# Primary production and nutrient cycling in lowland rainforests of the Golfo Dulce region

## Producción primaria y ciclo de nutrientes en bosques lluviosos de tierras bajas de la región de Golfo Dulce

Wolfgang WANEK, Sigrid DRAGE, Nina HINKO, Florian HOFHANSL,
Eva-Maria PÖLZ, Andrea RATZER & Andreas RICHTER

**Abstract**: Climate (rainfall, seasonality, temperature, and light) and soil fertility (geology, topography) exert the major controls on primary production in tropical rainforests. In this survey paper, we focus on the effect of topography and anthropogenic disturbance on forest primary production (litterfall, wood increment, and fine root production) and nutrient cycling (atmospheric deposition, through fall, stemflow, litter decomposition, soil nitrogen transformations) in the Esquinas forest, Piedras Blancas National Park, Costa Rica. Tree vegetation in the Esquinas forest showed the highest wood increments and among the highest litterfall rates published to date. These high rates of production are explained by high litterfall and decomposition rates, fast cycling of nutrients and continued supply of cations and phosphorus through high rates of weathering, tectonic uplift and erosion. The primary ravine forest showed the highest rates of primary production and the highest rates of nutrient cycling compared to secondary ravine forest and primary ridge forest. Topography had a major effect on soil fertility and plants responded by greater allocation to below-ground biomass and below-ground production to acquire soil resources at the ridge. Disturbance did not affect above or below-ground biomass >20 years later. However, biomass production was still greater than in primary rainforest on Inceptisols. Nutrient demand for biomass production evidently exceeded nutrient supply after disturbance as suggested by comparably higher nutrient use efficiencies than in primary forest in the same topographic position.

**Key words**: biomass, nutrient cycling, carbon stocks, productivity, lowland rainforest.

**Resumen:** Clima (lluvia, estacionalidad, temperatura y luz) y la fertilidad del suelo (geología, topografía) ejercen el control principal sobre la producción primaria en los bosques lluviosos tropicales. En este trabajo de investigación nos centramos en el efecto de la topografía y de las pertubaciones antropogénicas sobre la producción primaria del bosque (hojarasca, incremento de madera y producción de raices finas) y el ciclo de nutrientes (depositación atmosférica, precipitación directa, escurrimiento fustal, descomposición de la hojarasca, transformación del nitrógeno del suelo) en el bosque Esquinas, Parque Nacional Piedras Blancas, Costa Rica.

La vegetación arbórea en el bosque Esquinas mostró los mayores incrementos en madera y una de las mayores tasas de hojarasca publicadas hasta la fecha. Estas altas tasas de producción se explican por una elevada tasa de hojarasca y descomposición, rápido ciclo de nutrientes y un suministro continuo de cationes y P mediante altas tasas de desgaste, elevación tectónica y erosión. El bosque primario de barranco mostró una elevada tasa producción primaria y altas tasas en el ciclo de nutrientes comparado con el bosque secundario de barranco. La topografía tiene un importante efecto sobre sobre la fertilidad del suelo, y las plantas responden con una mayor producción y biomasa subterránea para adquirir los recursos del suelo. Las perturbaciones no afectan a la biomasa aérea o subterránea > 20 años más tarde. Sin embargo, la producción de biomasa fue aún mayor que en bosque lluvioso primario en Inceptisols. La demanda de nutrientes para la producción de biomasa, evidentemente superó la oferta de nutrientes después de una perturbación, tal como lo había sugerido comparativamente la alta eficiencia en el uso de nutrientes en un bosque primario en la misma posición topográfica.

**Palabras clave:** biomasa, ciclo de nutrientes, reserva de carbono, productividad, bosque lluvioso tropical de tierras bajas.

## Introduction

Tropical rainforests are key components of the global water and carbon cycles and are therefore highly relevant for global climatic processes. They account for an estimated 32% of terrestrial net primary production (NPP, FIELD et al. 1998). It is therefore of great interest to determine whether tropical rainforests act as sinks or sources of atmospheric carbon dioxide ($CO_2$) – a theme which is hotly debated (CLARK 2004). Micrometeorological measurements of ecosystem $CO_2$ exchange sug-

Stapfia **88**,
zugleich Kataloge der
oberösterreichischen
Landesmuseen
Neue Serie **80** (2008):
155-177

gest neotropical forests function as net $CO_2$ sinks (GOULDEN et al. 2004, LOESCHER et al. 2003, STEPHENS et al. 2007). Additionally, biometric measurements demonstrated increases in the above-ground standing biomass and net carbon sequestration in neotropical forest plots (BAKER et al. 2004a, MALHI et al. 2004, MILLER et al. 2004).

Net primary production and therefore also the sink capacity of tropical forests are controlled by several factors, whereof (1) soil fertility and (2) air temperature and precipitation are the most prominent (HARRINGTON et al. 2001, LOESCHER et al. 2003, VITOUSEK 1984, WORBES 1999). While the general relations between pedospheric and macroclimatic drivers and tropical forest productivity are well established, recent studies have uncovered large uncertainties in our understanding of tropical carbon and nutrient cycling processes, most prominently related to seasonal and intra-annual variations in climate (MOHAMED et al. 2004). For instance, inverse modelling of atmospheric $CO_2$ concentrations and long-term tree growth measurements revealed a clear climate signal in the productivity and sink strength of tropical rainforests (CLARK et al. 2003, POTTER et al. 2004, POTTER & KLOOSTER 1999). ENSO (El Nino Southern Oscillation) phenomena have reversibly turned the tropical biome from a sink into a source of atmospheric $CO_2$ (BOUSQUET et al. 2000). Efforts to detect responses of tropical forests to long-term climate change are increasing and the first signs thereof cannot be neglected (HIETZ et al. 2005, PHILLIPS 1996, PHILLIPS et al. 1998). Evidence for correlations between global primary productivity and short-term climate fluctuations are also accumulating (BEHRENFELD et al. 2001, BOUSQUET et al. 2000, CAO et al. 2004, POTTER & KLOOSTER 1999, RODENBECK et al. 2003). However, we lack a mechanistic understanding of the linkage between inter-annual climate variability, biogeochemical processes and the primary productivity of tropical rainforests (NEPSTAD et al. 2002, YAVITT et al. 1993). WOOD et al. (2005), for instance, demonstrated seasonal and inter-annual changes in leaf litter phosphorus in La Selva, which were linked to precipitation patterns and therefore indicated a linkage between vegetation, nutrient availability and uptake.

More than 10% of tropical land area has a slope exceeding 10° (PORDER et al. 2005a). Topography has therefore received increasing interest with regard to effects on microclimate, species composition, soil and vegetation chemistry, and hydrological and biogeochemical processes (CLARK et al. 1998a, PORDER et al. 2005b, SOLLINS 1998). For instance it has been demonstrated that topography greatly affects soil nutrient concentrations, decomposition rates and soil nutrient transformations (CLARK et al. 2002, COX et al. 2002, LUIZAO et al. 2004, SILVER et al. 1994). Heterogeneity in plant and soil patterns are mainly based on erosion-deposition processes, down-slope transport of leachates, and levels of chemical weathering (DYKES & THORNES 2000, PORDER et al. 2005b). It is therefore highly likely that topography also exerts a major control on net primary production (VIEIRA et al. 2004, WANG et al. 2003).

Anthropenic disturbance and land use change are among the factors most seriously affecting the biogeochemical functioning of tropical areas. Conversion of land proceeds at unprecedented rates, resulting in about 30% of the forest cover in Costa Rica ultimately being considered to be secondary forest (FAO 2000). Conversion of forest to pasture and logging activities lead to progressive losses of organic matter and to net $CO_2$ release through biomass burning and soil organic matter mineralisation, the affected pools recovering only slowly over decades (HUGHES et al. 2000, HUGHES et al. 1999, MCGRATH et al. 2001, PREGITZER & EUSKIRCHEN 2004). Moreover, due to the absence of trees with large diameter stems that hold a disproportionately large amount of total biomass secondary forests accumulate less biomass (and nutrients) in their above-ground plant parts during the first 20 years following degradation (GUARIGUATA & OSTERTAG 2001).

In the following part of this survey paper, we present data on primary production and nutrient cycling based on a case study in the Esquinas forest, Piedras Blancas National Park, Costa Rica and discuss general patterns in tropical rainforest biogeochemistry. There is still a large gap in studies of nutrient cycling in areas of high precipitation and temperature where forest NPP was reported to decline (SCHUUR 2003). Many of these forests stand on highly leached and weathered Oxisols and similar nutrient-poor soils. The Esquinas forest is therefore 'outstanding' in terms of high mean annual precipitation (>5800 mm) and temperature and the dominance of Inceptisols and Ultisols that are richer in nutrients than Oxisols.

## Case study

To study net primary productivity (NPP) in relation to (1) land use history, (2) topography, and (3) inter-annual climate changes, three forest types were selected in the Esquinas Forest ("Regenwald der Österreicher"), Piedras Blancas National Park, close to the Tropical Station (8°42'46" N, 83°12'90" W; 80-200 m above sea level) in February 2005. Within each forest type, i.e. primary ridge forest, primary ravine forest and secondary ravine forest, three sites were selected and subdivided into each four small plots (0.01 ha each). Secondary stands were formerly used as cacao plantations and for tree logging but have remained undisturbed for over 20 years. Primary ridge forest stands differ markedly from those along creeks in their microclimate due to the greater canopy openness and lower relative air humidity. Soils of ridge areas were classified as Acrisols (Ultisols) with 71% sand, 22% silt and 7% clay, soil pH ($CaCl_2$) ranging between 3.7 and 4.7, a cation exchange capacity of 13.1 cmol $kg^{-1}$ and base saturation decreased from 87% to 11% with soil depth to 0.5 m. Valleys are characterised by Cambisols (Inceptisols) with 36% sand, 30% silt, 34% clay; soil pH ranged between 4.7 and 5.0, the cation exchange capacity was 21.1 cmol $kg^{-1}$ and base saturation 93%. All trees greater than 10 cm d.b.h. (diameter at breast height) were tagged and their taxonomic affiliation determined to species level. Trees greater than 2.5 cm d.b.h. were included in this study in every fourth subplot. Tree height, tree girth (circumference), annual wood increment (dendrometer bands) and tree position in the plots were measured. Leaf area index was estimated using the SunScan system with BF3 sensor as a reference (Delta-T). Total above-ground standing biomass and stand-level wood growth were calculated using allometric equations (BROWN 1997); tree size distribution, tree gaps and litter stocks were recorded regularly through annual or half-yearly censuses. Wet and dry deposition, throughfall and stemflow and litterfall were monitored by standard methods, and fine root turnover was investigated by ingrowth cores, sequential coring and $^{15}N$ labelling (HENDRICKS et al. 1997). Litter decomposition, N transformation rates and soil respiration were studied. Microclimate data loggers were installed in the understory and in topsoil of each forest stand to continuously record air and soil temperature and moisture. At the field station, a fully automatic weather station monitors air temperature, relative humidity, precipitation intensity, PAR and global radiation. To better understand forest biomass and nutrient dynamics under current and future climate conditions, the project aims at a long-term (>10 years) analysis of climate patterns, net primary production and nutrient cycling. Details on vegetation composition and structure, climate and microclimate of the forest sites are presented in this volume.

## Net primary production and biomass distribution

BIOMASS DISTRIBUTION. – In general, total dry biomass for primary lowland wet/moist tropical forests ranges from 200 to 500 (1000) $Mg^{2+}$ $ha^{-1}$ (Table 1, and WADSWORTH 1997). Biomass allocation to different plant parts (foliage, branches, stems, roots) depends on the type of forest (climate, geology), tree size and species, and varies vertically within the rainforest canopy. Commonly, the major part of tree mass is found in stems, comprising 50-58% of total biomass and 67-77% of above-ground biomass of trees with d.b.h. > 10 cm. The proportion of branches varies widely from 23 to 34% of above-ground tree biomass. Foliage makes up the smallest fraction of above-ground tree biomass, ranging between 1 and 5%, however, yielding leaf area ratios (leaf area projected onto the soil surface) between 5 and 12 (22) (WADSWORTH 1997). Root biomass is also highly variable (VOGT et al. 1996), but on a global scale averages 19% of total forest biomass for tropical upland forests (CAIRNS et al. 1997). Again the most active part of below-ground biomass i.e. fine roots represents a small proportion, comprising 1-8% of total tree mass (VOGT et al. 1996). The relative biomass allocation between roots and shoots varies with stand/tree age and is a function of tree species or functional group. It is moreover affected by soil moisture, nutrient availability and texture (for refs. see CAIRNS et al. 1997). In extreme cases such as in tropical forests on Spodosol below-ground biomass can contribute 41-88% of total biomass (SANFORD & CUEVAS 1996).

In the Esquinas forest, below-ground allocation of tree biomass ranged from the lowest reported so far, 0.9 and 1.0% of total tree mass in the primary and secondary ravine forest plot to 2.2% in the primary ridge forest plot (Table 1). The low proportion of root biomass therefore points to the comparably low restriction of biomass production by below-ground reserves such as water and nutrients. Total above-ground biomass in the examined forests types in the Esquinas region ranged between 335 and 354 $Mg^{2+}$ $ha^{-1}$ and were among the higher values reported so far for 'undisturbed' tropical lowland rainforests (Table 1). However, the small area investigated (0.4 ha, n=3) is low for precise estimations of landscape scale variation in biomass distribution, and variances of the means were high.

The leaf area index (LAI, in $m^2$ projected leaf area $m^{-2}$ ground) is an important biomass proxy for photosynthetically active leaf area and scales globally with NPP (CHAPIN III et al. 2002, LINDROTH et al. 2008). In the Esquinas region, LAI was generally high and primary ravine forests had significantly higher LAI (8.3±0.3, n=60) than secondary ravine forests (6.9±0.2) and primary ridge forests (7.1±0.2). Landscape scale measurements of LAI at La Selva, Costa Rica, across 500 ha old-growth forest gave lower values with 6.0±0.3 (CLARK et al. 2008). Along an elevational transect (1050 to 3060 m a.s.l.) in Ecuador, LAI decreased from 5.1 to 2.9 while leaf lifespan increased with elevation and leaf biomass was not affected by elevation (MOSER et al. 2007).

**Table 1**: Biomass and necromass (dry matter) distribution in neotropical rainforests.

| Site | Forest/soil type | Rainfall (mm a$^{-1}$) | Altitude (m a.s.l.) | Above-ground biomass | Fine live roots | Coarse live roots | Root biomass | Soil organic matter (Mg$^{2+}$ ha$^{-1}$) | Soil depth | Coarse litter | Fine litter | Root necromass | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Esquinas. Costa Rica | Inceptisol. primary | 5850 | 90 | 335±87 | 1.3±0.8 | 2.1±3.6 | 3.4 | 215±18 | 30 | 2.7±1.0 | 3.5±0.5 | 1.2±0.9 | this study |
| Esquinas. Costa Rica | Inceptisol. secondary | 5850 | 90 | 352±71 | 1.2±0.6 | 2.1±2.2 | 3.3 | 159±18 | 30 | 6.9±3.2 | 4.7±0.8 | 0.6±0.4 | |
| Esquinas. Costa Rica | Ultisol. primary | 5850 | 160 | 354±122 | 3.1±1.3 | 5.0±6.1 | 8.1 | 213±15 | 30 | 2.7±0.7 | 4.2±0.7 | 2.6±1.0 | |
| Review tropical forests | | | | | | | | 188±99 | | 35.0±31.8 | | | (Pregitzer & Euskirchen 2004) |
| Review tropical forests | tropical evergreen | | | | 3.3±0.5 | | | | | | | | (Jackson et al. 1997) |
| La Selva. Costa Rica | Ultisol | 4000 | 80-150 | 264±80$^{1}$ | | | | | | | | | $^{1}$(DeWalt & Chave 2004) |
| La Selva. Costa Rica | Inceptisol | 4000 | 80-150 | 204±11 | 0.6-1.1$^{2}$ | | 2.4$^{3}$ | 370-448$^{7}$ | 100 | 52.8$^{7}$ | | | $^{2}$(Gower 1987) |
| Barro Colorado Island. Panama | Oxisol | 2600 | 120 | 232±38$^{1}$ | | | | | | | | | $^{3}$(Powers 2004) |
| Barro Colorado Island. Panama | Alfisol | 2600 | 120 | 196±54 | 3.5$^{4}$ | | 2.8$^{3}$ | | | | | | $^{4}$(Yavitt & Wright 2001) |
| Cocha Cashu. Brazil | Ultisol | 2165 | | 310±36$^{1}$ | | | | | | | | | |
| Cocha Cashu. Brazil | Entisol | 2165 | | 474±46 | <4.6$^{5}$ | | 5.0$^{3}$ | | | | | | $^{5}$(Powers et al. 2005) |
| KM41. Brazil | Spodosol | 2650 | | 263±68$^{1}$ | | | | | | | | | |
| KM41. Brazil | Oxisol | 2650 | | 276±21 | | | 8.0$^{3}$ | | | | | | |
| Tapajos. Brazil | Oxisol | 2000 | | 291-305 | 3.4-4.2 | 30-33 | 34-36 | | 12 (6) m | | | | (Nepstad et al. 2002) |
| KM80 Manaus. Brazil | 20 plots | 1900-3500 | 50-100 | 339-421 (398±30) | | | | | | | | | (Nascimento & Laurance 2002) |
| Marena plots. Panama | 54 plots | 1890-4000 | 20-810 | 169-464 (246±60) | | | | | | | | | (Chave et al. 2004) |
| Barro Colorado Island. Panama | | 2600 | 120 | 287 | | | | | | | | | (Chave et al. 2003) |
| Panama Canal. Panama | primary. 15 plots | | | 258 | | | | | | | | | (Condit et al. 2004) |
| Panama Canal. Panama | secondary. 4 plots | | | 278 | | | | | | | | | |
| La Selva. Costa Rica | primary. 18 plots | 4000 | 80-150 | 161 | | | | | | | | | (Clark & Clark 2000) |
| La Selva. Costa Rica | secondary. 2 plots | 4000 | 80-150 | 79-129 | | | | | | | | | (Nicotra et al. 1999) |
| Nouragues. French Guyana | 70 + 12 ha plot | 2760 | 200-400 | 230-416 (301±32) | | | 75±45 | | | | | | (Chave et al. 2001) |
| NW Amazonia | 20 plots | | | 182-259 (277±26) | | | | | | | | | (Baker et al. 2004a, Baker et al. 2004b) |
| C & E Amazonia | 17 plots | | | 250-379 (341±38) | | | | | | | | | |
| SW Amazonia | 19 plots | | | 125-289 (246±42) | | | | | | | | | |
| Puerto Rico | primary. 3 plots | 2000 | 730 | 173±33 | | | | | | | | | (Marin-Spiotta et al. 2007) |
| Puerto Rico | secondary. 10-80 yrs | 2000 | 730 | 53-272 | | | | | | | | | |
| Puerto Rico | wet tabonuco | 3500 | | 226 | | | 75 | | | | | | data compiled by (Cairns et al. 1997) |
| Puerto Rico | lower montane | 3920 | | 198 | | | 65 | | | | | | |
| Surinam | lowland | 2250 | | 415 | | | 66 | | | | | | |
| French Guyana | lowland | | | 323 | | | 42 | | | | | | |
| Venezuela | montane humid | 1500 | | 348 | | | 56 | | | | | | |
| Puerto Rico | lower montane | 3725 | | 223 | | | 69 | | | | | | |
| Brazil | lowland | 1770 | | 406 | | | 69 | | | | | | |
| Porce region. Colombia | primary. 33 plots | 2080 | 900-1500 | 259±41 | | | 83.6±17.3 | 176±5 | 30 | 14.7±2.2 | 7.3±0.9 | | (Sierra et al. 2007a)$^{6}$ |
| Porce region. Colombia | secondary. 77 plots | 2080 | 900-1500 | 46±4 | | | 25.5±3.1 | 131±5 | 30 | | | | |
| Los Tuxtlas. Mexico | primary | >4000 | 100-300 | 363±45 | | | | 376±29 | 100 | 14±5 | 6±0.4 | | (Hughes et al. 1999) |
| Los Tuxtlas. Mexico | secondary. 1-50 yrs | >4000 | 100-300 | 5-287 | | | | 252-489 | 100 | 0-13.5 | 2.1-7.7 | | |
| Venezuela | moist to montane forests | 1400 -3200 | 270 -3000 | | | | | | | 13.5-76.6 | | | (Delaney et al. 1998) |
| | | | | | | | | | | 9.5 (4.7-33.0) | | | (Martius & Bandeira 1998) |

$^{2}$Dead+live fine root biomass $^{3}$Root biomass 0-40 cm. Powers & Lerdau. pers. Obs. $^{6}$Back calculation of biomass from C pools by division by 0.45 (biomass) and 0.55 (SOM) $^{7}$Clark et al. 2002

NECROMASS AND ORGANIC MATTER DISTRIBUTION. – The main above-ground dry mass pools in a tropical rainforest are trees with d.b.h. >10 cm and the forest floor litter layer, whereas below-ground the root-mycorrhizae system and the mineral soil including soil organic matter represent the major organic matter pool. In the Esquinas forest, fine litter stocks ranged from 3.5 to 4.7 Mg$^{2+}$ ha$^{-1}$, coarse litter stocks from 2.7 to 6.9 Mg$^{2+}$ ha$^{-1}$, coarse woody debris (CWD, >10 cm diameter; data not shown) were largest and ranged from 21.1 to 26.2 Mg$^{2+}$ ha$^{-1}$, and root necromass contributed 0.6 to 2.6 Mg$^{2+}$ ha$^{-1}$ (Table 1). High necromass in CWD was also found in La Selva, Costa Rica (28.8 Mg$^{2+}$ ha$^{-1}$) (CLARK et al. 2002) and in undisturbed forests in Tapajos, Brazil (51-56 Mg$^{2+}$ ha$^{-1}$) (KELLER et al. 2004).

Expressed as a fraction of total carbon stock (dry mass × 0.45 for biomass and necromass carbon, dry mass × 0.55 for soil organic matter carbon) above-ground biomass contributed 54% to 59%, soil organic matter 34% (secondary forest) to 41%, below-ground biomass 0.5% to 1.2% and necromass 4% to 7%. Total carbon stocks were 257 Mg$^{2+}$ ha$^{-1}$ (secondary ravine forest) and 291-296 Mg$^{2+}$ ha$^{-1}$ (other forest types) to a soil depth of 30 cm in this study. In comparison, the mean total carbon stock for primary forests in Porce region, Colombia, was estimated to be 384±56 Mg$^{2+}$ C ha$^{-1}$ where soil organic carbon (0-4 m) provides 59%, below-ground carbon 10%, above-ground biomass 29% and standing litter stock 2% of the total carbon stock (SIERRA et al. 2007a). For adjacent secondary forests, a mean total carbon stock of 228±13 Mg$^{2+}$ C ha$^{-1}$ was estimated, with 84% in the soil organic carbon pool, 5% in below-ground biomass, 9% in above-ground biomass and 1% in standing litter stock (SIERRA et al. 2007a). Calculated to a soil depth of 30 cm, above-ground biomass in primary rainforests contributed 44%, necromass 3%, below-ground biomass 15% and soil organic matter 38.3% (total carbon stock 252 Mg$^{2+}$ ha$^{-1}$, SIERRA et al. 2007a), showing that the Esquinas forests had a higher proportion of above-ground biomass, similar soil organic matter but less below-ground biomass while the total carbon stocks were similar for primary rainforests.

PRODUCTIVITY. – Carbon balances and primary production of tropical forest have been studied in two ways, by (1) Eddy covariance measurement of $CO_2$ exchange between the forest and the atmosphere and by (2) long-term forest inventory records of biomass net changes (CLARK et al. 2001b). The data obtained by these approaches are often contradictory and it is therefore controversial whether tropical forests currently act as carbon sinks or sources.

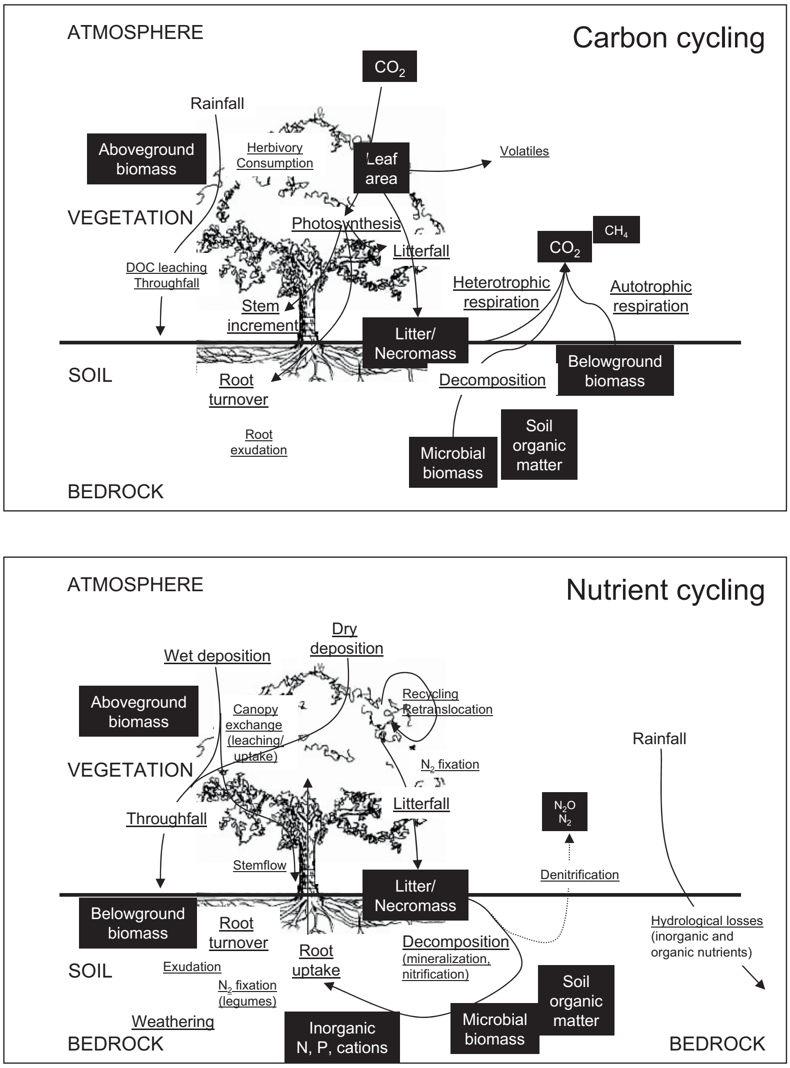

**Fig. 1**: Major pools and fluxes in the carbon and nutrient cycles of tropical rainforests. Fluxes are presented underlined, pools in black boxes.

Net primary production (NPP) is defined as the biochemical construction of new organic matter over a specific time interval (CHAMBERS et al. 2001). NPP is notoriously difficult to determine since the following component processes have to be considered to fully account for net primary production (NPP) in an ecosystem (CLARK et al. 2001a) (Fig. 1):

$NPP = NPP_{aboveground} + NPP_{belowground}$ , where

$NPP_{aboveground}$ is the sum of

above-ground increment (net increases in stem and branch wood and in leaves)

above-ground losses (fine litterfall + losses to consumers + volatile/leaching losses of organics), and

$NPP_{below\text{-}ground}$ is the sum of

below-ground increment (net fine and coarse root increment)

below-ground losses (root mortality + rhizodeposition + losses to herbivores and symbionts)

**Table 2**: Net primary production (dry matter) in neotropical forests.

| Site | Forest/soil type | Rainfall (mm $a^{-1}$) | Altitude (m a.s.l.) | Wood increment | Litterfall | Coarse litter prod. | TAG productivity ($Mg^{2+}$ $ha^{-1}$ $a^{-1}$) | Root production | tot NPP | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Esquinas. Costa Rica | Inceptisol. primary | 5850 | 90 | 15.0±3.9 | 13.0±2.8 | 0.4±0.2 | 28.4 | 1.8±0.4[1] (2.0[2]) | 30.2 | this study |
| Esquinas. Costa Rica | Inceptisol. secondary | 5850 | 90 | 24.6±4.2 | 10.7±1.2 | 3.5±0.4 | 28.8 | 1.6±0.4 (1.7) | 40.4 | [1]ingrowth cores |
| Esquinas. Costa Rica | Ultisol. primary | 5850 | 160 | 13.8±4.1 | 9.7±1.1 | 2.3±1.0 | 25.8 | 7.2±0.8 (2.1) | 33.0 | [2] by $^{15}N$ technique |
| Review tropical forests | | | | | | | | | 16.6±10.4 | (Pregitzer & Euskirchen 2004) |
| BCI. Panama | | 2600 | 120 | 7.2 | 12.1 | | | | | data compiled by (Malhi et al. 2004) |
| La Selva. Costa Rica | Inceptisol. Ultisol | 4000 | 80-150 | | 7.2-9.6 | 4.9[3] | | | | [3](Clark et al. 2002) |
| Tapajos. Brazil | Oxisol | 2000 | | 5.2 | 7.9 | | | | | |
| Bionte. Brazil | | | | 5.2 | 7.4 | | | | | |
| Caxiuana. Brazil | | | | 4.6 | 9.7 | | | | | |
| Mocambo. Brazil | | | | 5.1 | 9.9 | | | | | |
| Tapajos. Brazil | Oxisol. throughfall exclusion | 2000 | | 5.1-5.7 | 5.8-9.5 | 0.9-3.1 | 11.5-15.1 | | | |
| Fazenda Dimona. Brazil | | 2300 | | 4.4 | 8.4 | | 12.8 | | | |
| Paragominas. Brazil | | 1750 | | 2.6 | 9.2 | | 11.8 | | | |
| San Carlos. Venezuela | Oxisol | 3500 | 100 | 4.4 | 5.8 | | 10.2 | | | |
| Puu Kolekole. Hawaii | | 1210 | 2500 | 5.2 | 8.8 | | 14.0 | | | |
| Laupahoehoe. Hawaii | | 2500 | 1170 | 4.2 | 5.4 | | 9.6 | | | |
| Kohala. Hawaii | | 2500 | 1120 | 2.8 | 6.4 | | 9.2 | | | |
| Kokee. Hawaii | | 2500 | 1130 | 3.8 | 4.2 | | 8.0 | | | |
| Site 6. Hawaii | | 2600 | 1660 | 1.0 | 2.2 | | 3.2 | | | |
| Site 5. Hawaii | | 5800 | 700 | 0.6 | 1.8 | | 2.4 | | | |
| Chamela (low). Mexico | | 710 | 70-150 | 3.0 | 4.2 | | 7.2 | | | |
| Chamela (middle). Mexico | | 710 | 70-150 | 2.4 | 3.2 | | 5.6 | | | |
| Chamela (upper). Mexico | | 710 | 70-150 | 2.0 | 3.4 | | 5.4 | | | |
| Central Amazon. Brazil | 21 BIONTE/BDFFP plots | 2200 | 50-150 | 4.1±0.3 | 7.9±0.5 | 0.9±0.5 | 12.9 | | | (Chambers et al. 2001) |
| Piste de Saint-Elie. French Guyana | | 4000 | 0-100 | 2.9-3.2 | | 1.4-2.2 | | | | (Chave et al. 2001) |
| Hawaii. MAP transect | Inceptisol/Andisol | 2200 | 1300 | 0.5 | 9.0 | | 9.5 | 10.3[1] | | (Schuur & Matson 2001) |
| Hawaii. MAP transect | Inceptisol/Andisol | 5000 | 1300 | 0.0 | 4.5 | | 4.5 | 2.7 | | [1]soil respiration minus litterfall |
| Hawaii | control Eucalyptus plantation | 3600 | 350 | 19.6 | 8.2 | | 27.8 | 3.6 | | (Giardina et al. 2003) |
| Hawaii | fertilized Eucalyptus plantation | 3600 | 350 | 29.6 | 10.4 | | 40.0 | 5.4 | | |
| Hawaii. age gradient | 300 yrs | 1200 | 2500 | 5.0 | 5.5 | | 10.5 | 5.5[1] | | (Herbert & Fownes 1999) |
| Hawaii. age gradient | 1.4 $10^6$ yrs | 1200 | 2500 | 5.0 | 7.5 | | 12.5 | 6.0 | | [1]soil respiration minus litterfall |
| Porce region. Colombia | Entisol/ultisol. 33 plots. 2 years | 2080 | 900-1500 | 5.9-6.6 | 4.6-4.8 | (12.1) | 10.9-14.6 | 1.2-2.2 | | (Sierra et al. 2007b) |
| Neotropics. S-America | 104 RAINFOR plots | | | 3.0-11.0 (6.2) | | | | | | (Malhi et al. 2004) |
| Pico del Este. Puerto Rico | dwarf cloud forest | | 1000 | 0.45 | 3.1 | | 3.6 | 0.15 | | (Weaver et al. 1986) |
| Hawaii | | 2600-6000 | 760-1660 | 0.9-4.7 | 2.3-6.1 | | 5.8-10.8 | 4.2-6.0[1] | | (Raich 1998) |
| BCI. Panama | | 2600 | 120 | 5.3-7.1 | | | 0.5 | (+mortality 6.0) | | (Chave et al. 2003) |
| Santarem. Rio Branco. Manaus. Brazil | | | | | 3.8-5.2 | | | | | (Vieira et al. 2004) |
| Tapajos. Brazil | Oxisol. control plots | 2000 | | 5.3-5.8 | 5.8-6.6 | 1.2 | 11.5-11.9 | | | (Nepstad et al. 2002) |
| Tapajos. Brazil | | 2000 | | | | | | 1.5-2.3 | | (Silver et al. 2005) |
| San Carlos. Venezuela | Bana – Tierra Firme | 3570 | 100 | | | | | 2.4-11.2 | | (Cuevas & Medina 1988) |
| San Carlos. Venezuela | Oxisol | 3570 | 100 | | | | | 2.1 | | (Jordan & Escalante 1980) |
| San Carlos. Venezuela | gaps. understorey | 3500 | 120 | | | | | 0.1-4.7 | | (Sanford 1990) |
| BCI. Panama | | 2600 | 120 | | | | | 3.0 | | (Yavitt & Wright 2001) |
| BCI. Panama | | 2600 | 120 | | | | | 3.5 | | (Cavelier et al. 1999) |

Net increases in wood of stems and branches, fine and coarse litterfall, and net root increment generally comprise >80% of NPP and are therefore most often studied (CLARK et al. 2001b). Above-ground NPP is most frequently quantified as the sum of stand increment and litterfall. However, only few studies have reported estimates of below-ground NPP (BNPP) and above-ground NPP (ANPP) at the same time (see Table 2).

The major fractions of ANPP ranged from 1.8 to 12.0 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$ for fine litterfall, and from 0.6 to 11.0 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$ (plantations: 29.6) for stand increment. Caution has to be taken since some values of tree/stand increment did correct for tree mortality and in-growth, while others did not, thereby representing NPP of living trees only. The large wood increments in the Esquinas forest, ranging from 13.8 to 24.6 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$ are possibly related to the high productivity of this area but are also due to the absence of tree mortality (d.b.h. >10 cm) during the two observation years (2005-2007). Long-term tree fall in the area results in a forest turnover time of uphill forests of approximately 75 years (recensus of 0.1 ha plot after 13 years; Huber & Weissenhofer, pers. commun.) which is higher than the stand half-life of 34 years in La Selva (~2.0% mortality) (LIEBERMAN et al. 1985). An assumed annual mortality of 1% (median tree d.b.h. 28 cm) would result in a loss of live above-ground biomass of ~4 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$. Tree mortality will therefore significantly lower the long-term estimates of wood biomass increment in this forest. Moreover, wood increment was largest for the secondary forest (24.6 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$), demonstrating persistent biomass aggradation 20 years after disturbance. litterfall in the Esquinas forest was also among the highest reported so far (9.7-13.0 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$; Table 2), again pointing to the exceptionally high productivity in this area. LAI values between 6.9 and 8.3 also demonstrate the high potential for biomass production in the Esquinas forest. The high NPP in the Esquinas forest with a mean annual precipitation (MAP) of ~6000 mm actually contradicts the general trend in tropical forests where NPP increases up to MAP of 2500 mm and above that threshold decreases markedly (SCHUUR 2003). Again, this discrepancy can not be reconciled by climatic differences between this and other tropical forests but might be attributed to sporadic volcanic ash deposition (FIEBIG et al. 2007) and a combination of fast weathering and rapid land lift, tectonically-driven erosion leading to exposure of bed rock rich in P and other cations (BERN et al. 2005).

Other NPP components like above-ground losses by leaching, emissions of volatile organic compounds and losses to consumers have not been assessed though they may increase NPP estimates by >20% (CLARK et al. 2001b). Leaf herbivory accounted for 1.5% of total NPP in a recent study (SIERRA et al. 2007b) which may rise including other types of plant consumption such as sap-sucking, frugivory and herbivory by species other than ants. In this study canopy leaching of dissolved organic carbon (net throughfall) amounted to only 11±5 kg C $ha^{-1}$ $a^{-1}$, representing a minor portion of ANPP. Recently the importance of coarse litter production or structural losses e.g. branch fall and crown loss has been emphasised to comprise a quantitatively important component of ANPP, ranging from 0.9 to 4.9 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$ (Table 2) (CLARK et al. 2002) and up to 6.7 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$ in undisturbed Amazon forests (PALACE et al. 2008).

BNPP has been investigated by different methods e.g. root increment by sequential coring and root in-growth cores while total below ground C allocation was estimated by the indirect carbon balance method (difference between soil respiration and litterfall), thus actually representing the sum of root respiration and BNPP (RAICH & NADELHOFFER 1989). Both approaches yielded similar estimates (C balance: 2.7-10.3 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$; in-growth, coring: 1.3-11.1 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$), though they differ by the inclusion of root respiration in the C balance method (Table 2). Again, as reported above, for several components of BNPP, no data are available such as for rhizodeposition, root consumption by herbivores, and fine and coarse root production and mortality. These components may however account for a sizable portion of BNPP. The use of a $^{15}N$ tracer approach allows the differention of root production and mortality (HENDRICKS et al. 1997), producing similar figures (1.6-2.1 $Mg^{2+}$ $ha^{-1}$$a^{-1}$) for BNPP as by in-growth and sequential coring in two out of three forest types in the Esquinas forest.

The proportion of total productivity found below-ground varies considerably, ranging from 3% to 54% globally. In the tropics, broad-leaved evergreen forests on Oxisols (n=5) showed a relative fraction of below-ground NPP of total NPP of 49% (VOGT et al. 1996). In the Esquinas forest, this proportion was much lower, with 4 to 6% on the nutrient-rich Inceptisols at valley positions and 22% on nutrient-poor Ultisols on ridge positions (Table 2). The same pattern was also apparent for root biomass, implying greater C investments to below-ground where nutrients are scarce and aluminium toxicity may be high (FIEBIG et al. 2007).

In contrast to NPP, net ecosystem exchange (NEE) represents the net $CO_2$ flux from the ecosystem to the atmosphere and negative signs indicate ecosystem C uptake (CHAPIN III et al. 2002):

NEE = gross photosynthesis – (autotrophic respiration + heterotrophic respiration)

For tropical rainforests, little data is available on net ecosystem C exchange (NEE) over a full year. In a trop-

**Table 3**: Element fluxes in litterfall, bulk precipitation, throughfall and stemflow in neotropical rainforests. [1] litterfall dry mass calculated from litterfall C by dividing with 0.45

| Site | Forest/Soil type | Rainfall | Altitude | TF/SF | DW | $C_t$ | $N_t$ | $NO_3^-$ | $NH_4^+$ | DON | $P_i$ | $P_t$ | $H^+$ | $Na^+$ | $Mg^{2+}$ | $K^+$ | $Ca^{2+}$ | $Cl^-$ | S | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | (mm $a^{-1}$) | (m a.s.l.) | (% BP) | (kg element or dry mass $ha^{-1}$ $a^{-1}$) | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | |
| **Litterfall** | | | | | | | | | | | | | | | | | | | | |
| Esquinas. Costa Rica | Inceptisol. Primary forest | 5850 | 80 | | 13030 | 6040 | 180.0 | | | | | 9.88 | | 2.39 | 27.70 | 47.30 | 165.30 | | | this study |
| Esquinas. Costa Rica | Inceptisol. Secondary forest | 5850 | 80 | | 10670 | 4990 | 120.0 | | | | | 5.96 | | 2.20 | 18.00 | 39.10 | 150.00 | | | |
| Esquinas. Costa Rica | Ultisol. Primary forest | 5850 | 80 | | 9700 | 4470 | 100.0 | | | | | 4.43 | | 1.92 | 14.80 | 29.90 | 94.10 | | | |
| Mangrove. Belize | Mangrove | 930 | 0 | | 5200 | | 29.8 | | | | | 0.78 | | | 61.60 | 46.80 | 107.20 | | | (Hofmann et al., pers.commun.) |
| Monteverde. | | | | | | | | | | | | | | | | | | | | |
| Costa Rica | Cloud forest | 2300 | 1500 | | 7000 | | 93.0 | | | | | 6.00 | | | 15.00 | 12.00 | 115.00 | | | (Nadkarni & Matelson 1992) |
| Jamaica | Secondary | 2230 | 1300 | | | | 80.7 | | | | | 7.73 | | | | | | | | (McDonald & Healey 2000) |
| Mexico | tropical dry forest | 753 | 50-160 | | 3892 | | | | | | | 3.88 | | | 15.89 | 23.11 | 113.98 | | | (Campo et al. 2000, Campo et al. 2001) |
| Amazonia. Brazil | Forest edge | 1900-3500 | 50-100 | | 9500 | | 124.8 | | | | | 2.31 | | | 16.69 | 17.23 | 30.28 | | | (Vasconcelos & Luizao 2004) |
| Amazonia. Brazil | Forest interior | " | " | | 8820 | | 116.0 | | | | | 2.24 | | | 15.36 | 14.44 | 23.07 | | | |
| Amazonia. Brazil | Clayey soil | " | " | | 9310 | | 122.8 | | | | | 2.24 | | | 16.68 | 15.48 | 28.47 | | | |
| Amazonia. Brazil | Sandy soil | " | " | | 9000 | | 117.0 | | | | | 2.26 | | | 14.86 | 16.95 | 23.90 | | | |
| Amazonia. Brazil | Primary forest | | 44-50 | | 8715 | 4262 | 143.5 | | | | | | | | | | | | | (Martius et al. 2004) |
| Amazonia. Brazil | Secondary forest | | 44-50 | | 7380 | 4037 | 103.0 | | | | | | | | | | | | | |
| Cardoso Island. Brazil | Atlantic forest | 2200 | 140 | | 6310 | | 101.8 | | | | | 2.29 | | | 18.98 | 20.27 | 59.99 | | | (de Moraes et al. 1999) |
| Cardoso Island. Brazil | coastal lowland | 2200 | 0 | | 3930 | | 27.5 | | | | | 1.02 | | | 10.93 | 6.60 | 29.98 | | | |
| La Selva. Costa Rica | Inceptisol | 4300 | 80-150 | | 6600 | | 125.4 | | | | | 5.94 | | 3.30 | 13.20 | 21.78 | 52.80 | | 11.88 | (Wood et al. 2006) |
| La Selva. Costa Rica | Ultisol plateau | 4300 | 80-150 | | 7200 | | 115.2 | | | | | 5.04 | | 4.32 | 16.56 | 14.40 | 59.76 | | 12.24 | |
| La Selva. Costa Rica | Ultisol slope | 4300 | 80-150 | | 6500 | | 110.5 | | | | | 4.55 | | 3.90 | 13.00 | 15.60 | 46.15 | | 11.05 | |
| Colombia | Sedimentary plain | 3400 | 250 | | 6920 | | 78.9 | | | | | 1.10 | | 0.30 | 5.80 | 12.50 | 7.20 | | | (Tobon et al. 2004a) |
| Colombia | High terrace | 3400 | 250 | | 7640 | | 89.4 | | | | | 1.20 | | 0.20 | 7.00 | 19.90 | 10.70 | | | |
| Colombia | Low terrace | 3400 | 250 | | 8110 | | 107.8 | | | | | 2.40 | | 0.60 | 8.90 | 18.60 | 13.80 | | | |
| Colombia | Flood plain | 3400 | 250 | | 9770 | | 131.9 | | | | | 4.40 | | 1.50 | 18.60 | 30.30 | 69.40 | | | |
| Colombia | Lower montane forest | 1500 | | | 4300 | | 34.4 | | | | | 1.72 | | | | 15.05 | | | | Recalculated from data compiled by (Wood et al. 2006) |
| Trinidad | Mom excelsa forest | 1800 | | | 6900 | | 62.1 | | | | | 2.76 | | | 15.18 | 11.04 | 62.79 | | | |
| Brazil | Terra Firme | 1900 | | | 7300 | | 109.5 | | | | | 2.19 | | 5.11 | 14.60 | 14.60 | 18.25 | | | |
| Guatemala | Secondary Forest | 2000 | | | 10000 | | 140.0 | | | | | 7.00 | | | 35.00 | 24.00 | 212.00 | | | |
| Guatemala | Mature Forest | 2000 | | | 9000 | | 171.0 | | | | | 5.40 | | | 63.90 | 19.80 | 88.20 | | | |
| Panama | Tropcal moist | 2000 | | | 11300 | | | | | | | 11.30 | | 2.26 | 28.25 | 63.28 | 326.57 | | | |
| Colombia | Lower montane | 2500 | | | 7000 | | 77.0 | | | | | 4.90 | | | | 62.30 | | | | |
| Panama | Premontane wet | 2500 | | | 10500 | | | | | | | 16.80 | | 3.15 | 24.15 | 52.50 | 154.35 | | | |
| Colombia | Humid tropical | 3000 | | | 6600 | | 85.8 | | | | | 2.64 | | | 10.56 | 15.18 | 71.28 | | | |
| San Carlos. Venezuela | Terra Firme | 3565 | 120 | | 7600 | | 121.6 | | | | | 2.28 | | | 5.32 | 18.24 | 12.92 | | | |
| San Carlos. Venezuela | Tall Caatinga | 3565 | 100 | | 4000 | | 28.0 | | | | | 2.00 | | | 12.40 | 8.40 | 30.80 | | | |
| San Carlos. Venezuela | Bana | 3565 | 100 | | 2100 | | 12.6 | | | | | 0.42 | | | 5.25 | 9.87 | 15.54 | | | |
| Puerto Rico | Lower montane | 4200 | 750 | | 4800 | | | | | | | | | | 12.05 | 193.92 | 39.84 | | | |

| **Bulk precipitation** | | **Rainfall** | **Altitude** | **TF/SF** | **DW** | **DOC** | **$N_t$** | **$NO_3^-$** | **$NH_4^+$** | **DON** | **$P_i$** | **$P_t$** | **$H^+$** | **$Na^+$** | **$Mg^{2+}$** | **$K^+$** | **$Ca^{2+}$** | **$Cl^-$** | **S** | **Reference** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Esquinas. Costa Rica | Lowland | 5850 | 80 | | | 36 | 10.0 | 2.53 | 5.63 | 1.86 | 0.38 | | 1.44 | 9.97 | 4.47 | 9.28 | 17.28 | 8.64 | 4.71 | this study |
| Mangrove. Belize | Mangrove | 930 | 0 | | | 66 | 12.5 | 1.71 | 0.85 | 9.91 | 0.28 | | | 101.39 | 12.18 | 6.07 | 12.64 | 208.32 | 11.58 | (Wanek et al. 2007) |
| Yucatan. Mexico | Lowland | 1200 | 0 | | | | | 39.72 | 1.20 | | | | 0.55 | 28.80 | 3.12 | 1.32 | 3.12 | 47.64 | 12.72 | (Ceron et al. 2002) |
| Yucatan. Mexico | Lowland | 1200 | 0 | | | | | 1.92 | 1.08 | | | | 0.05 | 35.52 | 4.17 | 2.72 | 4.28 | 64.20 | 4.89 | (Bravo et al. 2000) |
| La Selva. Costa Rica | Lowland | 4000 | 35 | | | 28 | 9.6 | 2.30 | 3.36 | 3.98 | | | 0.18 | 25.02 | 3.60 | 2.82 | 5.45 | 46.86 | 9.50 | (Eklund et al. 1997) |
| Amazonia. Colombia | Lowland | 3400 | 200 | | | 134 | | 3.05 | 5.47 | | 0.32 | | 0.46 | 15.64 | 2.31 | 11.96 | 9.27 | 30.66 | 40.27 | (Tobon et al. 2004b) |
| Amazonia. Brazil | Lowland | 2500 | <100 | | | | 2.6 | | | | 0.75 | 0.80 | 0.23 | 25.76 | 3.77 | 3.23 | 5.71 | 54.58 | 6.26 | (Hölscher et al. 1998) |
| Amazonia. Brazil | Lowland | 2672 | <100 | | | | 5.3 | 1.35 | 1.61 | 2.39 | 0.02 | | | | 0.26 | 2.72 | 0.75 | | | (Schroth et al. 2001) |
| Amazonia. Brazil | Lowland | 2754 | <100 | | | 53 | 4.2 | 1.62 | 1.16 | 1.39 | 0.02 | 0.26 | 0.47 | 1.52 | 0.33 | 0.86 | 1.32 | 4.50 | 0.88 | (Williams et al. 1997) |
| Amazonia. Brazil | Lowland | 1983 | <100 | | | 38 | 2.2 | 0.92 | 0.33 | 0.97 | 0.01 | 0.18 | 0.22 | 0.96 | 0.24 | 0.54 | 0.95 | 3.24 | 0.51 | (Williams et al. 2004) |
| Amazonia. Brazil | Lowland | 2400 | <100 | | | | | | 0.49 | | | | | 0.74 | 0.06 | 0.38 | 0.58 | 1.79 | 2.45 | (Forti & Moreira-Nordemann 1991) |
| Rio Negro. Brazil | Lowland | 2083 | <100 | | | 28 | 8.3 | 3.45 | 0.82 | 0.44 | 0.31 | 0.30 | 0.21 | 2.44 | 0.37 | 0.73 | 2.46 | 1.56 | 3.13 | (Filoso et al. 1999) |
| Puerto Rico | Lower montane | 3407 | 390 | | | 219 | | 1.34 | 0.81 | | | 0.11 | | 55.64 | 7.45 | 3.20 | 11.61 | 106.43 | 16.95 | (McDowell et al. 1990) |
| Puerto Rico | Lower montane | 3500 | 390 | | | 34 | | 1.18 | 0.69 | | | 0.33 | 0.18 | 63.35 | 17.10 | 4.65 | 26.09 | 120.52 | | (McDowell 1998) |
| Panama | Montane | 3510 | 1200 | | | | 7.3 | | | | 0.70 | | | 63.51 | 4.06 | 13.51 | 27.87 | 34.50 | 13.16 | (Cavelier et al. 1997) |
| Colombia | Montane | 2115 | 2550 | | | | 18.0 | | 14.21 | | 0.72 | | | 24.13 | 3.24 | 7.94 | 10.09 | 19.37 | 26.27 | (Veneklaas 1990) |
| Colombia | Montane | 1453 | 3370 | | | | 12.2 | | 11.23 | | | | | 15.94 | 2.47 | 6.93 | 7.34 | 13.62 | 16.88 | |
| Costa Rica | Montane | 2812 | 2900 | | | | | 1.69 | 1.69 | | | | 0.14 | 4.53 | 1.09 | 6.71 | 4.51 | | | (Hölscher et al. 2003) |
| Costa Rica | Montane | 3191 | 1500 | | | | | 1.70 | 1.70 | | 0.05 | | 0.32 | 20.50 | 2.40 | 3.00 | 5.80 | | | (Clark et al. 1998c) |
| Ecuador | Montane | 2220 | 1900 | | | 91 | 5.9 | 1.13 | 2.64 | 0.19 | | 0.55 | | 18.99 | 1.24 | 3.73 | 3.92 | 11.90 | 0.36 | (Wilcke et al. 2001) |
| Mexico | tropical dry forest | 753 | 50-160 | | | | | | | | 0.16 | | | | 0.80 | 1.31 | 3.03 | | | (Campo et al. 2000) |
| **Throughfall** | | **Rainfall** | **Altitude** | **TF/SF** | | **DOC** | **$N_t$** | **$NO_3^-$** | **$NH_4^+$** | **DON** | **$P_i$** | **$P_t$** | **$H^+$** | **$Na^+$** | **$Mg^{2+}$** | **$K^+$** | **$Ca^{2+}$** | **$Cl^-$** | **S** | **Reference** |
| Esquinas. Costa Rica | Inceptisol. primary | 5850 | 80 | 88 | | 54 | 7.9 | 0.67 | 3.83 | 3.88 | 1.09 | | 0.26 | 5.11 | 6.73 | 49.88 | 18.62 | 12.20 | 3.63 | |
| Esquinas. Costa Rica | Inceptisol. second. | 5850 | 80 | 86 | | 50 | 7.5 | 0.44 | 4.12 | 2.99 | 0.51 | | 0.47 | 4.81 | 5.08 | 35.74 | 16.69 | 9.22 | 3.24 | this study |
| Esquinas. Costa Rica | Ultisol. primary | 5850 | 80 | 90 | | 43 | 6.0 | 0.62 | 2.63 | 2.73 | 0.31 | | 0.58 | 7.95 | 5.00 | 26.37 | 14.43 | 13.10 | 4.07 | |
| Mangrove. Belize | Mangrove | 930 | 0 | 84.5 | | 78 | 43.9 | 1.71 | 0.28 | 41.92 | 0.06 | | | 290.82 | 35.94 | 16.84 | 22.05 | 807.64 | 38.39 | (Wanek et al. 2007) |
| Puerto Rico | Lowland | 3500 | 390 | 59.0 | | 127 | | 0.18 | 3.35 | | | 0.38 | 0.01 | 81.22 | 26.85 | 51.59 | 45.36 | 142.22 | 0.00 | (McDowell 1998) |
| Amazonia. Colombia | Lowland, four forest types | 3400 | 200 | 87.0 | | 163 | | 9.81 | 11.43 | | 0.91 | | 0.36 | 16.33 | 5.82 | 37.47 | 10.43 | 23.94 | 56.02 | (Tobon et al. 2004b) |
| Amazonia. Brazil | Lowland | 2622 | <100 | 85.0 | | | 13.1 | | | | 0.18 | | | | 1.57 | 17.86 | 1.79 | | | (Schroth et al. 2001) |
| Amazonia. Brazil | Lowland | 2500 | <100 | 65.0 | | | 5.7 | | | | 0.81 | | 0.02 | 21.30 | 3.91 | 21.29 | 9.77 | 46.21 | 7.20 | (Hölscher et al. 1998) |
| Amazonia. Brazil | Lowland | 1983 | <100 | 84.0 | | 80 | 2.9 | 0.12 | 0.14 | 2.66 | 0.36 | 0.93 | | 2.87 | 2.67 | 8.66 | 17.42 | 15.43 | 2.83 | (Williams et al. 2004) |
| Amazonia. Brazil | Lowland | 2400 | <100 | 80.0 | | | | | 0.20 | | | | | 1.33 | 0.74 | 2.34 | 0.84 | 0.76 | 1.11 | (Forti & Moreira-Nordemann 1991) |
| Rio Negro. Brazil | Lowland | 2083 | <100 | 76.0 | | 0 | 35.0 | 2.74 | 0.66 | 6.56 | 2.12 | 1.55 | 0.05 | 3.83 | 2.70 | 27.70 | 5.54 | 5.38 | 5.13 | (Filoso et al. 1999) |
| Panama | Montane | 3510 | 1200 | 100 | | | 7.2 | | | | 2.15 | | | 131.18 | 7.60 | 63.22 | 35.07 | 49.60 | 6.07 | (Cavelier et al. 1997) |
| Colombia | Montane | 2115 | 2550 | 88.0 | | | 22.5 | | 16.75 | | 1.67 | | | 26.97 | 10.72 | 95.62 | 27.15 | 36.54 | 41.16 | (Veneklaas 1990) |
| Colombia | Montane | 1453 | 3370 | 82.0 | | | 10.5 | | 11.66 | | | | | 14.50 | 7.01 | 33.12 | 18.86 | 19.84 | 31.94 | |
| Costa Rica | Montane | 2812 | 2900 | 73.0 | | | | 9.03 | 0.82 | | | | 0.02 | 5.52 | 9.23 | 118.07 | 20.08 | | | (Hölscher et al. 2003) |
| Costa Rica | Montane | 3191 | 1500 | 65.0 | | | | 0.60 | 1.30 | | 0.48 | | 0.04 | 41.30 | 7.80 | 63.60 | 25.69 | | | (Clark et al. 1998b) |
| Ecuador | Montane | 2220 | 1900 | 43.0 | | 145 | 15.8 | 6.03 | 2.62 | 7.11 | | 4.30 | | 10.32 | 10.11 | 119.33 | 18.98 | 16.64 | 3.45 | (Wilcke et al. 2001) |
| Jamaica | Secondary | 2230 | 1300 | | | 254 | 11.0 | 2.27 | 4.81 | | 3.21 | 4.22 | | | | 67.62 | 21.55 | | | (McDonald & Healey 2000) |
| Mexico | tropical dry forest | 753 | 50-160 | | | | | | | | 0.35 | | | | | | | | | (Campo et al. 2000) |
| **Stemflow** | | **Rainfall** | **Altitude** | **TF/SF** | | **DOC** | **$N_t$** | **$NO_3^-$** | **$NH_4^+$** | **DON** | **$P_i$** | **$P_t$** | **$H^+$** | **$Na^+$** | **$Mg^{2+}$** | **$K^+$** | **$Ca^{2+}$** | **$Cl^-$** | **S** | **Reference** |
| Esquinas. Costa Rica | Inceptisol. primary | 5850 | 80 | 1 | | 2 | 0.2 | 0.01 | 0.05 | 0.11 | 0.01 | | 0.00 | 0.08 | 0.08 | 1.13 | 0.42 | 0.29 | 0.03 | |
| Esquinas. Costa Rica | Inceptisol. second. | 5850 | 80 | 1 | | 2 | 0.1 | 0.00 | 0.11 | 0.03 | 0.00 | | 0.00 | 0.07 | 0.17 | 1.16 | 0.29 | 0.29 | 0.03 | this study |
| Esquinas. Costa Rica | Ultisol. primary | 5850 | 80 | 1 | | 5 | 0.2 | 0.03 | 0.08 | 0.12 | 0.00 | | 0.01 | 0.20 | 0.30 | 1.55 | 0.48 | 11.20 | 0.13 | |
| Mangrove. Belize | Mangrove | 930 | 0 | 10.0 | | 121 | 6.8 | 0.15 | 0.11 | 6.50 | 0.01 | | | 28.58 | 2.88 | 1.66 | 2.08 | 96.90 | 5.65 | (Wanek et al. 2007) |
| Amazonia. Colombia | Lowland | 3400 | 200 | 2.0 | | 7 | | 0.32 | 0.63 | | 0.03 | | | 0.44 | 0.17 | 1.32 | 0.41 | 0.98 | 2.25 | (Tobon et al. 2004b) |
| Amazonia. Brazil | Lowland | 2500 | <100 | 23.0 | | | 1.0 | | | | 0.35 | | | 5.81 | 0.87 | 7.53 | 1.27 | 11.98 | 1.22 | (Hölscher et al. 1998) |
| Amazonia. Brazil | Lowland | 2622 | <100 | 1.0 | | | 0.2 | 0.03 | 0.04 | 0.13 | | | | | 0.04 | 0.21 | 0.03 | | | (Schroth et al. 2001) |
| Costa Rica | Montane | 2812 | 2900 | 2.0 | | | | 1.20 | 0.03 | | | | | 0.47 | 0.86 | 9.41 | 1.81 | | | (Hölscher et al. 2003) |

ical wet forest (La Selva, Costa Rica), net ecosystem-level carbon exchange was highly variable between years but not seasons, ranging from a slight carbon source (0.1 to –1.3 t C $ha^{-1}$ $a^{-1}$, 1998) to a moderate (–1.5 to –3.1 t C $ha^{-1}$ $a^{-1}$, 1999) and a strong carbon sink (–6.0 to –7.9 t C $ha^{-1}$ $a^{-1}$, 2000) (LOESCHER et al. 2003). The inter-annual changes were related to El Niño effects on the energy budget of this forest. Tropical moist forests in a Central Amazon rainforest exhibited annual NEE of –5.9 t C $ha^{-1}$ $a^{-1}$ (MALHI et al. 1998) and ranged from –1 to –8 t C $ha^{-1}$ $a^{-1}$ (ARAUJO et al. 2002). In a tropical moist forest in Tapajos, Pará, Brazil, large seasonal changes in NEE were found where $CO_2$ draw down was lower during the wet season than during the dry season, when litter respiration decreased due to litter desiccation (GOULDEN et al. 2004). The annual NEE flux was reported to be –3.9 t C $ha^{-1}$ $a^{-1}$ without correcting for the underestimation of flux on calm nights, indicated that the forest was a large carbon sink (MILLER et al. 2004). However, the above mentioned correction turned this forest into a slight C source (0.4 t C $ha^{-1}$ $a^{-1}$) (MILLER et al. 2004), pointing to large uncertainties in the annual NEE estimates in tropical rainforests (CLARK 2004). In Xishuangbana tropical rainforest, China, NEE was also higher in the dry season than in the wet season. The conversion between carbon sink and source occurred during the transition season. Annual NEE was –3.2 t C $ha^{-1}$ $a^{-1}$ (ZHANG et al. 2006).

NPP can be converted to NEE in the following way:

$NEE = NPP - R_h$, or $NPP = GPP - R_a$

where $R_h$ and $R_a$ are heterotrophic and autotrophic respiration and GPP is gross primary production. Heterotrophic respiration represents a large flux averaging 9.2 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$ in tropical rainforests (PREGITZER & EUSKIRCHEN 2004) and may equal or exceed NPP or be slightly lower than NPP. NEE therefore represents a small difference between two large fluxes, as shown by e.g. SIERRA et al. (2007b). They estimated NPP at 12.6±0.9 (2000-2001) and 12.9±1.0 t C $ha^{-1}$ $a^{-1}$ (2001-2002), and from measurements of different components of heterotrophic respiration (soil, fine litter, and coarse litter) estimated $R_h$ at –12.3±2.1 and –15.1±1.7 t C $ha^{-1}$ $a^{-1}$ for the respective time intervals. NEE therefore accounted for 0.3±1.2 (2000-2001) and –2.2±0.8 t C $ha^{-1}$ $a^{-1}$ (2001-2002). 95% confidence limits for the second intervals range from –1.9 to 2.6 t C $ha^{-1}$ $a^{-1}$, showing the large uncertainty in estimates of this globally important C flux. As outlined above, the interconversion of NEE and NPP for validation purposes remains difficult due to the many uncertainties in the measurement of both (CLARK et al. 2001a).

## Biogeochemistry and element input-output balances

Biogeochemistry represents the study of processes and reactions that govern the elemental composition of the natural environment, and the cycles of matter and energy. Nutrient cycling – the cycling of elements in ecosystems – describes fluxes of exchanging nutrients between pools in plants, soil, animals and decomposer micro-organisms (Fig. 1). In contrast to temperate forests, the greatest amount of organic matter and nutrients is stored in living biomass rather than the soil matrix, but contrary to predictions by earlier research, a substantial amount of organic matter and nutrients is contained in the below-ground rooting zone (Table 1) (WHITMORE 1998).

Despite many interactions among element cycles, substantial differences exist between the responses of different elements on specific controls. While processes such as nutrient uptake and release by plants and microorganisms are mostly governed by the same factors, input and losses occur along different pathways. The consequences are differences in the “openness” and “buffering capacity” of the main cycles of C, water, N and P (CHAPIN III et al. 2002). The carbon cycle is highly “open” but well “buffered” through the exchange of $CO_2$ with the atmosphere and its large pool in ecosystem biomass and soil organic matter. The water cycle also shows high “openness” caused by the dominating input and output fluxes, but lacks a notable storage capacity. Organisms therefore strongly depend on water input from precipitation and are less “buffered” against input deficiencies. In contrast, nutrient cycles are more closed in tropical rainforests with intensive internal cycling compared to relatively low inputs and losses (BRUIJNZEEL 1991, MCDOWELL 1998).

In the long term, the nutrient status of a tropical rainforest is controlled by the balance between nutrient inputs (deposition, weathering, and nitrogen fixation) and outputs (leaching, fixation, and volatilisation). During soil development, rock-derived elements are gradually lost (e.g. P, $Ca^{2+}$, $Mg^{2+}$, K) while being partly replenished from inputs from the atmosphere such as marine aerosols and dust (CHADWICK et al. 1999). Nitrogen represents a special case in that bedrock is (commonly) virtually N free and N is therefore introduced into soils and ecosystems by biological N fixation. Developing soils are therefore rich in cations and P but very low in N, resulting in N limitation or N:P limitation of plant production (HARRINGTON et al. 2001). With age, N accumulates in soils and vegetation, while deep weathering and leaching results in cation and P depletion, leading to P limitation of the productivity of old tropical rainforest ecosystems (HERBERT & FOWNES 1995, VITOUSEK & FARRING-

TON 1997). Phosphorus is further tied up in highly resistant organic compounds and by occlusion in secondary minerals. To understand the biogeochemical constraints of NPP, we therefore have to consider element input-output balances as well as the internal cycling of nutrients, both of which control the availability of essential nutrients to plant production. Nutrients also affect NPP or more generally C assimilation via stoichiometric constraints. For biomass production, higher plants need nutrients such as N and P in a specific ratio to C. The C:N:P ratio of tree foliage was 1.334:28:1 globally and 2.457:43:1 for tropical forests, reflecting lower P concentrations of tropical tree foliage (MCGRODDY et al. 2004). This also implies that globally rising atmospheric N and/or P deposition may not only promote NPP by increasing ecosystem N and P availability but may also trigger C sequestration in tropical forests, although this has not yet been demonstrated conclusively.

Nutrients are expected to limit NPP in different ways, by reducing leaf area index (LAI), by reducing photosynthetic capacity, or both (HARRINGTON et al. 2001). High NPP in tropical rainforests therefore indicates that the nutrient use by tropical forests is enhanced by several nutrient conserving mechanisms, increasing the retention of nutrients in the living or dead biomass pool (higher fraction of nutrient retranslocation, increased life span of fine roots and leaves, mycorrhizal association etc.). Plant species can also respond flexibly to changing nutrient availabilities e.g. by changing C allocation to leaf area or fine root production or by increasing nutrient retranslocation from senescent plant tissues (HARRINGTON et al. 2001, HERBERT & FOWNES 1999).

To maintain forest biomass and production at high levels, the trees' nutrient demands and ecosystem losses must therefore be met by internal recycling through nutrient release from decomposing fine litter, dead wood and roots, as well as from weathering and smaller inputs by wet and dry deposition and nitrogen fixation.

NUTRIENT INPUTS. – According to VITOUSEK (2004), weathering of primary minerals provides the major input of $Ca^{2+}$, $Mg^{2+}$ and P (and Si and Al) over the first 10.000 years of ecosystem development, while atmospheric deposition (plus volcanic sources) constitutes the most significant source for $K^+$, $Na^+$, N, $Cl^-$ and $SO_4^{2-}$. Biological $N_2$ fixation represents an important additional source for reactive N. Only later, after about 100.000 years of ecosystem development, atmospheric inputs of e.g. dust and rainfall become more important as an input of essential cations and P.

**Weathering**: Primary minerals are rich in rock-derived elements such as $Ca^{2+}$, $Mg^{2+}$, $K^+$, and P. Chemical weathering i.e. partial or complete dissolution of primary minerals results in a release of these elements while soils develop. Over time, the stocks of weatherable minerals in the part of geosphere that can be exploited by plants are depleted while e.g. cations and P are continuously lost by leaching of inorganic or organic forms. Weathering rates in the top metre of soil can exceed 10 kg $ha^{-1}$ $a^{-1}$ for $Ca^{2+}$ and 0.1 kg $ha^{-1}$ $a^{-1}$ for P over the first 10.000 to 100.000 years (CHADWICK et al. 1999). Only then, weathering rates have been reported to decline by up to seven orders of magnitude. Erosion, induced by tectonic uplift, can counteract the depletion of primary minerals and where uplift and erosion are moderate such as in Central America (2.1 to 6.5 m $kyr^{-1}$, GARDNER et al. 1992) continuously replete rock-derived elements (PORDER et al. 2006, PORDER et al. 2007).

**Deposition**: Atmospheric deposition of gases, aerosols, dust and precipitation represent a major input of elements to tropical rainforests, sustaining primary productivity in tropical forests on old, highly weathered soils such as in the Amazon basin (CHADWICK et al. 1999). Gaseous depositions primarily occur for N ($NO_x$, $NH_3$) and sulphur ($SO_2$), and as for aerosols (e.g. $(NH_4)_2SO_4$, $HNO_3$, $H_2SO_4$), quantification is prone to large uncertainties by methodology and modelling (MCMURRY 2000). Dust and aerosol deposition is an important input for P and cations, the major sources being marine aerosols, biomass burning, and long-distance transport of dust from arid areas (ARTAXO et al. 1998). Wet deposition by rainfall and occult precipitation has also been shown to contribute significantly to element inputs. Dry and wet deposition are negatively correlated, leading to enhanced nutrient concentrations in rainfall after prolonged dry periods (FILOSO et al. 1999, LOVETT & LINDBERG 1984). Nutrient concentrations in cloud and fog droplets are much higher than in rainfall, comprising an important nutrient input to tropical montane cloud forests (CARRILLO et al. 2002, CLARK et al. 1998c). However, wet and dry depositions are not unusually measured separately but in the form of bulk precipitation (Table 3). It must be borne in mind that dry deposition is not fully accounted for in bulk precipitation but also contributes to throughfall fluxes; material that has been dry deposited during rain-free periods is washed off during the next shower, therefore showing up in rainwater intercepted by the canopy. Bulk precipitation added on average 0.4 kg P $ha^{-1}$ $a^{-1}$ to neotropical rainforests, and represented an input of 2.9 kg $Mg^{2+}$, 4.3 kg $K^+$, 7.0 kg $Ca^{2+}$ and 7.3 kg N $ha^{-1}$ $a^{-1}$ (Table 3). These values are close to those found for the Esquinas forest though atmospheric inputs of N (+37%), $Mg^{2+}$ (+55%), $K^+$ (+116%) and $Ca^{2+}$ (+147%) were higher, partly due to the vicinity of the sea. Compared to internal recycling of nutrients (litterfall plus net throughfall), bulk deposition fluxes are generally small and, based on the ratio of internal recycling to bulk deposition, were small in the Esquinas forest for P (18.2) and N (13.0), intermediate for $K^+$ and $Ca^{2+}$ (7.2-7.9) but high for $Mg^{2+}$ (4.8). Bulk deposition therefore constituted a significant flux in the nutrient cycle of $Mg^{2+}$, and less so of $K^+$ and $Ca^{2+}$.

**$N_2$ Fixation**: Most undisturbed lowland rainforests are considered to be N sufficient i.e. not N-limited; continuous N losses by nitrate leaching and denitrification therefore occur and have to be replenished (VITOUSEK 2004). To keep ecosystem N pools high, or to allow recovery of the forest biomass-N pool after disturbance (logging), the input of combined N via $N_2$ fixation by prokaryotes is crucial. Symbiotic N fixers (e.g. rhizobia in legume nodules) play the most important role but cyanobacteria-lichen associations as well as free-living cyanobacteria and heterotrophic $N_2$ prokaryotes on leaf surfaces (phyllosphere), litter and the root-soil interface (rhizosphere) are also considered significant in tropical rainforests (CLEVELAND et al. 1999, PONS et al. 2007). The best estimates of symbiotic $N_2$ fixation by legumes are 4-7 kg N $ha^{-1}$ $a^{-1}$ in lowland tropical rainforests (PONS et al. 2007, ROGGY et al. 1999). The natural $^{15}N$ abundance method (see also GEHRING & VLEK 2004) was applied to quantify $N_2$ fixation by tree legumes in the Esquinas forest (SCHEMBERA & WANEK 2002, data not shown). Leaf $\partial^{15}N$ signatures of legumes in all three forest types ranged between –0.5‰ and –0.9‰ (SE 0.4) and for non-fixers they were 0.1‰ (secondary forest), –1.2‰ (primary ravine) and –1.8‰ (primary ridge forest). Due to the small isotopic differences between $N_2$ fixing legumes und non-$N_2$ fixing legumes (or other reference plants), we however refrained from further calculations of legume N fixation. In contrast to natural $^{15}N$ abundance techniques, enriched $^{15}N$ tracers allow accurate estimations of N fluxes. Based on $^{15}N_2$ incorporation, estimates of epiphyll-covered leaf area (LAI) and micro-climatological data, phyllosphere $N_2$ fixation was estimated to range between 7.2 (ravine forest) and 0.1 kg N $ha^{-1}$ $a^{-1}$ (ridge forest) in the Esquinas forest (WANEK 2000, data not shown). Molecular analysis demonstrated that autotrophic $N_2$ fixers (cyanobacteria) and heterotrophic diazotrophs (Gamma-Proteobacteria) were dominant in the leaf-associated diazotrophic communities (FÜRNKRANZ et al. 2008). Depending on the host species and microclimate, $N_2$ fixation by epiphylls was reported to be 0.2 to 5.0 kg N $ha^{-1}$ $a^{-1}$ (CARPENTER 1992, FREIBERG 1998).

NUTRIENT LOSSES. – Nutrient losses occur primarily via three pathways, (1) leaching through soils to streams, (2) gaseous losses of C and N by microbial processes and (3) erosion. Other pathways may be important such as biomass removal by harvest and biomass loss through volatilisation/suspension by fire.

**Hydrological outputs**: Losses of dissolved nutrients follow different flow paths, and depending on the prevailing rainfall regime, catchment losses occur mostly via saturation overland flow and interflow (strong rainfall) or base flow (rain-free periods) (ELSENBEER 2001). The composition of water exported via these flow paths differs markedly, base flow being dominated by ions released during weathering of bedrock e.g. $SiO_2$, DIC (dissolved inorganic carbon) and $Ca^{2+}$ while (sub)surface flow and storm flow is enriched with inorganic N ($NO_3^-$), $Na^+$, $K^+$ and $SO_4^{2-}$ (LESACK 1993, SALMON et al. 2001).

Hydrological outputs represent a major loss pathway of elements but this has not been estimated in detail in the Esquinas forest so far. Initial studies (Tschelaut 2005, pers. commun.) suggest, however, that the 'Quebrada Negra', a small stream draining a watershed (~600 ha, 30 L $s^{-1}$ base flow) which is mainly stocked with primary rainforest in the vicinity of the experimental plots, represents a rather small output for $NO_3^-$ (0.22 kg $ha^{-1}$ $a^{-1}$), $NH_4^+$ (0.03), dissolved organic N (DON; <0.05), $P_i$ (0.11), dissolved organic P (DOP; 0.02), $K^+$ (2.1), $Ca^{2+}$ (66 ), $Mg^{2+}$ (15) and $Na^+$ (19 kg $ha^{-1}$ $a^{-1}$).

The flux of dissolved organic matter plays an important role in soil formation and nutrient dynamics, but its controls are poorly understood (NEFF et al. 2000). Dissolved organic matter export by rivers can represent the major pathway of N losses in pristine landscapes (HEDIN et al. 1995, VITOUSEK 2004). The contribution of DON to total dissolved N flux ranged from 75% to 95%, that of DOP to total dissolved P flux between 30% and 70% in Hawaiian rainforests (NEFF et al. 2000). In contrast to hydrological $NO_3^-$ losses, DON and DOP losses belong to demand-independent pathways of N and P losses i.e. are independent of plant or microbial demand (VITOUSEK 2004). These pathways persist even when ecosystems are strongly nutrient-limited and the demand for an element therefore actually exceeds the supply of that element. Such losses can therefore sustain P or N limitation or constrain N accumulation in an ecosystem, as indicated in Hawaii (VITOUSEK 2004).

**Erosion**: Erosion represents the displacement of particulate materials by wind and water, through downward movement in response to gravity. Land lift and disturbance can greatly increase erosion processes and thereby initiate the loss of the uppermost soil layers which contain a significant fraction of the ecosystem nutrient pool locked up in the form of soil organic matter. On steep slopes, erosion can become a determinant of nutrient budgets even in primary rainforest where, for instance, annual soil loss reached 2.9 t $km^{-2}$ in Costa Rican forests (JANSSON & STROMBERG 2004). Most loss of soil material occurred during strong rain events only, e.g. of the annual soil loss, 50-87% was lost during two storms (JANSSON & STROMBERG 2004). Due to fast land lift in the Corcovado region of 2.1-6.5 m $kyr^{-1}$ during the Quaternary (GARDNER et al. 1992), erosion has to be assumed to play an important rôle in counteracting the weathering of bedrock in the Esquinas forest; moreover, erosion leads to redistribution of minerals, elements and radionuclides between upland sites and alluvial terraces (FIEBIG et al. 2007), amplifying the effect of topography on soil fertility and vegetation dynamics.

**Gaseous losses**: Losses of elements that occur in a gaseous form are most prominent for C and N, though irrelevant for most other nutrient elements. Gaseous losses represent the major pathway of ecosystem C output but a minor one for N. Litter and soil organic matter decomposition are driven by microbial processes where a major fraction of C assimilated by plants is released as $CO_2$ via microbial respiration to the atmosphere. Heterotrophic respiration represents a major flux in the ecosystem C cycle that equals or often slightly exceeds NPP (see: Net ecosystem exchange) (SIERRA et al. 2007b). Soil temperature and moisture are the major abiotic factors determining soil respiration (BEKKU et al. 2003, LI et al. 2006), while litter quality and quantity, as well as the structure of microbial community, also strongly affect heterotrophic respiration (e.g. MENYAILO et al. 2003). Organic matter decomposition and soil C losses ($CO_2$ efflux) were also shown to be sensitive to soil nutrient status, with nutrient addition adversely affecting soil respiration in two rainforest ecosystems (CLEVELAND & TOWNSEND 2006, MO et al. 2008). In the Esquinas forest, soil respiration (in situ) ranged from 2.8 to 5.1 µmol $CO_2$ $m^{-2}$ $s^{-1}$, with no significant difference between sites (dry season 2008). The values were lower than measured in a primary rainforests near Manaus, with an annual mean of 6.45 µmol $CO_2$ $m^{-2}$ $s^{-1}$ (SOTTA et al. 2004). Investigations focusing on the partitioning of soil respiration into autotrophic (root and rhizosphere) respiration and heterotrophic respiration (soil organic matter derived) indicated that up to 50% of soil respiration is directly driven by plant photosynthesis and root activity (LI et al. 2006, SILVER et al. 2005).

Methane ($CH_4$) efflux from soils is commonly low in terms of the C cycle (VON FISCHER & HEDIN 2007), though tropical forest soils reportedly served as a net source of methane to the atmosphere if more than 0.04% of total carbon mineralisation was by methanogenic pathways.

The abundance of available N in many soils of tropical lowland rainforests has been linked to large losses of nitrogenous gases such as $N_2O$ and NO (MCSWINEY et al. 2001, PARSONS et al. 1993). Losses of nitrogen oxides ($N_2O$ and NO) and $N_2$ were previously estimated to account for a small proportion of ecosystem N flux only, being 1-4 kg N $ha^{-1}$ $a^{-1}$, in a hill slope forest in Puerto Rico (CHESTNUT et al. 1999). In contrast, natural $^{15}N$ abundance measurements and modelling suggested large gaseous N losses from tropical rainforests via denitrification of $NO_3^-$, even in presumably N-limited montane tropical rainforests (HOULTON et al. 2006). Based on this evidence, denitrification was responsible for 24% to 53% of total ecosystem N losses in forests ranging in MAP from 2200 to 4100 mm.

**Fire and harvest**: Fire and harvest remove marked amounts of nutrients from forests, elements that are irreversibly removed from the ecosystem and are replaced only slowly by atmospheric deposition, weathering and $N_2$ fixation. While above-ground biomass accrual is rapid and within ~12-14 years, above-ground biomass in secondary forests can reach 25-50% of primary forests, soil organic matter pools and nutrient pools (particularly P) recover more slowly (FELDPAUSCH et al. 2004, SIERRA et al. 2007a). However, biomass recovery can be faster if disturbance is less severe such as after selective logging, though the removal of large tree individuals that contain a large proportion of elements has frequently been under-estimated (MARTINELLI et al. 2000). In the Osa region, deforestation led to a decrease of forested area on the Corcovado peninsula from 97% (1979) to 89% (1997), and human activities have left only 44% of the remaining forest on the peninsula in a mature state, while most of the forest outside the Corcovado National Park has been altered (SANCHEZ-AZOFEIFA et al. 2002).

Soil charcoal provides historical evidence for fire, and was shown to be most abundant at the wettest lowland sites (60-500 m) and less at montane elevations (> 1000 m) at an elevational transect at the Volcan Barva, Costa Rica (TITIZ & SANFORD 2007). Old-growth forests have therefore been disturbed infrequently but multiple times as a consequence of anthropogenic and natural fires. Losses of elements due to fire can be large, due to direct volatile losses of biomass nutrients and due to subsequent leaching losses of nutrients from ash when the biotic sink is negligible (HUGHES et al. 2000, MALMER & GRIP 1994).

INTERNAL NUTRIENT CYCLING. – Processes involved in the internal cycling of elements include uptake and assimilation of nutrients by plants and microbes, their subsequent release by decomposition of dead biomass, and conversion processes from organic to inorganic elemental forms. Sources of nutrients for internal cycling include litterfall and litter decomposition processes and the input of canopy leachates via throughfall and stemflow. Root litter decay, microbial transformation processes and nutrient uptake are the major below-ground processes in internal element cycles (WHITMORE 1998).

Nitrogen, P and $Ca^{2+}$ are transferred to the soil mainly via litterfall (Table 3). In contrast, leaching inputs of nutrients to the forest floor via throughfall and stemflow have been reported to be significant in ecosystem nutrient cycles of $K^+$ and $Mg^{2+}$ (CHUYONG et al. 2004, TOBON et al. 2004b) (Table 3). The amount of elements recycled internally in litterfall as a fraction of total recycled (litterfall plus net throughfall) was 99%-100% for P and C, 88%-91% for $Ca^{2+}$ and N, 78% for $Mg^{2+}$ and 40% for $K^+$ (neotropical average; Table 3), demonstrating the importance of the litterfall pathway as the primary route of internal nutrient recycling. Unfortunately, we are only aware of one study estimating fine root decay as below-ground contribution to internal nutrient recycling (TOBON et al. 2004a). The poor understanding of the rates and controls of root life span and turnover therefore goes with a lack of prediction of C flow and nutrient cycling dynamics in fine roots at the ecosystem scale (GUO et al. 2008).

**Litterfall**: Litter provides the central nutrient source for nutrient cycling in tropical rainforests, where soils are highly weathered and nutrient-poor (MARTIUS et al. 2004). The litter layer on the forest floor is made up of coarse and fine litter in different stages of decay and a usually well developed thin humus layer on top of the mineral soil. Coarse litter and coarse woody debris consists of dead wood, palm leaves and big fruits and is very heterogeneous in space and time (CLARK et al. 2002). Fine litter includes mostly leaves, small twigs, flowers and fruit parts and is more uniformly distributed (e.g. DENT et al. 2006). The nutrient content in leaf litter and reproductive litter material is generally higher than in dead wood litter (CUEVAS & LUGO 1998). Since leaves account for the largest fraction of fine litterfall (41%-62%, Esquinas forest), factors influencing leaf senescence and abscission such as seasonality of climate and soil fertility govern the general patterns of litterfall (CUEVAS & LUGO 1998). Nutrient resorption before leaf fall varies among species, leading to a discrepancy between species impact in litter input and nutrient return to the forest floor. Leaf litter nutrient cycling is further positively related to soil fertility as are litterfall and litter nutrient concentrations (WOOD et al. 2006).

While litterfall dry mass in the Esquinas forest ranged among the highest reported so far (>10 $Mg^{2+}$ $ha^{-1}$ $a^{-1}$), phosphorus return via litterfall (4.4 to 9.9 kg $ha^{-1}$ $a^{-1}$), particularly of primary ravine forest, was also in the highest range, only exceeded by lowland and premontane moist forest in Panama (Table 3) (GOLLEY et al. 1975). In La Selva, a wet lowland tropical rainforest at the Atlantic coast in Costa Rica, P fluxes in litterfall were ~5 kg $ha^{-1}$ $a^{-1}$ (WOOD et al. 2006). Nitrogen fluxes in litterfall covered much of the reported range, though those of primary rainforests in valleys were again among the highest found (Table 3), pointing to very fast N cycling and high N availability in the forests studied. Fluxes of $Mg^{2+}$, $K^+$ and $Ca^{2+}$ were similar to those found for other neotropical rainforests (Table 3). Therefore, the litterfall data indicate strongly that NPP of the forest types studied here was linked – for tropical forests – to high availability of cations and N and P.

**Throughfall and stemflow**: Throughfall is defined as the proportion of incident gross precipitation that penetrates or drips through a plant canopy while stemflow is the residual amount of rainwater that runs down tree stems and constitutes a localised point input of water and nutrients (PARKER 1983). The rest of incident gross precipitation is intercepted by the canopy and lost via evaporation (MARIN et al. 2000). Despite the multitude of throughfall and stemflow studies worldwide, as reviewed by LEVIA & FROST (2003, 2006), the elucidation of underlying processes that alter nutrient concentrations and fluxes still lags behind, since they remain difficult to interpret (LOVETT et al. 1996).

Elements in throughfall and stemflow derive from three processes: (1) passage of incident precipitation through the canopy, (2) wash-off of dry deposited materials such as particles and gases, and (3) solute exchange between intercepted rainfall and canopy surfaces like foliage, woody parts, epiphytes and microorganisms (HANSEN et al. 1994, LOVETT & LINDBERG 1984). Fluxes of dissolved nutrients are strongly correlated with (1) the amount, duration and intensity of precipitation penetrating the canopy, and (2) the amount of dry deposition as linked to duration of antecedent rain-free period. The clear positive correlations between net fluxes of most elements and rain volumes, however, suggest that the process of leaching is dominant in most cases, whereas the contribution of dry deposition is probably small since it would be expected to be largely independent of rainfall. Throughfall chemistry mainly depends on factors like latitude, elevation, seasonality, proximity to the sea, species composition, forest age and local land use (LEVIA & FROST 2006) which affect dry deposition and/or canopy exchange. stemflow chemistry is basically controlled by factors like species assemblage, seasonality, meteorological conditions and canopy structure (LEVIA & FROST 2003).

For discussions of internal nutrient recycling, net throughfall flux (NTF) has to be considered. Net throughfall flux is defined as the difference between throughfall flux (TF) and bulk precipitation flux (BP): NTF = TF – BP = CE + DD and represents the integral of the processes of uptake or leaching of nutrients during canopy exchange (CE) and dry deposition (DD). NTF therefore shows whether a certain element is enriched or depleted during the passage through the canopy layer. A positive result points to net leaching and/or dry deposition processes whilst a negative one demonstrates uptake of solutes exceeding dry deposition. Due to the impact of dry deposition, direct comparisons of NTF with litterfall have to be taken cautiously. In the Esquinas forest, throughfall represented between 87% and 92% and stemflow between 0.7% and 1.0% of bulk precipitation volume. Negative NTF fluxes in the Esquinas forest (calculated from Table 3) pointed to net canopy retention and were evident for $NH_4^+$, $Na^+$, $NO_3^-$ and $SO_4^{2-}$. In contrast, leaching and dry deposition resulted in net enrichment of the following solutes: $K^+$, dissolved organic carbon and N (DOC, DON), $Mg^{2+}$, $Cl^-$ and inorganic P. Enrichment or depletion of elements strongly relies on soil nutrient status and on the mobility of solutes: while N, $Ca^{2+}$ and P are mainly immobilised in cell walls or in cell plasma, other solutes (e.g. $K^+$, DOC) are more susceptible to leaching from the canopy layer due to their high abundance and exchange rates during processes of cell physiology. Similar patterns of nutrient uptake and release by the canopy have been observed by others (FILOSO et al. 1999, TOBON et al. 2004b). The contribution of net throughfall to above-ground nutrient cycling was however very low – ranging from zero for elements being depleted during canopy passage (e.g. $Na^+$, N), negligible for C (0.2%), P (4%) and $Mg^{2+}$ (5%), but 42% for $K^+$. Stemflow contributed only 1 to 10% to solute deposition to the forest floor, due to small volumetric flows (Table 3; exception: $Cl^-$ deposition at ridge position). In total, essential elements were mainly recycled via the litterfall pathway; only a small but significant fraction has been recycled by canopy processes via throughfall. In contrast to litterfall, however, element fluxes in throughfall and stemflow can be significant in the short term as solutes are directly available for microbial and plant use, while litter nutrients have to be released through litter decomposition into soluble forms.

**Decomposition:** Decomposition refers to a sequence of processes which break down organic matter – leaching, fragmentation and chemical alteration – producing nutrients in available forms for plant and microbial production and releasing $CO_2$ to the atmosphere. Without decomposition, large quantities of detritus would accumulate on the forest floor, locking up nutrients in unavailable stocks (CHAPIN III et al. 2002). Nutrient cycling would halt as would mineral supply to primary producers. litterfall and litter decomposition are therefore key processes in terrestrial nutrient cycling. The rate of decomposition is determined by litter quality and the physical environment, where litter quality reflects the concentrations of nutrients (N, P) and structural and defense compounds (lignin, phenols etc) (AERTS 1997, AUSTIN & VITOUSEK 2000). More nutrient-rich leaves with fewer physical and chemical defences decompose more rapidly than tougher, nutrient-poor leaves (CONSTANTINIDES & FOWNES 1994, DENT et al. 2006). Therefore, traits associated with high stand-level nutrient use efficiency are often associated with low decomposition rates (SANTIAGO & MULKEY 2005).

Litter decay usually shows two phases, with a negative exponential curve of mass loss in the beginning, followed by more asymptotic linear curves caused by the relative accumulation of recalcitrant material in the remaining litter with time (BERG et al. 1984, CORNU et al. 1997). Leaching represents the initial step of decomposition, where small water-soluble organic compounds and ions dissolve in water and are transported into the soil. Leaching losses are great in humid rainforests due to their high precipitation and induce a pulse of microbial growth and respiration in times of high litterfall. Fragmentation is performed primarily through feeding activities of soil invertebrates, but is also supported by wetting-drying processes. The disruption of cellular structures and protective layers facilitates microbial colonisation and increases the litter surface exposed for break down. During organic matter depolymerisation and microbial processing, organic material is converted to inorganic minerals, which are subsequently available for plant or microbial uptake (ALLISON & VITOUSEK 2004). The initial actors in this last step of decomposition are fungi, which, together with bacteria, account for 80% to 90% of decomposer biomass (ZHANG & ZAK 1998).

There are two major ways to study decomposition: (1) the turnover rate $K_L$ of the litter stock is calculated as the ratio of litterfall rate to standing stock of litter (SCOTT et al. 1992), (2) based on litter bag experiments, the decomposition constant k is calculated by fitting mass loss against time using single or double exponential models (COUTEAUX et al. 2002). OLSON postulated that in steady state ecosystems, rates of litterfall and decomposition are in equilibrium and $K_L$ gives an indicator of the decomposition constant k (OLSON 1963). Mature rainforests can be seen as being in a steady state, whereas this assumption does not fit for successional stages like secondary forests. In the Esquinas forest, k values of mixed species leaf litter of the respective sites ranged from 1.1 to 1.8 ($t_{0.5}$ half lives 145-230 d), and that of *Vochysia ferruginea* single species litter from 0.64 to 0.75 for the three sites ($t_{0.5}$ 339-395 d).

**Table 4**: Soil characteristics of three rainforest sites in the Esquinas forest. Costa Rica. Mean values sharing the same letter within a row are not significantly different from each other. ($P > 0.05$. Kruskal Wallis test. Bonferroni Multiple range test.) Soil samples have been taken from the upper 5 cm during the wet and dry season 2005. All values are means with SE ($n = 18$).

| | **Primary Ravine Forest** | | | | **Secondary Ravine Forest** | | | | **Primary Ridge Forest** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| pH ($CaCl_2$) | 3.68 | ± | 0.04 | A | 3.56 | ± | 0.04 | A | 3.28 | ± | 0.02 | B |
| Bulk density (g $cm^{-3}$) | 0.61 | ± | 0.08 | A | 0.49 | ± | 0.06 | B | 0.41 | ± | 0.06 | B |
| Carbon conc. (% DW) | 7.78 | ± | 0.41 | A | 4.80 | ± | 0.40 | B | 8.59 | ± | 0.71 | A |
| Nitrogen (% DW) | 0.64 | ± | 0.03 | A | 0.37 | ± | 0.02 | B | 0.62 | ± | 0.03 | A |
| C/N ratio | 12.4 | ± | 0.8 | ns | 12.6 | ± | 0.5 | ns | 13.8 | ± | 1.1 | ns |
| Nitrate (mg $kg^{-1}$) | 49.6 | ± | 8.93 | B | 8.98 | ± | 1.43 | A | 18.8 | ± | 5.11 | A |
| Phosphate (mg $kg^{-1}$) | 2.08 | ± | 0.39 | ns | 4.80 | ± | 1.23 | ns | 0.69 | ± | 0.05 | ns |
| Ammonium (mg $kg^{-1}$) | 11.5 | ± | 1.5 | A | 6.87 | ± | 0.90 | A | 24.4 | ± | 3.8 | B |
| Potassium (mg $kg^{-1}$) | 122.0 | ± | 13.7 | ns | 199.8 | ± | 46.4 | ns | 172.6 | ± | 77.7 | ns |
| Gross N mineralization (mg N-$NH_4$ $kg^{-1}$ $day^{-1}$) | 54.0 | ± | 15.1 | | 60.8 | ± | 3.8 | ns | 33.0 | ± | 6.9 | ns |
| Gross nitrification (mg N-$NO_3$ $kg^{-1}$ $day^{-1}$) | 2.24 | ± | 0.35 | | 1.33 | ± | 0.77 | ns | 2.33 | ± | 0.91 | ns |

Different forest types across a gradient of soil nutrient supply in a tropical rainforest in Malaysia showed k values for mixed species leaf litter from 1.35 on the nutrient poorest site to 2.55 on the nutrient richest one; the half-lives were 187 days and 99 days (DENT et al. 2006), respectively.

Turnover rates $K_L$ for leaf litter were 1.43 $yr^{-1}$ and 2.27 $yr^{-1}$ for both ends of the nutrient supply gradient (DENT et al. 2006). In the Esquinas forest, total fine litter had a turnover rate $K_L$ of 3.7 (primary ravine forest) and ~2.3 $yr^{-1}$ (secondary ravine and primary ridge forest), being markedly higher as in former study. $K_L$ values were 1.2-1.5 for fine litter in primary rainforests at three topographic positions close to Manaus and 2.0 on Maraca Island in the Brazilian Amazon (LUIZAO et al. 2004, SCOTT et al. 1992). Coarse litter decomposed much more slowly with a $K_L$ of 0.15-0.87 $yr^{-1}$ in the Esquinas forest. Turnover times of coarse litter were therefore slow but comparable or higher than the average for coarse woody debris of 9 years at La Selva, Costa Rica (CLARK et al. 2002) and the range of 0.12-0.47 $yr^{-1}$ for large to small size classes of coarse woody debris found in Tapajos, Brazil (PALACE et al. 2008).

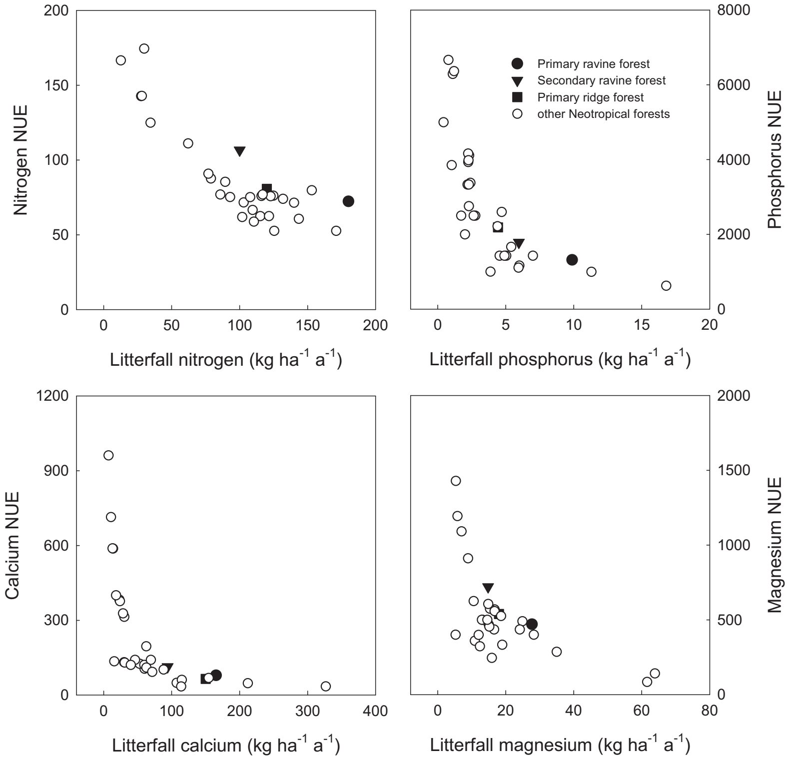

**Fig. 2**: Relationship between nutrient fluxes in litterfall (kg $ha^{-1}$ $a^{-1}$) and nutrient use efficiencies (NUE) of litter production (kg dry mass $kg^{-1}$ nutrient content) in neotropical rainforests (○) for N, P, $Ca^{2+}$, and $Mg^{2+}$. Filled symbols are for primary ravine forest on Inceptisol (●), secondary ravine forest on Inceptisol (▼) and primary ridge forest on Ultisol (■) in the Esquinas forest, Piedras Blancas National Park, Costa Rica.

Nutrient release during decomposition of litter follows complex pathways and controls (CONSTANTINIDES & FOWNES 1994); N and P (and $Ca^{2+}$) often accumulate during the initial phases while mass is lost (CORNU et al. 1997, DENT et al. 2006). Over the course of years it can therefore happen that net release of macro elements is detectable and adds to the available soil nutrient pools (AUSTIN & VITOUSEK 2000, PARTON et al. 2007).

**Nutrient use efficiency**: Nutrient availability generally determines the efficiency of nutrient use for most tree species. Therefore efficient within-stand nutrient economy of an element indicates its limiting status for primary production, while inefficient within-stand cycling of a specific nutrient implies no limitation of a nutrient (VITOUSEK 1982, 1984). The term "efficient within-stand cycling" means that relatively more C is fixed per unit nutrient or a larger fraction of nutrients is resorbed by plants before shedding of senescent plant parts (HARRINGTON et al. 2001). Moreover, limited nutrient losses from the system through rapid nutrient uptake by roots, mycorrhizae and decomposers also support efficient within-stand cycling (KINGSBURY & KELLMAN 1997, VITOUSEK 1982). Studies of litterfall and litter nutrient content have often been applied to investigate the efficiency of nutrient cycling. VITOUSEK (1984) suggested the ratio dry mass/nutrient content – the inverse of nutrient concentration – in litterfall as a proxy of a forest ecosystem's nutrient economy as a whole and termed it "nutrient use efficiency" (NUE). In the Esquinas forest, phosphorus NUE was rather low at 1320 (primary ravine), 1790 (secondary ravine) and 2190 (primary ridge), while in neotropical rainforests, phosphorus NUE ranged from 625 to 6660 (mean 2890) (Fig. 2). Nitrogen NUE was between 72 and 107, being well within the range reported for other neotropical rainforests (53-175, mean 87). Calcium NUE ranged from 65 to 113, again being similar or at the lower end of other neotropical rainforest sites studied (34-961, mean 235). Within the Esquinas forest, NUE for N, P and $Ca^{2+}$ were all greater at the ridge site implying lower availability of these nutrients in Ultisols. There was also a trend towards higher NUE for P and N in the secondary forest than in the primary forest on Inceptisols. In comparison with other neotropical forests, the Esquinas forest stands were rather inefficient in their N, P and $Ca^{2+}$ use while showing among the highest rates of nutrient cycling in litterfall (Fig. 2), both pointing to high availability of these nutrients for forest growth and production.

## Conclusions

The Esquinas forest holds a special position within the neotropical rainforest continuum, due to its extraordinarily high mean annual precipitation and high mean annual temperature. Previous reviews of biogeochemistry (SCHUUR 2003) have suggested that at high levels of precipitation, NPP in tropical rainforests will decline, which was clearly not the case here. In contrast, trees showed the highest wood increments and among the highest litterfall rates published to date. These high rates of production are explained by high litterfall and decomposition rates, fast cycling of nutrients and therefore high nutrient availability. Low constraints of NPP by nutrients are also illustrated by low nutrient use efficiencies for N, P, $Ca^{2+}$ and others (Fig. 2). We further suggest that the Esquinas forest is well supplied with cations and P through high rates of weathering, tectonic uplift and erosion. Topography had a major effect on soil fertility and plants responded by greater allocation to below-ground biomass and below-ground production to acquire soil resources at the ridge compared to the ravine site. Disturbance did not affect above – or below-ground biomass >20 years later. However, biomass production was still greater than in primary rainforest on Inceptisols, and nutrient demand for biomass production evidently exceeded nutrient supply as suggested by a draw-down of available soil nitrate and comparably higher nutrient use efficiencies as in primary forest at the same topographic position (Table 4).

## Acknowledgements

This project was supported by the University of Vienna by providing travel funds and the Austrian Academy of Sciences, Commission of Interdisciplinary Ecological Studies (Title: Carbon and element cycling in a tropical lowland rainforest, Costa Rica). The authors are highly grateful to Werner Huber and Anton Weissenhofer who helped to establish the plots and to determine trees to the species level. Moreover, thanks to Erich Mursch-Radlgruber (Institute of Meteorology, University of Natural Resources and Applied Life Sciences, Vienna) who provided part of the microclimate loggers.

## References

AERTS R. (1997): Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. — Oikos **79**: 439-449.

ALLISON S.D. & P.M. VITOUSEK (2004): Extracellular enzyme activities and carbon chemistry as drivers of tropical plant litter decomposition. — Biotropica **36**: 285-296.

ARAUJO A.C., NOBRE A.D., KRUIJT B., ELBERS J.A., DALLAROSA R., STEFANI P., von RANDOW C., MANZI A.O., CULF A.D., GASH J.H.C., VALENTINI R. & P. KABAT (2002): Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rainforest: The Manaus LBA site. — Journal of Geophysical Research-Atmospheres **107**: 8090.

ARTAXO P., FERNANDES E.T., MARTINS J.V., YAMASOE M.A., HOBBS P.V., MAENHAUT W., LONGO K.M. & A. CASTANHO (1998): Large-scale aerosol source apportionment in Amazonia. — Journal of Geophysical Research-Atmospheres **103**: 31837-31847.

AUSTIN A.T. & P.M. VITOUSEK (2000): Precipitation, decomposition and litter decomposability of Metrosideros polymorpha in native forests on Hawai'i. — Journal of Ecology **88**: 129-138.

BAKER T.R., PHILLIPS O.L., MALHI Y., ALMEIDA S., ARROYO L., di FIORE A., ERWIN T., HIGUCHI N., KILLEEN T.J., LAURANCE S.G., LAURANCE W.F., LEWIS S.L., MONTEAGUDO A., NEILL D.A., VARGAS P.N., PITMAN N.C.A., SILVA J.N.M. & R.V. MARTINEZ (2004a): Increasing biomass in Amazonian forest plots. — Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **359**: 353-365.

BAKER T.R., PHILLIPS O.L., MALHI Y., ALMEIDA S., ARROYO L., di FIORE A., ERWIN T., KILLEEN T.J., LAURANCE S.G., LAURANCE W.F., LEWIS S.L., LLOYD J., MONTEAGUDO A., NEILL D.A., PATINO S., PITMAN N.C.A., SILVA J.N.M. & R.V. MARTINEZ (2004b): Variation in wood density determines spatial patterns in Amazonian forest biomass. — Global Change Biology **10**: 545-562.

BEHRENFELD M.J., RANDERSON J.T., MCCLAIN C.R., FELDMAN G.C., LOS S.O., TUCKER C.J., FALKOWSKI P.G., FIELD C.B., FROUIN R., ESAIAS

W.E., KOLBER D.D. & N.H. POLLACK (2001): Biospheric primary production during an ENSO transition. — Science **291**: 2594-2597.

BEKKU Y.S., NAKATSUBO T., KUME A., ADACHI M. & H. KOIZUMI (2003): Effect of warming on the temperature dependence of soil, respiration rate in arctic, temperate and tropical soils. — Applied Soil Ecology **22**: 205-210.

BERG B., EKBOHM G. & C. MCCLAUGHERTY (1984): Lignin and holocellulose relations during long-term decomposition of some forest litters – Long-term decomposition in a Scots Pine forest. 4. — Canadian Journal of Botany **62**: 2540-2550.

BERN C.R., TOWNSEND A.R. & G.L. FARMER (2005): Unexpected dominance of parent-material strontium in a tropical forest on highly weathered soils. — Ecology **86**: 626-632.

BOUSQUET P., PEYLIN P., CIAIS P., le QUERE C., FRIEDLINGSTEIN P. & P.P. TANS (2000): Regional changes in carbon dioxide fluxes of land and oceans since 1980. — Science **290**: 1342-1346.

BRAVO H.A., SAAVEDRA M.I.R., SANCHEZ P.A., TORRES R.J. & L.M.M. GRANADA (2000): Chemical composition of precipitation in a Mexican Maya region. — Atmospheric Environment **34**: 1197-1204.

BROWN S. (1997): Estimating Biomass and Biomass Change of Tropical Forests: A Primer. UN FAO Forestry Paper **134**. — Food and Agricultural Organization of the United Nations, Rome.

BRUIJNZEEL L.A. (1991): Nutrient input-output budgets of tropical forest ecosystems: a review. — Journal of Tropical Ecology **7**: 1-24.

CAIRNS M.A., BROWN S., HELMER E.H. & G.A. BAUMGARDNER (1997): Root biomass allocation in the world's upland forests. — Oecologia **111**: 1-11.

CAMPO J., MAASS J.M., JARAMILLO V.J. & A.M. YRIZAR (2000): Calcium, potassium, and magnesium cycling in a Mexican tropical dry forest ecosystem. — Biogeochemistry **49**: 21-36.

CAMPO J., MAASS M., JARAMILLO V.J., MARTINEZ-YRIZAR A. & J. SARUKHAN (2001): Phosphorus cycling in a Mexican dry forest ecosystem. — Biogeochemistry **53**: 161-179.

CAO M.K., PRINCE S.D., SMALL J. & S.J. GOETZ (2004): Remotely sensed interannual variations and trends in terrestrial net primary productivity 1981-2000. — Ecosystems **7**: 233-242.

CARPENTER E.J. (1992): Nitrogen fixation in the epiphyllae and root nodules of trees in the lowland tropical rainforest of Costa Rica. — Acta Oecologica **13**: 153-160.

CARRILLO J.H., HASTINGS M.G., SIGMAN D.M. & B.J. HUEBERT (2002): Atmospheric deposition of inorganic and organic nitrogen and base cations in Hawaii. — Global Biogeochemical Cycles **16**: 1076.

CAVELIER J., JARAMILLO M., SOLIS D. & D. DELEON (1997): Water balance and nutrient inputs in bulk precipitation in tropical montane cloud forest in Panama. — Journal of Hydrology **193**: 83-96.

CAVELIER J., WRIGHT S.J. & J. SANTAMARIA (1999): Effects of irrigation on litterfall, fine root biomass and production in a semideciduous lowland forest in Panama. — Plant and Soil **211**: 207-213.

CERON R.M.B., PADILLA H.G., BELMONT R.D., TORRES M.C.B., GARCIA R.M. & A.P. BAEZ (2002): Rainwater chemical composition at the end of the mid-summer drought in the Caribbean shore of the Yucatan Peninsula. — Atmospheric Environment **36**: 2367-2374.

CHADWICK O.A., DERRY L.A., VITOUSEK P.M., HUEBERT B.J. & L.O. HEDIN (1999): Changing sources of nutrients during four million years of ecosystem development. — Nature **397**: 491-497.

CHAMBERS J.Q., DOS SANTOS J., RIBEIRO R.J. & N. HIGUCHI (2001): Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. — Forest Ecology and Management **152**: 73-84.

CHAPIN III F.S., MATSON P.A. & H.A. MOONEY (2002): Principles of Terrestrial Ecosystem Ecology. — Springer Verlag, New York.

CHAVE J., CONDIT R., AGUILAR S., HERNANDEZ A., LAO S. & R. PEREZ (2004): Error propagation and scaling for tropical forest biomass estimates. — Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **359**: 409-420.

CHAVE J., CONDIT R., LAO S., CASPERSEN J.P., FOSTER R.B. & S.P. HUBBELL (2003): Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. — Journal of Ecology **91**: 240-252.

CHAVE J., RIERA B. & M.A. DUBOIS (2001): Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. — Journal of Tropical Ecology **17**: 79-96.

CHESTNUT T.J., ZARIN D.J., MCDOWELL W.H. & M. KELLER (1999): A nitrogen budget for late-successional hillslope tabonuco forest, Puerto Rico. — Biogeochemistry **46**: 85-108.

CHUYONG G.B., NEWBERY D.M. & N.C. SONGWE (2004): Rainfall input, throughfall and stemflow of nutrients in a central African rainforest dominated by ectomycorrhizal trees. — Biogeochemistry **67**: 73-91.

CLARK D.A. (2004): Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. — Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **359**: 477-491.

CLARK D.A., BROWN S., KICKLIGHTER D.W., CHAMBERS J.Q., THOMLINSON J.R. & J. NI (2001a): Measuring net primary production in forests: Concepts and field methods. — Ecological Applications **11**: 356-370.

CLARK D.A., BROWN S., KICKLIGHTER D.W., CHAMBERS J.Q., THOMLINSON J.R., NI J. & E.A. HOLLAND (2001b): Net primary production in tropical forests: An evaluation and synthesis of existing field data. — Ecological Applications **11**: 371-384.

CLARK D.A., PIPER S.C., KEELING C.D. & D.B. CLARK (2003): Tropical rainforest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984-2000. — Proceedings of the National Academy of Sciences of the United States of America **100**: 5852-5857.

CLARK D.B. & D.A. CLARK (2000): Landscape-scale variation in forest structure and biomass in a tropical rainforest. — Forest Ecology and Management **137**: 185-198.

CLARK D.B., CLARK D.A., BROWN S., OBERBAUER S.F. & E. VELDKAMP (2002): Stocks and flows of coarse woody debris across a tropical rainforest nutrient and topography gradient. — Forest Ecology and Management **164**: 237-248.

CLARK D.B., CLARK D.A. & J.M. READ (1998a): Edaphic variation and the mesoscale distribution of tree species in a neotropical rainforest. — Journal of Ecology **86**: 101-112.

CLARK D.B., OLIVAS P.C., OBERBAUER S.F., CLARK D.A. & M.G. RYAN (2008): First direct landscape-scale measurement of tropical rainforest Leaf Area Index, a key driver of global primary productivity. — Ecology Letters **11**: 163-172.

Clark K.L., Nadkarni N.M., Schaefer D. & H.L. Gholz (1998b): Atmospheric deposition and net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. — Journal of Tropical Ecology **14**: 27-45.

Clark K.L., Nadkarni N.M., Schaefer D. & H.L. Gholz (1998c): Cloud water and precipitation chemistry in a tropical montane forest, Monteverde, Costa Rica. — Atmospheric Environment **32**: 1595-1603.

Cleveland C.C. & A.R. Townsend (2006): Nutrient additions to a tropical rainforest drive substantial soil carbon dioxide losses to the atmosphere. — Proceedings of the National Academy of Sciences U.S.A. **103**: 10316-10321.

Cleveland C.C., Townsend A.R., Schimel D.S., Fisher H., Howarth R.W., Hedin L.O., Perakis S.S., Latty E.F., von Fischer J.C., Elseroad A. & M.F. Wasson (1999): Global patterns of terrestrial biological nitrogen ($N_2$) fixation in natural ecosystems. — Global Biogeochemical Cycles **13**: 623-645.

Condit R., Aguilar S., Hernandez A., Perez R., Lao S., Angehr G., Hubbell S.P. & R.B. Foster (2004): Tropical forest dynamics across a rainfall gradient and the impact of an El Nino dry season. — Journal of Tropical Ecology **20**: 51-72.

Constantinides M. & J.H. Fownes (1994): Nitrogen mineralization from leaves and litter of tropical plants: relationship to nitrogen, lignin and soluble polyphenol concentrations. — Soil Biology & Biochemistry **26**: 49-55.

Cornu S., Luizao F., Rouiller J. & Y. Lucas (1997): Comparative study of litter decomposition and mineral element release in two Amazonian forest ecosystems: litter bag experiments. — Pedobiologia **41**: 456-471.

Couteaux M.M., Sarmiento L., Bottner P., Acevedo D. & J.M. Thiery (2002): Decomposition of standard plant material along an altitudinal transect (65-3968 m) in the tropical Andes. — Soil Biology & Biochemistry **34**: 69-78.

Cox S.B., Willig M.R. & F.N. Scatena (2002): Variation in nutrient characteristics of surface soils from the Luquillo Experimental Forest of Puerto Rico: A multivariate perspective. — Plant and Soil **247**: 189-198.

Cuevas E. & A.E. Lugo (1998): Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species. – Forest Ecology and Management **112**: 263-279.

Cuevas E. & E. Medina (1988): Nutrient dynamics within Amazonian forests. 2. Fine root growth, nutrient availability and leaf litter decomposition. — Oecologia **76**: 222-235.

de Moraes R.M., Delitti W.B.C. & Y.S. de Vuono (1999): Litterfall and litter nutrient content in two Brazilian tropical forests. — Revista Brasileira de Botânica **22**: 9-16.

Delaney M., Brown S., Lugo A.E., Torres-Lezama A. & N.B. Quintero (1998): The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. — Biotropica **30**: 2-11.

Dent D.H., Bagchi R., Robinson D., Majalap-Lee N.& D. Burslem (2006): Nutrient fluxes via litterfall and leaf litter decomposition vary across a gradient of soil nutrient supply in a lowland tropical rainforest. — Plant and Soil **288**: 197-215.

Dewalt S.J. & J. Chave (2004): Structure and biomass of four lowland neotropical forests. — Biotropica **36**: 7-19.

Dykes A.P. & J.B. Thornes (2000): Hillslope hydrology in tropical rainforest steeplands in Brunei. — Hydrological Processes **14**: 215-235.

Eklund T.J., Mcdowell W.H. & C.M. Pringle (1997): Seasonal variation of tropical precipitation chemistry: La Selva, Costa Rica. — Atmospheric Environment **31**: 3903-3910.

Elsenbeer H. (2001): Hydrologic flowpaths in tropical rainforest soilscapes – a review. — Hydrological Processes **15**: 1751-1759.

Fao (2000): Bibliografia comentada. Cambios en la cobertura forestal. Costa Rica. Working paper 36. — Food and Agriculture Organisation, Rome, Italy.

Feldpausch T.R., Rondon M.A., Fernandes E.C.M., Riha S.J. & E. Wandelli (2004): Carbon and nutrient accumulation in secondary forests regenerating on pastures in central Amazonia. — Ecological Applications **14**: S164-S176.

Fiebig M., Hrachowitz M., Kugler H., Mentler A., Ottner F., Pamperl S., Sieghardt M. & W.E.H. Blum (2007): Soil properties and distribution of radionuclides of selected soil profiles from Southern Costa Rica. — Neues Jahrbuch für Geologie und Paläontologie Abhandlungen **243**: 283-297.

Field C.B., Behrenfeld M.J., Randerson J.T. & P. Falkowski (1998): Primary production of the biosphere: Integrating terrestrial and oceanic components. — Science **281**: 237-240.

Filoso S., Williams M.R. & J.M. Melack (1999): Composition and deposition of throughfall in a flooded forest archipelago (Negro River, Brazil). — Biogeochemistry **45**: 169-195.

Forti M.C. & L.M. Moreira-Nordemann (1991): Rainwater and throughfall chemistry in a "Terra Firme" rainforest: central Amazonia. — Journal of Geophysical Research **96**: 7415-7421.

Freiberg E. (1998): Microclimatic parameters influencing nitrogen fixation in the phyllosphere in a Costa Rican premontane rainforest. — Oecologia **117**: 9-18.

Fürnkranz M., Wanek W., Richter A., Abell G., Rasche F. & A. Sessitsch (2008): Nitrogen fixation by phyllosphere bacteria associated with plants and their colonizing epiphytes of a tropical lowland rainforest in Costa Rica. — ISME Journal **2**: 561-570.

Gardner T.W., Verdonck D., Pinter N.M., Slingerland R., Furlong K.P., Bullard T.F. & S.G. Wells (1992): Quaternary uplift astride the aseismic Cocos ridge, Pacific coast, Costa Rica. — Geological Society of America Bulletin **104**: 219-232.

Gehring C. & P.L.G. Vlek (2004): Limitations of the 15N natural abundance method for estimating biological nitrogen fixation in Amazonian forest legumes. — Basic and Applied Ecology **5**: 567-580.

Giardina C.P., Ryan M.G., Binkley D. & J.H. Fownes (2003): Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. — Global Change Biology **9**: 1438-1450.

Golley F.B., Mcginnis J.T., Clements R.G., GChild .L. & M.J. Duever (1975): Mineral cycling in a tropical moist forest ecosystem. — University of Georgia Press, Athens.

Goulden M.L., Miller S.D., da Rocha H.R., Menton M.C., de Freitas H.C., Figueira A. & C.A.D. DE Sousa (2004): Diel and seasonal patterns of tropical forest CO2 exchange. — Ecological Applications **14**: S42-S54.

Gower S.T. (1987): Relations between mineral nutrient availability and fine root biomass in two Costa Rican tropical wet forests: a hypothesis. — Biotropica **19**: 171-175.

Guariguata M.R. & R. Ostertag (2001): Neotropical secondary forest succession: Changes in structural and functional characteristics. — Forest Ecology and Management **148**: 185-206.

Guo D.L., Mitchell R.J., Withington J.M., F. P.-P. & J.J. Hendricks (2008): Endogenous and exogenous controls of root life span, mortality and nitrogen flux in a long-leaf pine forest: root branch order predominates. — Journal of Ecology **96**: 737-745.

Hansen K., Draaijers G.P.J., Ivens W.P.M.F., Gundersen P. & N.F.M. van Leeuwen (1994): Concentration variations in rain and canopy throughfall collected sequentially during individual rain events. — Atmospheric Environment **28**: 3195-3205.

Harrington R.A., Fownes J.H. & P.M. Vitousek (2001): Production and resource use efficiencies in N- and P-limited tropical forests: A comparison of responses to long-term fertilization. — Ecosystems **4**: 646-657.

Hedin L.O., Armesto J.J. & A.H. Johnson (1995): Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. — Ecology **76**: 493-509.

Hendricks J.J., Nadelhoffer K.J. & J.D. Aber (1997): A 15N tracer technique for assessing fine root production and mortality. — Oecologia **112**: 300-304.

Herbert D.A. & J.H. Fownes (1995): Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. — Biogeochemistry **29**: 223-235.

Herbert D.A. & J.H. Fownes (1999): Forest productivity and efficiency of resource use across a chronosequence of tropical montane soils. — Ecosystems **2**: 242-254.

Hietz P., Wanek W. & O. Dünisch (2005): Long-term trends in cellulose d13C and water-use efficiency of tropical Cedrela and Swietenia from Brazil. — Tree Physiology **25**: 745-752.

Hölscher D., Köhler L., Leuschner C. & M. Kappelle (2003): Nutrient fluxes in stemflow and throughfall in three successional stages of an upper montane rainforest in Costa Rica. — Journal of Tropical Ecology **19**: 557-565.

Hölscher D., Sa T.D.D., Moller., R.F., Denich M. & H. Folster (1998): Rainfall partitioning and related hydrochemical fluxes in a diverse and in a monospecific (Phenakospermum guyannense) secondary vegetation stand in eastern Amazonia. — Oecologia **114**: 251-257.

Houlton B.Z., Sigman D.M. & L.O. Hedin (2006): Isotopic evidence for large gaseous nitrogen losses from tropical rainforests. — Proceeding of the National Academy of Sciences U.S.A. **103**: 8745-8750.

Hughes R.F., Kauffman J.B. & D.L. Cummings (2000): Fire in the Brazilian Amazon 3. Dynamics of biomass, C, and nutrient pools in regenerating forests. — Oecologia **124**: 574-588.

Hughes R.F., Kauffman J.B. & V.J. Jaramillo (1999): Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. — Ecology **80**: 1892-1907.

Jackson R.B., Mooney H.A. & E.D. Schulze (1997): A global budget for fine root biomass, surface area, and nutrient contents. — Proceedings of the National Academy of Sciences of the United States of America **94**: 7362-7366.

Jansson M.B. & K. Stromberg (2004): Surface runoff and soil loss in tropical rainforest and pasture, Costa Rica, and indices explaining their variations. — Zeitschrift Fur Geomorphologie **48**: 25-51.

Jordan C.F. & G. Escalante (1980): Root productivity in an Amazonian rainforest. — Ecology **61**: 14-18.

Keller M., Palace M., Asner G.P., Pereira R. & J.N.M. Silva (2004): Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. — Global Change Biology **10**: 784-795.

Kingsbury N. & M. Kellman (1997): Root mat depths and surface soil chemistry in southeastern Venezuela. — Journal of Tropical Ecology **13**: 475-479.

Lesack L.F.W. (1993): Export of nutrients and major ionic solutes from a rainforest catchment in the Central Amazon basin. — Water Resources Research **29**: 743-758.

Levia D.F. & E.E. Frost (2003): A review and evaluation of stemflow literature in the hydrologic and biogeochemical cycles of forested and agricultural ecosystems. — Journal of Hydrology **274**: 1-29.

Levia D.F. & E.E. Frost (2006): Variability of throughfall volume and solute inputs in wooded ecosystems. — Progress in Physical Geography **30**: 605-632.

Li Y.Q., Xu M. & X.M. Zou (2006): Heterotrophic soil respiration in relation to environmental factors and microbial biomass in two wet tropical forests. — Plant and Soil **281**: 193-201.

Lieberman D., Lieberman M., Peralta R. & G.S. Hartshorn (1985): Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. — Journal of Ecology **73**: 915-924.

Lindroth A., Lagergren F., Aurela M., Bjarnadottir B., Christensen T., Dellwik E., Grelle A., Ibrom A., Johansson T., Lankreijer H., Launiainen S., Laurila T., Molder M., Nikinmaa E., Pilegaard K., Sigurdsson B.D. & T. Vesala (2008): Leaf area index is the principal scaling parameter for both gross photosynthesis and ecosystem respiration of Northern deciduous and coniferous forests. — Tellus Series B-Chemical and Physical Meteorology **60**: 129-142.

Loescher H.W., Oberbauer S.F., Gholz H.L. & D.B. Clark (2003): Environmental controls on net ecosystem-level carbon exchange and productivity in a Central American tropical wet forest. — Global Change Biology **9**: 396-412.

Lovett G.M. & S.E. Lindberg (1984): Dry deposition and canopy exchange in a mixed oak forest as determined by analysis of throughfall. – Journal of Applied Ecology **21**: 1013-1027.

Lovett G.M., Nolan S.S., Driscoll C.T. & T.J. fahey (1996): Factors regulating throughfall flux in a New Hampshire forested landscape. — Canadian Journal of Forest Research **26**: 2134-2144.

Luizao R.C.C., Luizao F.J., Paiva R.Q., Monteiro T.F., Sousa L.S. & B. Kruijt (2004): Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. — Global Change Biology **10**: 592-600.

Malhi Y., Baker T.R., Phillips O.L., Almeida S., Alvarez E., Arroyo L., Chave J., Czimczik C.I., di Fiore A., Higuchi N., Killeen T.J., Laurance S.G., Laurance W.F., Lewis S.L., Montoya L.M.M., Monteagudo A., Neill D.A., Vargas P.N., Patino S., Pitman N.C.A., Quesada C.A., Salomao R., Silva J.N.M., Lezama A.T., Martinez R.V., Terborgh J., Vinceti B. & J. Lloyd (2004): The aboveground coarse wood productivity of 104 neotropical forest plots. — Global Change Biology **10**: 563-591.

Malhi Y., Nobre A.D., Grace J., Kruijt B., Pereira M.G.P., Culf A. & S. Scott (1998): Carbon dioxide transfer over a Central Amazonian rainforest. — Journal of Geophysical Research-Atmospheres **103**: 31593-31612.

Malmer A. & H. Grip (1994): Converting tropical rainforest to forest plantation in Sabah, Malaysia. 2. Effects on nutrient dynamics and net losses in streamwater. — Hydrological Processes **8**: 195-209.

MARIN-SPIOTTA E., OSTERTAG R. & W.L. SILVER (2007): Long-term patterns in tropical reforestation: Plant community composition and aboveground biomass accumulation. — Ecological Applications **17**: 828-839.

MARIN C.T., BOUTEN W. & J. SEVINK (2000): Gross rainfall and its partitioning into throughfall, stemflow and evaporation of intercepted water in four forest ecosystems in western Amazonia. — Journal of Hydrology **237**: 40-57.

MARTINELLI L.A., ALMEIDA S., BROWN I.F., MOREIRA M.Z., VICTORIA R.L., FILOSO S., FERREIRA C.A.C. & W.W. THOMAS (2000): Variation in nutrient distribution and potential nutrient losses by selective logging in a humid tropical forest of Rondonia, Brazil. — Biotropica **32**: 597-613.

MARTIUS C. & A.G. BANDEIRA (1998): Wood litter stocks in tropical moist forest in central Amazonia. — Ecotropica **4**: 115-118.

MARTIUS C., HOFER H., GARCIA M.V.B., ROMBKE J. & W. HANAGARTH (2004): litterfall, litter stocks and decomposition rates in rainforest and agroforestry sites in central Amazonia. — Nutrient Cycling in Agroecosystems **68**: 137-154.

MCDONALD M.A. & J.R. HEALEY (2000): Nutrient cycling in secondary forests in the Blue Mountains of Jamaica. – Forest Ecology and Management **139**: 257-278.

MCDOWELL W.H. (1998): Internal nutrient fluxes in a Puerto Rican rainforest. — Journal of Tropical Ecology **14**: 521-536.

MCDOWELL W.H., SÁNCHEZ C.G., ASBURY C.E. & C.R.R. PÉREZ (1990): Influence of sea salt aerosols and long range transport on precipitation chemistry at El Verde, Puerto Rico. — Atmospheric Environment **24a**: 2813-2821.

MCGRATH D.A., SMITH C.K., GHOLZ H.L. & F.D. OLIVEIRA (2001): Effects of land-use change on soil nutrient dynamics in Amazonia. — Ecosystems **4**: 625-645.

MCGRODDY M.E., DAUFRESNE T. & L.O. HEDIN (2004): Scaling of C: N: P stoichiometry in forests worldwide: Implications of terrestrial redfield-type ratios. — Ecology **85**: 2390-2401.

MCMURRY P.H. (2000): A review of atmospheric aerosol measurements. — Atmospheric Environment **34**: 1959-1999.

MCSWINEY C.P., MCDOWELL W.H. & M. KELLER (2001): Distribution of nitrous oxide and regulators of its production across a tropical rainforest catena in the Luquillo Experimental Forest, Puerto Rico. — Biogeochemistry **56**: 265-286.

MENYAILO O.V., LEHMANN J., CRAVO M.D. & W. ZECH (2003): Soil microbial activities in tree-based cropping systems and natural forests of the Central Amazon, Brazil. — Biology and Fertility of Soils **38**: 1-9.

MILLER S.D., GOULDEN M.L., MENTON M.C., da ROCHA H.R., de FREITAS H.C., FIGUEIRA A. & C.A.D. DE SOUSA (2004): Biometric and micrometeorological measurements of tropical forest carbon balance. — Ecological Applications **14**: S114-S126.

MO J., ZHANG W., ZHU W., GUNDERSEN P., FANG Y., LI D. & H. WANG (2008): Nitrogen addition reduces soil respiration in a mature tropical forest in southern China. — Global Change Biology **14**: 403-412.

MOHAMED M.A.A., BABIKER I.S., CHEN Z.M., IKEDA K., OHTA K. & K. KATO (2004): The role of climate variability in the inter-annual variation of terrestrial net primary production (NPP). — Science of the Total Environment **332**: 123-137.

MOSER G., HERTEL D. & C. LEUSCHNER (2007): Altitudinal change in LAI and stand leaf biomass in tropical montane forests: a transect study in Ecuador and a pan-tropical meta-analysis. — Ecosystems **10**: 924-935.

NADKARNI N.M. & T.J. MATELSON (1992): Biomass and nutrient dynamics of fine litter of terrestrially rooted material in a neotropical montane forest, Costa Rica. — Biotropica **24**: 113-120.

NASCIMENTO H.E.M. & W.F. LAURANCE (2002): Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. — Forest Ecology and Management **168**: 311-321.

NEFF J.C., HOBBIE S.E. & P.M. VITOUSEK (2000): Nutrient and mineralogical control on dissolved organic C, N and P fluxes and stoichiometry in Hawaiian soils. – Biogeochemistry **51**: 283-302.

NEPSTAD D.C., MOUTINHO P., DIAS M.B., DAVIDSON E., CARDINOT G., MARKEWITZ D., FIGUEIREDO R., VIANNA N., CHAMBERS J., RAY D., GUERREIROS J.B., LEFEBVRE P., STERNBERG L., MOREIRA M., BARROS L., ISHIDA F.Y., TOHLVER I., BELK E., KALIF K. & K. SCHWALBE (2002): The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. — Journal of Geophysical Research-Atmospheres **107**: 8085.

NICOTRA A.B., CHAZDON R.L. & S.V.B. IRIARTE (1999): Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. — Ecology **80**: 1908-1926.

OLSON J.S. (1963): Energy, storage and the balance of producers and decomposers in ecological systems. — Ecology **44**: 322-331.

PALACE M., KELLER M. & H. SILVA (2008): Necromass production: studies in undisturbed and logged Amazon forests. — Ecological Applications **18**: 873-884.

PARKER G.G. (1983): Throughfall and stemflow in the forest nutrient cycle. — Advances in Ecological Research **13**: 57-133.

PARSONS W.F.J., MITRE M.E., KELLER M. & W.A. REINERS (1993): Nitrate limitation of $N_2O$ production and denitrification from tropical pasture and rainforest soils. — Biogeochemistry **22**: 179-193.

PARTON W., SILVER W.L., BURKE I.C., GRASSENS L., HARMON M.E., CURRIE W.S., KING J.Y., ADAIR E.C., BRANDT L.A., HART S.C. & B. FASTH (2007): Global-scale similarities in nitrogen release patterns during long-term decomposition. — Science **315**: 361-364.

PHILLIPS O.L. (1996): Long-term environmental change in tropical forests: increasing tree turnover. — Environmental Conservation **23**: 235-248.

PHILLIPS O.L., MALHI Y., HIGUCHI N., LAURANCE W.F., NUNEZ P.V., VASQUEZ R.M., LAURANCE S.G., FERREIRA L.V., STERN M., BROWN S. & J. GRACE (1998): Changes in the carbon balance of tropical forests: Evidence from long-term plots. — Science **282**: 439-442.

PONS T.L., PERREIJN K., van KESSEL C. & M.J.A. WERGER (2007): Symbiotic nitrogen fixation in a tropical rainforest: 15N natural abundance measurements supported by experimental isotopic enrichment. — New Phytologist **173**: 154-167.

PORDER S., ASNER G.P. & P. VITOUSEK (2005a): Ground-based and remotely sensed nutrient availability across a tropical landscape. — Proceedings of the National Academy of Sciences of America **102**: 10909-10912.

PORDER S., CLARK D.A. & P.M. VITOUSEK (2006): Persistence of rock-derived nutrients in the wet tropical forests of La Selva, Costa Rica. — Ecology **87**: 594-602.

PORDER S., PAYTAN A. & P. VITOUSEK (2005b): Erosion and landscape development affect plant nutrient status in the Hawaiian Islands. — Oecologia **142**: 440-449.

PORDER S., VITOUSEK P.M., CHADWICK O.A., CHAMBERLAIN C.P. & G.E. HILLEY (2007): Uplift, erosion, and phosphorus limitation in terrestrial ecosystems. — Ecosystems **10**: 158-170.

Potter C., Klooster S., Steinbach M., Tan P.N., Kumar V., Shekhar S. & C.R. de Carvalho (2004): Understanding global teleconnections of climate to regional model estimates of Amazon ecosystem carbon fluxes. — Global Change Biology **10**: 693-703.

Potter C.S. & S.A. Klooster (1999): Detecting a terrestrial biosphere sink for carbon dioxide: Interannual ecosystem modeling for the mid-1980s. — Climatic Change **42**: 489-503.

Powers J.S. (2004): New perspectives in comparative ecology of neotropical rainforests: Reflections on the past, present, and future. — Biotropica **36**: 2-6.

Powers J.S., Treseder K.K. & M.T. Lerdau (2005): Fine roots, arbuscular mycorrhizal hyphae and soil nutrients in four neotropical rainforests: patterns across large geographic distances. — New Phytologist **165**: 913-921.

Pregitzer K.S. & E.S. Euskirchen (2004): Carbon cycling and storage in world forests: biome patterns related to forest age. — Global Change Biology **10**: 2052-2077.

Raich J.W. (1998): Aboveground productivity and soil respiration in three Hawaiian rainforests. — Forest Ecology and Management **107**: 309-318.

Raich J.W. & K.J. Nadelhoffer (1989): Belowground carbon allocation in forest ecosystems: Global trends. — Ecology **70**: 1346-1354.

Rodenbeck C., Houweling S., Gloor M. & M. Heimann (2003): $CO_2$ flux history 1982-2001 inferred from atmospheric data using a global inversion of atmospheric transport. — Atmospheric Chemistry and Physics **3**: 1919-1964.

Roggy J.C., Prevost M.F., Garbaye J. & A.M. Domenach (1999): Nitrogen cycling in the tropical rainforest of French Guiana: comparison of two sites with contrasting soil types using d15N. — Journal of Tropical Ecology **15**: 1-22.

Salmon C.D., Walter M.T., Hedin L.O. & M.G. Brown (2001): Hydrological controls on chemical export from an undisturbed old-growth Chilean forest. — Journal of Hydrology **253**: 69-80.

Sanchez-Azofeifa G.A., Rivard B., Calvo J. & I. Moorthy (2002): Dynamics of tropical deforestation around national parks: Remote sensing of forest change on the Osa Peninsula of Costa Rica. — Mountain Research and Development **22**: 352-358.

Sanford R.L. (1990): Fine root biomass under light gap openings in an Amazon rainforest. — Oecologia **83**: 541-545.

Sanford R.L. & E. Cuevas (1996): Root growth and rhizosphere interactions in tropical forests. — In: Mulkey S.S., R.L. Chazdon & A.P. Smith (eds), Tropical Forest Plant Ecophysiology, Springer, New York: 268-301.

Santiago L.S. & S.S. Mulkey (2005): Leaf productivity along a precipitation gradient in lowland Panama: patterns from leaf to ecosystem. — Trees **19**: 349-356.

Schroth G., Elias M.E.A., Uguen K., Seixas R. & W. Zech (2001): Nutrient fluxes in rainfall, throughfall and stemflow in tree-based land use systems and spontaneous tree vegetation of central Amazonia. — Agriculture Ecosystems & Environment **87**: 37-49.

Schuur E.A.G. (2003): Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. — Ecology **84**: 1165-1170.

Schuur E.A.G. & P.A. Matson (2001): Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. — Oecologia **128**: 431-442.

Scott D.A., Proctor J. & J. Thompson (1992): Ecological studies on a lowland evergreen forest on Maraca Island, Roraima, Brazil. II. Litter and nutrient cycling. — Journal of Ecology **80**: 705-717.

Sierra C.A., del Valle J.I., Orrego S.A., Moreno F.H., Harmon M.E., Zapata M., Colorado G.J., Herrera M.A., Lara W., Restrepo D.E., Berrouet L.M., Loaiza L.M. & J.F. Benjumea (2007a): Total carbon stocks in a tropical forest landscape of the Porce region, Colombia. – Forest Ecology and Management **243**: 299-309.

Sierra C.A., Harmon M.E., Moreno F.H., Orrego S.A. & J.I. del Valle (2007b): Spatial and temporal variability of net ecosystem production in a tropical forest: testing the hypothesis of a significant carbon sink. — Global Change Biology **13**: 838-853.

Silver W.L., Scatena F.N., Johnson A.H., Siccama T.G. & M.J. Sanchez (1994): Nutrient availability in a montane wet tropical forest – spatial patterns and methodological considerations. — Plant and Soil **164**: 129-145.

Silver W.L., Thompson A.W., Mcgroddy M.E., Varner R.K., Dias J.D., Silva H., Crill P.M. & M. Keller (2005): Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. — Global Change Biology **11**: 290-306.

Sollins P. (1998): Factors influencing species composition in tropical lowland rainforest: Does soil matter? — Ecology **79**: 23-30.

Sotta E.D., Meir P., Malhi Y., Nobre A.D., Hodnett M.& J. Grace (2004): Soil CO2 efflux in a tropical forest in the central Amazon. — Global Change Biology **10**: 601-617.

Stephens B.B., Gurney K.R., Tans P.P., Sweeney C., Peters W., Bruhwiler L., Ciais P., Ramonet M., Bousquet P., Nakazawa T., Aoki S., Machida T., Inoue G., Vinnichenko N., Lloyd J., Jordan A., Heimann M., Shibistova O., Langenfelds R.L., Steele L.P., Francey R.J. & A.S. Denning (2007): Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO2. — Science **316**: 1732-1735.

Titiz B. & R.L. Sanford (2007): Soil charcoal in old-growth rainforests from sea level to the continental divide. — Biotropica **39**: 673-682.

Tobon C., Sevink J. & J.M. Verstraten (2004a): Litterflow chemistry and nutrient uptake from the forest floor in northwest Amazonian forest ecosystems. — Biogeochemistry **69**: 315-339.

Tobon C., Sevink J. & J.M. Verstraten (2004b): Solute fluxes in throughfall and stemflow in four forest ecosystems in northwest Amazonia. — Biogeochemistry **70**: 1-25.

Vasconcelos H.L. & F.J. Luizao (2004): Litter production and litter nutrient concentrations in a fragmented Amazonian landscape. — Ecological Applications **14**: 884-892.

Veneklaas E.J. (1990): Nutrient fluxes in bulk precipitation and throughfall in two montane tropical rainforests, Colombia. — Journal of Ecology **78**: 974-992.

Vieira S., de Camargo P.B., Selhorst D., da Silva R., Hutyra L., Chambers J.Q., Brown I.F., Higuchi N., Dos Santos J., Wofsy S.C., Trumbore S.E. & L.A. Martinelli (2004): Forest structure and carbon dynamics in Amazonian tropical rainforests. — Oecologia **140**: 468-479.

Vitousek P. (2004): Nutrient Cycling and Limitation. Hawai'i as a Model System. — Princeton University Press, Oxford and Princeton.

VITOUSEK P.M. (1982): Nutrient cycling and nutrient use efficiency. — The American Naturalist **119**: 553-572.

VITOUSEK P.M. (1984): Litterfall, nutrient cycling, and nutrient limitation in tropical forests. — Ecology **65**: 285-298.

VITOUSEK P.M. & H. FARRINGTON (1997): Nutrient limitation and soil development: Experimental test of a biogeochemical theory. — Biogeochemistry **37**: 63-75.

VOGT K.A., VOGT D.J., PALMIOTTO P.A., BOON P., OHARA J. & H. ASBJORNSEN (1996): Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. — Plant and Soil **187**: 159-219.

von FISCHER J.C. & L.O. HEDIN (2007): Controls on soil methane fluxes: Tests of biophysical mechanisms using stable isotope tracers. — Global Biogeochemical Cycles **21**: GB2007.

WADSWORTH F.H. (1997): Primary forests and their productivity. — Forest production for tropical America, United States Department of Agriculture (USDA), Washington: 63-99.

WANEK W., HOFMANN J. & I.C. FELLER (2007): Canopy interactions of rainfall in an off-shore mangrove ecosystem dominated by Rhizophora mangle (Belize). — Journal of Hydrology **345**: 70-79.

WANG H.Q., HALL C.A.S., SCATENA F.N., FETCHER N. & W. WU (2003): Modeling the spatial and temporal variability in climate and primary productivity across the Luquillo Mountains, Puerto Rico. — Forest Ecology and Management **179**: 69-94.

WEAVER P.L., MEDINA E., POOL D., DUGGER K., GONZALES-LIBOY J. & E. CUEVAS (1986): Ecological observations in the dwarf cloud forest of the Luquillo Mountains in Puerto Rico. — Biotropica **18**: 79-85.

WHITMORE T.C. (1998): An introduction to tropical rainforests. — Oxford University Press, Oxford, U. K..

WILCKE W., YASIN S., VALAREZO C. & W. ZECH (2001): Change in water quality during the passage through a tropical montane rainforest in Ecuador. — Biogeochemistry **55**: 45-72.

WILLIAMS M.R., FILOSO S. & P. LEFEBVRE (2004): Effects of land-use change on solute fluxes to floodplain lakes of the central Amazon. — Biogeochemistry **68**: 259-275.

WILLIAMS M.R., FISHER T.R. & J.M. MELACK (1997): Chemical composition and deposition of rain in the Central Amazon, Brazil. — Atmospheric Environment **31**: 207-217.

WOOD T.E., LAWRENCE D.& D.A. CLARK (2005): Variation in leaf litter nutrients of a Costa Rican rainforest is related to precipitation. — Biogeochemistry **73**: 417-437.

WOOD T.E., LAWRENCE D. & D.A. CLARK (2006): Determinants of leaf litter nutrient cycling in a tropical rainforest: Soil fertility versus topography. — Ecosystems **9**: 700-710.

WORBES M. (1999): Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. — Journal of Ecology **87**: 391-403.

YAVITT J.B., WIEDER R.K. & S.J. WRIGHT (1993): Soil nutrient dynamics in response to irrigation of a Panamanian tropical moist forest. — Biogeochemistry **19**: 1-25.

YAVITT J.B. & S.J. WRIGHT (2001): Drought and irrigation effects on fine root dynamics in a tropical moist forest, Panama. — Biotropica **33**: 421-434.

ZHANG L.M., YU G.R., SUN X.M., WEN X.F., REN C.Y., SONG X., LIU Y.F., GUAN D.X., YAN J.H. & Y.P. ZHANG (2006): Seasonal variation of carbon exchange of typical forest ecosystems along the eastern forest transect in China. — Science in China Series D-Earth Sciences **49**: 47-62.

ZHANG Q. & J.C. ZAK (1998): Potential physiological activities of fungi and bacteria in relation to plant litter decomposition along a gap size gradient in a natural subtropical forest. — Microbial Ecology **35**: 172-179.

Address of authors:

Wolfgang WANEK
Sigrid DRAGE
Nina HINKO
Florian HOFHANSL
Eva-Maria PÖLZ
Andrea RATZER
Andreas RICHTER
Department of Chemical
Ecology and Ecosystem Research
University of Vienna
Althanstraße 14
A-1090 Vienna, Austria
E-mail: wolfgang.wanek@univie.ac.at

Zeitschrift/Journal: Stapfia

Jahr/Year: 2008

Band/Volume: 0088

Autor(en)/Author(s): Wanek Wolfgang, Drage Sigrid, Hinko Nina, Hofhansl Florian P., Pölz Eva-Maria, Ratzer Andrea, Richter Andreas

Artikel/Article: Primary production and nutrient cycling in lowland rainforests of the Golfo Dulce region 155-177