positions. Aboveground litter production appeared to be limited by nitrogen (N), potassium (K), and phosphorus (P) and was related mainly to available nutrient stocks of the organic layer, although stocks of K and P were larger in the mineral soil. We could not confirm our hypothesis that total and relative TBCA increase when nutrient supply declines. TBCA decreased with elevation and from lower slope toward the ridges and was controlled more by soil moisture and temperatures than available nutrients. The decline in TBCA with increasing elevation corresponded with an increment in fine root biomass which we explain with higher root longevity. Together with slow decomposition rates in the organic layers, this may contribute to the large carbon storage in organic layers of tropical montane forest soils.

4.2 Introduction

Total belowground carbon allocation (TBCA) for the production and maintenance of roots and mycorrhiza can make up more than 30% of the gross primary productivity (Gower et al., 1996; Giardina and Ryan, 2002) and may equal or exceed aboveground C allocation to leaves and aboveground respiration in forest ecosystems (Davidson et al., 2002; Giardina and Ryan, 2002). Long term C sink strength of a forest is determined by net changes in the storage of decay resistant C (Schlesinger and Lichter, 2001), but controls on belowground carbon allocation remain poorly quantified (Davidson et al., 2002; Giardina and Ryan, 2002; Litton et al., 2007). Despite its importance for the forest carbon cycle, large uncertainties remain, of how

environmental conditions influence the amount of TBCA and the ratio between TBCA and aboveground C allocation (Raich, 1998). According to allocation theory, plants countervail growth limitations by investing more C into the components where limitation occurs. If nutrients become a more limiting factor to plant growth than light and CO_2, relatively more C will be invested belowground, into roots (Raich, 1998). A corresponding increase in the ratio of TBCA: aboveground primary productivity (APP) may either be the result of lower aboveground C allocation at constant TBCA (Giardina et al., 2003), of higher root activity at constant APP (Keith et al., 1997a; Litton et al., 2007), or of a combination of both mechanisms (McConnaughay & Coleman, 1999). Fertilization experiments showed that increased nutrient supply leads to a decline of TBCA (Keith et al., 1997a; Keith et al., 1997b), or left it unchanged (Giardina et al., 2003). On the other hand, there is evidence, that higher nutrient supply may increase TBCA along with GPP (Raich, 1998; Litton et al., 2007; Aragao et al., 2009).

Aboveground primary productivity of tropical montane forests decreases with elevation, which has been related to decreasing temperatures, increasing soil moisture and lower availability of macronutrients such as nitrogen (N), phosphorous (P), and potassium (K) (Bruijnzeel & Veneklaas, 1998; Tanner et al., 1998). The low nutrient availability is often linked to the occurrence of thick organic layers, and slow mineralization rates of organic matter at higher elevations and on ridge positions (Wilcke et al., 2002; Hertel et al., 2003; Purbopuspito et al., 2006; Arnold et al., 2009). Furthermore N and P availability have been found to be depending on soil age, where N limitation occurs on younger soils as they occur on mountain slopes, whereas P limitation is more pronounced on deeply weathered soils of the lowlands (Walker & Syers, 1976). Parallel to the decline in APP with elevation, large increases in root biomass have been reported for tropical montane forests (Röderstein et al., 2005; Leuschner et al., 2007; Girardin et al., 2010; Hertel & Leuschner, 2010). It is however still unclear whether those increases in root biomass are caused by higher fine root productivity and higher TBCA (Röderstein et al., 2005; Leuschner et al., 2007) or by an increase in residence time of the root material with elevation as shown from a study in the Peruvian Andes (Girardin et al., 2010).

Here we investigate how environmental conditions, especially nutrient availability affected TBCA in tropical montane forests of southern Ecuador. We used the indirect C-mass balance approach proposed by Raich & Nadelhoffer (1989) to estimate TBCA and measured soil

respiration and aboveground litterfall over one year. We determined TBCA together with availability of N, P and K on 54 plots along an elevation gradient (1000 m to 3000 m elevation) and topographic gradients covering the three main landscape positions lower slope, midslope and ridge. We tested the hypothesis that absolute and relative belowground carbon allocation (TBCA: aboveground productivity) increases with decreasing nutrient availability along the elevation and topographic gradients.

4.3 Methods

4.3.1 Study area and experimental design

The study area is located in the Cordillera del Consuelo, which forms part of the eastern chain of the Andes in southern Ecuador. Three study sites were selected along an elevation gradient from 1000 m to 3000 m (Table 4.1): 990-1200 m a.s.l. (hereafter called the '1000 m site'), 1800-2100 m a.s.l. (hereafter called the '2000 m site') and 2800-3000 m a.s.l. (hereafter called the '3000 m site'). At each elevation, we installed 18 plots along a topographic gradient covering the three main landscape positions lower slope, midslope and ridge. Natural vegetation at the 1000 m site was a premontane rain forest, with Moraceae, Rubiaceae and Melastomataceae being the most important tree families. The 2000 m site was covered with lower montane rain forest with Lauraceae, Euphorbiaceae, Melastomataceae and Rubiaceae as most important tree families. At 3000 m natural vegetation was an upper montane rain forest with Cunoniaceae, Clusiaceae and Melastomataceae as most important tree families (Homeier et al., 2008). Along the major environmental gradients (elevation and topography) not only tree species composition, but also forest structure changed. Decreasing stand height and mean diameter at breast height (dbh) and increases in stem density with elevation are typically found with elevation and from the lower slope positions to the ridge positions (Homeier et al., 2010) and (Table 4.1).

Table 4.1: Site characteristics, forest structure and forest productivity of the topographic positions across the elevation gradient.

	1000 m			2000 m			3000 m		
	Lower slope	Midslope	Ridge	Lower slope	Midslope	Ridge	Lower slope	Midslope	Ridge
Coordinates	04° 06' S, 78° 58' W			03° 58' S, 79° 04' W			04° 06' S, 79° 11' W		
Elevation a.s.l. (m)	990-1200			1800-2100			2800-3000		
Air temperature (°C) [a]	19.4			15.7			9.4		
Precipitation (mm yr^{-1}) [a]	2230			1950			4500		
Organic layer thickness (cm) [b]	2.5 (0.7)	2.6 (1.0) A	6.5 (1.9) A	4.0 (0.9) a	12.2 (3.1) aB	24.0 (2.9) bB	6.6 (0.7) a	14.2 (1.6) abB	22.2 (3.4) bB
Mean dbh (≥10 cm) [b]	22.6 (1.4)	22.6 (1.9) A	18.7 (1.4) A	23.8 (2.6) a	19.0 (0.6) bAB	16.8 (0.6) bAB	24.0 (1.8) a	15.9 (0.3) bB	14.7 (0.7) bB
Stem density (400 m^2) [b]	32.8 (3.5)	36.0 (3.0)	22.6 (7.4) A	30.4 (3.6) a	45.4 (2.8) b	45.4 (3.6) bAB	34.4 (6.8)	49.3 (7.3)	56.7 (4.8) B
Tree basal area (m² ha^{-1}) [b]	44.8 (5.0)	57.2 (15.0)	20.3 (7.2)	48.9 (8.6)	40.4 (4.3)	29.2 (3.0)	44.8 (4.6)	28.1 (4.2)	28.6 (4.2)
Total litter production (Mg ha^{-1}yr^{-1}) [b]	7.0 (0.3) aA	8.6 (0.5) bA	6.4 (0.5) aA	9.5 (0.5) aB	9.8 (0.6) aB	7.1 (0.3) bA	4.7 (0.2) C	4.8 (0.5) C	4.5 (0.2) B
Basal area increment (m² ha^{-1}yr^{-1}) [b]	0.6 (0.1)AB	0.8 (0.2)A	0.7 (0.2)A	0.9 (0.2)aB	0.8 (0.1)aA	0.4 (0.1)bAB	0.4 (0.03)A	0.3 (0.1)B	0.3 (0.1)B

[a] Moser et al. (2007)

[b] Means (± SE, n = 6) within rows followed by different letter indicate significant differences among topographic positions at each elevation (small letters) and differences among elevations at each topographic position (capital letters) (two-way ANOVA with Fischer LSD test at $P \leq 0.05$).

For most of the study area, Paleozoic metamorphic schist and sandstone with some quartz veins form the parent material for soil development. Only at the 1000 m site soil parent material of half of the plots consists of deeply weathered granitic rock of the Jurassic Zamora granitoide formation (Litherland et al., 1994). Organic layer thickness increased with elevation and from lower slope positions to ridge positions (Table 4.1). At the ridge positions of the 2000 m and 3000 m sites and to some extend at the ridges of the 1000 m site, soils displayed Humic and Histic characteristics (thick organic layers). Soils at well-drained positions of the 1000 m and 2000 m sites were Eutric or Dystric Cambisols. Soils with hydromorphic properties (Stagnic Cambisols or Planosols) were found on the ridges of the 2000 m site and at all topographic positions of the 3000 m site (Chapter 2.4.1).

4.3.2   Experimental Design

At each elevation we established 18 plots, six at each landscape position (lower slope, midslope and ridge positions). All plots were situated in mature, closed-canopy forest that was representative of the respective topographic position. At each plot we installed four chamber bases for gas exchange measurements and six litter traps in a stratified random design along two orthogonal transects.

4.3.3   Total and available soil nutrients

We determined total and available phosphorus (P_{tot} and P_{av}) and total potassium (K_{tot}) on composite soil samples consisting of four subsamples per plot taken with an auger within one-meter distance of the chamber bases. Depending on the depth of the organic layer, we took one or two depths from the organic layer (0-10 cm and if present also 10-20 cm depth) and two depths of the mineral soil (0-10 cm and 10-20 cm depth). Available potassium (K_{av}) of the mineral soil and total soil nitrogen (N) were assessed from soil samples taken by horizon from soil profiles situated at the outer border of the plots. All soil samples were dried at 45 °C for three days, sieved and stored in plastic bags until analysis in Germany. Analysis of soil P_{tot} and K_{tot} concentrations was done using Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP-AES, Spectro Analytical Instruments, Kleve, Germany) after pressure digestion in 65% HNO_3 (Heinrichs et al., 1986). We determined P_{av} using the modified Hedley fractionation

method (Tiessen & Moir, 1993), extracting 0.5 g of soil succeeding with an anion exchange resin and 0.5 M sodium bicarbonate ($NaHCO_3$). Instead of the membrane shaped anion exchange resin used by Thiessen and Moir (1993) we used one gram (moist weight) of pellet-shaped anion exchange resin (DOVEX® 1x8 20-50 mesh, SERVA Electrophoresis GmbH, Heidelberg, Germany), which was sewed into a polyester gauze bag (Wullfen, 1989). Phosphorus concentration in the fractions was measured using ICP-AES. Based on Cross and Schlesinger (1995) we defined plant-available P as the sum of P in the resin and $NaHCO_3$ fractions. We obtained K_{av} from the determination of the exchangeable cations from sieved soil samples by measuring K concentration in percolates of soils with unbuffered 1 M NH_4Cl using ICP-AES (König & Fortmann, 1996). Total carbon (C_{tot}) and total nitrogen (N_{tot}) were determined using a CNS Elemental Analyzer (Elementar Vario EL, Hanau, Germany). Nutrient stocks were calculated under consideration of bulk density, which was determined for mineral soil using steel cores (250 cm^3) and for the organic layer by measuring the thickness and dry weight of an area of 400 cm^2 (Blake & Hartge, 1986; Schlichting & Stahr., 1995).

4.3.4   Soil respiration

We measured soil respiration bi-monthly over a period of one year (May 2008 – May 2009) using static closed chambers with a base area of 0.044 m^2 and a closed chamber volume of 13 liters. Chamber bases were installed six months prior to the first measurement, by inserting them approximately 0.02 m into the soil, and remained in place until the end of the sampling period. Chamber lids were equipped with a Luer-Lock sampling port and a vent for pressure equilibration. Gas samples were taken 2, 14, 26, and 38 minutes following chamber closure using pre-evacuated glass containers (60 ml). Pressure was checked with a manometer during sampling to assure that containers had been evacuated properly and were filled to atmospheric pressure. Soil temperature and gravimetric soil moisture were determined concomitantly to every soil respiration measurement. Gas samples were analyzed within 48 hours following sampling using a gas chromatograph (Shimadzu GC-14B, Duisburg, Germany) equipped with an electron capture detector (ECD) combined with an autosampler (Loftfield et al., 1997). Gas concentrations were calculated by comparing integrated peak areas of samples with four standard gases (350, 700, 1500, 5000 $\mu L\ L^{-1}$ standard concentrations of CO_2; Deuste Steiniger GmbH, Mühlhausen, Germany). CO_2 emissions were calculated by fitting both linear and quadratic

regression models if CO_2 concentrations increased asymptotically (Wagner et al., 1997). Based on the Akaike Information Criterion the quadratic model was found to be statistically more adequate and therefore applied in about 50% of the cases. By applying this data screening and model fitting, we minimized underestimations of CO_2 emissions that may have occurred by using linear models uncritically with static chamber flux data (e.g. Livingston et al., 2006). Volumetric gas fluxes were converted to mass fluxes by multiplying net gas fluxes by the density of air and the ratio of chamber volume to soil surface area (Köhler et al., 2009b). Annual fluxes were calculated from the average of the bi-monthly measurements.

4.3.5   Aboveground productivity and litter quality

Aboveground productivity was estimated by summing up fine litter production (litter < 2 cm) and aboveground wood increment both expressed in kg C h^{-1} yr^{-1}. Total litter was collected monthly (bi-weekly at 1000 m) from six litter traps (60 x 60 cm) per plot. Total litter, including leaves, twigs, epiphytes, flowers and fruits, was dried at 60˚C and weighed. Aboveground litterfall C input was calculated by multiplying C concentrations of the litter and total annual litter fall for each plot. Wood increment was determined by measurement of tree basal area increment of all trees with a diameter >10cm over one year and by measuring wood density using an Pilodyn 6J wood tester (PROCEQ SA, Zürich, Switzerland) as suggested by Chave et al. (2008). Aboveground biomass was estimated according to models provided by Chave et al. (2005) applying the moist forest category model for the 1000 m and 2000 m sites and the wet forest category model at the 3000 m site. C content of the wood was estimated to be 50% (Link, 2010). Total litterfall of December 2008 was collected, ground and sent to Germany for analysis. Litter samples of the six litter traps were proportionally pooled for each plot. Carbon and N concentrations were determined using a CNS Elemental Analyzer (Elementar Vario EL, Hanau, Germany). Total P and K concentrations in litter were measured using ICP-AES after pressure digestion as described for soil samples. Additionally we used soil C:N, C:P and C:K ratios as an index for nutrient availability.

4.3.6   Total belowground carbon allocation

Total belowground carbon allocation (TBCA) is all carbon transferred belowground for belowground productivity (root building, root exudates, root and mycorrhiza mortality) and root respiration. We estimated TBCA using the C-mass balance approach proposed by Raich and Nadelhoffer (1989).

$$\text{TBCA} = \text{R soil} - \text{aboveground litterfall C,} \qquad (1)$$

Where R soil is soil respiration (CO_2 emissions from the soil), which consists of heterogenic respiration (decomposition by microbes) and root respiration. Aboveground litterfall C is the carbon input via litterfall (Raich and Nadelhoffer, 1989; Davidson et al., 2002). This approach may only be used under the assumption that soils are in steady state with respect to total organic carbon storage, because only then annual inputs of detritus from above and belowground are approximately equal to annual respiration of decomposers within the soil. Other fluxes into or out of the soil (dry and wet precipitation, leaching, runoff, erosion) are minor in comparison to the major fluxes and thus have little influence on the carbon budget (Raich and Nadelhoffer, 1989). Davidson et al. (2002) suppose that soil C stocks in forest stands that have not undergone major disturbance during the last several decades are likely approaching a steady state. As our plots are situated under mature forest without natural gaps or signs of anthropogenic disturbance, we assume that the forest sites of our study are in a steady state.

4.3.7   Statistical analysis

For testing elevation and topography effects on annual C fluxes and data that were measured once (i.e. soil characteristics) we used two-way analysis of variance (two-way ANOVA). Data were tested for normality and heteroscedasticity and transformed if necessary. For multiple comparisons after ANOVA we applied the Tukey HSD test. The relationships among soil characteristics and annual C fluxes were assessed by linear and non-linear regression (2-parameter exponential asymptotic regression, yield function after Mitscherlich: $y = a * (1 - \exp(-b * x))$). Regressions were carried out on the means of six plots for each topographic position at the 2000 m and the 3000 m site and separate for the two different geological substrates at the 1000 m site (n = 12; 3 topographic positions of 2 elevations and 3 topographic

positions of two substrates at one elevation). Linear and non-linear regression were used because linear mixes effects models (LME) and non-linear mixed effects models (NLME) did not improve the fit of the models on the 12-point database. The effects of geological substrate on nutrient concentrations and annual C fluxes were assessed using one–way ANOVA. Linear mixed effects models were applied to test the effect of soil depth on the amount of total and available nutrients, including topographic positions nested into the elevations as spatial random factor. We used LME to account for the hierarchical study design by including different error variances of the different spatial scales (Crawley 2009). Linear mixed effects models were tested for autocorrelation effects by including a first order autoregressive structure and for heteroscedasticity of residual variance by including variance functions (Bliese & Ployhart, 2002). Model residuals were tested for normal distribution, and data were transformed if necessary.

4.4 Results

4.4.1   Soil total and available nutrients

Soil depths had a strong influence on total and available nutrient stocks at all elevations and topographic positions ($P < 0.001$). Generally total and available nutrient stocks were lower in the organic layer compared to the mineral soil ($P < 0.001$; Table 4.2). We found no differences of nutrient concentrations between the two depths of the organic layer (where present), therefore we used data from the upper organic layer (0–10 cm) for further investigation. Stocks of P_{av}, P_{tot} and K_{tot} within the organic layer were not different between the geological substrates of the 1000 m site. At both mineral soil depths (0-10 cm and 10-20 cm) P_{tot} and K_{tot} stocks of the schist material were higher ($P \leq 0.01$) than of the granite material (Table 4.4). Soil P_{av} and K_{av} stocks of the schist material were only higher in the deeper mineral soil ($P = 0.03$ for P_{av} and $P = 0.05$ for K_{av}) (Table 4.4). Total P, P_{av} and K_{tot} stocks were influenced by elevation at all three soil depths ($P \leq 0.01$), with highest P and K stocks at the 2000 m site and lowest values at the 3000 m site. Available K of the two mineral soil depths did not change with elevation (Table 4.2). Available and total nutrient stocks on granite at the 1000 m site did not differ between topographic positions in neither of the soil depth, whereas on schist P_{tot}, P_{av}, K_{tot}, and K_{av} stocks at both

mineral soil depths were highest at the midslope position (Table 4.4). At 2000 m and 3000 m soil P_{tot} and P_{av} were influenced by the topographic position ($P \leq 0.05$) with decreasing nutrient contents toward the ridges at all soil depths (Table 4.2). Soil K_{tot} stocks at all soil depths at 2000 m were highest at the lower slope positions, whereas soil K_{av} stocks did not change between the topographic positions at 2000 m and 3000 m (Table 4.4).

Different geological substrate at the 1000 m site did not affect C:N ratios of the organic layer and the two mineral soil depths. C:N ratios of the organic layer and the two mineral soil depths were affected by elevation as well as topography with increasing ratios with elevation ($P < 0.001$ for elevation and topography effect on C:N ratio of all three soil depths, Table 4.2). At the 1000 m site C:N ratios of the organic layer were not different between topographic positions at neither of the geological substrates, whereas both mineral soil depths on granite and the 10-20-cm soil depth on schist showed highest C:N ratios at the ridge positions. At the 2000 and 3000 m site C:N ratios of all three soil depths increased toward the ridges. The lower slope and midslope positions at the 2000 m site showed lowest C:N ratios at all soil depths (Table 4.2).

Organic layer thickness did not correlate with total or available K and P stocks at any of the soil depths and showed only weak correlation with the C:N ratio of the organic layer ($P = 0.003$, $R^2 = 0.31$, data not shown).

Table 4.2: Nutrient input, C:nutrient ratios in aboveground litterfall and C:N ratios, available and total phosphorus (P) and potassium (K) stocks at different soil depths and of the topographic positions along the elevation gradient.

	1000 m			2000 m			3000 m		
	Lower Slope	Midslope	Ridge	Lower Slope	Midslope	Ridge	Lower Slope	Midslope	Ridge
Litterfall									
C:N	31.6 (0.9)A	32.6 (2.1)A	35.8 (2.4)A	24.8 (2.4)aA	27.0 (2.2)aA	39.6 (2.2)bA	43.8 (1.8)aB	55.5 (5.0)bB	77.9 (3.1)cB
C:K	83.8 (4.8)A	81.1 (2.8)A	88.8 (10.2)A	70.6 (3.7)aA	100.3 (17.1)aB	140.9 (10.2)bB	161.2 (12.5)B	182.0 (17.4)B	198.5 (8.1)C
C:P	713.4 (46.0)A	683.9 (43.8)A	843.6 (72.7)A	408.5 (58.5)aB	499.2 (85.8)aA	906.0 (66.2)bA	901.0 (58.0)aB	1403.4 (94.9)bB	1820.6 (183.8)bB
Aboveground litterfall N (kg ha^{-1} yr^{-1})	116.4 (7.7)A	136.6 (7.9)A	100.6 (6.6)A	196.78 (14.4)aB	191.7 (21.7)aB	97.4 (6.1)bA	56.7 (3.3)aC	46.9 (4.8)aC	31.8 (2.2)bB
Aboveground litterfall K (kg ha^{-1} yr^{-1})	3.4 (0.2)A	3.4 (0.1)A	3.3 (0.3)A	3.6 (0.2)aA	3.0 (0.5)abA	2.1 (0.2)bB	1.7 (0.1)B	1.6 (0.2)B	1.5 (0.1)B
Aboveground litterfall P (kg ha^{-1} yr^{-1})	5.9 (0.5)A	7.0 (0.9)AB	4.6 (0.2)A	12.3 (1.0)aB	11.9 (2.5)aA	4.3 (0.4)bA	2.8 (0.2)aC	1.8 (0.2)bB	1.5 (0.3)bB
Organic Layer									
P $_{tot}$ (kg ha^{-1})	51.6 (19.0)AB	61.3 (13.4)A	52.9 (25.7)A	91.8 (19.8)aA	70.3 (26.5)aA	16.9 (1.3)bAB	24.5 (2.6)aB	15.1 (1.4)aB	10.9 (1.2)bB
P $_{av}$ (kg ha^{-1})	7.5 (3.4)A	10.7 (3.0)	8.96 (3.3)	21.3 (4.5)aB	12.5 (4.9)ab	5.2 (0.6)b	8.0 (1.0)aAB	5.1 (0.6)b	3.6 (0.3)b
K $_{tot}$ (kg ha^{-1})	403.9 (180.7)AB	299.9 (96.8)A	344.4 (228.8)	708.5 (206.7)aA	257.6 (53.6)aA	46.9 (6.9)b	104.5 (19.7)B	70.4 (7.0)B	80.1 (22.9)
C:N	18.5 (0.7)A	18.6 (1.5)A	20.5 (0.7)A	15.7 (0.8)aB	15.6 (0.6)aA	21.1 (0.7)bA	20.5 (0.8)aA	23.9 (1.4)bB	26.7 (1.3)cB
Mineral Soil (0-10cm)									
P $_{tot}$ (kg ha^{-1})	167.8 (38.0)A	349.5 (225.8)A	127.6 (15.9)A	350.8 (37.2)aB	241.3 (47.7)aA	89.2 (12.3)bA	85.7 (5.7)aA	62.6 (12.6)abB	40.8 (7.1)bB
P $_{av}$ (kg ha^{-1})	11.5 (2.0)A	23.5 (11.1)	10.2 (0.9)	41.7 (7.4)aB	34.6 (7.1)ab	17.3 (5.2)b	31.0 (8.2)aB	14.9 (3.0)ab	11.6 (2.0)b
K$_{tot}$ (Mg ha^{-1})	2.1 (0.6)A	3.2 (1,7)	1.6 (0.5)A	11.1 (2.2)aB	3.5 (0.9)b	5.4 (1.2)abB	2.1 (0.3)A	2.8 (0.6)	1.9 (0.4)A
K $_{av}$ [b] (kg ha^{-1})	40.6 (11.8)	63.5 (6.8)	9.3 (1.4)	25.5 (6.3)	22.8 (11.3)	16.5 (2.1)	27.6 (3.6)	28.4 (6.1)	29.7 (3.5)
C:N	16.3 (0.6)aA	15.0 (0.7)a	21.3 (1.2)bB	13.2 (1.1)B	14.1 (1.5)	17.0 (0.8)A	14.2 (0.2)aAB	18.0 (1.1)b	22.3 (1.0)cB
Mineral soil (10-20 cm)									
P $_{tot}$(kg ha^{-1})	187.4 (75.6)	331.9 (223.0)A	116.6 (18.8)A	300.1 (26.5)a	244.8 (56.9)aAB	89.9 (15.6)bAB	103.0 (12.3)a	57.3 (11.0)abB	54.9 (11.3)bB
P $_{av}$(kg ha^{-1})	19.0 (10.7)	17.6 (6.9)AB	8.5 (1.4)	33.8 (5.7)a	33.7 (6.1)aA	10.2 (2.8)b	25.1 (2.8)a	7.3 (1.6)bB	11.1 (2.3)b
K $_{tot}$ (Mg ha^{-1})	3.1 (0.9)A	3.4 (1.8)	2.0 (0.7)A	11.2 (1.8)aB	3.7 (1.1)b	6.7 (1.4)abB	3.2 (0.3)A	3.7 (0.9)	3.8 (0.5)AB
K $_{av}$ [b] (kg ha^{-1})	29.3 (7.7)	13.7 (NA)	5.8 (0.2)	18.5 (4.8)	14.2 (6.7)	8.4 (1.1)	23.5 (7.3)	10.2 (4.3)	16.6 (2.8)
C:N	14.1 (0.8)aA	13.2 (1.9)a	21.5 (1.2)bA	8.5 (1.8)B	13.1 (1.7)	14.3 (1.5)B	14.5 (0.8)aA	17.2 (0.7)a	21.6 (1.5)bA

[a] Means (± SE, n = 6) within rows followed by different letter indicate significant differences among topographic positions at each elevation (small letters) and differences among elevations at each topographic position (capital letters) (two-way ANOVA with Tukey HSD test at $P \leq 0.05$).

[b] K_{av} determination using the NaHCO$_3$ extracts of the Hedley fractionation

[c] K_{av} determination via measurement of cation exchange capacity from soil profiles

4.4.2   Litter quality

Total nutrient content in aboveground litterfall (kg ha^{-1} yr^{-1}) was influenced by elevation and topography (P < 0.001 for the elevation effect and P ≤ 0.02 for the topographic effect on K, P and N content in aboveground litterfall). Nutrient input via litterfall was highest at the lower and midslope positions of the 2000 m site and was generally lowest at the ridge positions at all elevations. Phosphorous concentration of aboveground litterfall was linearly correlated with P$_{tot}$ stocks of the organic layer (P = 0.001, R^2 = 0.63, Figure 4.1 a) and followed a saturation function with P$_{tot}$ concentrations of the two mineral soil depths (P < 0.001, R^2 ≤ 0.71). Potassium concentration of aboveground litterfall followed a saturation function with K$_{tot}$ stocks of the organic layer (P < 0.01, R^2 = 0.59, Figure 4.1 b) but did not correlate with K$_{av}$ at the mineral soil depths. Soil P$_{av}$ content at all soil depths correlated linearly with P concentration in aboveground litterfall with weaker relationships for P$_{av}$ in the mineral soil compared to the organic layer (P < 0.01, R^2 = 0.80 in the organic layer, Figure 4.1 c; P = 0.04, R^2 = 0.30 at 0-10 cm, P < 0.01, R^2 = 0.60 at 10-20 cm depth, data not shown). Nitrogen concentration in aboveground litterfall was closely correlated to the C:N ratio, and thus N availability of the organic layer (Figure 4.1 d, P < 0.001, R^2 = 0.91).

At the 1000 m site carbon: nutrient ratios in litterfall (C:N, C:K and C:P) were generally lower in plots over schist material than over granite . Litterfall C:nutrient ratios were influenced by elevation and topography (P < 0.001 for elevation and topography effect on C:N, C:K and C:P ratios in aboveground litterfall). They were lowest at the lower slope and midslope positions of the 2000 m site and increased toward the ridges at the 2000 m and the 3000 m sites (Table 4.2). We found no difference in C:N, C:K and C:P ratios between topographic positions at the 1000 m site (schist and granite). Carbon:nutrient concentration in aboveground litterfall showed best relations with the available and total nutrient stocks in the organic layer. Aboveground litterfall C:K ratio correlated positively with the K$_{tot}$ stocks of the mineral soil (P = 0.02, R^2 = 0.30 for K$_{av}$, and P = 0.02, R^2 = 0.39 for K$_{tot}$). C:P ratio of the aboveground litterfall showed linear correlations with the organic layer stocks of P$_{av}$ and P$_{tot}$ (P = 0.01, R^2 = 0.46 for P$_{av}$ and P = 0.01, R^2 = 0.46 for P$_{tot}$), whereas it followed exponential decay functions with P$_{tot}$ content of the two mineral soil depths (P < 0.001, R^2 = 0.88 for 0-10cm depth and P < 0.001, R^2 = 0.88 for 10-20 cm depth). We found very close linear correlations between C:N ratios of the aboveground litterfall and the C:N ratio of the organic layer (P < 0.001,

$R^2 = 0.84$) and weaker linear correlations with C:N ratios of the mineral soil ($P \leq 0.04$, $R^2 = 0.30$ for both mineral soil depths).
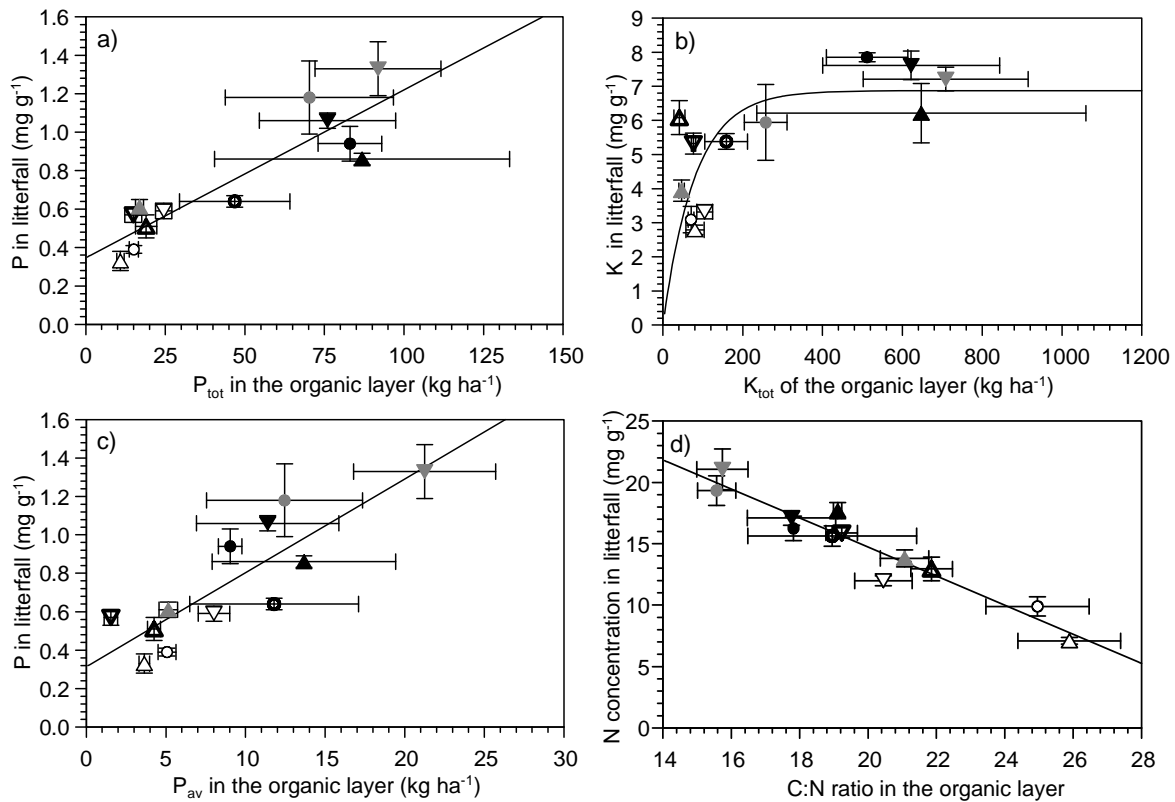
Figure 4.1: Relationship between litterfall nutrient concentration and total and available nutrient stocks of the organic layer (means ± standard error), with a) total phosphorus (Y = 0.35 + 0.01 *x, P < 0.01, $R^2 = 0.79$), b) total potassium (Y = a * (1 - exp (–b * x)), a = 6.9 ± 0.5, b = 0.01 ± 0.003, P < 0.01, $R^2 = 0.87$) c) available phosphorus (Y = 0.31 + 0.05 *x, P < 0.01, $R^2 = 0.70$), d) C:N ratio (38.41 – 1.18 * x, P < 0.001, $R^2 = 0.91$), of the topographic positions across the elevation gradient. Symbols used for data are: full black, schist material 1000 m; open granite material 1000 m, full grey, 2000 m; white, 3000 m; ▼ Lower Slope, ● Midslope, ▲ Ridge

4.4.3 Soil respiration

Soil respiration decreased with increasing elevation (P < 0.001) and from the lower slopes to the ridges(P < 0.03) (Table 4.3). Soil respiration ranged from 10.3 (0.8) Mg C ha^{-1} yr^{-1} at the lower slopes at 1000 m to 3.7 (0.5) Mg C ha^{-1} yr^{-1} at the ridges of the 3000 m site. Different geological substrate at the 1000 m site did not affect soil respiration (Table 4.4). Multiple regression analysis revealed that

temperature, gravimetric moisture content and C:N ratio of aboveground litterfall together influenced soil respiration significantly ($P \leq 0.001$) and explained about 63% of spatial CO_2 flux variability. Soil stocks and concentrations of P_{tot}, P_{av}. K_{tot} and K_{av} did not influence soil respiration, whereas we found linear correlations between soil respiration and C:nutrient ratios of the litterfall ($P = 0.003$, $R^2 = 0.56$ for C:N, $P = 0.002$, $R^2 = 0.60$ for C:K and $P = 0.02$, $R^2 = 0.40$ for C:P, Figure 4.2 a-c) and the C:N ratio of the organic layer ($P = 0.02$, $R^2 = 0.35$). We found a good correlation of soil respiration rates with organic layer thickness ($P < 0.01$, $R^2 = 0.63$, Figure 4.4 b).
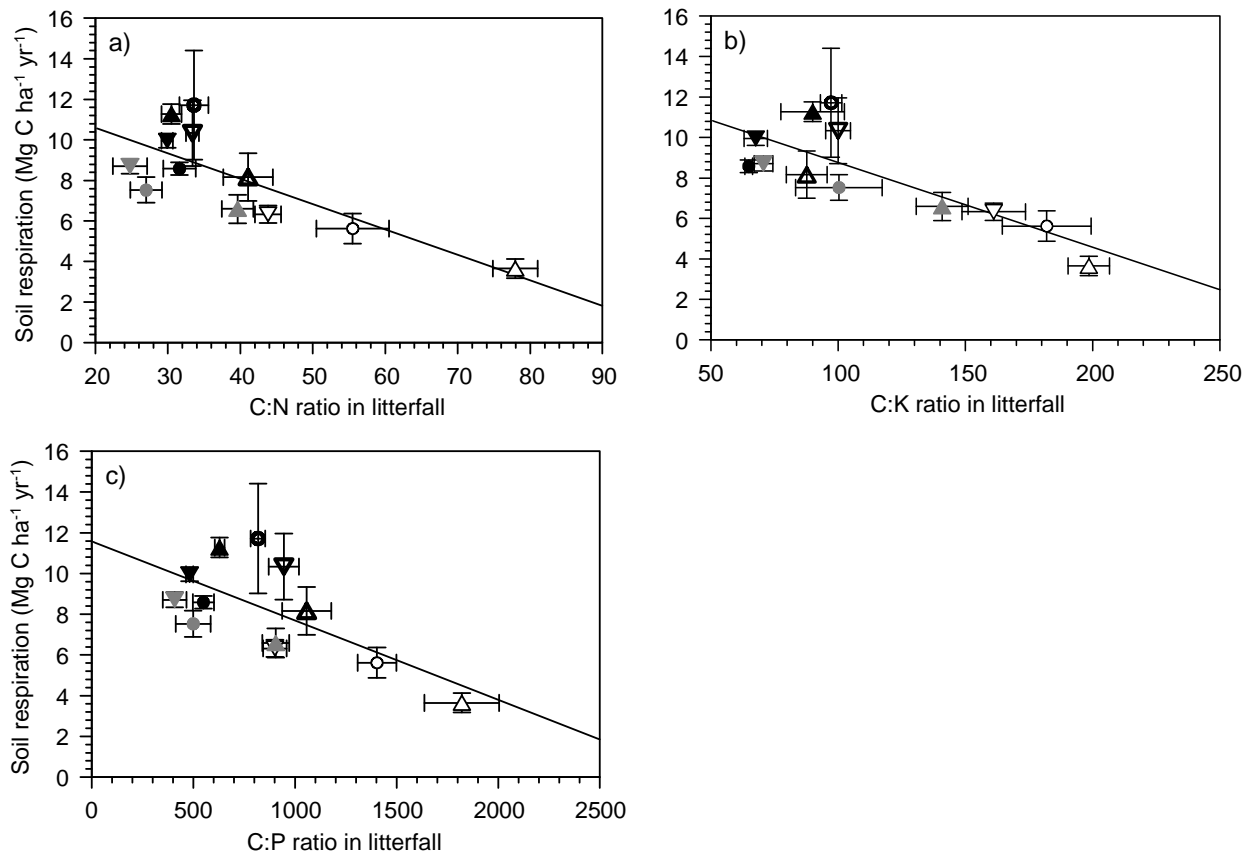
Figure 4.2: Relationship between soil respiration (means ± standard error) and a) C:N ratio in litterfall (y = 13.1 - 125.4 * x, P = 0.003, R^2 = 0.56), and b) C:K ratio in litterfall (y = 13.0 – 41.9 * x, P = 0.002, R^2 = 0.60), c) C:P ratio in litterfall (y = 11.6 - 3.9 * x, P = 0.02, R^2 = 0.40) and d) organic layer thickness (y = 10.4 – 244.1 * x, P = 0.002, R^2 = 0.62) of the topographic positions across the elevation gradient. Symbols used for data are: full black, schist material 1000 m; open granite material 1000 m, full grey, 2000 m; white, 3000 m; ▼ Lower Slope, ● Midslope, ▲ Ridge.

Table 4.3: Carbon fluxes (Mg C ha^{-1} yr^{-1}) of the topographic positions across the elevation gradient.

	1000 m			2000 m			3000 m		
	Lower slope	Midslope	Ridge	Lower slope	Midslope	Ridge	Lower slope	Midslope	Ridge
Soil respiration	10.3 (0.8)aA	10.3 (1.4)aA	9.8 (0.9)aA	8.8 (0.4)aA	7.6 (0.6)aAB	6.7 (0.7)aB	6.4 (0.4)aB	5.7 (0.8)abB	3.7 (0.5)bC
Aboveground litter production	3.7 (0.2)abA	4.4 (0.2)aA	3.4 (0.3)bA	4.8 (0.3)aB	5.0 (0.3)aA	3.8 (0.1)bA	2.5 (0.1)aC	2.6 (0.3)aB	2.5 (0.1)aB
AGB	6.9 (0.5)A	7.1 (0.5)A	6.0 (0.9)A	7. 9 (0.8)aA	7.0 (0.5)abA	5.1 (0.3)bA	3.4 (0.2)B	3.1 (0.4)B	2.9 (0.1)B
TBCA	6.6 (0.9)aA	5.8 (1.5)a	6.4 (0.8)aA	4.1 (0.3)aB	2.6 (1.0)a	2.9 (0.7)aB	3.9 (0.4)aB	3.1 (0.7)a	1.2 (0.5)bB
TBCA: Aboveground productivity	1.0 (0.2)AB	0.9 (0.2)	1.1 (0.1)A	0.5 (0.1)A	0.4 (0.2)	0.6 (0.1)B	1.2 (0.1)aB	1.1 (0.3)ab	0.4 (0.2)bB

Means (± SE, n = 6) within rows followed by different letter indicate significant differences among topographic positions at each elevation (small letters) and differences among elevations at each topographic position (capital letters) (two-way ANOVA with Tukey HSD test at $P \leq 0.05$).

Table 4.4: Carbon fluxes, available and total nutrient stocks at different soil depths of two different geological substrates at the 1000 m site

	1000 m Schist			1000 m Granite		
	Lower slope	Midslope	Ridge	Lower slope	Midslope	Ridge
Soil respiration (Mg ha^{-1} yr^{-1})	10.1 (03)a	8.7 (0.3)b	11.4 (0.5)a	10.4 (1.6)	11.8 (2.7)	8.3 (1.2)
Aboveground litterfall C (Mg ha^{-1} yr^{-1})	3.9 (0.2)	4.7 (0.4)	4.0 (0.2)A	3.5 (0.3)ab	4.1 (0.2)a	2.9 (0.2)bB
TBCA (Mg ha^{-1} yr^{-1})	6.2 (0.3)a	4.0 (0.5)b	7.4 (0.7)a	7.0 (1.9)	7.7 (2.7)	5.4 (1.3)
TBCA: Aboveground litterfall C	1.6 (0.1)ab	0.9 (0.2)a	1.9 (0.3)b	2.1 (0.8)	1.9 (0.7)	1.9 (0.6)
Litterfall						
C:N	29.9 (0.8)A	31.6 (2.3)	30.5 (1.4)A	33.4 (0.9)B	33.6 (2.0)	41.1 (3.4)B
C:K	67.6 (4.6)A	64.9 (1.5)A	90.0 (12.5)	100.0 (4.9)B	97.2 (4.2)B	87.7 (8.0)
C:P	481.6 (17.6)A	549.8 (52.0)A	629.5 (24.4)A	945.1 (74.4)B	818.0 (35.6)B	1057.7 (121.0)B
Aboveground litterfall N (kg ha^{-1} yr^{-1})	129.1 (8.4)	149.3 (10.3)	131.2 (10.1)A	103.6 (7.0)a	123.8 (5.4)a	70.0 (3.1)bB
Aboveground litterfall K	3.9 (0.2)A	4.0 (0.1)A	3.3 (0.5)	2.8 (0.2)B	2.8 (0.1)B	3.2 (0.2)

(kg ha^{-1} yr^{-1})						
Aboveground litterfall P	0.8 (0.1)A	0.9 (0.1)	0.6 (0.01)A	0.4 (0.04)B	0.5 (0.03)	0.3 (0.02)B
(kg ha^{-1} yr^{-1})						
Organic Layer						
P tot (kg ha^{-1} yr^{-1})	76.0 (21.4)	83.0 (10.0)	86.8 (46.4)	14.9 (2.7)	46.8 (17.3)	19.0 (3.3)
P av (kg ha^{-1} yr^{-1})	11.4 (4.5)	9.0 (0.7)	13.7 (5.8)	1.5 (0.4)	11.8 (5.3)	4.3 (0.4)
K tot (kg ha^{-1} yr^{-1})	622.1 (222.0)	511.5 (102.1)	647.4 (412.1)	76.5 (5.2)	158.8 (53.5)	41.5 (13.7)
C:N	17.8 (1.3)	17.8 (NA)	19.1 (0.1)A	19.2 (0.5)	19.0 (2.5)	21.9 (0.6)B
Mineral Soil 0-10cm						
P tot (kg ha^{-1} yr^{-1})	23.5 (29.9)aA	1.0 (NA)bA	149.9 (16.7)a	84.1 (9.6)B	123.8 (9.7)B	105.2 (21.9)
P av (kg ha^{-1} yr^{-1})	4.2 (2.2)a	56.7 (NA)bA	11.2 (0.9)a	7.4 (0.4)	12.4 (0.7)B	9.2 (1.4)
K tot (Mg ha^{-1} yr^{-1})	3.3 (0.1)aA	8.2 (NA)bA	2.7 (0.2)aA	0.9 (0.1)aB	1.5 (0.2)bB	0.5 (0.1)aB
K av [b] (kg ha^{-1} yr^{-1})	2.0 (17.9)ab	101.3 (NA)aA	11.2 (0.8)b	19.3 (5.7)	25.6 (6.8)B	7.3 (1.9)
C:N	16.3 (0.6)	14.5 (1.5)	19.0 (0.9)A	16.4 (1.2)a	15.6 (0.1)a	23.6 (0.8)bB
Mineral Soil 10-20cm						
P tot (Mg ha^{-1} yr^{-1})	311.3 (114.9)a	1.0 (NA)bA	144.8 (22.6)a	63.5 (7.6)	109.0 (6.4)B	88.5 (21.3)
P av (kg ha^{-1} yr^{-1})	31.9 (20.2)	37.9 (NA)A	10.1 (2.1)	6.1 (1.0)	10.9 (1.6)B	7.0 (1.5)
K tot (Mg ha^{-1} yr^{-1})	5.1 (0.7)ab	8.7 (NA)aA	3.4 (0.4)bA	1.2 (0.3)ab	1.6 (0.2)aB	0.6 (0.1)bB
K av [b] (kg ha^{-1} yr^{-1})	47.5 (12.0)	NA	10.0 (0.3)A	11.2 (3.4)	13.8 (NA)	1.6 (0.2)B
C:N	14.7 (0.9)a	13.3 (1.3)a	18.6 (0.8)bA	13.5 (0.8)a	13.1 (2.4)a	24.5 (1.7)bB

NA No data not available, NA for standard errors if the mean is one repetition

[a] K_{av} determination using the NaHCO3 extracts of the Hedley fractionation

[b] K_{av} determination via measurement of cation exchange capacity from soil profiles

4.4.4 Aboveground productivity

Different substrate at the 1000 m site influenced aboveground litter production (P = 0.03), with lower productivity over granite. Litter C concentrations and total litter production were correlated negatively (P = 0.03, R^2 = 0.35) along the environmental gradients. Both elevation and topography affected aboveground litter production (P ≤ 0.001) with highest productivity at the lower slope and midslope position of the 2000 m site and lowest values at all positions of the 3000 m site (Table 4.3). Aboveground litter production followed a saturation function with K_{tot} of the organic layer (P = 0.01, R^2 = 0.65, Figure 4.3 c), and P_{tot} in the mineral soil (P < 0.001, R^2 = 0.85 at 0-10 cm, Figure 4.3 f, and P = 0.001, R^2 = 0.67 at 10-20 cm, data not shown). Linear correlations were found with P_{tot} and P_{av} stocks in the organic layer (P < 0.01, R^2 = 0.61 for P_{tot} and P = 0.01, R^2 = 0.41 for P_{av} Figure 4.3 b, d) and with K_{tot} at 0-10cm depth (P < 0.03, R^2 = 0.31; Figure 4.3 e). Weaker linear correlations were found with P_{av} of the mineral soil depths (P = 0.06, R^2= 0.24 at 0-10 cm, P = 0.04, R^2= 0.31 at 10-20 cm soil depth, data not shown). Aboveground litter production also correlated with C:nutrient ratios of litterfall (P = 0.005, R^2 = 0.52 for C:K and P = 0.001, R^2 = 0.64 for C:P and P < 0.001, R^2 = 0.75 for C:N) and the C:N ratio of the organic layer (P < 0.001, R^2 = 0.74, Figure 4.3 a). Correlations with C:N ratios of the mineral soil were less pronounced (P < 0.03, R^2 = 0.33 for 0-10 cm depth and P < 0.02, R^2 = 0.38 for the 10-20 cm depth). Soil respiration and aboveground litter production did not correlate along the environmental gradients.

Aboveground productivity, estimated as the sum of aboveground litter production and wood increment, followed the trends shown for aboveground litter productivity, with highest values at the at the lower slope and midslope position of the 2000 m site and lowest values at all positions of the 3000 m site (Table 4.3). We found significant influence of both elevation and topography on aboveground productivity (P ≤ 0.005).
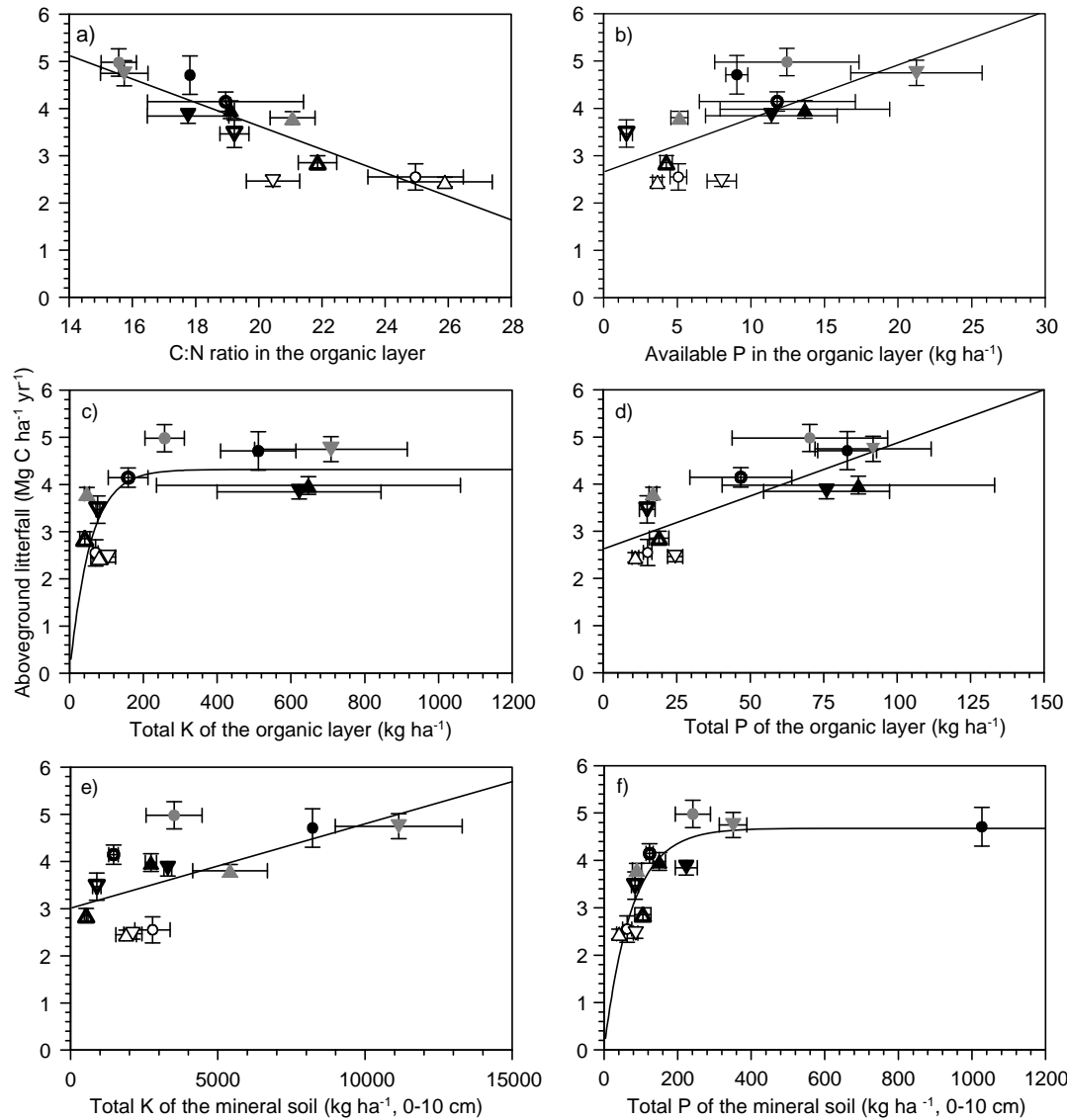
Figure 4.3: Relationship between aboveground litterfall and nutrient stocks (means ± standard error) and a) C:N ratio in the organic layer (8.61 – 248.70 * x, P < 0.01, R^2 = 0.74), b) available phosphorus in the organic layer (Y = 2.7 + 113.1 * x, P = 0.01, R^2 = 0.41), c) total potassium in the organic layer (y = a * (1 - exp (–b * x)), a = 4.3 ± 0.4, b = 0.02 ± 6.2*10⁻⁶, P < 0.001, R^2 = 0.65), and d) total phosphorus in the organic layer (Y = 2.6 +22.5*x, P < 0.01, R^2 = 0.61), e) total potassium in the mineral soil (0-10 cm depth) (y = 3.0+0.2*x, P = 0.03, R^2 = 0.32) and, f) total phosphorus in the mineral soil (0-10 cm depth) (y = a * (1 - exp (–b * x)), a = 4.7 ± 0.6, b = 0.01 ± 4.7*10⁻⁶, P < 0.001, R^2 = 0.85) of the topographic positions across the elevation gradient. Symbols used for data are: full black, schist material 1000 m; open granite material 1000 m, full grey, 2000 m; white, 3000 m; ▼ Lower Slope, ● Midslope, ▲ Ridge.

4.4.5   Total belowground carbon allocation

TBCA, as estimated by the difference between soil respiration and litterfall C, decreased from 6.6 Mg C ha^{-1} yr^{-1} at the 1000 m site to 1.2 Mg C ha^{-1} yr^{-1} at the 3000 m site and was highest at the lower slope positions of all elevations (Table 4.3). Absolute TBCA did not correlate with any of the nutrient contents at neither soil depths, but was negatively correlated with gravimetric soil moisture content ($P = 0.002$, $R^2 = 0.60$, Figure 4.4 c) and organic layer thickness ($P = 0.003$, $R^2 = 0.58$, Figure 4.4 d). We found a weak linear correlation of absolute TBCA with C:K ratio of litterfall ($P = 0.04$, $R^2 = 0.29$), whereas C:N and C:P ratios of the litterfall did not influence TBCA. TBCA showed no correlation with aboveground litter production. The ratio between TBCA and aboveground productivity, as determined from the sum of litter production and wood increment (relative TBCA), ranged between 0.4 and 1.2. Elevation influenced relative TBCA ($P < 0.005$), while we did only find a topographic effect at the 3000 m site ($P = 0.02$). Relative TBCA was lowest at all positions of the 2000 m site, and at the ridge position of the 3000 m site (Table 4.3). We did not find any correlation of relative TBCA with total or available nutrients in the soil. Multiple regression analysis showed that C:N ratio in litter, P concentration in litter and gravimetric soil moisture together accounted for 38% of the variability in relative TBCA data (including ^{15}N signature of litterfall 45%).
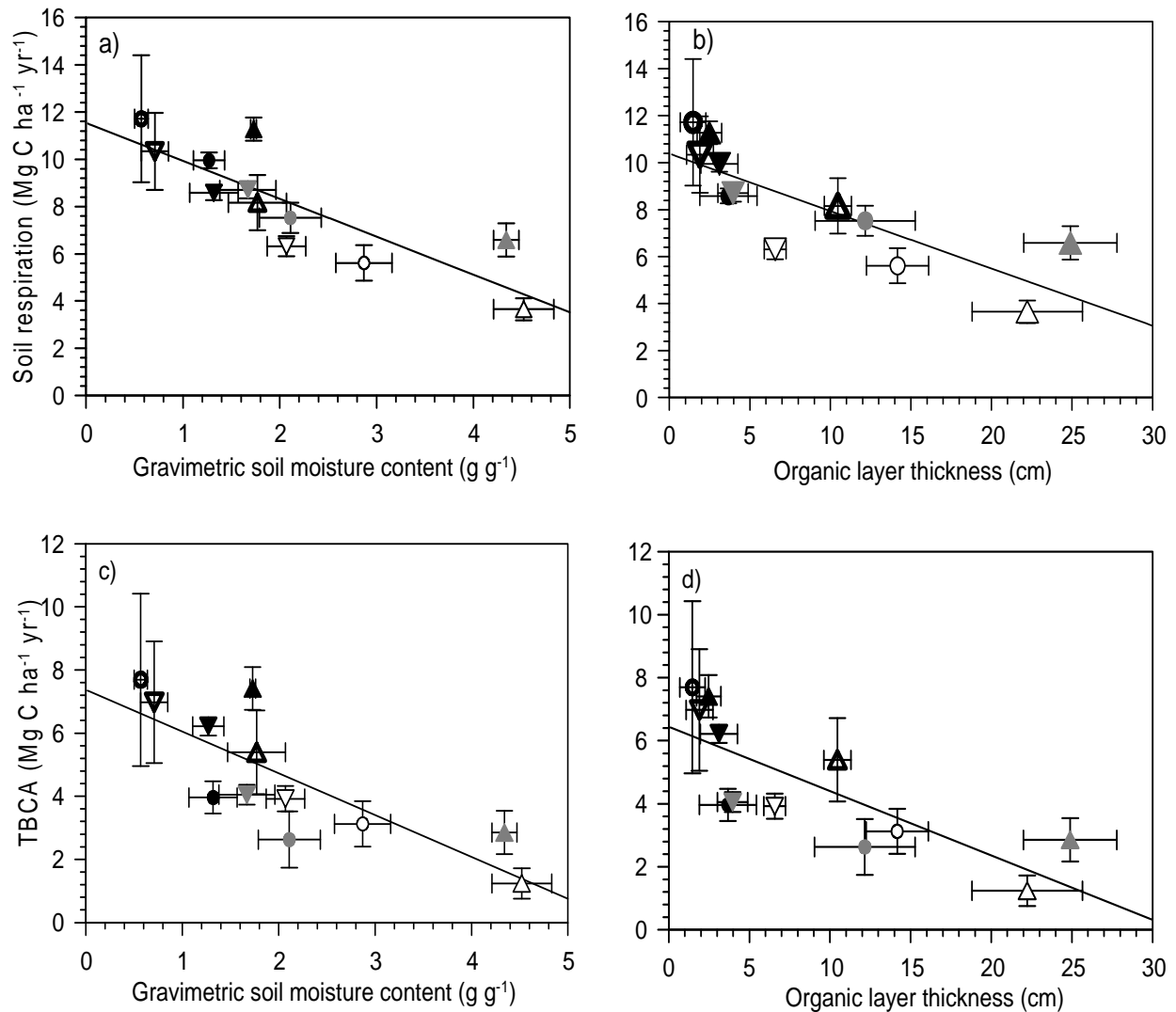
Figure 4.4: Relationship (means ± standard error) between a) soil respiration and gravimetric soil moisture content (y = 9.7 – 1.4 * x, P < 0.005, R^2 = 0.65) b) soil respiration and organic layer thickness (y = 10.4 – 244.0 * x, P < 0.002, R^2 = 0.63), c) TBCA and gravimetric soil moisture content (y = 7.4 – 1.3 * x, P < 0.01, R^2 = 0.60), and d) organic layer thickness (y = 6.4 - 0.2 * x, P < 0.01, R^2 = 0.58) of the topographic positions across the elevation gradient. Symbols used for data are: full black, schist material 1000 m; open granite material 1000 m, full grey, 2000 m; white, 3000 m; ▼ Lower slope, ⬤ Midslope, ▲ Ridge.

4.5 Discussion

4.5.1   Soil respiration

Soil respiration measured along our elevation gradient was lower than reported for tropical lowland forests (Raich & Schlesinger, 1992; Köhler et al., 2009a) but fitted into the range of CO_2 fluxes given for tropical montane forests (0.65 – 1.4 kg C ha^{-1} yr^{-1}) of Panama, Colombia, Hawaii and China (Cavelier & Penuela, 1990; Raich, 1998; McGroddy & Silver, 2000; Werner et al., 2006; Köhler et al., 2009a). Large parts of the measured soil respiration derived from the decomposition of surface litter, as the correlations of indices of litter quality were significant in contrast to nutrient availability in the organic layer. We could not confirm the positive correlation between soil respiration and aboveground litterfall found by Raich & Schlesinger (1992) for a wide range of ecosystems. This lack of correlation suggests that the main controlling factors of soil respiration and aboveground litter production are not the same in this ecosystem. Furthermore, this corroborates with findings from Hawaiian forests (Schuur et al., 2001) that increased carbon storage (thick organic layers) was not due to high productivity but due to a decrease in decomposition rates. The positive correlation between organic layer thickness and soil respiration with soil moisture and temperature imply that C-turnover and the and mineralization rates of the organic layer were rather limited by temperature and soil moisture than limited by substrate input as suggested by Raich & Schlesinger (1992). Aboveground litterfall on the other hand was clearly nutrient limited in wide parts of the study region. Linear correlation of aboveground litter production with nitrogen and phosphorus availability mainly in the organic layer are an indication for N and P limitation of tree productivity in the whole investigated area, whereas the saturation functions described by aboveground litter production and available K indicate limitations only for parts of the study area.

4.5.2   Soil nutrient availability and aboveground productivity

Thick organic layers, as they were found in our study area, are common in tropical montane forests (Grubb, 1977; Purbopuspito et al., 2006; Arnold et al., 2009) and imply low mineralization rates and thus low nutrient availability (Edwards & Grubb, 1977). Such unfavorable soil conditions and impaired nutrient supply combined with low temperatures are

suggested to hamper tree productivity in montane rain forests (Leuschner et al., 2007). Indeed, the positive correlations of aboveground litter productivity and litter P and K concentrations with soil nutrient availability in our study area suggest that tree productivity of these tropical montane rain forests is nutrient limited (Tanner et al., 1998). Although it has to be noted, that K-limitation was probably not given within the entire investigated area. Despite such nutrient limitation and the higher available nutrient contents in the mineral soil, plants seem to obtain nutrients mainly from the organic layer. This assumption is supported by several findings. First, we found closer positive correlations of aboveground litter production with the available nutrients of the organic layer relative to the mineral soil depths. Further evidence for this crucial role of the organic layers as nutrient supplier comes from the studies reporting the occurrence of highest fine root densities within the organic layer of tropical montane forests in Costa Rica and Panama (Cavelier, 1992; Vance & Nadkarni, 1992; Hertel et al., 2003). Within our study area, at least 80% of the fine root biomass of a soil profile was located within the organic layer and the uppermost 20 cm of the mineral soil (Röderstein et al., 2005). Of these 80% about two thirds were found within the organic layer (estimate from graphics in Röderstein et al.(2005)). A possible explanation for this paradox nutrient acquisition may be the increasing occurrence of water logging in the mineral soil with elevation (Schrumpf et al., 2001) and toward the ridge positions. Hertel et al. (2003) suggest that the high root densities in the organic layer may advance a self–enforcing feedback process as they themselves provided large amounts of decomposing organic material with root death in a old growth montane forest in Costa Rica. A similar process, strengthened by a limited mixing of the organic layer with the mineral soil due to low biological activity (Wilcke et al., 2002), may, for our study area, result in a nutrient cycling system between plants and soil, that is largely uncoupled from the mineral soil.

4.5.3   Total belowground carbon allocation

TBCA of our sites were lower than for most lowland sites (Davidson et al., 2002; Litton et al., 2007) and comparable to the values reported by Raich (1998) for comparable elevations in a tropical montane forest in Hawaii. The lack of correlations between aboveground litter production and TBCA in our tropical montane site could not confirm the link between belowground and aboveground primary productivity found by Raich & Nadelhoffer (1989) and Litton et al. (2007). The authors suggested that an increase of primary productivity would lead to

a parallel increase in TBCA and aboveground litter production, leaving the ratio TBCA: aboveground litter production constant for a wide range of ecosystems (Davidson et al., 2002). Neither could we confirm our hypothesis that relatively more carbon is allocated belowground than aboveground when nutrient supply declines.

The decrease in TBCA along the elevation gradient seems contradictory to the increasing fine root biomass and increasing root/shoot ratios with elevation, which have been reported for tropical montane forests (Hertel et al., 2003; Hertel & Leuschner, 2010) including our study area (Röderstein et al., 2005; Leuschner et al., 2007). Although we cannot completely dismiss the possibility of methodological problems, our measurements of aboveground productivity and soil respiration, as well as our estimates for TBCA were within the range of values reported from other tropical montane forests (Raich, 1998). Large root biomass has often been assumed to be synonymic with increases in root productivity and reduction in fine root longevity (Malhi et al., 2004; Leuschner et al., 2007). However, this assumption seems not to hold true for our study area, as the increase in fine root biomass with increasing elevation and toward the ridges went along with a decline in TBCA. One explanation might be that root productivity makes up only about 30% of TBCA (Nadelhoffer & Raich, 1992), with much less known about the other carbon fluxes, such as C allocated to mycorrhizae, root exudates and coarse root production (Gower et al., 1996). Another explanation could be increasing root longevity with increasingly adverse environmental conditions. Together with low decomposition rates in the organic layers, this may lead to higher and longer-term storage of organic C in the soil. A third possible explanation for the discrepancy between high root density and low TBCA is that TBCA might be underestimated by the carbon balance approach, especially at the highest elevation and the very poor ridge positions of the 2000 m site due to very low soil respiration rates.

In summary, we found a clear dependence of aboveground productivity and soil respiration on nutrient availability, and that nutrient cycling is mainly constricted to the organic layers and litter layer. The results obtained from our estimations of TBAC were controversial. Consequently, more direct measurements of root productivity rates especially in altitudes above 2000 m are needed to ascertain if the carbon balance approach by Raich & Nadelhoffer (1989) to estimate TBCA on a global scale, is applicable to tropical montane rain forests on a regional scale.

4.6 References

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SYNTHESIS

5.1 Synthesis and discussion of the major results

Soil trace gas fluxes were within the range reported from other tropical montane forests and showed rather spatial than temporal pattern

The results from Chapter 2 to 4 show that none of the investigated gases displayed a clear seasonal pattern, which might be related to the absence of a pronounced dry season and the resulting relatively stable soil moisture content. A lack of seasonality in soil trace gas fluxes has also been reported from montane forests in Indonesia (Purbopuspito et al. 2006; Veldkamp et al. 2008). The overview of soil trace gas fluxes in tropical montane forests in Table 5.1 shows that apart from the remarkably large N_2O fluxes of the lower slope at 2000 m (14.5 ± 2.1) N-oxide fluxes from the Ecuadorian soils were within the range reported from other tropical montane forests at comparable elevations. The annual CH_4 mean fluxes at the 2000 and 3000 m sites were within the ranges reported from Indonesia, whereas uptake rates at the 1000 m site were 24 - 55% higher than the means of other studies. Soil respiration data (CO_2 emissions) correspond to rates from Colombia, Hawaii, Puerto Rico and Panama. Soil CO_2 emission and CH_4 uptake rates declined with increasing elevation, whereas N_2O emissions were highest at the intermediate site, probably due to the high soil N availability. The effect of topography on trace gas fluxes was less pronounced and more complex. While CO_2 emissions followed the expected, however not statistically significant trend of decreasing emissions from the lower slopes toward the ridges, such a decline of N-oxide emissions was only observed at 2000 m for N_2O, and at 3000 m for NO. CH_4 uptake was not significantly influenced by topography at neither elevation.

Table 5. 1: Compilation of published soil trace gas emissions from old growth tropical montane forest soils*

Country, site	Slope position	Soil type	Elevation a.s.l m	Climate Mean ann. Precip. mm	Climate Mean ann. Temp ˚C	N_2O	Soil trace gas fluxes NO $\mu g\ m^{-2}\ h^{-1}$	CH_4	CO_2 $mg\ m^{-2}\ h^{-1}$	Reference
Colombia	upper slope		700	853	24				137.50	Cavelier and Penuela, (1990)
Australia, Kauri Creek	slope:12-14˚	Ustochrept	700-900	1594	21	49.77		-36.0	131.55	Kiese et al. (2008), Kiese and Butterbach -Bahl. (2002)
Hawai'i, Mauna Loa	lower slope	Acrudoxic Hydrudand	760	6000	19				101.60	Raich, (1998)
China	slope: 5-35˚	lateritic red/ yellow soils	770	1493	22	6.0		-29.5	68.8	Werner et al. (2006)
Congo	hillside		900	1500				-46.8		Delmas et al. (1992)
Ecuador, Bombuscaro	lower slope	Dystropept	990-1200	2000	20	1.90	0.75	-62.56	117.12	This study
Ecuador, Bombuscaro	midslope	Dystropept	990-1200	2000	20	3.53	1.11	-61.15	117.01	This study
Ecuador, Bombuscaro	ridge	Humitropept/ Dystropept	990-1200	2000	20	4.14	0.72	-67.29	111.87	This study
Puerto Rico	ridges/upper slope	Ultisols	1000	5000	21				96.77	McGroddy and Silver, (2000)
Australia, Maasy Creek	slope:18–20˚	Kandihumult	1020	2350	20	42.81			161.4	Breuer et al. (2000)
Hawai'i, Puu Makaala		Hydrandept	1112	3800	17	2.50				Riley and Vitousek (1995)
Hawai'i, Kohala		Placandept	1122	2540	16	4.50				Riley and Vitousek (1995)
Hawai'i, Kauai			1134	2410	16	3.10				Riley and Vitousek (1995)
Hawai'i, Kilauea		Dystrandept	1176	2410	16	0.13				Riley and Vitousek (1995)
Indonesia, Sulawesi	lower slope	Entisols and Fluvisols	1190	1590	23	12.67	5.48	-27.97		Purbopuspito et al. (2006)
Panama, Fortuna	slope <15%	Andosols	1200	5532	20	14.84	1.14		107.30	Köhler et al. (2009b, 2009a)
Hawai'i, Kilauea		Volcanic ash	1200	2200	16	0.60				Matson and Vitousek (1987)
Hawai'i, Kilauea		Volcanic ash	1200	3500	16	1.85				Matson and Vitousek (1987)
Hawai'i, Mauna Loa		Volcanic ash	1200	4500	16	1.80				Matson and Vitousek (1987)
Hawai'i, Molokai		Placandept	1267	2500	16	1.63				Riley and Vitousek (1995)
Hawai'i, Maui	slope <5%	Andisols	1300	4050	16	1.82	0.00			Holtgrieve et al. (2006)
Hawai'i, Maui	slope <5%	Andisols	1320	3350	16	8.41	2.00			Holtgrieve et al. (2006)

Location	Slope	Soil								Reference
Hawai'i, Maui	slope <5%	Inceptisols	1370	2200	16	11.14	87.00			Holtgrieve et al. (2006)
Indonesia, Sumatra	slope:17-31˚	Andisols	1540	~2500	25	3.83		-36.30		Ishizuka et al. (2005)
Hawai'i, Mauna Loa		Histosols	1600	2600	13				87.90	Raich, (1998)
Hawai'i, Mauna Loa		Histosols	1600	2600	13				74.20	Raich, (1998)
Indonesia, Sulawesi		Inceptisols	1800		18	3.31	1.94	-37.90		Purbopuspito et al. (2006)
Ecuador, ECSF	lower slope	Dystropept/ Eutropept	1800-2100	2200	15	14.54	1.11	-25.77	100.46	This study
Ecuador, ECSF	midslope	Dystropept	1800-2100	2200	15	3.68	1.13	-49.54	86.76	This study
Ecuador, ECSF	ridge	Albaquults	1800-2100	2200	15	1.15	0.14	-30.75	76.48	This study
Indonesia, Sulawesi	upper slope	Inceptisols	2470		15	11.53	2.05	-16.55		Purbopuspito et al. (2006)
Ecuador, Cajanuma	lower slope	Typic Albaquults	2800-3000	5400	10	1.63	0.19	-6.89	73.06	This study
Ecuador, Cajanuma	midslope	Aquic Dystropepts	2800-3000	5400	10	1.34	0.06	-17.99	65.07	This study
Ecuador, Cajanuma	ridge	Histic Albaquults	2800-3000	5400	10	-0.53	-0.02	-11.05	42.24	This study

*This listing is not meant to be complete, but to give an overview of the range of published data

Nutrient availability affected soil trace gas fluxes

Soil N-oxide, CH_4 and CO_2 fluxes were positively correlated to indices of N availability in soil and litterfall along the elevation and topographic gradients. Soil respiration was also positively correlated to C:K and C:P ratios in litterfall, and negatively correlated to soil moisture content and organic layer thickness. The positive relationship between N-oxide emissions and N availability (Chapter 2) confirms hypothesis 1, and corroborates the conceptual 'hole-in-the-pipe'- model, which states that higher soil N availability will lead to higher N losses via N-oxide emissions (Davidson et al. 2000; Firestone & Davidson 1989). Field-measured atmospheric CH_4 uptake was positively correlated to CO_2 emissions, P concentration in the mineral soil and mineral N contents in the soil. This surprising positive correlation between field-measured atmospheric CH_4 uptake and N availability falsifies hypothesis 4. Instead of an ammonia inhibition effect, I found evidence, that more favorable conditions for microbial activity (e.g. higher litter quality) enhanced soil respiration, mineralization and nitrification rates, as well as atmospheric CH_4 uptake by soils. This conclusion is supported by the positive correlation between soil respiration and atmospheric CH_4 uptake. The relationships of litter quality and soil moisture with soil respiration (Chapter 4), as well as the first results of a decomposition experiment in the study area suggest that microbial activity and decomposition was mainly limited by litter quality in these TMFs (Homeier & Werner, unpublished data). In summary, I found that trace gas fluxes were influenced by nutrient availability along the environmental gradients in the investigated TMF. This finding was consistent for N-oxides, CO_2, and CH_4 throughout the study period; although not all indices of nutrient availability correlated with all trace gas fluxes.

Aboveground tree productivity was closely related to N, P and K availability, whereas belowground carbon allocation did not show any interdependencies

Confirming hypothesis 2, indices of aboveground forest productivity (litter production and tree basal area increment) were positively correlated with indices of nitrogen availability (δ ^{15}N signature and C:N ratios in litterfall), irrespective of elevation and topographic position. Litter production was also positively correlated with available P in the organic layer. Available K described a saturation function with aboveground litter production, which indicates that at some

sites K was not a limiting factor. Concentrations of P and K in litterfall correlated with the availability of the respective nutrient in the organic layer. These results, presented in Chapter 2 and Chapter 4, suggest that forest productivity was not limited by one nutrient alone, but both N and P could be limiting at all study sites and K was also potentially limiting at most sites. This confirms findings from other studies in TMFs, that tree growth in montane forests is mainly N and P limited (Cavelier et al. 2000; Grubb 1977; Homeier et al. 2010; Tanner et al. 1992). Nitrogen addition experiments carried out in tropical montane forests, including forests close to our study sites, also showed increases in aboveground forest productivity following fertilization indicating nutrient limitation (Adamek et al, 2009, Homeier et al., unpublished data). The good correlations found in the study are also due to the wide range of nutrient availabilities found along the environmental gradients.

Contradicting hypothesis 7, TBCA decreased with increasing elevation and from lower slopes to the ridges. The lack of correlations with soil N, P and K availability (Chapter 4) suggests that TBCA was not affected by the investigated nutrients. Instead, TBCA was inversely correlated with organic layer thickness and soil moisture content. These results seem to disagree with allocation theory which states that plants countervail growth limitations by investing more C into the respective plant structures able to reduce limitation (Raich 1998). Hence, relatively more C should be invested below ground (i.e. into roots) than into leaves, if nutrients limited plant growth stronger than light and CO_2, (Raich 1998). The increase in root/shoot ratio and root biomass found with elevation in our study area suggests that root productivity and TBCA should also increase (Leuschner et al. 2007; Röderstein et al. 2005). However, considering our findings of a decrease in absolute TBCA with increasing altitude, this assumption seems not to hold true for the investigated forests and the larger root biomass may better be explained by increasing root longevity. Together with low decomposition rates in the organic layers, this may lead to higher and longer-term storage of organic C in the soil.

In summary the results presented in Chapter 2 and Chapter 4 show, that aboveground litter production and TBCA are not directly linked through nutrient availability and that the decrease in aboveground productivity was probably not balanced by an increase in TBCA.

Tree basal area increment as promising proxy to estimate soil N-oxide fluxes in N limited ecosystems

As indicated by the positive correlation, tree productivity and soil N-oxide emissions were linked through N availability (Chapter 2). This result confirms hypothesis 3 and suggests that forest productivity may be a suitable predictor of soil N-oxide emissions in N limited tropical montane forests. Information on ecosystem productivity, especially on litter production, is available for a wide range of forest ecosystems. However, since litterfall is quite variable and some studies reported extremely high litter production rates with high standard errors (Purbopuspito et al. 2006) it may not be the predicting parameter of choice. Instead, tree basal area increment, which showed closer correlations with soil N-oxide emissions than litter production in the studied site, may be a better long-term measure of forest productivity. It is important to note that predictive relationships can only be expected if N limits forest productivity because, in N-rich ecosystems, additional N will further enhance N-oxide emissions but not affect forest productivity.

Soil organic layers showed potential to consume atmospheric methane

Methane uptake rates of the incubated organic layer samples from the 1000 m site confirmed the widely accepted notion that organic layers consume only little, if any, atmospheric CH_4 (Adamsen & King 1993; Brumme & Borken 1999; Butterbach-Bahl & Papen 2002b; Saari et al. 1998). In contrast, organic layer samples from the 2000 m and 3000 m site revealed substantial potential for oxidizing CH_4 at atmospheric concentrations. Largest uptake rates were found in the lowermost organic layers just above the mineral soil suggesting a high abundance of methanotrophic bacteria in these samples (Chapter 3). This deep location of the maximum CH_4 uptake capacity is remarkable. It may result form ammonia inhibition in the upper organic layers or from the sensitivity of microorganisms to temperature and moisture changes, which are larger in the upper organic layer (Butterbach-Bahl & Papen 2002b; Schnell & King 1994). Potential uptake of atmospheric CH_4 in the underlying mineral soil was lower than in the lower organic layers, possibly because of the better aeration of the latter. Contradicting hypothesis 6, soil organic layers may strongly influence the CH_4 budget of tropical montane rain forests.

5.2 Implications for ecosystem response to environmental change

The results obtained in this study show that nutrient and C cycling of TMFs is not spatially homogeneous throughout the ecosystem. This implies that environmental changes such as elevated N input or climate change have different impact on TMFs not only at different elevations, but also at distinct topographic positions. Forests at lower slope positions reveal more open N cycles and might therefore respond more sensitively to elevated N input, with enhanced gaseous and leaching losses of N. In contrast, the tight N cycling and high net microbial N immobilization at ridge positions and at higher elevations might not be overcome for some time. Elevated N input may also lead to higher CH_4 uptake rates on the ridges, as this process was shown to be N limited, whereas ammonia inhibition of CH_4 oxidation might gain importance at the lower slopes. Improved litter quality and enhanced mineralization and nitrification rates following elevated N input might lead to a decrease of organic layer thickness and to changes in carbon sequestration. Enhanced mineralization rates and nutrient availability following N fertilization may increase gross primary productivity and change carbon allocation pattern along the elevational and topographic gradients. They might result in a shift from belowground to aboveground C allocation and to primarily in increasing aboveground C allocation at less nutrient-limited sites, whereas higher gross primary productivity might lead to an overall increment of belowground and aboveground productivity at stronger nutrient limited sites.

Predicted increases in air temperature and atmospheric CO_2 concentrations are likely to affect biochemical cycling and ecosystem functioning, although possibly less pronounced in the tropics compared to other biomes. Especially decomposition rates in tropical forest soils have been shown to be sensitive to temperature changes. One possible consequence of higher decomposition rates, resulting from temperature increases are higher soil respiration rates and a decline in soil carbon storage. To which degree increasing net primary productivity and increased plant C fixation balance the additional C losses is regulated by the availability of potentially limiting nutrients. Another consequence of higher decomposition rates is the increase in nutrient availability especially of N, which is covalently bonded with C in the organic matter. Enhanced N availability influences forest growth, carbon storage, and also trace gas fluxes. One possible scenario following elevated atmospheric CO_2 concentrations and higher temperatures might include higher net primary productivity at less nutrient limited sites, which, on longer time

scales, could lead to nutrient limitations and the change in carbon allocation from aboveground to belowground plant structures. Enhanced decomposition of the organic matter accumulated at the ridge positions and higher altitudes lead to higher nutrient availability, to a decrease in soil carbon storage and possibly to higher leaching and gaseous nutrient losses. However, predicting the consequences of temperature increase and higher atmospheric CO_2 concentrations on forest productivity and carbon allocation is difficult due to complex feedback processes between soil organic matter, soil microorganisms and plants and due to the high tree species diversity of the study area. Different tree species have been shown to react differently on nutrient additions in a close-by nutrient manipulation experiment. While some species showed increased growth and litter productivity following fertilization on a nutrient limited site, other tree species did not. Less speculative is the implication that plant species distribution may change due to higher nutrient availability and higher temperatures. Lowland species may infiltrate to higher elevations and fast growing, nutrient demanding species might replace slow growing, well adapted plant species from the ridge forests. Such shifts in plant species composition could lead to the disappearance of very specialized species and to a decrease in plant diversity of TMFs.

5.3 Suggestions for future research

The results obtained in this study contribute to the understanding of nutrient and carbon cycling of tropical montane forests and provide valuable information for the prediction and modeling of their soil trace gas fluxes. For future research I suggest to focus on the investigation of processes involved in soil N and C turnover and allocation, which will allow for an improved estimation of environmental change impacts on TMF ecosystems. The following important, open and new questions arising from this study should be addressed.

What is the total amount of N turnover and N retention rates?

While net mineralization and nitrification rates, are a good index for plant available N, they do not reveal the total amount of N turnover and N retention rates in the soil. Central processes of the N cycle, such as gross mineralization, immobilization and nitrification, have been successfully investigated by means of the ^{15}N pool dilution technique (Corre et al. 2003;

Davidson et al. 1991; Sotta et al. 2008). Additionally, ^{15}N tracing using small amounts of highly enriched $^{15}NH_4^+$ give insight into the pathway of mineralized nitrogen, the immobilization and leaching as well as gaseous losses. These methods might also provide information on the specific role of the organic layer for N transformation processes and provide a more appropriate measure to characterize possible inhibition of CH_4 uptake in the upper organic layers than the traditionally used soil extractable ammonium.

Where is main soil N turnover concentrated and does this location change with topographic position along the elevation gradient?

Natural abundances of ^{15}N of forest ecosystems can also be consulted for further investigation of the soil N cycle (Poertl et al. 2007). Several microbial processes in the soil discriminate against the isotopically heavy ^{15}N isotope (Mariotti et al. 1981; Nadelhoffer & Fry 1988). Hence, faster mineralization rates lead to relatively higher ^{15}N enrichment of the residual material, reflecting cumulative N losses (Hogberg and Johannisson 1993) and indicating openness of the ecosystem N cycle (Vitousek et al. 1989). In forest soil profiles, δ^{15}N signatures have been shown to shift to more enriched values with depth, indicating faster mineralization of isotopically depleted organic N in the upper soil layers and an enrichment of residual soil organic matter in ^{15}N at deeper depths (Nadelhoffer & Fry 1988; Vervaet et al. 2002). I expect less negative enrichment factors for sites with slower N cycling. First calculations with data from my study site suggest that N cycling may be decoupled from the mineral soil. Natural abundance of ^{15}N data and enrichment factors of our study site could be combined with data from the nearby fertilization experiment to explore if nutrient application stimulates soil N cycling and possibly reduces the decoupling of mineral soil and organic layer.

How is carbon partitioned between plant organs and how do these pattern change with elevation and along topographic gradients?

Isotopic tracer techniques may also be used for a more direct estimation of belowground C allocation. Plain et al. (2009) and Hogberg et al. (2010) presented approaches to pulse-label full-grown single trees or even forest patches in situ over a time period of a few hours. Trees exposed

to a ^{13}C-CO$_2$ labeled atmosphere take up the labeled ^{13}C and translocate it into plant tissues including roots, from where it becomes available to soil microorganisms. Measuring ^{13}C in leaves, roots, soil microorganisms and soil CO$_2$ efflux may help to understand C partitioning. This approach allows for tracing C fluxes to different groups of soil organisms and determination of residence times in different tree and soil compartments. Consequently it may facilitate estimations on the contribution of TMF in terms of belowground C sequestration. Although this approach is methodologically challenging it might improve estimates received from indirect methods such as root washing, determination of root biomass and root necromass, by including root exudation and mycorrhizal fungi. Other tracing methods, such as the injection of ^{13}C labeled glucose into plant tissues, might be easier to handle and lead to similar results, but they imply an additional carbon input to plant tissue.

Which mechanisms are responsible for the deep location of the maximum CH$_4$ oxidation potential in soil organic layers at high elevations?

The deep location of the maximum CH$_4$ oxidation potential in soil organic layers may be a result of one or both of the following mechanisms. First, in the upper organic layer the potential to oxidize diffusing atmospheric CH$_4$ is reduced due to processes, such as NH$_4^+$ inhibition, or adverse soil conditions impeding microbial growth. Second, water logging of the underlying mineral soil after heavy rainfall creates anaerobic conditions, and temporally turns the mineral soil into a CH$_4$ source. Evidence for possible NH$_4^+$ inhibition may be provided by the determination of gross mineralization and nitrification rates, as well as the measurement of NH$_4^+$ concentrations in the upper organic layer. Frequent measurements of soil-air CH$_4$ concentrations could be conducted to examine a possible reverse of soil functioning as CH$_4$ sink into a source after wet periods. Additionally, chloroform fumigation extraction of soil samples, the identification of microbial bacteria, analysis of phospholipid fatty acids composition and DNA extractions from cell cultures may provide information on the abundance and type of methanotrophic bacteria in different soil depths. This data may contribute to the identification of a prevailing form of methanotrophic oxidation (low or high affinity oxidation) in the respective soil depths.

In addition to process-based investigations fertilization experiments including N, P and K additions could be realized at the different topographic positions along the elevation gradient. The results of such experiments allow for a more direct investigation of the respective nutrient limitations on plant growth, plant regeneration dynamics and bacterial activity. Furthermore, nitrogen fertilization experiments are valuable to examine possible impacts of elevated N-inputs on TMF ecosystem functioning, including trace gas fluxes, carbon sequestration, nutrient cycling and nutrient losses, forest productivity, regeneration dynamics and plant species composition.

5.4 References

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DECLARATION OF ORIGINALITY AND CERTIFICATE OF AUTHORSHIP

I, Katrin Wolf, hereby declare that I am the soil author of this dissertation entitled "Trace gas fluxes from tropical montane rain forest soils". It has not previously been submitted in any form for another degree at any university or other institute of tertiary education. Information derived from the published and unpublished work of other authors has been appropriately acknowledged in the text and a list of references is given in the bibliography. I certify that the manuscripts presented in the chapters 2, 3 and 4 have been written by me as first author.

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