Diplomarbeit

Solute fluxes via Bulk Precipitation, Throughfall & Stemflow in a humid tropical lowland rainforest, Costa Rica

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„Der wahre Wissenschaftler besitzt eine seltene, indianische Weisheit und kennt die Natur besser aufgrund seiner feineren Organe. Er wird besser riechen, schmecken, sehen, hören und fühlen können als andere Menschen. Er wird tiefere differenziertere Erfahrungen machen. Wir lernen nicht, indem wir Schlüsse ziehen und etwas ableiten, noch indem wir die Prinzipien der Mathematik auf die Philosophie anwenden, sondern durch direkten Umgang mit einer Sache." (**Henry David Thoreau** † 6.Mai 1862)

Danksagung

Ich möchte mich bei meiner Familie und meinen Freunden für ihre Liebe, und ihr ungebrochenes Verständnis bedanken das dieser Arbeit Tribut zollte.

Especialimente quiero dar las gracias al Estacion Tropical La Gamba y mi corazon Victor Cruz, sin quien este trabajo ne puede ser realizado...
– tschanflees -

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General Introduction in tropical ecology

Geology & Climate

The tropics (from Greek: *tropai heliou* = solstitial regions) are situated between the latitudes of the Tropic of Cancer (22.5°N) on the northern hemisphere, and the Tropic of Capricorn (22.5°S) on the southern hemisphere. The Greek word indicates the oscillation (tropos = turn) of the sun between the two tropics within the period of one year. Besides the latitudinal gradient there is also a vertical gradient caused by the ascent and descent of the land mass and thus topography is taking strong influence on the predominant climate. Hence it is understood that within this “tropical belt” there is not only tropical landscape, e.g. tropical rainforests, but also alpine tundra like at the peaks of the Andes in northern Chile or dry areas like the Saharan Desert in Western Africa and the area of northern Australia. Regions in these latitudes, however, often are designated as ‘hot spots’ of biodiversity since they are inhabited by a variety of fauna and flora. The driving force inducing the tropical climate originates in the temperature controlled movement of air masses (convection) generated by solar radiation. In detail the warm moist air mass of the so-called ‘Hadley Cell’ is lifted in equatorial low pressure areas to the tropopause and carried poleward until at around 30° N or S where it descends in a cooler high pressure area, travelling along the earth’s surface back to its origin, creating the ‘trade winds’ (Hadley 1735).

In general tropical rainforests can be found near equatorial regions where there is high humidity and high amounts of rainfall. These are usually caused by warm and wet air masses ascending mountain ridges, getting colder and therefore releasing rainwater which they have taken up previously at sites of high evaporation from ocean surfaces. In most regions tropical climate can be divided into two seasons, a rainy ‘wet season’ and an arid ‘dry season’, throughout the year. In case of the Neotropics wet season lasts approximately from January to March and dry season from September to November.

Costa Rica in particular is distinguished by exceptional high biodiversity, forming a land bridge between both North and South American continents sharing its coasts with two oceans the Atlantic and the Pacific Ocean. In past ages this isthmus admitted the exchange of diverse species between the variable habitats. Inhabiting 5 percent of the world’s total biodiversity CR is believed the land comprising the highest numbers of species. Only 3 million years ago CR and its surrounding countries was only a volcanic archipelago formed by plate tectonics, as the Caribbean plate moved westwards overriding the Cocos plate, located in the Pacific Ocean, a process that still lasts down to the present day. Nowadays the Mesoamerican countries still connect the northern and southern part of America urging the Atlantic’s warm surface currents to turn and form the ‘golf stream’ that provides Europe with a much warmer climate of approximately 10°C than would be expected for areas situated in these latitudes.

Tropical Biodiversity

For the present state a rise in species numbers can be assumed in tropical latitudes mainly due to the fact that the temperature oscillates more in the ranges of day and night than throughout the year. Therefore there is no season of low productivity as in winter in higher latitudes. Looking back over geological time scales it must be taken into consideration that a lack of ice ages and thus the possibility of exchanging species through longitudinal migrations in the Neotropics, as a refugee area, mirror major advantages for species inventories (Erkens, Chatrou et al. 2007). On the contrary the genesis of landscape patches in patterns of mountain ranges and deep valleys could lead to a high rate of endemism through ‘island-like’ formations (Barbara, Martinelli et al. 2007; Morawetz & Raedig 2007). Overall the benefits of tropical climate could cause a broader range of species staying in competition for the same existing niches and thus lead to a co-evolution of many more species than elsewhere, considering the fact that mild disturbance usually leads to highest diversity (Rosenzweig & Brown 1995).

Other factors explaining tropical species diversity:

1) Feeding guilds:

Tropical birds for instance often feed in preying formations called “feeding guilds” providing a whole range of different species with mostly ground dwelling arthropods (Poulin, Lefebvre et al. 1992).

2) Plant-Animal Interactions:

Best known interactions between these to life-forms are probably plant-ant interactions, where different species of both live in symbioses feeding and protecting each other. In case of the plant genus *Cecropia* and the ant genus *Atzteka*, the hollow plant tissues of the stems provide a dry and safe home to the eusocial insects living in colonies, whereas the ants in turn protect the plant from herbivores which gives them a huge advantage in concurrence for light making them grow faster than surrounding plant species (Fischer, Richter et al. 2002; Fischer, Wanek et al. 2003; Schaber 2007). In further studies on the plant genus *Passiflora* it could be observed that the facultative symbiosis with various ant species reduced herbivory pressure (Thurner 2007).

3) Tropical land conversion:

For many birds and insect-groups it has been shown that the conversion of tropical landscape from pristine forests to agricultural areas has lead to a rise in species numbers for the short term (Schulze, Waltert et al. 2004). Nevertheless these results have to be interpreted carefully since mostly a rise of common or abundant species-numbers was encountered, whereas rare or endemic species have vanished (Schneeweihs & Hofhansl 2007).

Tropical Soils

The tropical rainforests' high biodiversity and productivity of the above-ground biomass is understood when associated with the nutrient poor soils of these landscapes.

In general the genesis of tropical pedobiomes can be characterized by undisturbed development over geological periods and leads to a high degree of weathering and low availability of nutrients in the soil. This major nutrient loss is due to uniform high temperatures and precipitation throughout the year, which have led to deep-reaching chemical weathering of the parent material and formed rather acidic soils named 'Ultisols'. The main fraction of an Ultisol is composed of the clay mineral kaolinite, characterized by a low nutrient retention capacity. Only in ravines and sediment deposition sites moderately weathered Inceptisols can be found, exhibiting a better nutrient supply (Pamperl 2001). When parent material has weathered, only aluminium and iron oxides namely haematite, goethite and ferrihydrite remain, giving the tropical soils its typical yellow-reddish colour. These remaining compounds show a high anion exchange capacity in neutral and acid conditions and can bind phosphorus nearly irreversibly decreasing its availability for plant growth and enhancing phosphorus limitation of primary production so that soils become increasingly limited in this element (Chapin III 2002).

Nutrient cycling

Prevalent processes influencing ecosystem fluxes are closely related to effects of seasonality, like e.g. the flowering of tropical plants representing a nutrient input, and even throughfall (rainfall passing through the canopy layer) in some regions is capable to provide tropical ecosystems with up to 50% of overall nutrient input, besides the major part from leaf litter fall.

As a matter of the seasonal fluctuations in climatic conditions, as mentioned before, nutrient cycling in tropical rainforests shows a faster turn over than in any other ecosystem. The internal cycling rates of elements - describing fluxes of nutrients that are exchanged between pools in plants, soils and decomposer micro-organisms - exceed those of inputs and outputs. In general these processes are described by uptake and release of nutrients by plants and micro-organisms during decomposition processes of dead biomass, conversion processes from organic to inorganic material and exchange to ionic surfaces in the soil matrix. Nutrient inputs are generated by chemical weathering of parent material, atmospheric deposition and biological fixation of atmospheric compounds. Nutrient losses occur mainly through wash off and leaching from canopy leaves, epiphytes, decomposed litter and soils into stream- and groundwater (Chapin III 2002).

Nutrient cycles in tropical forests are considered as highly efficient compared to temperate forests, out of two reasons: 1) relatively more carbon is fixed per unit nutrient or a larger fraction of nutrients is re-absorbed by plants before shedding of senescent plant parts and 2) rapid nutrient uptake by roots, mycorrhizas and decomposers admits only small amounts of nutrient losses (Vitousek 1984).

Despite of environmental factors like climate and temperature nutrient cycling is also influenced by chemical and biological drivers namely soil composition and bacteria or fungi (Attiwill & Adams 1993). Decomposition activity of the latter is in turn influenced by environmental factors like temperature, moisture and oxygen level so that tropical rainforests generally exhibit small nutrient pools (e.g. litter layers) and high cycling rates (Whitmore 1998).

Overall nutrient cycling rates are on the one hand driven by nutrient supply from the soil, limited by climatic factors or soil chemistry, and on the other hand by nutrient demand of vegetation, which itself is constrained by water limitation or low vegetation density after disturbance (Chapin III 2002). Whilst biomass development and regeneration capacity depend on the rates and patterns of nutrient cycling (Vitousek & Sanford 1986), the nutrient which is most limiting for production usually determines cycling rates of overall nutrients on ecosystem scale (Chapin III 2002).

Since there are substantial differences between responses of different elements on specific controls concerning input and losses along different pathways, the consequences are differences in the “openness” and “buffering capacity” of the different cycles of carbon, water, nitrogen and phosphorus. The carbon cycle is described by the exchange of CO_2 with the atmosphere and its huge pool in ecosystem biomass and soil and therefore displays an open system. The water cycle is also dominated by high input and output fluxes, but lacks a notable storage capacity, making organisms strongly dependent on water input from the atmosphere. Nitrogen and phosphorus exhibit a relatively closed cycling, with high amounts of recycling compared to in- and outputs (Chapin III 2002).

It was exemplified that nitrogen content in leaf litter is consistently higher in tropical lowland rainforests compared to temperate or montane tropical rainforests, as indicated by a lower dry mass/nitrogen ratio in litterfall (Vitousek 1984). This suggests that nitrogen is not re-absorbed as efficiently as phosphorus before the leaves are shed and therefore is not a limiting resource in these habitats (Vitousek 1984). Furthermore it is believed that low phosphorus content in litterfall and very high dry mass/phosphorus ratios indicate highly efficient cycling of phosphorus in tropical rainforests and points to phosphorus- but not nitrogen limited forest production (Vitousek 1984). This assumption is further encouraged by tracer-experiments, indicating that plants' fine roots can absorb dissolved nutrients, which were earlier released from decomposed litter or canopy leaching (Stark & Jordan 1978). Recent studies suggested that the uptake of nutrients, especially phosphorus, is enhanced by mycorrhiza-microbes that are symbiotically associated with the plants' fine roots (Herrera 1978). Nevertheless the formation of insoluble precipitates with iron, aluminium and calcium decreases phosphorus availability in highly weathered tropical soils. Especially at low pH between 4 and 5, where phosphorus occurs predominantly as $H_2PO_4^-$, in the preferred ionic form for plant uptake, it reacts with aluminium, iron or manganese to insoluble compounds (Cuevas & Lugo 1998; Luizao, Luizao et al. 2004; Martius, Höfer et al. 2004). Other elements like calcium are not as manoeuvrable and therefore allocated in the plants' tissue, thus it shows a slow turn over, returning to the forest floor mostly via litterfall (Vitousek 1984).

Litter decomposition

As soils are highly weathered and do not serve for tropical plants' nutrient supply, litter exhibits the most important nutrient source for the highly limited ecosystems (Martius, Höfer et al. 2004). Nutrient content in leaf litter and reproductive material litter is generally higher than in dead wood litter (Cuevas & Lugo 1998) and mainly provides supply of carbon, nitrogen, phosphorus and calcium of the forest floor. Mean total carbon stock for tropical primary forests was estimated to be 383,7 +/- 55,5 Mg C ha^{-1} with soil organic carbon providing 59%, total belowground carbon 10%, total aboveground biomass 29% and total standing litter stock 2% of total carbon (Sierra, del Valle et al. 2007).

Therefore studies of litterfall and litter nutrient content are often conducted to investigate the efficiency of nutrient cycling in order to compare different systems. The ratio of dry mass to nutrient content, so called 'nutrient use efficiency' (NUE), was defined as a reliable indicator to calculate a forest ecosystem's nutrient budget (Vitousek 1984). But also other indicators are used to determine an ecosystem's nutrient status like initial nutrient concentration (Taylor, Parkinson et al. 1989; Vitousek, Turner et al. 1994), or carbon/nitrogen ratios (Edmonds 1980) and carbon/phosphorus ratios.

Interestingly, the most limiting nutrient is always the one which shows the highest internal cycling rates, since its availability is most limited and usually shows low in- and output. In other words, nutrient availability generally determines the efficiency of nutrient use for most tree species (Turner 1977) and so efficient nutrient economy of an element indicates its limiting status for primary production, while inefficient cycling of a specific nutrient implies no limitation of a nutrient (Grubb 1977; Vitousek 1982). In this way it is possible to determine the importance of different nutrients in different ecosystems by calculating turnover rates with defined indicators.

Generally litterfall can be understood as a plants response to environmental conditions and therefore is highly related to periods of drought and climatic conditions. The shedding of leaves differs from species to species or even on individual's level, since species often follow different life-strategies or individuals are affected by differing site factors. Water limitation, for instance, will lead to an unintentional loss of leaves during dry periods, but also heavy storms can induce a nutrient pulse in the same way. Apart from nutrient status litterfall could be a successful defence against herbivores (e.g. ants), parasites or pathogens. And also the re-absorption of nutrients from leaves before abscission differs between species, which leads to an unequal impact of nutrient recycling via litterfall among species (Cuevas & Lugo 1998). When looking for pathways of nutrient fluxes via litterfall these facts must be considered, indicating a difference in litter quality to the ecosystem.

Decomposition - the break down of organic matter – converts macromolecules into nutrients available for plants, releasing carbon dioxide to the atmosphere (Chapin III 2002). The break-down must be considered as a complex process which is handled by a community of micro-organisms depending on various environmental factors such as temperature, moisture, nutrient availability and biotic interactions (Swift, Andren et al. 1998). The decay of litter can be generally described by three processes: 1) Leaching, at the very beginning of decomposition, removing soluble compounds out of leaves, representing a major input of nutrients to the forest floors and it's microbial community, 2) Fragmentation by soil invertebrates and 3) the lysis of cells which enhance microbial colonization and increase the exposed surface for further decomposition.

The re-conversion of biologically derived organic material into inorganic minerals is managed by fungi and bacteria which together account for 80 to 90% of the decomposers biomass. Fungi have a competitive advantage over bacteria in decomposition of low quality litter, due to their network of hyphen and their unique enzymatic system which is capable to compose nearly all plant derived material. Bacteria on the contrary are privileged at nutrient rich sites because of their rapid growth ability and preferred uptake of low molecular compounds (Chapin III 2002).

In the case of nitrogen, the conversion is provided by mineralization and nitrification of dissolved organic nitrogen (DON) to ammonium (NH_4^+) or nitrite (NO_2^-) and nitrate (NO_3^{2-}) respectively. DON consists of a mixture of compounds, containing amino acids, and can be taken up by plants and micro-organisms equally. When a system becomes nitrogen limited microbes will incorporate most DON into their biomass and thus immobilize nitrogen from the system. Therefore the balance between mineralization and immobilization controls net mineralization of nitrogen and must be considered when interpreting data on this subject (Chapin III 2002).

Besides litter fall, the most important pathways of nutrient cycling (up to 50% in some tropical wet forests) originate from *canopy leaching* and *atmospheric dry deposition* and nutrients inserted via throughfall and stemflow to the forest floor (Parker 1983; Levia & Frost 2003). On the one hand, litterfall, litter decomposition processes and the input of canopy leachates via throughfall and stemflow exhibit *autochthonous sources* of nutrients (Whitmore 1998). On the other hand, *external nutrient inputs* into the soil are derived from atmospheric dry and wet deposition, chemical fixation or the weathering of parent materials.

Atmospheric deposition

Representing an external nutrient pulse, atmospheric deposition generally divides into *wet-* and *dry- deposition*. Whereas wet deposition consists of substances dissolved in precipitation and represents a minor source of total nutrient input, dry deposition is composed of aerosols, gases and particulate forms of ions which are deposited onto the forests' canopy. Accumulated materials can either enter the nutrient cycle through wash off of the canopy layer running off to the forest floor, or through uptake by leaves via stomata or epicuticules. There are diverse forms of nutrient uptake like diffusion in case of dissolved aerosols, absorption of gases or processes of ion exchange leading to differences in uptake rates which themselves are strongly influenced by the duration of rain free periods, wind speed and direction (influencing deposition velocity) and particularly canopy structure.

On the one hand, ionic solute inputs can either derive from local sources (non sea salt ions: K^+, Ca^{2+}) or even distribute over long distances (sea salt ions: Na^+, Mg^{2+}, Cl^- and SO_4^{2-} from ocean surfaces) until their deposition on the canopy leaves' surface and subsequent introduction to the forest's nutrient cycle by the following precipitation event (Eklund, McDowell et al. 1997). On the other hand, origin of deposited materials can either deduce from natural sources like soil processes due to geology and climate or anthropogenic alteration through combustion of fossil fuels or agricultural fertilization (Lovett 1992). Furthermore major nutrient accumulation can take place by massive short term inputs of: (1) volcanic ash derived from earlier eruptions (Kellman, Hudson et al. 1982; Veneklaas 1990; Eklund, McDowell et al. 1997) leading to enrichment of SO_4^{2-}, (2) artificial inputs of aerosols SO_2, NO, NO_2, NH_3, HNO_3 due to human activities and (3) NO_3^-, NH_4^+, Ca^{2+} and K^+ which especially correspond to biomass burning (Clark, Nadkarni et al. 1998b).

In the tropics in particular, the input of nitrogen and phosphorous play a key role as most tropical systems are reported to be limited by these nutriments due to high turnover rates and weathering of soil resources. Taking into account that nitrogen makes up to

78% of atmospheric gases, but mostly is present in unavailable and non-reactive (N_2) or reduced forms (NH_4^+ and NH_3), a further significant pathway of nitrogen input is given by the fixation of atmospheric N_2 on surface areas (up to 25% of total leaf N content) by cyan bacteria and other epiphyllous organisms like algae or lichens where fixation rates strongly correlate with forest stand age due to colonization rates of epiphylls (Bentley & Carpenter 1984). Nevertheless dry deposition of N primarily occurs through gaseous HNO_3 and NH_3, representing the major N input, since these forms of N can be absorbed more easily by plants' surfaces (Lovett 1992; Hill, Shepson et al. 2005).

Generally it can be assumed that 40-50% of deposited inorganic N is retained by the forests' canopy through epiphytes and microbial immobilization in temperate latitudes (Garten, Schwab et al. 1998). This percentage is even exceeded in the tropics where 80% of NO_3^--N and 61% of NH_4^+-N from atmospheric N deposition were retained by the canopy and accumulated canopy litter and humus accounted for 80% of this retention (Clark, Nadkarni et al. 1998a).

In contrast to nitrogen input via dry deposition, only a small contribution to the vegetations total N demand occurs via wet deposition (Wilson & Tiley 1998), therefore throughfall measurements usually underestimate the atmospheric deposition of N compounds (Hansen 1996).

Canopy exchange

As already mentioned the major pathways of ion exchange can be specified by uptake or leaching of dissolved substances from the leaves' surface of the forest canopy. Many characteristics of the canopy affect the modality and velocity of exchange processes. For a given site differences in nutrient availability might occur on the species level as certain species follow differing life strategies. For instance leaves of evergreen trees will exhibit higher lignin contents in order to endure longer than deciduous species. These assumptions are confirmed as sclerophylly and re-translocation of foliage nutrients from senescent leaves to other plant parts before abscission where found to differ between species (Jordan & Herrera 1981; Vitousek & Sanford 1986). Furthermore exchange processes and rates vary due to tissue age and foliage nutrient content reflecting earlier metabolic processes (Tukey 1970). In general nutrient loss increases with maturity of plant tissue and nutrients accumulated in excess are leached more easily.

Other factors like differences in canopy structure, nutrient and water availability but particularly microclimatic conditions, especially due to light spots in gaps of fallen trees induce the patterns and variability in physical and chemical parameters. Canopy roughness for instance, where a variable stand of uneven tree sizes usually leads to a high value of roughness, arises from development of different tree strata and thus is increasing the total surface area for possible nutrient exchange by high spatial variability.

Extraordinary diversity in tropical rainforests is thought to derive from the fact that the canopy contains about 10% of known vascular plant species and that plants within a canopy of tropical rain forests follow different life strategies (Whitmore 1998). Besides multilayer tree strata and huge emergent trees, which overcome the average level of the canopy, epiphytes account for one third of vascular plant biodiversity in the tropics (Gentry & Dodson 1987). Epiphytic plants usually do not affect their host plants since they do not attach to their phloem, but assimilate nutrients either through atmospheric dry deposition or aerial roots taking up substances out of the crown soils which derived from dead organic matter trapped in branches of trees or epiphytes. Moreover it is proven that epiphytes obtain notable amounts of nutrients from wash off of dry deposited material and from leaching of foliage solutes of higher plants (Wania, Hietz et al. 2002) with morphologically and physiologically adapted leaves to trap water and nutrients or plant detritus from allochthonous and autochthonous sources. In case of several genera of bromeliads, for instance, it was shown that they are capable to accumulate nutrients in so called “water tanks” which are made of their thick leaves that are arranged in funnel like structures (Richardson, Richardson et al. 2000; Inselsbacher, Aguetoni Cambui et al. 2007).

Furthermore leaves themselves (phyllosphere) are colonized by so called epiphylls (e.g. bio films of bacteria, algae and even lichens, mosses and ferns) which are believed to significantly contribute to interception losses and therefore represent internal water storage of tropical forest ecosystems. Bryophytes for instance absorb more than 20-fold compared to foliage, probably due to the lack of epicuticular waxes (Wanek, Pörtl et al. 2003). A similar pattern was examined for nutrients, where an extensive bidirectional transfer of nitrogen between epiphylls and host leaves was found to take strong influence on the control of N fluxes in the lower canopy of a tropical ravine forest (Wanek, Pörtl et al. 2003; Wanek & Portl 2005). Therefore it is evident that uptake processes do not occur only through stomata but along the whole leaf surface.

The magnitude of water and nutrient fluxes inside the canopy, however, is mainly affected by non-vascular plants (mosses, liverworts and lichens) since they account for the biggest part of the vegetation’s biomass (Hölscher, Köhler et al. 2004). In this way it is assumed that the canopy acts as a kind of nutrient conservation mechanism to secure nutrient availability for forest growth and production (Jordan, Golley et al. 1980) and that epiphytes play an important role in the retention of valuable nutrients especially during periods of low nutrient availability (Coxson & Nadkarni 1995). Nutrient capital retained by canopy epiphytes was investigated to be more or less of the same value as from canopy foliage showing that nutrient pools in epiphytes are crucial (Nadkarni 1984), especially exemplified since foliar and epiphytic inputs on equal stages also derive from sudden impacts when branches or whole host trees fall in the course of succession (Nadkarni & Matelson 1992; Coxson & Nadkarni 1995).

Nutrient exchange processes

Although the fate of nutrients is manifold; either retained, leached or re-emitted to the atmosphere (Draaijers, Erisman et al. 1997) uptake or leaching of nutrients is represented mainly by 3 mechanisms:

1) Diffusion: The occurrence of an ionic gradient between tissues or surface areas leads to a charge dependent exchange of ionic nutrients along this so called diffusion gradient. This is probably the most common form of uptake and leaching since it derives from a physical and therefore *passive* process.

2) Ion exchange: In contrast to diffusion this process can both be *passive* and *active* where the plant's driving force derives from enzymatic reactions controlling the proton pump which allows the cell to incorporate charged particles from outside the cell membranes.

3) Absorption of atmospheric gases: Exchange of gaseous forms of nutrients proceeds between surface areas connected through a gaseous phase, in which gases can be taken up being bound to chemical carriers or by dissolution in the phase's water layer and further diffusion. In tropical latitudes especially, uptake of gaseous nitrogen is enhanced by epiphyll microbes.

Although amounts of nutrients in precipitation are considerably lower than those released via litterfall the contribution of *throughfall* and *stemflow* to nutrient inputs into the forest floor is of significant importance due to the typical high inner cycling rates of tropical rainforests and strongly weathered soils (Tobón 2004). Whereas nitrogen, calcium and phosphorus mainly derive from litterfall since either immobilized in cell walls or in cell plasma protected from leaching through cell walls, particularly potassium is leached from the forest canopy due to high abundance and exchange rates during processes of cell physiology (Veneklaas 1991; Johnson 1992; Cavelier, Jaramillo et al. 1997; Tobón 2004) and thus mainly derives from throughfall.

Throughfall

The amount of incident precipitation that passes the canopy and is thereby enriched or depleted of nutrients is called throughfall. About 2 to 5% of rainwater is volatized or retained by treetops, epiphytes and other surfaces and therefore designated as interception loss. The residual amount of precipitation passes the leaf layer and either falls down to the forest floor as throughfall or runs down along branches and tree trunks as stemflow. Various studies reported that throughfall contributed to the bigger part of around 80 to 90 percent, whereas stemflow only accounted for about 1 percent of total precipitation, the rest being lost by interception (Jordan, Golley et al. 1980; Chuyong, Newbery et al. 2004a).

Throughfall is calculated as:

$$TF = BP + CE + DD$$

and therefore consists of Bulk Precipitation (BP) Canopy Exchange (CE) and Dry Deposition (DD). In order to find out about exchange processes and to compare ecosystems or differing sites within one system it was found to be useful to calculate the net throughfall, which is given by the equation:

$$NTF = TF – BP = CE + DD$$

It becomes obvious that nutrient input in net throughfall is mostly influenced by canopy exchange processes, through the duration and intensity of antecedent storm events, and the number of incident days without precipitation exaggerating the amount of accumulated nutrients that are deposited as aerosols onto the canopy layer during dry deposition (Lovett & Lindberg 1984).

Generally it is acknowledged that chemicals in throughfall and stemflow derive from three processes:

1) passage of incident precipitation through the canopy,

2) washoff of dry deposited materials as particles, gases or cloud droplets and

3) exchange between canopy surfaces like foliage, woody parts, epiphytes and microorganisms (Parker 1983; Lovett & Lindberg 1984; Hansen, Draaijers et al. 1994; Lovett, Nolan et al. 1996b).

Positive values indicate a net enrichment, pointing to a loss of nutrients of the canopy leading to an accumulation of chemicals in throughfall, whereas negative values refer to nutrient uptake by the canopy surface. Whilst leaching and uptake activities show more or less a clear patterning, depending mostly on amount of incident rainfall and earlier deposition of aerosols, it is difficult to quantify and differentiate between the processes of canopy exchange and dry deposition. Nevertheless it is important to distinguish between the two since dry deposition represents an input of external sources to the ecosystem, whilst canopy exchange displays an intrasystem transfer of internal sources (Lovett, Nolan et al. 1996b). Although various models were established to calculate these factors, it is complicated to compare results among each other, since sampling design often differs between studies (Hansen, Draaijers et al. 1994). Moreover cycling processes are believed to be highly dynamic due to temporal and spatial variability and influenced by factors deriving from various sources mirrored by atmospheric, hydrological, chemical and biological conditions as well as human activities (Parker 1983; Potter, Ragsdale et al. 1991; Tobón 2004). Therefore resolving differences in net fluxes are mainly caused by differences in precipitation volumes, leaching rates, dry deposition, or uptake rates (Veneklaas 1990).

In order to be capable of dividing the different sources of nutrient input and calculate the magnitude of dry deposition and canopy exchange for a given forest site, the following equation was modelled (Lovett, Nolan et al. 1996b):

$$NTF_x = a + b1*A + b2*P + b3*C_x + b4*C_{H+}$$

where NTF is net throughfall flux, the factors a, b1, b2, b3, b4 are indicating the slope of the calculated linear model, for A being the antecedent dry period, P the magnitude of precipitation and C_x and C_{H+} the concentration of the element investigated and the pH-value, respectively. With this model it is possible to characterize the influences of DD, CE, ionic concentration and pH to the underlying exchange processes in throughfall for both inter-event and seasonal studies. Furthermore it is feasible to estimate the amount of dry deposition and canopy exchange after investigating only a set of precipitation events for the whole study period by multiplying the values for A (DD) and P (CE) with the amount of dry days (in hours) and magnitude of precipitation (in mm) that were investigated throughout the study period. With this knowledge one can interpret whether a certain element rather derives from deposition or exchange processes and such indicates external or internal sources. Several studies investigated that 50-90% of event-event variation where explained by the three independent variables: P, C_x, C_H (Lovett, Nolan et al. 1996b).

Considering all the before mentioned, however, further questions provoke concerning possible caveats and biases (Lovett & Lindberg 1984):

1) in the calculation of precipitation amount and chemistry, CE and DD are assumed to be linear although most kinetics in nature seem to follow an exponential function,
2) the accumulated material is assumed to wash off completely and quickly (<2mm events excluded) thus retained material of dry deposition is not included in NTF and thus might underestimate data
3) dry deposition includes material that migrates (inside the leaves to surfaces) and also includes material accumulated inside collectors during the antecedent dry period (e.g. particulate debris from the canopy)

As a result of this set of mutually interacting biotic and abiotic factors, throughfall volumes and solute concentrations usually do vary temporarily and spatially. On the one hand abiotic factors affecting hydrology and solute fluxes are broadly conceptualized as micrometeorological and relate to precipitation event characteristics as event magnitude, duration and intensity, wind speed and direction. On the other hand biotic factors, accounting for variable throughfall volume and solute inputs, are the result of species-specific traits like interception storage, plant area index (PAI = the sum of LAI and woody area index), canopy hydrophobicity, canopy structure and species composition. Whereas the abiotic factors vary irregularly as a function of precipitation event characteristics, the biotic factors are more uniform and constant influencing throughfall variability in a regular and predictable manner. Although abiotic and biotic factors influencing nutrient disposition are often treated separately it must be emphasized that they are mutually interacting and thus interpretation and understanding of nutrient fluxes still remains difficult (Levia Jr 2006).

Nevertheless, a general pattern that could be observed was that fluxes of dissolved nutrients are highly correlated with (1) amount, duration and intensity of precipitation penetrating the canopy (Parker 1983; Reiners & Olson 1984; Potter, Ragsdale et al. 1991; Lovett, Nolan et al. 1996b; Tobón 2004) and (2) the amount of antecedent dry deposition. 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 (Veneklaas 1990). For instance a short intense event of precipitation usually leads to a decrease in nutrient concentrations in throughfall, exhibiting a dilution of washed off particles, whereas a long lasting event of rainfall of low intensity leads to an increase of nutrients due to longer residence times of solvents and therefore exchange processes (Tukey 1970; Lovett & Schaefer 1992; Hansen, Draaijers et al. 1994). Several studies investigating intra-event fluxes, reported that ion concentrations in throughfall in the initial phase of a rain event (the first 2 mm) were highest after long dry periods indicating that both deposited and foliar material are more easily leached in the early phases of wetting (Hansen, Draaijers et al. 1994). Moreover the efficiency of leaching was influenced by the amount, intensity and chemical composition of precipitation as well (Tukey 1970).

Nevertheless, both leaching and dry deposition rates are influenced by canopy structure and foliage characteristics (Veneklaas 1990). So it is conceptional that variability in throughfall amounts may also be attributed to canopy architecture and branch inclination angle (Navar, Charles et al. 1999), bark morphology and drainage impediments (e.g. peeling bark) (Crockford & Richardson 2000), herbivory (Price & Carlyle-Moses 2003), canopy gaps (Crockford & Richardson 2000; Loescher, Powers et al. 2002), leaf texture (e.g. hairs) and hydrophobicity (epicuticular waxes) of vegetative surfaces. As a result of adaptation the leaves of different plant species are highly variable. Some species tend to develop thin broad shaped annual leaves that will be discarded during times of droughts and therefore will be easily leached, whereas others will invest much of their metabolites and build up long-lasting, stiff and scleromorphe leaves to reduce water loss and thus contribute to solute nutrient retention. Another example for altering the nutrient budget would be leaves of some tree species that are either densely covered with hairs which therefore would increase water retention and limit displacement under windy conditions (Levia Jr 2006) or posses epicuticular waxes, where moisturising of smooth and waxy leaf surfaces is less than those of pubescent or wax-less surfaces (Tukey 1970). But also within the individual's scale differences emerge taking influence on nutrient states, as even the age of the leaves plays a role in terms of nutrient exchange, as older or damaged leaves are usually more susceptible to leaching than younger ones. This is due to the fact that mature leaves comprise larger pools of nutrients than young foliage, which can utilize those nutrients more quickly for growth (Tukey 1970).

Other biotic factors such as type of vegetation and species composition, as well as canopy structure and covering of epiphytic biomass, indicated by the leaf area index (LAI) as a surrogate for canopy density and therefore estimating the given surface of rainwater interception and also exchange processes, are influencing the forest's nutrient supply. Thus it is understood that interception was generally lower in the dry season by a decrease of leaf numbers than during the wet season where more precipitation was intercepted by the canopy (Lovett & Lindberg 1984; Veneklaas 1990; Cavelier, Jaramillo et al. 1997). This is also mirrored in terms of nutrient concentrations for which was observed that concentrations in net throughfall were higher during the growing season than in times of dormancy (Potter, Ragsdale et al. 1991). As a bigger overall leaf surface leads to enhanced nutrient input the term canopy roughness is introduced, pointing to the fact that dry deposition is enhanced with the number of species with different crown structures. The greater the canopy roughness and thus higher dry deposition rates will occur the more precipitation is intercepted by the canopy leading to a greater area of canopy exchange processes and thus nutrient disposition (Parker 1983; Lovett & Lindberg 1992; Hansen, Draaijers et al. 1994). In recent studies it was assumed that ion concentrations of wet deposition are overestimated since the roughness of the upper canopy layer generates vortices and turbulent mass flow (Forti & Moreira-Nordemann 1991). Contrariwise, Hansen (Hansen 1996) reported that due to these turbulent air movements less incident precipitation was collected and that ion concentrations above the canopy and from an open field were similar. To summarize this it was supposed that there were no differences in precipitation volumes but large differences in dry deposition, resulting from the fact that a change in aerodynamic roughness of the forest canopy compared to open landscape worked as a trap for particulate matter. Thus it is not surprising that there were differences in fluxes between forest interior and forest edge, the latter having larger inputs of potassium, sodium, chloride, calcium and magnesium (Levia Jr 2006).

A further important factor of nutrient disposition is that solutes may be absorbed in the canopy by epiphytes, foliage or canopy roots. A large part of the epiphytic mass is dead organic matter with abundant animal life. The organic matter will partly decompose and nutrients may be taken up by epiphytes or may be leached. The amounts of decomposing organic matter and growing epiphytes will influence the balance between nutrient release and uptake (Veneklaas 1990). Supporting this assumption it was proofed that significant variability of TF volumes was attributed to disparate coverage by epiphytes foliage and branches (Nadkarni, Schaefer et al. 2004) where mean normalized TF was found to decrease with increases of foliage depth along transects (Levia & Herwitz 2002). In another study epiphyte abundance in an upper montane rainforest in CR was found to differ as a function of succession, with old-growth forest having the largest epiphyte load and TF nutrient inputs (Hölscher, Köhler et al. 2003) where presence of epiphytes favoured larger portions of TF than SF. Especially during increased rainfall intensity an increase of the spatial variability of throughfall was observed beneath an old-growth tropical forest, because these tropical forest canopies are attributed to be highly diverse and geometrically complex and thereby have a great number of potential drip points (Loescher, Powers et al. 2002). Within rainforests the tropical montane cloud forest therefore is believed to account to the ecosystems with the highest plant diversity in the world (Gentry & Dodson 1987). It is thought to contain at least as many species of plants as tropical lowland rainforests (Henderson, Churchill et al. 1991) although this forest has a surface area of only 1/20 of the Amazon basin (Cavelier, Jaramillo et al. 1997).

As so many factors take influence on hydrology and fluxes of nutrients, all the previously mentioned would suggest that different species of trees inhabiting different habitats will likely have differential effects on TF water and solute inputs and thus contribute to spatial variability of TF fluxes (Brown & Iles 1991; Cape, Brown et al. 1991; Schroth, da Silva et al. 1999). This is especially supported by a study which pointed out that on the species scale TF inputs differed significantly between *Bactris gasipaes* [Kunth] (peach palm fruit) and *Bertholletia excelsa* [Humboldt & Bonpland] (Brazil nut) within a multistrata agroforestry system (Schroth, da Silva et al. 1999). For nutrient composition, however, results are contradictory, since this assumption could not be accredited as species composition took no significant influence on nutrient input between primary and secondary forest stands in a tropical lowland rainforest (this study). Although inter-specific variations in TF solute concentrations have been observed among European tree species (Brown & Iles 1991; Stadler, Michalzik et al. 1998; Robertson, Hornung et al. 2000) and this context was approved between monoculture agro-forest systems, there was no relation of nutrient inputs to species composition in the tropical forest stands probably due to the high diversity of about 200 tree species per hectare.

Another interesting fact is that the presence of herbivores has lead to a further complexity in terms of nutrient cycling within forest ecosystems as their presence did not only reduce the canopy’s total leaf area but also did alter solute fluxes by segregation of metabolites. For instance in a coniferous forest infested by aphids nitrogen-containing ions as DON, nitrate and ammonium were observed to decrease in throughfall, whereas

DOC inputs have been positively correlated with aphid density (Levia Jr 2006). It was exemplified that an increase of CO2 from 560 to 760 ppm was found to increase DOC inputs via TF by 48 %; particularly forests infested by phytophagous insects will transfer even more DOC to the forest floor in the future with elevated atmospheric CO2 concentrations, and thus further alter the cycling of DOC (Hunter, Linnen et al. 2003). At endemic densities however insect herbivores where found to increase canopy throughfall inputs of nitrate, whereas throughfall inputs of ammonium remained constant (Parker 1983; Attiwill & Adams 1993; Levia Jr 2006). For frugivores it was similarly demonstrated that presence and feeding activity during fruiting times altered the chemical enrichment of throughfall compared to non-fruiting times (Tobón 2004).

Moreover nutrient inputs where found to vary among forest stands, depending on the relative location and proximity to their sources, either deriving from natural pools as ocean surfaces and volcanoes or agricultural, urban and industrial areas in case of anthropogenic origin (Levia Jr 2006). Factors that affect throughfall chemistry under this conditions are slope aspect, elevation and climatic conditions (Chiwa, Oshiro et al. 2003). For instance throughfall deposition of especially nitrate and sulphate was found to be higher in forests with slopes oriented toward urban areas than facing mountainous terrain due to increased quantities in dry deposition (Puckett 1991; Rodrigo & Avila 2002; Avila & Rodrigo 2004).

Considering all this factors and uncertainties of estimating throughfall fluxes already mentioned it is advisable to think of the right sampling strategy to exclude sampling errors before trying to differentiate various natural sources for variability in data. Thus sampling strategy and number of gauges rather than type, is considered to be more important in gaining the correct magnitude of throughfall input in wooded ecosystems (Neal 1990; Reynolds & Neal 1991; Price & Carlyle-Moses 2003). The number of gauges required to satisfactorily asses throughfall solute inputs can vary depending on the specific solute being measured (Kostelnik, Lynch et al. 1989; Puckett 1991). For instance mean number of fixed gauges for sampling in a mixed hardwood forests would be 19, 111, and 11 for nitrate, potassium and throughfall volume, respectively (Rodrigo & Avila 2001). Other researchers using fixed gauges found that after a certain point increases of gauge numbers had a diminishing return and found the critical number to be approaching 30 gauges (Czarnows.Ms & Olszewsk.Jl 1970; Kimmins 1973; Lloyd & Marques 1988; Forti & Neal 1992). Moreover it has been suggested that random positioning of gauges after each collection on a precipitation basis is (1) more accurate (Rodrigo & Avila 2001) and (2) can reduce the number of gauges required to adequately sample the mean (Lin, Hamburg et al. 1997; Rodrigo & Avila 2001), than maintaining throughfall gauges in fixed positions. If gauges are repositioned, however, canopy structure is no longer constant and differences in measurements cannot solely be attributed to meteorological conditions and thus inter-event differences would be more difficult to explain. Another fact is that much larger numbers of gauges are necessary to sample small precipitation events (<2mm) than bigger ones (>4mm) (Price & Carlyle-Moses 2003), which confirms that throughfall volume is less variable with increased precipitation (Forti & Neal 1992; Price & Carlyle-Moses 2003; Carlyle-Moses 2004).

Further potential bias in throughfall sampling:

1) wind loss associated with turbulence around the collector orifice
2) splash loss as a function of depth and diameter of the collector
3) retention of collector surfaces leading to an undermeasurement of actual volume
4) evaporation from collectors.

Whereas splash loss and evaporation should be of concern to investigators, gauge undercatch due to wind loss is rather minimal because of generally low wind speeds inside forests and plantations.

Finally it is recommended that studies of throughfall variability have a duration of at least one year in order to capture variation of nutrient inputs as a function of season and corresponding changes in precipitation regimes and canopy leaf area (Parker 1983).

Stemflow

The small amount (<1%) of incident precipitation running down branches and tree trunks to the forest floor is called stemflow. As already mentioned earlier stemflow only contributes to a small amount of about 1-10 percent of total water input to the forest floor (Herwitz & Levia 1997). Though SF represents a small fraction of total amount of rainwater these inputs can exhibit local excesses and probably supply the plant and surrounding microbes at firsthand (Levia & Frost 2003) mirrored by the fact that SF was observed to account for about 20% of total groundwater recharge (Taniguchi, Tsujimura et al. 1996).

Both TF and SF have been documented to significantly impact biochemical cycles (Parker 1983; Soulsby, Helliwell et al. 1997) being the two major hydrological processes transferring water and nutrients from the canopy to the soil. In turn nutrient content of the soil was argued to influence nutrient concentrations in SF and TF (Timmons, Verry et al. 1977). In general the spatial variability of SF is greater than that of TF, both decreasing as a function of precipitation magnitude (Lloyd & Marques 1988). Nutrient inputs of SF at the bases of selected trees have been documented to be 30-40 times larger than those of TF (Durocher 1990). Therefore especially SF is of hydrological and biochemical importance in forest and agricultural ecosystems exhibiting a localized point input of water and nutrients (Herwitz 1991b; Levia & Herwitz 2000). As fertilizer applications may be leached from the soil at the tree base, they should be spread between tree trunks instead of around the boles of individual trees (Hölscher, Köhler et

al. 2003), where concentrations of nutrients (K^+, Ca^{2+}, Mg^{2+}, DON) in stemflow will be significantly higher than in throughfall anyway (Hölscher, Köhler et al. 2003).
Whereas TF chemistry has been found to depend on factors like latitude, elevation, seasonality, proximity to the sea, species composition, forest age and local land use – SF chemistry has been found to be controlled by factors like species assemblage (Herwitz 1991b; Levia & Herwitz 2000), seasonality (Soulsby, Helliwell et al. 1997), meterological conditions (Lindberg & Lovett 1992; Levia & Herwitz 2000) and canopy structure (Crockford, Richardson et al. 1996a; Levia & Herwitz 2002).

Seasonal influences are evidently altering nutrient composition in SF. SF yields in deciduous forests were greater during winter than in summer simply because of lower precipitation amounts, lower rates of evaporation and leaf abscission in the dormant season (Neal, Robson et al. 1993).

Furthermore several studies have approved that nutrient content and water contingent vary highly dependant on *stem diameter and species*. Therefore it’s not surprising that stemflow volume differed significantly between trees reaching the upper canopy and sub-canopy since height of trees was found to positively correlate with stem diameter (Schroth, Elias et al. 2001). Despite of this coherency, the greater amount of stemflow flux is mostly attributed to trees showing small widths in diameter due to their higher abundance. In this way the quantity of the small but numerous trees overrules the higher quality (amount) of nutrient input of single emergent trees in terms of nutrient disposition to the forest floor. Thus stemflow was found to be especially important for nutrient fluxes in vegetation with high stem density such as fallows (Jordan 1978). The same pattern was also obtained for climax vegetation as in an tropical old growth forest trees with less than ten centimetre in diameter accounted for 80% of stemflow volumes (Hölscher, Köhler et al. 2003). In a Costa Rican tropical montane forest high nutrient flux within stemflow in secondary forest stands were likewise due to small canopies and the inclined branches of young *Quercus* tree species, channelling rainwater to their trunks. Whereas large canopies and more horizontal branching patterns of adult trees did not. This effect was explained thereby that water travelling along branches of tall trees will most likely pass through the epiphyte vegetation which might absorb and partly re-evaporate water and thus lead to lower amounts of stemflow (Hölscher, Köhler et al. 2003). Generally steeper branch inclinations were observed to increase SF volumes in tropical dry forests (Aboal, Morales et al. 1999; Crockford & Richardson 2000). As a matter of adhesion and inclination, leachate concentrations were found to be significantly greater from branches inclined at 20° than at 5° or 38° which was attributed to the increased residence time of intercepted precipitation and lower probability of branch drip (Levia & Herwitz 2002).

Moreover there was a large difference among stands in the relative contribution of stemflow to the total element flux with net precipitation probably due to variation of water fluxes within stemflow and the concentrations of nutrients in it. For instance stemflow accounted for different percentages of potassium fluxes in net precipitation at forest stands of different stages of succession, ranging from 5% in an old growth forest to 17% in early stage forests with highest percentages in secondary forests. Comparison of nutrient fluxes with net precipitation among successional stages of a tropical upper montane rainforest, however, showed only small differences in the total quantity of nutrient fluxes. Nevertheless the internal partitioning of fluxes into stemflow and throughfall was very different with generally high stemflow values observed in the secondary forests probably due to the higher abundance of small upcoming trees in the course of succession and thus their lower branch inclination and canopy height (Levia & Frost 2003).

Highly variable SF quantities in a particular ecoregion are likely the result of site-specific differences, 3d geometry of canopy structure and stand densitiy (Olson, Reiners et al. 1981; Herwitz 1987; MartinezMeza & Whitford 1996), presence of epiphytes (Veneklaas 1990) species composition (Navar, Charles et al. 1999) variation in bark texture (Aboal, Jimenez et al. 1999; Navar, Charles et al. 1999) and precipitation event frequency, duration, magnitude and intensity (Crockford & Richardson 2000; Kuraji, Punyatrong et al. 2001). On the one hand SF production increases with the magnitude of a precipitation event (Xiao, McPherson et al. 2000; Kuraji, Punyatrong et al. 2001) once the interception storage capacity is reached, but on the other hand can also decrease with the intensity of the incident gross precipitation due to higher probability of branch drip of, thus becoming TF (Crockford & Richardson 2000). Whereas nutrient concentrations in SF were relatively low in high intensity precipitation events of short duration, events of longer duration and low intensity were generally high due to longer contact times with the bark (Levia & Herwitz 2000). It seems that residence time is the key factor controlling the extent of chemical enrichment, but further research will bring to light whether this is true or not (Levia & Frost 2003). Total SF input at the tree base, however, is likely to be greater during events of higher magnitude, due to shorter contact time reflecting a greater ion concentration gradient and diffusion from the bark (Levia & Herwitz 2000). In general meteorological conditions determine the physical properties of intercepted precipitation, TF and SF since they affect the surface tension and viscosity of the water film directly as a function of air temperature (Levia & Frost 2003). Thus increased residence time on bark surfaces due to colder air temperatures will lead to nutrient enrichment (Levia & Herwitz 2000).

Apart from species-specific traits influencing SF enrichment like branch inclination and canopy geometry, there are physiological differences in *bark tissue* chemistry and bark porosity causing differences in SF yield and leachate chemistry (Levia & Frost 2003). These characteristics will determine the time span the bark is wetted and thus its water-holding capacity and air drying rate. Canopy storage is a key factor in determining the quantity of intercepted precipitation but bark has an even greater water-holding capacity than foliar surfaces. For instance Herwitz (1985) found inter-specific differences between water-holding capacities of tropical trees dependent on bark texture (Herwitz 1985). Generally rough-barked species will store greater quantities of water and generate smaller SF yields, enhancing the residence time of intercepted rain-water and thus increasing nutrient enrichment. Therefore bark thickness and morphology are two key factors influencing SF leachate chemistry (Crockford, Richardson et al. 1996b; Levia & Herwitz 2000). Significant enrichment of K^+ and Mg^{2+} during dormant season was accounted to colder air temperatures and thus increased kinematic viscosity and surface tension lengthening the residence time of intercepted precipitation (Levia & Frost 2003). In addition greater SF leachate losses of *Eucalyptus melliodora* were attributed to its debarking process, as the newly exposed nutrient rich bark is leaching greater nutrient quantities (Levia & Herwitz 2000). For the genus *Populus* and *Acer*, mean SF leaching was also found to be greater from dead standing trees than from living trees by a factor of 46 for P, 3 for NO_3^- and 1.5 for K^+ (Watters & Price 1988).

Generally differences in nutrient composition were attributed to organisms - particularly lichens, mosses and fungi - that inhabit the rougher barks, sequestering particularly P in their metabolic processes (Zhang & Mitchell 1995). Epiphytic lichens, for instance, were found to take up N containing anions and also influence cat-ion nutrient cycling by uptake and retention processes (Levia & Herwitz 2002).

Furthermore tree species with adventitious roots were observed to have greater SF leachate concentrations than species without, and therefore this was hypothesized to be an evolutionary adaptation of some species to recover highly enriched drainage water (Herwitz 1991a).

SF quantities are also influenced by *wind speed and direction* since yield increases with wetted tree stem area (Crockford & Richardson 2000) and the effective crown area was shown to change as a function of wind direction (Herwitz & Slye 1995). Thus SF yield may be spatially and temporally variable within a forest or culture due to its dependence on wind direction and canopy position of individual tree crowns (Levia & Frost 2003). In a simulation experiment investigating vertical raindrop inputs, up to 98% of SF was produced in the upper half of the canopy (Hutchinson & Roberts 1981) that is usually most exposed to wind and weather.

Furthermore storm damage could particularly lead to higher nutrient inputs since newly exposed vegetative tissue caused by branch breakage seem to affect SF chemistry significantly (Levia & Frost 2003). Thus originated canopy gaps increase SF yield by exposing a greater surface area to incident precipitation (Crockford & Richardson 2000).

Stemflow is usually measured by collecting drainage from forest trees using flexible tubing cut in half longitudinally and wrapped around a tree trunk in a downward spiral (Herwitz 1988; Levia & Herwitz 2000; Nakanishi, Shibata et al. 2001). The tubing is nailed or stapled to the tree trunk and silicone sealant is applied to seal the collar to the trunk to avoid water losses (Herwitz & Levia 1997). Collected samples should been analyzed soon after each precipitation event to minimize erroneous data.

To quantify the extent of chemical enrichment of SF drainage, Levia & Herwitz (2000), developed an enrichment ratio:

$$E = (C_s S) / (C_p P_g B_a)$$

where E is the enrichment ratio, C_s the chemical concentration, S is SF volume collected, C_p is the chemical concentration of bulk precipitation, P_g is the depth equivalent of gross precipitation and B_a is the trunk basal area. This ratio admits to interpret the enrichment of SF drainage in relation to the magnitude of the precipitation event and the basal area and therefore standardizes SF chemical inputs per unit area. Thereby it is possible to compare different sites within or between forest ecosystems (Levia & Herwitz 2000).

To be furthermore capable of separating the two phases of initial nutrient enrichment and later leaching processes of a certain precipitation event, the drainage of nutrients was modelled using non-linear regression and determined by dividing the area under the curve into two integrals. The first integral represents the steady decrease in SF concentration during dilution. The second represents the amount of nutrients that is leached or absorbed. Leaching was found to attribute from 30 - 80% depending on the respective nutrient in SF drainage from *Fagus sylvatica* (European beech) (Kazda 1990). Finally in order to properly analyse nutrients collected in SF and TF funnels the maximum storage time of nutrients must be considered, as base cat-ions can be stored up to 6 months, but nitrate for 2 days only and pH should be measured within 2 hours (American Public Health Association 1995).

Hydrological and nutrient fluxes in SF are of such great variability that studies should last for at least several years to gather all seasonal and spatial variations for valuable interpretation of data (Levia & Frost 2003). It was exemplified that SF affects biochemical cycling of nutrients by constituting a local point input of water and solutes influencing the soil solution chemistry, nutrient status, moisture and groundwater recharge. Nutrient composition in SF is a result of interactions of various variables like meteorological conditions, seasonality, species composition and particularly canopy structure.

As SF is believed to have a considerable effect on plant productivity and yield particularly through leaching fertilizers near the plant stem, a comprehensive understanding might result in an accurate modelling for agricultural purposes (Lovett, Nolan et al. 1996b). Further research on SF partitioning and calculation of models could lead to a better understanding of nutrient composition and thus support management of water resources for municipal, agricultural and industrial uses.

Nutrient composition

Differences of nutrient composition in *throughfall* and *stemflow* were elucidated to result from various sources depending on variable factors. For instance variability in nutrient cycles will be influenced by chemical and physical attributes of the respective element investigated. On the one hand chemical distinctions will result from charge, configuration and linkage to other ligands or resolve from interactions with aqueous solutes as canopy exchange processes, which could be related to chemical composition of precipitation. On the other hand abiotic conditions such as elevation, temperature or climate will either affect whole groups of nutrients or lead to amplification or deletion of underlying factors which in turn favour certain conditions.

Whereas nutrient concentrations in throughfall are mainly affected by stormsize as diluted with magnitude of precipitation or accumulated with increasing time of dry deposition, there are some minor but still important factors in pathways of nutrient disposition:

General coherences for canopy exchange and deposition processes of plant nutrients were that ion concentrations in bulk precipitation did influence the dissolubility of ions as affecting internal reactions and balances. The first demonstration that foliar leaching of cat ions increases in response to increases in precipitation acidity was supplied in a study of Lovett in 1996, where they showed that acidity of precipitation had a positive effect to H retention, as well as NH_4^+ concentrations had a positive effect to NH_4^+ retention but NO_3^- concentrations showed no effect on NO_3^- retention (Veneklaas 1990). Other studies approved that when concentrations of certain nutrients in precipitation were high net fluxes were more likely to be positive, whilst low concentrations in rainwater lead to a negative net flux and thus uptake of nutrients (Cadle, Marshall et al. 1991; Sutton, Fowler et al. 1995).

Generally the uptake of nitrogen occurs either through stomata and leaf cuticles in form of NH_3 and gaseous HNO_3 or by dissolution in water films, where surface deposited material usually is washed off by precipitation (Bentley 1987). Whereas movement of newly fixed nitrogen by epiphyllous cyan bacteria to the host leaf occurs rather via epidermal cells and ectodesmata than through stomata, as was earlier assumed (Parker 1983; Wilson 1992; Wilson & Tiley 1998).

In terms of nutrient fluxes, for nitrogen in particular concentrations of inorganic N in incident rainfall decreased as it passed through the canopy which lead to the suggestion that N was taken up by canopy components (Coxson 1991; Lovett, Nolan et al. 1996a). Other studies investigated that increase in ammonium concentration in a simulated rain solution had a significant effect on the efflux of ammonium from the canopy and that the net retention of NO_3^- exceeded that of NH_4^+ due to leaching from litter and humus of the canopy (Lovett, Nolan et al. 1996b). In a coniferous forests release of inorganic N was also found to be related to nitrogen concentration in the foliage and it was figured out that needles prefer the uptake of NH_4^+ rather than the uptake of NO_3^- by the reason that cuticle surfaces possess a net negative charge which therefore attract cat ions. Furthermore the correlation effects of forest type and nutrients NO_3^- and NH_4^+ were strong since uptake of N resolves from an active exchange process, whereas ion exchange of K^+, TOC and H remains passive (Clark & Clark 1994).

Interestingly epiphytic bryophytes, vascular epiphytes, litter and humus were attributed to account for about 80% of inorganic N retained by the canopy (Vance & M. 1990; Vance & Nadkarni 1992). Epiphytes are believed to initially retain N and thereby buffer pulses of inorganic nitrogen before reaching the forest floor (Clark, Nadkarni et al. 1998b). Increased inputs of nitrogen initially stimulate the growth of epiphytes and host trees and are subsequently stored in the highly recalcitrant canopy and soil org matter (Chuyong, Newbery et al. 2004b). This seems to be confirmed as trees with high ectomyccorhizal and epiphytic bryophyte masses showed significantly lower nitrogen solute inputs (Johnson 1992). In addition presence of corticolous lichens inhabiting the bark tissue of trees lowered nitrate-nitrogen inputs to the forest floor compared to trees with little or no lichen coverage (Levia 2002).

As potassium is the main nutrient used for stomata opening and closing processes (Lovett & Schaefer 1992) it is understood that canopy exchange processes are of major importance for K^+ cycling, since it occurs generally in ionic form, thus is highly osmotic and reacts in cat ion exchange processes between H^+ and base cat ions (Mecklenburg, Tukey et al. 1966).

On the contrary Ca^{2+} and Mg^{2+} are usually immobilized in structural tissues or enzyme complexes and therefore less susceptible to leaching and exchange processes. The major portions of leached calcium were believed to derive from recently absorbed calcium available in exchangeable forms located in plant’s tissue outside cell walls as it is dislocated from roots to foliage (Lovett, Nolan et al. 1996b).

Both Ca^{2+} and Mg^{2+}, however, significantly correlated with acidity, so that increasing acidity of precipitation lead to increased leaching of Ca^{2+} and Mg^{2+}. Since there was no significant effect for K^+ and Na^+ it was assumed that there was little impact on monovalent ions, but major influence on polyvalent ones, similar to soil ion-exchange processes (Clark, Nadkarni et al. 1998b).

Especially in the tropics the influence of seasonal variations on dispersal of nutrient inputs, resulting from differences in precipitation amounts, is determined by distinct wet and dry seasons. Aside form simple dilution effects, ions of H, Ca^{2+} and K^+ were found to be less reduced in precipitation of small storm-sizes indicating sources during wet season (Veneklaas 1990; Campo-Alves 2003).

For instance, throughfall fluxes of potassium, phosphorous and magnesium were found to be higher at lower elevation than at higher elevation sites in tropical forest sites in Mexico and Colombia, suggesting that lowland sites have a decreased tendency to cycle nutrients as efficiently as sites of higher elevation (Grubb 1977; Vitousek 1984; Vitousek & Sanford 1986). Thus low net throughfall fluxes of N and P may be associated with an economic use of these elements by trees and epiphytes, which would be in accordance with the conclusions of (Veneklaas 1990), suggesting limited availability and efficient use of N and P in high altitude tropical forests (Clark, Nadkarni et al. 1998b).

Location and proximity of forest sites relative to the origin of nutrient sources were reported to be of certain importance. Thus factors like evaporation, clouding and wind distribution will lead to changes in patterns of precipitation and deposition in altering the impact of horizontal distances. First approval for this assumption was that the molar ratio of Na^+ and Mg^{2+} to seawater was 0,137 to 0,123 indicating that this solutes derived from wind driven aerosols from marine sources (Eklund, McDowell et al. 1997). Therefore nutrients Na^+, Cl^- and Mg^{2+} are often closely related to the sea nearby due to evaporation of sea salt ions which are distributed by the wind and deposited in the form of aerosols onto the forests canopy. Furthermore sea-salt aerosols accounted for 97% of Cl^- and 88% of Mg^{2+} whilst Na^+ and Cl^- were most abundant ions in deposition and had highest average concentration (McDowell, Sánchez et al. 1990). Obviously other sources must exist besides deposition of marine aerosols since elements like Ca^{2+} and K^+ would be expected to show a similar behaviour as Na^+ (Veneklaas 1990), which was not the case and thus higher Na^+ concentrations are probably caused by terrestrial influences (Eklund, McDowell et al. 1997). In order to be capable to separate the different sources of nutrients, it was proposed to divide accumulated nutrients into sea-salt and non-sea-salt derived aerosols. Typically non-seasonal fractions did not show seasonal fluctuations as deriving from unaffected sources, whereas sea-salt fractions did strongly correlate with precipitation in dry and wet season in connection with differing rainfall amounts. For instance non sea-salt fractions of SO_4^{2-}, Ca^{2+} and K^+ were 73% 76% and 62% of total ion amounts, respectively showing no strong correlation among any of the non-sea-salt ions and also no seasonal trends. In contrast seasonal trends have been observed for sea-salt ions Na, Cl^-, Mg^{2+} and DIN (Ewel, Berish et al. 1981).

Other natural and artificial sources have been designated to be responsible for nutrient inputs to forest ecosystems. In general it was observed that burning of vegetation results in considerable loss of N and other ions (Lobert, Scharffe et al. 1990) as plant tissue is volatized as NO, NH_3, HCN and other organic N compounds (Andreae, Browell et al. 1988; Guyon, Graham et al. 2003). Further studies reported that biomass burning was the source of DOC, NO_3^-, NH_4^+, SO_4^{2-} and K^+ in aerosols (Andreae, Browell et al. 1988; Maenhaut, Salma et al. 1996). The burning of forests lead to particulate emission of K^+, Cl^-, SO_4^{2-} (Yamasoe, Artaxo et al. 2000), organic material and NH_4^+, K^+, NO_3^-, SO_4^{2-} and organic anions like formate, acetate and oxalate (Guyon, Graham et al. 2004). Comparing seasonal influences, however, gained insight into relative dominance of shifts from pyrogenic emissions in the dry season to biogenic emissions in the wet season (Eklund, McDowell et al. 1997).

In certain cases volcanic emissions where found to account particularly for inputs of SO_4^{2-} and NO_3^- since uncorrelated to anthropogenic sources and also could be related to wind direction measurements (Eklund, McDowell et al. 1997). Otherwise enhanced N, P and S concentrations lead to the assumption to be air pollutants and hence derive from anthropogenic sources, such as agriculture and stock farming. To emphasize this a Principle component analysis (PCA) showed that the relation of accumulated nutrients (K^+, DOC, DON, NH_4^+ and NO_3^-) in throughfall, contributing most to calculated factor 1, was probably the effect of agricultural dust since concentrations of K^+ and Ca^{2+} were derived primarily from non sea-salt sources, whilst factor 2 was build up of SO_4^{2-}, Cl^- and H (Clark, Nadkarni et al. 1998b).

Since it is difficult to differentiate sources of aerosol origin we will further have to evaluate the different effects of deforestation, land use change and agricultural practices on rates of N emissions before we can estimate the individual contribution of anthropogenic activities to precipitation chemistry solely (Ellingson, Kauffman et al. 2000). To give some insight on the effect of artificial nutrient inputs, however, nitrogen deposition via throughfall ranged from <9kg ha yr in northern Scandinavia and Britain to >30 kg ha yr in forests of Netherlands and northern Germany. As a major contributor land use change - mainly the conversion of forest to agricultural lands - and increasing biomass burning are assumed to be responsible for increased N emissions to the atmosphere throughout tropical latitudes (Clark, Brown et al. 2001a).

Climate change and tropical carbon budget

As a result of permanently ongoing net primary production and heterotrophic respiration, tropical rainforests contribute to a major part to the world’s carbon budget deriving from terrestrial ecosystems (Melillo, McGuire et al. 1993; Field, Behrenfeld et al. 1998). Together they account for 32-36 % of terrestrial net primary production (NPP) (Dixon 1994). About 59% of the global carbon pool in forests is stored in tropical regions (Clark, Brown et al. 2001b) and is likely to be released, in turn affecting the global carbon cycling, when atmospheric CO2 concentration is furthermore altered. Estimates of Net Primary Production in diverse tropical forests range from 1.7 Mg $C.ha^{-1}.yr^{-1}$ to 21.7 Mg $C.ha^{-1}.yr^{-1}$ (Clark 2004a). Although numerous studies have already been conducted it is not clear to date whether tropical forests exhibit net carbon sources or sinks, as different studies exemplified controversial results (Clark 2004a).

The coherences become clear when the interconnection of soil, microbial biomass and plant physiology is elucidated:

Net primary (NPP) production is the difference between total forest PS (GPP) and plant respiration (Ra) (Clark 2004a).

$$NPP = GPP - R_a$$

The combined effects of photosynthesis and autotrophic respiration responses to temperature could strongly decrease tropical forest NPP with rising temperatures (Clark 2004a). Net ecosystem exchange (NEE) is the difference between NPP and heterotrophic respiration (Rh)

$$NEE = NPP - R_h$$

NEE, although not measured directly, appears to increase exponentially with increasing temperature in both tropical and temperate ecosystems (Holland, Neff et al. 2000). Continued warming will bring ongoing declines in the ratio $GPP:R_a$ and so a continuing shift in NEE towards increased carbon emissions for tropical rainforests (Clark, Piper et al. 2003).

Thus it is understood that even small changes in the ratio between photosynthesis and respiration will affect the rate of accumulation of atmospheric CO2 (Petit, Jouzel et al. 1999). Nevertheless, as the current CO2 concentration is higher than during the past 420.000 years (Clark 2004a) exhibiting a 32 % increase over pre-industrial levels, it seems obvious that there must be a consequence to temperature and climate. According to this assumption in records maintained since 1861, the 1990's were the warmest decade and 1998 was the warmest year (Folland, Rayner et al. 2001). Especially the very strong El Nino events of 1982/83 and 1997/98 showed both record-high temperatures and record-low rainfall (Harrison & Vecchi 2001). Even though mean surface temperatures and precipitation for global tropical land regions have been anticorrelated over the last two decades, years of temperature peaks have usually also been years of anomalously low rainfall (Los, Collatz et al. 2001).

Since there is a high probability that both atmospheric CO2 and global mean temperatures will continue increasing substantially during this century (Albritton 2001), expected greenhouse gas emissions make it virtually certain that atmospheric CO2 concentrations will exceed 450 ppm by 2100 in turn enhancing global warming. Even higher values could result if there shows decreasing sink strength in terrestrial ecosystems as been projected by some coupled climate-vegetation models for 980 ppm (Cox, Betts et al. 2000) and 790 ppm (White, Cannell et al. 2000). Thus simulations projected a mean temperature increase of about 2.5 °C in tropical forests at 700 ppm CO2 (Bounoua, Collatz et al. 1999) or of more than 4.5 degrees for some tropical land areas by 2100 (White, Cannell et al. 2000) respectively. It is also very likely that continued warming will involve large short term temperature excursions that might bring higher temperatures earlier than indicated by the smoothed projected trends based on increasing greenhouse gas concentrations (Clark 2004a).

This could be of particular importance thinking of the still unsettled interaction between the ENSO cycle and altered climatic conditions (Fedorov & Philander 2000). It is likely that the continued warming will amplify the oscillating effect, leading to an increase of both frequency and severity of future events (Cole 2001). The integrated response to all this changes could either lead to increased productivity and total carbon storage or on the contrary to decreased productivity and total carbon losses to the atmosphere (Clark 2004a).

Another open issue yet unknown is whether photosynthetic active radiation has been changing in either total amount or quality (Clark 2004a). Although satellite data indicated a large increase in incoming solar radiation between 1980 and 1990 (Chen, Carlson et al. 2002; Wielicki, Wong et al. 2002; Nemani, Keeling et al. 2003) there are significant uncertainties. Increased proportion of diffuse light for instance has been linked to greater efficiency of forest carbon uptake, and increased aerosols and cloud cover have raised the diffuse fraction of incoming light in many regions of the world (Roderick, Farquhar et al. 2001; Gu, Liu et al. 2003).

In experiments dealing with elevated concentrations of CO2, however, photosynthetic rates increased about 30%. For instance in an 6-8 year old forest mesocosm, carbon uptake was found to be significantly higher at 900 ppm than at 450 ppm, whereas night time respiration did not differ between the CO2 levels (Rosenthal 1998). Whilst no increase in biomass production could be detected (Lovelock, Virgo et al. 1999) there was a 20% increase in total non structural carbohydrates (TNSC) suggesting local carbon saturation. Even stronger increases of 40% and 60 % for these substances and also increased seedling growth after 15 month of exposure at doubled CO2 were observed in a similar study (Wurth, Winter et al. 1998). In the only open top chamber study of 10 tropical forest species during 6 months, seedlings grew from 20 centimetre to 2 meter at doubled ambient CO2 but no enhancement of biomass accumulation was observed. Instead results showed a decrease in leaf area index, leaf starch concentration, increases in leaf C:N ratio and increase of photosynthetic rates (Lovelock, Winter et al. 1998). Other in situ experiments likewise showed decreased biomass production or LAI, which strongly contrast numerous studies under elevated Co2 on individually potted plants. Therefore these results seem inappropriate for scaling up due to restriction to small plants, atypically high availability of water and nutrients, growth in the absence of plant competition, herbivory, pathogen pressure and other real world processes. More realistic experiments under elevated CO2 have suggested that tropical forests will show a decrease in leaf tissue quality and little or no enhancement of biomass production rates (Clark 2004a). The consistent response of plant growth under elevated CO2 resulting in an increase of TNSCs, either in leaves or in twigs, and thus an increase of C:N ratios and such decreased litter qualities could have far reaching consequences on nutrient cycling, herbivory and other forest processes.

According to first expectations species in states of late succession tended to respond less intense than pioneer and mid-succession species (Lovelock, Winter et al. 1998). An important and interesting analogy in experiments with different plant sizes showing differing results was that all experiments produced a significant shift in community composition in the elevated CO2 treatment.

Furthermore it was observed that PS shows a characteristic parabolic response to temperature, since above the temperature optimum for a given plant species or ecotype PS decreases markedly owing to a combination of factors (Baldocchi & Amthor 2001). Measurements of canopy leaves have documented a sharp decline in PS at temperatures above 26-34 °C (Fetcher, Strain et al. 1983; Huc & Guehl 1989; Graham, Mulkey et al. 2003). Such temperatures are already experienced as canopy leaf temperatures can be 1-7 °C above air temperatures (Koch, Amthor et al. 1994; Grace, Malhi et al. 1996). With global warming these temperatures will continue to rise and thus it is likely that the future will bring periods when canopy leaf temperatures in tropical lowland forests reach levels where the photosynthetic apparatus is damaged (40-55°C), since such damage can easily occur after exposures of only 30 minutes.

There are a series of factors influencing the increased heating or damage of leaf surfaces. Decrease of stomatal conductance with increasing CO2 levels, for instance, could further raise leaf temperatures and have particularly strong effects on species already near their thermal limits (Bazzaz 1998). Especially OGF forests, constituting the biggest C sink, might show a strong negative response to increased warming (Clark 2004a).

Since the frequency of day-time periods where temperature exceeds 26-34 °C is believed to have been generally increasing through recent years, and in turn might lead to further damage of the PS apparatus, observed PS responses suggest that daytime C-uptake is significantly decreased at such temperatures (Clark 2004a).

On the contrary autotrophic respiration shows very different short term temperature response from that of PS – as temperature increases, respiration increases exponentially (Clark 2004a). Measurements confirmed that respiration rates increased (8-24 %) with a temperature rise of 1 and 3°C respectively for 2 tropical canopy species (Ryan, Hubbard et al. 1994). Evidently autotrophic respiration plays a large role in the forest's carbon budget, since it is likely to be at least 50-60 % of GPP (Amthor, Koch et al. 2001).

Although some studies concluded that tropical forest plants or microbes could show significant acclimatization of their respiration response, and so the increase of ecosystem respiration with temperature could be much less than indicated by short term measurements (Gifford 2003) it seems more probable that this is not the case. Tropical plants were characterized to be particularly ill-equipped to adjust to ever higher temperatures due to their relatively constricted ambient temperature range (Hogan, Smith et al. 1991). Thus tropical species also showed narrower tolerances than temperate species as the maximum photosynthetic capacity of the two most thermophile tropical species was strongly depressed to only 30-40% of the species maximum (Read & Busby 1990), whereas temperate species were able to maintain 80 % of their maximum PS rates over much larger temperature ranges (Cunningham & Read 2003). In addition palaeorecords suggested a higher sensitivity of tropical lowland forests to warming, based on much stronger floristic shifts with quite small temperature changes during the Pleistocene (Bazzaz 1998).

Another important temperature response is the production of biogenic volatile organic compounds (BVOCs) of tropical forest trees (Warneke, Karl et al. 1999). These substances particularly consist of isoprene but also acetone, methanol and methyl chloride (Geron, Guenther et al. 2002; Yokouchi, Ikeda et al. 2002). For isoprene, one of the major contributors temperature response of emission by tropical plants has been found to be exponentially with very strong increases occurring at leaf temperatures of 27-40°C (Harley, Monson et al. 1999; Keller & Lerdau 1999; Geron, Guenther et al. 2002). At high temperatures of above 38°C tropical forest canopy loses 8-25% of total assimilated carbon via isoprene (Sharkey & Yeh 2001; Geron, Guenther et al. 2002). Surveys have determined 29-50% of tested tropical plant species to be significant isoprene emitters (Keller & Lerdau 1999; Lerdau & Throop 1999).

These observations point to the possibility of severe negative effects on the productivity and net carbon exchange of tropical forests due to combined effects of several physiological responses of plants and microbes to rising temperature in the course of global warming (Clark 2004a). Thus entailed changes in quality and quantity of above and belowground litter inputs could have complex potential effects on microbial respiration and nutrient cycling (Holland, Neff et al. 2000; Kirschbaum, Simioni et al. 2003).

Since recent years of peak temperatures have also been years of anomalously low rainfall, the amount of dry season rainfall has been decreasing markedly since 1948 for both El Nino and non-Nino years (Clark 2004a) resulting in decreased forest productivity and increased tree mortality (Nepstad, Moutinho et al. 2002). Water stress generally increased carbon losses through isoprene emissions (Harley, Monson et al. 1999) and lead to strong decrease in the above ground biomass increment, canopy thinning and decreased PS capacity for some tree species in large scale forest drought experiments (Nepstad, Moutinho et al. 2002). Changes of light quality and quantity would also be likely to alter forest carbon balance (Fan, Wofsy et al. 1990; Graham, Mulkey et al. 2003), since studies approved not only a change in the C:N-ratio of leaves but also increases in leaf phenols (Coley, Massa et al. 2002) which both probably negatively affect nutrient cycling.

By monitoring the performance of old growth tropical rainforest by repeatedly measuring the diameters of all trees above a minimum size and further estimation of the above ground biomass from generalized biomass models over all species based on harvested tropical forest trees it is possible to calculate the aboveground carbon storage of a certain forest ecosystem. Interestingly above-ground biomass was found to have been significantly increasing in the Neotropics but not in the paleotropics (Phillips, Malhi et al. 1998) probably due to differences in methods. Adjusting for species differences regarding wood densities, however, indicated net increases of about 0,6+/-0,3 Mg C ha yr and substantially greater increases in potential still sucessional forest plots (Baker, Phillips et al. 2004).

In order to produce reliable measurements calculating CO2 fluxes, the state of the art method is believed to be adjusted by *eddy covariant towers*. These measurements have produced good estimates of significant net CO2 uptake but a major problem is the overwhelming predominance of still air conditions at night in ca 80 % of nights (Loescher, Oberbauer et al. 2003) and 92% of night hours making the eddy covariance technique inoperable (Clark 2004a) as the same dataset for a given forest indicates NEE values that differ by more than 4 Mg C ha yr depending on the treatment of data from periods of still air (Clark 2004a). Nevertheless combined models of biometric and eddy covariance approaches attribute forests to be a net CO2 source or only small sink.

Another method to calculate current responses of tropical rainforests are *inversion calculations* based on the CO2 or O2:N2 concentrations and isotopic variation in atmospheric gas samples being collected at sites around the world (Clark 2004a). The model involves the uptake and emissions of carbon or oxygen by the world’s oceans and terrestrial ecosystems combined with a model of global atmospheric transport. It becomes evident that the large oscillation of the CO2 concentration as observed in the long-time record at Mauna Loa (Keeling, Whorf et al. 1995) reflects the metabolism of forst ecosystems of the northern hemisphere (Clark 2004a). Carbon uptake dominates during the productive summer months and respiration in the winter and therefore the amplitude of this oscillation declines from the Arctic to the South Pole, mirroring the lack of land masses in the southern hemisphere. This means that shifts in the relationship of photosynthesis and respiration could greatly affect the rate and level of CO2 accumulation in the atmosphere. Moreover will plant respiration and heterotrophic respiration respond to temperature more strongly than photosynthesis does leading to a rise in atmospheric CO2 concentration and thus constitute a biotic positive feedback to the global warming (Houghton, Davidson et al. 1998; Woodwell, Mackenzie et al. 1998).

Other studies based on inversion calculations estimated a net carbon flux from the terrestrial tropics varying from a net sink of -1.8 Pg C yr to a net source of +6.7 Pg ha yr due to strong interannual variation linked to changes in mean tropical temperature and rainfall (Clark, Piper et al. 2003).

Overall interannual variation in tropical tree growth was highly significantly negatively correlated with the atmospheric CO2 anomaly such that years of anomalously poor tree growth were also years of peak net emissions. Supporting these findings, satellite-derived measurements of vegetation greenness indicated reduced productivity of tropical ecosystems in warmer years (Los, Collatz et al. 2001).

Eventually existing data are still insufficient to fathom whether tropical rainforests are net carbon sinks or sources, but there is evidence that there are strong negative impacts on this biome from ongoing climatic and atmospheric changes, particularly altered by anthropogenic interferences, which will lead to decreases in plant tissue quality, affecting nutrient cycling and elevated tree mortality urging tropical forests to net sources of atmospheric CO2 as warming proceeds (Clark 2004b).

As already mentioned tropical forests could be shifting their carbon balance in response to the effects of anthropogenic greenhouse gas emissions such that they respond to the increase of atmospheric CO2 by building up more biomass and accumulating more C in the soil (Phillips, Malhi et al. 1998). As forest ecosystems have been estimated to account for 35% of global plant productivity tropical forest could on the one hand act as brakes on the rate of global warming by decreasing atmospheric greenhouse gas content but on the other hand if they become emitters they might accelerate the pace of global warming. The annual increase of atmospheric CO_2 is the result of several large CO fluxes which are directly affected by humans through (1) emissions from fossil fuel combustion and cement production and (2) land-use change principally due to tropical deforestation. Although much larger quantities of C are cycled between the atmosphere and the world’s oceans and terrestrial ecosystems neither one of them affect atmospheric CO2 if their C uptake equals their emission. Most analyses indicate that both, terrestrial and marine ecosystems have been acting as carbon sinks over the last decades. Therefore terrestrial ecosystems and especially the tropics certainly constitute the most important terrestrial ecosystems in terms of CO2 uptake. In fact it is difficult to accurately quantify the tropical deforestation C flux but it is ascertained that only small imbalances between photosynthesis and respiration could also produce substantial net C emissions to the atmosphere (Levia Jr 2006).

The real difficulty in estimating C fluxes of tropical ecosystems is that one would have to harvest, dry and weight hundreds of plants including their roots, dead wood and litter and moreover analyze multiple soil samples. Even if this is done a further complication is that forests depending on their successional stage, different ages and growth will vary greatly in their average wood density, tree height, soil depth and other parameters. In order to calculate reliable carbon fluxes deriving from human delinquency one would need to estimate how much new biomass was produced in the same time interval by building up plantations or by regrowing young forests on altered landscapes.

Nevertheless we have to remember that tropical C emissions are mainly regulated by three fluxes: (1) C uptake by photosynthesis, (2) C emission by respiration of both plants and heterotrophic organisms and (3) net emissions from tropical land-use change. Thus response of tropical forests to the ongoing changes will probably result in a shift in C balance towards increased gas emissions, leading to a positive feedback to global warming, as tropical ecosystems convert from carbon sinks to carbon sources in the course of tropical land conversion (Clark 2004a).

Study Aims

This study wants to contribute to the question of how tropical forest ecosystems affect the earth’s climate by altering the distribution of solar radiation, surface albedo, sensible and latent heat flux, and especially the hydrologic cycle (Hardy & Albert 1995; Herwitz, Levia et al. 2004; Levia & Underwood 2004) since large tracts of relatively undisturbed tropical forests are of continental and global significance to climate because of their ability to alter the exchange of energy, water momentum and trace gases (Bonan, Oleson et al. 2002; Fisch, Tota et al. 2004).

Especially knowledge of hydrological processes in wooded ecosystems, as partitioning into incident gross precipitation, throughfall and stemflow is of major importance in terms of nutrient cycling and moreover could constitute a key component for successful watershed management that provides high quality drinking water and flood protection for a large portion of the world’s population. These processes are not static and stressors like land cover change from vegetation decline, bio-geographic shifts due to climate change, deforestation etc. will likely impact the quantity and quality of water available to human populations. Thus it is necessary to better understand temporal and spatial variability of hydrology and solute inputs in wooded ecosystems.

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Solute fluxes via Bulk Precipitation, Throughfall & Stemflow in a humid tropical lowland rainforest, Costa Rica

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Abstract

Tropical rainforests are considered to play major roles as sinks in the planet's carbon budget; therefore numerous studies try to quantify the input, cycling and dispersal of nutrients. By calculating present states and turnover rates we will be able to foresee the impact of shifts in nutrient fluxes in future scenarios (e.g. global warming caused by the alteration of pristine landscapes) which may invert the current status insofar as tropical regions might soon act as carbon source instead.

In this study measurements of Bulk Precipitation, throughfall and stemflow were used to investigate nutrient fluxes in three forest sites in different stages of succession. Collectors for throughfall (n=45), stemflow (n=36), soil water content (n=9) and litter percolate (n=6) were put into three forest sites of 0.12 hectares each, and sampled on event basis up to intervals of two weeks over a period of 2 years.

Nutrients (H^+, Na^+, HH_4^+, K^+, Mg^{2+}, Ca^{2+}, Cl^-, NO_3^{2-}, CO_3^{2-}, SO_4^{2-}, PO_4^{3-}, DOC and DON) were determined by HPLC (Dionex) and tested statistically to investigate significant differences between sites by one-way and two-way ANOVA, after log normalization of data, and Tuckey-HSD post-hoc test.

Here, we constitute an innovative approach for the quantification of nutrient inputs via net throughfall fluxes (NTF) deriving from BP and DD, based on the multiple regression model (Lovett & Lindberg 1984) which announced that the role of canopy exchange is of major importance in terms of tropical nutrient cycling, whereas the influence of dry deposition was weak since largely independent of rainfall. We moreover investigated the major controls on NTF such as soil fertility, topography, canopy structure and species assemblage. The use of a Sun Scan probe (estimating canopy closure) did reveal significant differences between forest sites, but spearman-rank correlation of NTF and canopy closure showed no significant coherency. Investigating species inventory, Fisher's alpha diversity index, ANOSIM and SIMPER analysis indicated differences in species composition between pristine and secondary forests. However, relating resemblance matrices showed no significant influence of species assemblages on nutrient composition of forest sites. The clustering of nutrients revealed by PCA gave insight on origin and sources of associated solutes in NTF.

Key words: Throughfall, stemflow, Net flux, tropical lowland rainforest, Costa Rica, Canopy exchange, Dry deposition, ANOVA, Multiple Regression, PCA, LAI, Spearman-Rank correlation, ANOSIM, SIMPER

Introduction

Tropical forests are of global significance to climate because of their ability to alter the exchange of energy, water momentum and trace gases (Beringer, McIlwaine et al. 2002; Fisch, Tota et al. 2004). At regional and local scales forests affect the distribution of solar radiation, surface albedo, sensible and latent heat flux, and the hydrologic cycle (Hardy & Albert 1995; Herwitz, Levia et al. 2004; Levia & Underwood 2004). These processes are not static and stressors like land-use change, bio-geographic shifts due to climate change and deforestation will likely impact the quantity and quality of water available to human populations (Levia Jr 2006). Therefore knowledge of hydrological processes in wooded ecosystems, e.g. the partitioning of incident gross precipitation (BP) in evapotranspiration, throughfall (TF), stemflow (SF) and runoff constitutes a key component to successful watershed management schemata (Levia Jr 2006).

Tropical rainforests also contribute significantly to the world's carbon budget (Clark, Brown et al. 2001a), accounting for 32-36 percent of terrestrial net primary production (NPP) (Melillo, McGuire et al. 1993; Field, Behrenfeld et al. 1998). Estimates of net primary production in diverse tropical forests range from 1.7 to 21.7 Mg $C*ha^{-1}*yr^{-1}$ (Clark, Brown et al. 2001b). About 59% of the global carbon pool in forests is stored in tropical regions (Dixon 1994). Net primary production of forests is globally strongly controlled by climate (temperature and precipitation) though data are still scarce for tropical rainforests (Schuur 2003) and the impact of other factors is not well understood.

Two dominant gradients were found in tree composition and function across the Amazon, one along a major gradient in soil fertility and the other in dry season length (ter Steege, Pitman et al. 2006). Similar patterns have been shown in the Amazon along climatic and soil fertility gradients for aboveground biomass and wood density while NPP was only related to soil nutrient availability at the regional scale in the Amazon (Baker, Phillips et al. 2004a; Baker, Phillips et al. 2004b; Malhi, Baker et al. 2004). Moreover, nutrient limitation of forest NPP was conclusively demonstrated in Hawaii across wide climatic gradients (precipitation, altitude and/or temperature) but also along substrate age gradients ranging from 100s to millions of years (Harrington, Fownes et al. 2001) (Vitousek 2004 Hawaii). Nutrients are therefore a key determinant of forest productivity and of the functioning of tropical rainforests in global carbon cycle. To understand current and future responses of tropical rainforests to global changes, external nutrient inputs, losses and internal cycling processes of nutrients have to be better understood.

In order to sustain high NPP there must be a relatively closed cycling of nutrients, particularly since tropical soils are usually highly weathered and thus extremely poor in nutrients (primarily nitrogen and phosphorus). Therefore continuous losses of nutrients from the system would lead to further nutrient depletion (Vitousek 1984). The cycling of nutrients occurs via dead plant material in litterfall, root turnover and soluble elements in TF and SF and these together represent the major pathways in a tropical forest’s nutrient cycle. TF is defined as the proportion of incident gross precipitation that penetrates or drips through a plant canopy while SF is the residual amount of rainwater that runs down tree stems and constitutes a localized point input of water and nutrients (Parker 1983). The rest is intercepted by the canopy and lost via evaporation (Jordan, Golley et al. 1980; Chuyong, Newbery et al. 2004). The flux of nutrients in TF and SF is relatively easy to measure and studies produced a good general understanding of the role of TF. For instance, it was shown that the production and decomposition of fine (and coarse) litter represents the major source of autochthonous nutrient input in tropical ecosystems, however, TF can account for up to 50 percent of the total nutrients released and cycled aboveground (Tobón 2004).

Despite this multitude of TF studies worldwide (review Levia and Herwitz 2000) the elucidation of underlying processes that alter nutrient concentrations and fluxes still lagged behind since they remain difficult to interpret (Parker 1983; Lovett, Nolan et al. 1996). It is generally acknowledged that elements in TF and SF derive from three processes:

(1) the 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 (Parker 1983; Lovett & Lindberg 1984; Hansen, Draaijers et al. 1994; Lovett, Nolan et al. 1996; Chapin III 2002).

Nevertheless, a general pattern that could be observed was that fluxes of dissolved nutrients are highly correlated with (1) the amount, duration and intensity of precipitation penetrating the canopy (Parker 1983; Reiners & Olson 1984; Potter, Ragsdale et al. 1991; Lovett, Nolan et al. 1996; Tobón 2004) and (2) the amount of antecedent dry deposition. 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 (Veneklaas 1990).

There have been only few attempts to dissect the contribution of dry deposition and canopy exchange to throughfall chemistry, most thereof based on the canopy budget model or the multiple regression model. For temperate and boreal forests it was shown that TF chemistry mainly depends on factors like latitude, elevation, seasonality, proximity to the sea, species composition, forest age and local land use (Parker 1983;

Levia Jr 2006) that affect dry deposition and/or canopy exchange. SF chemistry is basically controlled by factors like species assemblage (Herwitz 1991; Levia & Herwitz 2000), seasonality, meteorological conditions (Levia & Herwitz 2000) and canopy structure (Levia & Herwitz 2002). Species effects were more clearly visible in temperate and boreal forest due to low species richness, and large differences between deciduous and coniferous species. In tropical rainforests the mechanistic understanding of throughfall and stemflow hydrochemistry is much less developed, and species diversity is much higher:

It was exemplified that soil fertility, canopy structure and land use had significant influences on the nutrient availability and cycling rates in tropical rainforests (Filoso, Williams et al. 1999; Hölscher, Köhler et al. 2003; Hölscher, Köhler et al. 2004). Generally litterfall exhibits the major pathway of internal nutrient cycling for most elements, however, external inputs via DD and internal enrichment via CE processes can make up a big portion of additional nutrient input (Tobón 2004). Whereas nitrogen, calcium and phosphorus mainly derive from litterfall since either immobilized in cell walls or in cell plasma, particularly potassium and DOC is leached from the forest canopy due to high abundance and exchange rates during processes of cell physiology (Veneklaas 1991; Johnson 1992; Cavelier, Jaramillo et al. 1997; Tobón 2004) and thus mainly derives from throughfall. Although there have been many studies on nutrient cycling via TF and SF in tropical regions only few observed that there were differences in nutrient dispersal via CE and DD due to seasonal distinctions of wet and dry season (Filoso, Williams et al. 1999), soil fertility and topography (Tobón 2004), canopy structure and species composition (Hölscher, Köhler et al. 2003). Moreover nutrient inputs were found to vary among forest stands, depending on the relative location and proximity to their sources, either deriving from natural pools as ocean surfaces and volcanoes or agricultural, urban and industrial areas in case of anthropogenic origin (Filoso, Williams et al. 1999; Levia Jr 2006).

Nevertheless there is still particularly a gap in studies of nutrient cycling (litterfall and throughfall) in areas of high precipitation and temperature where forest NPP was reported to decline (Schuur 2003). However, most studies in high rainfall tropical rainforests were performed on Oxisols not on nutrient rich soils such as Inceptisols and Ultisols. The Esquinas forest, Parque National Piedras Blancas, in SW Costa Rica is particularly suited for such an undertaking, since tree diversity is high (140-210 spp. >10 cm dbh), MAP is >5800 mm and MAT is about 28 °C and due to ongoing tectonic land lift and moderate erosion forests stock on more nutrient rich Ultisols and Inceptisols.

This study wants to contribute to the following research questions:

(1) What is the contribution of DD to external nutrient inputs by BP which, due to methodological difficulties, has not been assessed in detail for tropical rainforests.
(2) What is the magnitude of nutrient inputs via litterfall and NTF?
(3) What are the major controls of nutrient fluxes via net throughfall?
    a. ratio between CE and DD, uptake or leaching processes
    b. canopy structure (via estimation of PAI)
    c. species composition of forest sites
    d. how is a.-c. affected by season, topography and stage of succession
    e. origin and sources of associated solutes

Material & Methods

Study Area

The study was conducted at the Tropical Research Station La Gamba (TRSLG; 8°42'46'' N, 83°12'09'' W, 70 m.a.s.l.) situated at the borders of the 'Parque Nacional Piedras Blancas' national park, covering an area of approximately 142 km^2, reaching from the Golfo Dulce's seashore to the village of La Gamba, in the province Puntarenas in the Southwest of Costa Rica (Figure 1). The vegetation is mainly characterized by a wet tropical lowland rainforest (Holdridge 1967) covering from sea level up to 580 meters altitude. Ultisols and Inceptisols are the major soil types typically found in the region (Vasquez 1989). Ultisols are strongly acidic and weathered soils, appearing especially on ridges and upper slopes, and are replaced by the moderately weathered, younger Inceptisols in lower slopes and ravines (Pamperl 2001).

Mean annual temperature is 28.1°C and ranges from 22.9°C to 34.2°C on monthly average (Weber, Huber et al. 2001). Mean annual temperature inside the forest was 25.2°C, monthly averages ranging from 22.3 to 28°C, and humidity was high (97.7%) throughout the year (Weissenhofer 1996). Average annual bulk precipitation was 5769mm (recorded at the Tropical Field Station La Gamba) with a short dry season from January to March (monthly mean precipitation approx. 180mm), and a wet season from September to November (monthly mean precipitation about 800mm) (Figure 2).

Study design

To study patterns in nutrient cycling study plots where randomly established in three different forest sites consisting of primary ravine (PRa), primary ridge (PRi) and secondary ravine (SRa) forest (Figure 1). We setup plots as squares of 20x20 meters, separated by a distance of 10m, and divided into subplots of 10x10 meters each, or plots as rectangles of 10x40 meters subdivided into subplots of 10x10 m and separated by 10-30 m due to spatial restriction at the ridge site. Distances between sites were approx. 1.5 km and each site was covered by 0.12 hectare of survey area. Inside these subplots all tree species above 10 cm diameter at breast height (dbh) where labelled and determined to species level. In one of the four subplots trees between 2.5 and 10 cm in dbh were labelled and determined to species level. Herbarium specimens were deposited in the National Herbarium at the Museo Nacional (San Jose, Costa Rica) and at the Biologiezentrum Linz (Upper Austria, Austria). A foto-herbarium is available at the TRSLG. To investigate possible differences in stemflow trees were grouped into 4 different classes of diameter (2.5-10cm, 10-20cm, 20-30cm and >30cm).

Furthermore global site factor & canopy closure as well as plant area index (PAI) were estimated by taking hemispherical photographs and PAR measurements by a SunScan probe v1.02R (Delta-T-devices Ltd) on days of uniform overcast skies. A digital camera (Nikon Coolpix 8100 with FC-E9 fisheye adaptor lens 183°) was balanced horizontally and directed to the geographic north. For evaluation of canopy closure we employed the software Hemiview (Delta-T-Devices 1999) and Sidelook (Nobis 2005) using the following setup: solar transmission coefficients: transmittivity 0.4, diffuse proportion 0.45, external solar flux 1370 W/m2, diffuse distribution: SOC, standard overcast sky; picture settings: threshold 182, radiant 911, rotation 0.0 (north), Magnetic declination 0.5 east).

Finally each site was equipped with collectors for throughfall (TF, 15 collectors per site), stemflow (SF, 12), soil water (SW, 3) and zero tension meters for collection of litter percolate (LP, 3), respectively. Sampling for hydrochemistry was performed on an event basis (n=30) in February to April and August to October 2005 after every rainstorm; additionally BP, TF & SF volumes were sampled also on an event basis every two weeks for the rest of the study year. Precipitation events below 5 mm were discarded in consideration of minimum canopy interception storage.

Sampling design

Bulk deposition samplers (n=3) were placed in the open area surrounding the TRSLG to quantify the amount and chemistry of open precipitation. They consisted of plastic (PVC) tubes of 20.5 cm in diameter and 100 cm length that were fixed each to two steel posts using cable ties. Polyethylene bags (80 L, thickness 0.2 mm) were inserted and fixed with rubber straps, the opening being at 1.5 m height aboveground. The bags allowed rainwater collection of up to 300 mm per event. Polyethylene bags were displaced every month or when leaky or contaminated. When bags were new the first sampling event was discarded due to wash out polymer plasticizers. To avoid contamination during sampling the collectors where covered with a wire net (mesh width 10mm) to keep litter and other material off the traps. Between each sampling period the collectors were kept closed with polyethylene caps to avoid unintended collection of rainwater and further contamination when no samples were taken. Collectors were opened every 3-7 days until a rainfall event occurred and was collected, otherwise collectors were closed.

Throughfall collectors (n=45) were made of the same design as BP collectors. Throughfall was sampled placing these traps in every subplot and also in the middle of each plot, so that every plot was equipped with 5 traps (15 collectors per site).

Stemflow collectors (n=36) were either made of 0.5 L polyethylene bottles which where previously cut on one side and put around stems in case of the stem class comprising the smallest trees (2.5-10 cm). Bottles were mounted upside down, sealed to the stem by sanitary silicone and connected to collection bottles (1-5 L, PE) using silicone tubing. In the case of trees >10 cm dbh flexible tubing (garden hose) was cut in half longitudinally and fixed tightly around the tree trunks in a steeply sloped upward spiral in order to avoid overflow. The tubing was stapled to the tree trunk and silicone sealant was applied sealing the collar to the trunk to avoid water losses. After setup the first two rain events collection were discarded due to probable contamination of samples with ingredients from the sealant. Collection vessels (allowing sampling of up to 25 L in the case of the largest stem class >30 cm) were connected to the flexible tubes when sampling was performed or disconnected in between sampling events. Nylon nets (mesh width 0.2mm) were put between tubes and sampling vessels to prevent contamination by coarse and fine material. SF bottles and vessels where washed with tap water after each sampling event.

Litter percolate was collected with so called ‘zero-tension-meters’ (n=9) which consisted of plastic boxes put at equal horizon with the soil surface and covered by a wire gauze (mesh size 10 mm). The litter layer was carefully removed before installation of the boxes and put back on top of the wire net so that only water running through the litter layer was sampled. Litter percolate was also sampled on an event basis and samples were retrieved using syringes connected to silicone tubing.

Soil water samples (n=9) were also taken on an event basis using ceramic soil suction tubes (USM tensiometers SKP-100) positioned to 10 cm soil depth. Suction tubes were connected to collector bottles that where evacuated with a hand operated vacuum pump to a pressure of minus 40 kilopascal.

After each event total amount of water per collector was determined volumetrically using measuring cylinders. Of each collector two sample aliquots (15 mL) were transferred into 20 mL scintillation vials and stabilized against microbial transformation by addition of $HgCl_2$ (30 µM end concentration, for TOC/TN analysis) or Hg-Phenyl acetate (30 µM end concentration, for ion chromatography) and stored at -20 °C immediately after collection.
Chemical Analyses

Directly after sample collection the pH was measured at TRSLG using a Sentron ArgusX ph meter. The following chemical analyses were performed at the Department of Chemical Ecology and Ecosystem Research, University of Vienna, Austria. Inorganic cations (Na^+, NH_4^+, K^+, Ca^{2+}, Mg^{2+}) and anions (Cl^-, NO_3^-, SO_4^{2-}, PO_4^{3-}) were analysed by HPLC (high pressure liquid chromatography, DX 500, Dionex, Vienna, Austria) and conductivity detection. Anions were separated on an anion exchange column (AS11, 4x250 mm, Dionex) using a linear KOH gradient (2 to 30mM in 6 min, total run time 10 min). Cations were separated on a cation exchange column (CS16, 5x250 mm, Dionex) by an isocratic method with methanesulfonic acid as eluent (30mM methanesulfonic acid for 26 min and 40 °C). NPOC (non purgable organic carbon) and TDN (total dissolved nitrogen) content of samples were determined using a TOC-$V_{CPH/CPN}$/ TNM-1 analyzer (Shimadzu, Japan). Inorganic carbon was automatically removed during measurement through addition of 2 N HCl and purging with synthetic air (CO_2 free). DON was calculated by subtracting DIN (dissolved nitrate and ammonium) from measured TDN.

Calculations

Volume-weighted mean concentrations (VWM, Table 1) of each sampling collector were used to express mean solute concentration of throughfall and rainfall during the study period and were calculated as:

$$(1)\ VWM = \frac{\Sigma^{n}_{i=1} (C_i * V_i)}{\Sigma^{n}_{i=1} V_i}$$

in order to be able to compare nutrient fluxes between forest sites, since the collected amount of water and solute concentrations will naturally differ between collectors as a result of the differences in vegetation composition and structure.

Annual nutrient fluxes (Table 2) were then expressed by multiplication of VWM values per trap with the TF:BP quotient of respective trap volumes over the sampling interval (30 events) and annual precipitation volume.

Throughfall is the amount of open bulk precipitation (BP) that is not retained by the vegetation but passes the canopy layer and thus is altered in hydrochemistry due to exchange processes in canopy exchange (CE) and dry deposition (DD):

$$(2)\ TF = BP + CE + DD$$

Net throughfall flux (Figure 3) is defined as the difference between the solute flux in throughfall and in bulk precipitation:

$$(3)\ NTF = TF - BP = CE + DD$$

and represents the integral of processes of uptake or leaching of nutrients during canopy exchange (CE) and dry deposition (DD), showing 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.

To calculate the contribution of CE & DD to annual inputs (Figure 4) we computed a regression model based on the following equation (Lovett & Lindberg 1984):

$$(4)\ NTF_x = a + b1*A + b2*P$$

Factor a represents the intercept of the model. Factors b1 and b2 are respectively indicating the slope of the calculated linear model, for A being antecedent dry period and P the magnitude of precipitation, respectively. With this model it is possible to characterize the influences of DD and CE on the underlying exchange processes in TF for both inter-event and seasonal studies. With this knowledge one can further interpret whether a certain element rather derives from deposition or exchange processes and therefore from external or internal sources in terms of nutrient cycling (Veneklaas 1990; Lovett, Nolan et al. 1996; Filoso, Williams et al. 1999). Here, positive annual values of canopy exchange indicate net enrichment pointing of nutrients by leaching within the canopy, whereas negative values point to nutrient uptake processes or retention of nutrients within the canopy.

It is thereby possible to estimate the amount of annual fluxes of respective dry deposition and canopy exchange by investigating only a set of precipitation events for the whole study period by multiplying the values for b1 (DD) and b2 (CE) with the amount of dry days (80 days during the study period) and magnitude of precipitation (5720 mm during the study period).

Furthermore we hereby constitute an innovative approach for the quantification of annual fluxes of respective BP and DD by calculating a correction factor (f):

$$(5)\ f = \frac{BP + DD}{BP}$$

which indicates the contribution of DD to total nutrient inputs (wet & dry deposition) that until now very likely was underestimated by former studies.

Statistical Analysis

Statistical analyses such as one-way analysis of variance (ANOVA), two-way ANOVA, principal component analysis (PCA) and multiple range tests were computed with STATGRAPHICS PLUS 5.0 (Statpoint-Inc 2000) and STATISTICA for Windows 7.5 (STATSOFT 2005). Statistical analysis investigating species assemblages were computed with PRIMER 6.0 (Clarke & Gorley 2006).

Differences in rainwater quantity and nutrient fluxes between study sites were investigated by one-way *ANOVA* after testing whether the assumptions underlying ANOVA were met by Levene's Test (homogeneity of variance) and test for normality (after log-transformation of data). Furthermore a two-way-ANOVA was conducted to test for inter-correlation of stemflow volumes or nutrient fluxes between sites and stem classes. Tukey HSD multiple range tests at the 95% level were calculated to test for differences between sites. Kruskal-Wallis ANOVA was calculated for data which after log-transformation still were not normally distributed.

A *principal component analysis* (PCA) was computed to investigate which ions contributed most to the variability in net throughfall fluxes of single collectors. Thus ion clustering is believed to indicate common sources of nutrient fluxes in throughfall (e.g. sea-salt-ions or canopy leaching).

A *multiple regression* model (see Equation 4) was computed to differentiate nutrient input to the forest ecosystem that derives either from exchange processes or deposition of aerosols. Interpretation of values of probability and correlation coefficients was accomplished using ANOVA. The amplitude of calculated b values shows which factor (exchange or deposition) had a greater impact on net throughfall fluxes.

A *spearman-rank correlation*, normalising non-parametric data by the formation of ranks, investigated the coherence of ion fluxes and distribution of leaves above a given throughfall trap by considering canopy closure as a surrogate for local leaf area index (LAI).

Since fitting best for species rich areas, as it accounts especially for rare single species (singletons), *fisher's alpha index* was computed to exhibit differences in species assemblages of study sites. Analysis of similarity (ANOSIM) based on correlating Bray Curtis matrices (Non-metric-multidimensional Scaling) and Spearman-Rank Correlations showed whether forest plots form clusters according to forest site. Analysis of Similarity Percentage (SIMPER) was applied to estimate percentages of similarity and reveal most dissimilar species between forest sites. After Bray Curtis distances of square rooted data were calculated for ionic composition and tree diversity, respectively, the two matrices where related by spearman-matrix-rank correlation to test for significant relationships between nutrient fluxes and tree species assemblage of the different forest sites.

Results

I) Hydrology

An analysis of variance testing differences in TF volumes, ranging from 5 to 300 mm, between forest sites showed no statistical significant differences. TF comprised between 87 and 92% of BP volume, on an annual basis (Figure 5). A Kruskal-Wallis ANOVA was computed showing no differences in stemflow volumes between sites, ranging between 0.7 and 1.0% of BP volume (Figure 5). However differences in stem classes between sites were found ($H_{(36)}=17.1$, $p=0.0007$); stem class 1 (2.5-10 cm dbh) produced higher SF volume on a tree basis compared to class 2 (10-20 cm) and class 3 (20-30 cm) but was not different from class 4 (above 30cm). To test for interaction between between factors site and stem class in stemflow volume a two-way ANOVA was computed with log-transformed data. Whilst there were no effects of site*class ($P=0.461$) and site ($P=0.452$), stem class significantly affected SF volume ($P<0.001$).

IIa) Nutrient concentrations (volume weighted means, VWM)

Generally variations in nutrient concentration between collectors where relatively high with CVs ranging between 8-57% for BP, 20-160% for TF, 35-345% for SF, 18-165% for LP, 5-109% for SW within sites. Two-way ANOVAs could not be calculated since any transformation tested did not result in normal distribution of VWMs. One-way ANOVA of VWMs combined for site revealed significant differences between sample types (BP, TF, SF, SW, LP) with highest values in SF for all nutrients except NO_3 which was similar at all sites (H: $F_{(4)}=16.1$, $p<0.001$; Na: $F_{(4)}=28.7$, $p<0.001$; NH_4: $F_{(4)}=31.7$, $p<0.001$; K: $F_{(4)}=45.0$, $p<0.001$; Mg: $F_{(4)}=59.0$, $p<0.001$; Ca: $F_{(4)}=63.8$, $p<0.001$; Cl: $F_{(4)}=18.1$, $p<0.001$; SO4: $F_{(4)}=6.1$, $p<0.003$; PO_4: $F_{(4)}=10.1$, $p<0.001$; DOC: $F_{(4)}=53.6$, $p<0.001$; DON: $F_{(4)}=9.7$, $p=0.004$; TDN: $F_{(4)}=30.0$, $p<0.001$).

One-way ANOVAs were calculated to test for differences in VWM between sites. One-way ANOVA of TF samples showed significant differences of solutes between sites for Na ($F_{(44)}=6.3$, $p=0.01$) being highest at site PRi (C), Ca ($F_{(44)}=5.5$, $p=0.012$) being lowest at site PRi (C), NO_3 ($F_{(44)}=6.0$, $p=0.004$) being lowest at site SRa (A) and PO_4 ($F_{(44)}=7.4$, $p=0.003$) being highest at site PRa (B). One-way ANOVA of VWMs of SF samples showed significant differences of solutes for Mg ($F_{(35)}=5.3$, $p=0.006$) being highest at site SRa, and Cl ($F_{(35)}=6.9$, $p=0.03$), SO_4 ($F_{(35)}=5.6$, $p=0.018$) and DOC ($F_{(35)}=4.4$, $p=0.019$) being highest at site PRi. One-way ANOVA of VWMs of SW samples showed significant differences of nutrients for NH_4 ($F_{(8)}=6.7$, $p=0.039$) being highest at site PRi (C) and NO_3 ($F_{(8)}=15.1$, $p=0.039$) being highest at site PRa (B). No significant differences between sites were found for VWMs of LP samples.

IIb) Nutrient fluxes

BP inputs of dissolved ions ranged from 0.4 (PO_4) to 17.3 kg per hectare and year (Ca). Inputs for dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) were 36.2 and 10 kg per hectare and year, respectively. TF fluxes of dissolved ions ranged from 0.6 (PO_4) to 16.6 kg per hectare and year (Ca). Values for DOC and TDN were 48.9 and 7.1 kg per hectare and year, respectively (Table 2). There were significant differences in solute fluxes between bulk precipitation and throughfall (full model: $F_{(39)}=3.9$, $p<0.001$). Compared to throughfall, bulk precipitation showed higher fluxes of H (BP>PRa), Na (BP>SRa) and NH_4 (BP>PRi). However the biggest differences were found in fluxes of K and NO_3, where NO_3 was highest and K was lowest in BP compared to TF at all sites. A further Kruskal-Wallis ANOVA was computed for Cl, SO_4 and DOC since these elements were not normally distributed, revealing a significantly lower SO_4 flux in BP compared to TF in SRa. Statistical analysis of TF fluxes between sites produced the same significant differences as shown before for VWM of TF at different sites i.e. Na being highest at site PRi, Ca being lowest at site PRi, NO_3 being lowest at site SRa and PO_4 being highest at site PRa (Table 2).

SF fluxes of dissolved ions were much lower ranging from 0.006 (PO_4) to 3.92 kg per hectare and year (Cl). Inputs of DOC and TDN were on average 2.9 and 0.2 kg per hectare and year, respectively (Table 2). For all solutes, therefore, SF flux comprised between 0.2 – 10.7% of TF flux except for Cl^- (85.5%). One-way ANOVA of SF fluxes showed significant differences of solutes for Mg ($F_{(35)}=5.3$, $p=0.006$) being highest at site SRa, and Cl ($F_{(35)}=6.9$, $p=0.03$), SO_4 ($F_{(35)}=5.6$, $p=0.02$) and DOC ($F_{(35)}=4.4$, $p=0.02$) being highest at site PRi. Combining forest sites, nutrient fluxes differed significantly for trees of different diameter (full model: $F_{(36)}=2.1$, $p=0.005$); fluxes of Na, NH_4, K, Ca, SO_4 and PO_4 where higher for trees with 2.5 to 10 cm diameter at breast height compared to to trees with 20-30 cm dbh. To analyse the interactions in solute fluxes between forest sites and between diameter classes of stems a *two-way ANOVA* was computed. Whilst site*stem class had no significant effect, the factor ‘site’ ($F_{(24)}=2.5$, $p=0.01$) and the factor ‘stem class’ showed a significant effect on fluxes of solutes in stemflow ($F_{(36)}=2.6$, $p=0,002$).

Solute fluxes in net throughfall were calculated as the difference of TF flux minus BP flux. Positive NTF values indicated pronounced net increases of K and DOC, with lower enrichments found for Cl, Mg, DON and PO_4 (in decreasing order). In contrast negative values of NTF pointed to marked net retention and/or uptake of Na, NH_4, NO_3, SO_4 and H (Figure 3). Statistics of site-specific differences in NTF conform to the same values as given above for TF fluxes. A multiple linear regression of event-based NTF, event precipitation and antecedent dry days was calculated to show whether canopy exchange or dry deposition had a greater impact on NTF. Whereas the model was highly significant for most solutes, for PO_4 it was not. CE led to significant retention of Na and Cl, and less of Ca, SO_4, NH_4, Mg and NO_3 (in decreasing order). Furthermore, CE resulted in marked leaching of DOC and K and less so of DON and PO_4. DD contributed to the inputs of most elements but especially for Na, DOC, Cl and Ca but not to DON (Figure 4, Table 3).

III) Sources of nutrient input in net throughfall

A principal component analysis was calculated to assess different or common sources of solutes in net throughfall (NTF). At a threshold of 0.5 (Eigenvalue) factor 1 was found to group solutes such as K, Mg, Ca, DON and DOC i.e. plant nutrients and dissolved organic matter that are attributable to leaching from canopy components, Factor 2 showed clustering of typical sea-salt ions (Na, Cl, Mg, SO_4) together with NO_3, while factor 3 was determined by NH_4 and PO_4 which may be related to biomass burning. Factor 4 was determined by solutes H and K which were negatively correlated, indicating exchange of H for K through ion-exchange processes in the canopy (Table 4). Together they accounted for 73.5 % of total variance. The factor values were then tested with further ANOVAs for differences between forest sites. Factor 1 showed highest values at SRa, differing from PRi. Factor 2 was highest at site PRi, differing from SRa. Factor 3 was highest at the PRa site and lowest at PRi. For factor 4 no differences between sites were evident (Figure 6).

IV) Effects of seasonality, vegetation structure and species assemblage

One way ANOVA of VWM showed that concentrations of most solutes (except NH_4, Ca) were significantly higher ($p<0.001$; n=3 events of approximately 610mm) in the dry season than in the wet season (n=3 events of about 1350mm). Similarly seasonality also affected throughfall fluxes, being significantly higher for Cl, NO_3, SO_4, PO_4 ($p<0.001$) and DOC ($p<0.01$) during the dry season and for NH_4, Ca ($p<0.001$) and Mg ($p=0.01$) during the wet season.

LAI values (Table 5) determined by SunScan system, based on light absorbance by the canopy, were highest for PRa compared to SRa and PRi ($F_{(2)}=15$, $p<0.001$). Despite the higher LAI values at PRa, levels of canopy closure calculated by hemispherical photography and tested by ANOVA did not differ between sites. The Spearman-Rank correlation of canopy closure measured above each TF collector and water or solute flux in throughfall was not significant (Table 6).

Fisher’s alpha value demonstrated that trees between 2.5 and 10 cm in diameter at breast height showed only little difference in species diversity among sites (Fisher´s alpha 20-26), while trees species above 10 cm dbh did (Fisher´s alpha 11-86, Table 5).

A Principle Component Analysis (PCA, data not shown) investigating the most characteristic tree species on the respective study site showed that for trees below 10 cm dbh, component 1 explained 88.6 percent of variance, where the four most relevant species were *Vochysia ferruginea* (Eigenvalue 0.86), *Croton schiedeanus* (0.4), *Bactris gasipaes* (0.14) and *Mabea occidenta* (0.14) being the most abundant species at PRi. For trees above 10 cm dbh component 1 explained 74.5 percent of variance, was highest at SRa and was dominated by *Vochysia ferruginea* (0.87), *Guatteria amplifolia* (0.19), *Guarea grandifolia* (0.15) and *Carapa guianensis* (0.15).

Analysis of similarities (ANOSIM) between sites showed weak differences (high similarity) for trees between 2.5 and 10cm dbh (Global Model's R = 0.87, p = 0.001). PRa differed from PRi and PRa (R = 0.79-1.00, p = 0.03) whilst SRa and PRi showed no differences in species assemblage (R = 0.63, p = 0.10). For trees above 10cm in dbh species assemblages showed greater differences between sites (Global Model's R = 0.10, p = 0.002) with generally high differences in species between all sites (R = 0.01, p = 0.003-0.02; Table 19).

Analysis of Similarity Percentage (SIMPER) confirmed that for trees below 10 cm dbh forests differed most significantly in species composition (Average dissimilarity: PRa/PRi: 100%, SRa/PRa: 98.2% and SRa/PRi: 92.1%). Dominant species that contribute to similarity within sites and dissimilarity between sites are given in Table 7. Finally, relating Bray Curtis distance matrices of tree species and ionic composition by Spearman-matrix-rank correlation showed no influence of species composition on ionic composition in throughfall (Table 8).

Discussion

1. Quantification of BP and DD inputs

In this study we introduced an innovative approach to quantify and separate the annual input of allochthonous derived (external) nutrients in BP and DD, the latter being derived from the multiple regression model to differentiate the component fluxes in NTF. We clearly show that inputs by BP, representing a combination of wet deposition and a small contribution of DD flux while BP collectors are open, have to be corrected by a factor f of approximately 1.3 to 3.6 depending on the element analyzed in this study. For essential nutrients such as nitrogen (NH_4, NO_3), sulphur (SO_4) and phosphorus (PO_3), values for this correction factor ranged from 1.3 and 1.8, whereas for base cations (K, Ca and Mg) from 1.3 to 1.6. Corrections for external inputs of Na and Cl were highest, with 3.6 and 2.6, respectively. The results therefore indicate that previous calculations of external nutrient inputs to tropical forest ecosystem have been profoundly underestimated.

Moreover there are only few studies on tropical forests that conducted the calculation of the multiple regression approach (Lovett & Lindberg 1984) to quantify the amount of DD and CE in NTF. Comparing our results with those of other studies the correction factor exceeded ours for specific solutes by far. For instance in an off-shore mangrove ecosystem dominated by *Rhizophora mangle* (Wanek, Hofmann 2007); calculation of BP from nutrient concentrations in Table 2 and precipitation volume during the observation period, DD from Table 5) values for the correction factor ranged from 2.2 to 3.4 for base cations (K, Ca and Mg) and was 2.8 for SO_4. Sea-salt derived solutes i.e. Na and Cl were underestimated by a factor of 2.9 and 3.8. At a more remote site in a flooded forest archipelago at the Negro River in Brazil (Filoso et al. 1999; BP and NTF derived from Table 3, DD calculated as NTF – CE, CE was calculated by multiplying the averge canopy exchange factor times precipitation volume during the observation period) correction factors were even higher, ranging between 1.5 and 35 for cations (Na, K, Ca and Mg) were 1.6 and 6.8 for SO_4 and PO_4. Although situated far from the coast values for Na and Cl input had to be corrected by 1.6 and 3.2.

It is noticeable external inputs of fundamental nutrients (N, P) at the mangrove site were estimated correctly based on BP only since the DD component was negligible, which may be related to their extremely low concentration in sea water. Interestingly the underestimation of K, Mg, NH_4, NO_3 and PO_4 inputs seemed exceptionally high at the remote archipelago forest site which grows on relatively nutrient-poor soils. It has been suggested by Filoso et al. (1999) that DD of these solutes mainly derives from enhanced biogenic sources (e.g. biomass burning, emissions from soils and vegetation) during the dry (and wet) season.

2. Nutrient inputs via litterfall, TF and SF

Comparison of nutrient inputs to the forest floor from litterfall versus TF showed that litterfall generally represents a higher fraction of input with a more pronounced seasonal pattern. In the Esquinas forest, a peak of leaf litterfall was observed, during as well as at the end of the dry season on all forest sites (Drage 2008, pers. comm.) though MAP is >5800 mm, there is no month with precipitation <200 mm and a pronounced dry season is therefore missing. Moreover topography, climate seasonality and successional stage where found to be the major variables affecting litter dynamics in tropical forests (Luizao, Luizao et al. 2004). The SRa forest showed significantly higher litter production than the PRi forest but highest rates of nutrient cycling were consistently recorded for the PRa forest. Thus successional stage and topography determined the spatial variability in litterfall but also the total carbon and nitrogen concentration of soils (Drage 2008, pers. commun.).

Inputs of nutrients to the forest floor in litter fall declined in the order C>N>Ca>K>Mg and Na and therefore ranged among the highest reported for tropical forest sites, probably due to the nutrient rich characteristics of Inceptisols. Whereas internal cycling of N, Ca and P mainly is associated with litterfall since either immobilized in cell walls or in cell plasma, other nutrients (e.g. K) are more susceptible to leaching of the canopy layer due to high abundance and exchange rates during processes of cell physiology (Veneklaas 1991; Johnson 1992; Cavelier, Jaramillo et al. 1997; Tobón 2004) and thus mainly cycle via throughfall and stemflow (Parker 1983; Levia & Frost 2003). Although cycling of nutrients in throughfall is considerably lower than that released by litterfall the contribution of throughfall and stemflow to nutrient inputs to the forest floor is of significant importance due to the typical high inner cycling rates of tropical rainforests on strongly weathered soils (Tobón 2004). For instance, Chuyong et al. (2004) reported that the percentage of rain-based input (TF+SF) to gross inputs including litterfall was 76-78% (K), 39-45% (Mg), 33-37% (P), 25-29% (Ca) but only 2-5% (N) for two different forest sites in Cameroon.

However, in terms of internal cycling litterfall has to be compared to CE, not TF or NTF. On this there is no literature or data available. The same multiple regression model would allow such first comparisons between litterfall and CE. Due to the lack of litterfall nutrient fluxes (data pending, Drage et al.) the CE data suggest the following: there is no contribution of CE where elements are taken up actively, e.g. Na, NH_4+NO_3, Mg, Ca, Cl and SO_4, but only to elements that are leached from the canopies i.e. K, PO_4, DON and DOC. Naturally the contribution of CE to internal cycling of C is negligible, and DON efflux is partly counterbalanced by NH_4 and NO_3 uptake.

SF only contributes to a small proportion (1-10%) to total water input and make up 0.2 to 11% of TF flux to the forest floor (Herwitz & Levia 1997). In the Esquinas forest the hydrological flux in SF was <1% of BP and nutrient fluxes in SF were also well below 5% of that in TF at all sites. SF is therefore excluded from further discussion.

3. Controls of nutrient cycling in NTF based on the CE/DD model

In ecosystem ecology the following state factors have been defined: climate, time, topography, parent material and potential biota (Chapin XXX). It is these factors that determine ecosystem type, vegetation composition and ecosystem processes, and we here adopted a revised scheme (FIG 7) to investigate the major controls of external and internal nutrient inputs and therefore controls of NTF via DD and CE. DD and CE represent the common mechanisms that regulate the chemical composition and deposition via NTF (Lovett & Lindberg 1984; Filoso, Williams et al. 1999). It has been suggested that CE is mainly affected by species assemblage, vegetation structure, soil fertility and concentration of solutes in precipitation, whereas DD is primarily altered by climate (seasonality) and exposure of the canopy layer (REFerence). Both DD and CE vary in space and time since they are related to biological characteristics of the forest (i.e. stand age, soil fertility, plant nutrient status, presence of insects, leaf area and epiphyte activity).

3.1 Ratio between CE and DD, uptake or leaching processes

A multiple linear regression of NTF determined the relative importance of CE and DD and denoted the solutes of Na>Cl>DOC>K>Ca>DON>SO_4 to be controlled primarily by canopy exchange processes. NTF of solutes indicated an enrichment in TF in the order of K>DOC>Cl>Mg>DON and PO_4 which may either be due to DD and leaching or DD exceeding canopy uptake. Ca fluxes were more variable. Only in the case of DOC, K, DON and PO_4 this net throughfall enrichment was linked with solute leaching. In the case of Cl and Mg DD was dominant thereby masking the uptake of these elements from rainfall. Uptake rates can therefore be substantial where NTF is positive, and the application of the multiple regression model allows a clear separation of the underlying processes, and thereby of the controls of NTF in tropical rainforests. Particularly K and DOC are considered to be highly soluble substances that are washed out from canopy leaves and plant material (Tobón 2004), explaining the highest positive CE fluxes at our sites.

In contrast, negative NTF of Na>TDN>NH_4>NO_3>SO_4 and H pointed to net uptake of solutes from throughfall after passing the canopy layer, where canopy uptake clearly exceeds DD. Again the multiple regression model demonstrated that besides solutes that exhibit negative NTF some solutes are also taken up while NTF was positive, e.g. Cl, Ca and Mg. Negative CE (uptake) was highest for Na and Cl and decreased for Ca, SO_4, NH_4, Mg and NO_3. Nitrogen such as TDN, NH_4 and NO_3 is the major plant nutrient and in strongly nutrient limited forests, canopy uptake may supplement nutrients for plant growth. For instance, in boreal forests canopy uptake of N has been reported to meet up to 30% of the annual demand for net primary production (Lovett & Lindberg 1993). Similarly, uptake of essential nutrients such as N and P was found across a strong N to P limitation gradient in mangroves (Wanek et al. XXX) or across a soil nutrient gradient from nutrient-rich alluvial soils to nutrient-depleted upland terraces (Tobon, Sevink et al. 2004). Interestingly, P was leached at all three sites, though lowland rainforest are considered to be rather P than N limited (Tanner, Vitousek et al. 1998). Na is probably retained by epiphytes, cryptogams and other canopy components. It was reported that Na can show high rates of adhesion due to its physical and chemical characteristics and is quickly taken up in exchange for other solutes (Eklund, McDowell et al. 1997; Hölscher, Köhler et al. 2004; Tobon, Sevink et al. 2004). In a Brazilian forest archipelago high rates of exchange of ions were reported in the forest canopy (especially H and K), whereas Na and Mg were commonly low in foliar concentration and less susceptible to leaching than K (Filoso, Williams et al. 1999; Levia Jr 2006). Besides simple dilution effects, H, K and Ca were found to be less depleted in TF of small storm-sizes pointing to their major origin from canopy exchange during the wet season (Veneklaas 1990; Campo-Alves 2003). The retention of H is probably a result of ion exchange with base cations and NH_4 in the leaf canopy which decreases the acidity of rain and results in an enrichment of base cations and organic acids. Moreover, principal component analysis of annual NTF based on individual throughfall traps yielded a PCA factor 4 that was represented by the highly exchangeable elements H and K and was not related to any forest site. Therefore, the effects of ion-exchange processes where not related to spatial differences between forest types but to physiological processes of overriding importance (Tobón 2004).

Generally extended periods of contact increase the retention of NO_3 and NH_4, while increased acidity of rainwater enhances the permeability of the leaf canopy and cation exchange processes (Filoso, Williams et al. 1999). Thus, NO_3 and NH_4 can be either leached or retained in forest canopies, depending on the concentration gradient between canopy and rainfall and length of contact time. Ca showed both enrichment and depletion in NTF depending on the investigated forest site, being depleted only at PRi; overall Ca uptake and DD were high but closely counterbalanced at the three sites, and Ca leaching depended on the nutrient status of the forest site (Filoso, Williams et al. 1999). Interestingly major portions of enriched calcium are believed to derive from recently absorbed calcium which is available in exchangeable forms located in plant's tissue outside of cell walls as it was transported from roots to foliage (Lovett, Nolan et al. 1996). In contrast this study unequivocally demonstrated strong Ca uptake not leaching.

Dry deposition contributed most for inputs of Na>DOC>Cl>Ca>NH4>SO4>K>Mg. Na, Cl, Mg and SO_4 are the major components of sea water, and external inputs are therefore commonly related to DD of marine aerosols. K and Ca are only minor solutes in sea water, and marine concentrations of NH_4 and DOC are negligible. These components are closely linked with biogenic emissions and biomass burning (Artaxo, Fernandes et al. 1998). Generally it is assumed that DD is of less importance than CE for base cations since they do not occur in gaseous phases and there is low aeolean transport of soil and dust particles in remote areas of continuous forests (Filoso, Williams et al. 1999). CE was therefore the dominant source of base cations to NTF, while DD was important only during dry season (Filoso, Williams et al. 1999). Although for SO_4 and Cl, DD was reported to be the main contributing source to NTF (Filoso, Williams et al. 1999) this was not the case in our study where CE fluxes dominated. It was shown that DD changes seasonally with anthropogenic biomass burning during the dry season since forest burning increases emissions of NOx, organic C and other elements such as K and P and thus DD of these compounds (Clark, Brown et al. 2001b). There was also a small DD flux of PO_4 (this study) but again the larger portion derived from leaching. PO_4 leaching can be enhanced in the wet season (or at sites of very high MAP) where the net loss from the forest canopy is increased by the greater magnitude of heavy precipitation events (Filoso, Williams et al. 1999). Interestingly, we found no DD component for DON, and NTF of DON was controlled by CE, i.e. canopy leaching. The major source of DON to NTF is considered to be foliar leaching or phyllosphere (surface) processes such as N_2 fixation by free-living diazotrophic organisms (Fürnkranz 2008).

3.2 Canopy cover and structure

Canopy cover and related estimates are a major determinant of NTF, through increasing the surface area to which aerosols are deposited and where nutrients can be exchanged. Schroth et al. (1999) clearly demonstrated this relationship for tropical mono- and polycultures with canopy cover ranging between 7 and 100%. In this study leaf area indices were very high and varied between 6.9 and 8.3. LAI was significantly higher at the PRa forest site reflecting the spatial geometry and greater structural heterogeneity of the ravine forest due to the prolonged stage of vegetation development. It was also PRa were highest NTF values were found for PO_4 and a trend towards increased NTF of DOC, K, Mg and Ca compared to the other sites. A greater variability in canopy structure at PRa, implied by higher coefficients of variation of LAI, canopy closure and tree height, also results in greater canopy roughness. Canopy roughness may further increase NTF by enhancing DD (and CE) processes and thus nutrient deposition (Parker 1983; Lovett & Lindberg 1992; Hansen, Draaijers et al. 1994). However, on a individual throughfall trap basis, we found no correlation between canopy closure and NTF of any solute. At this small scale the variation in NTF is therefore not accounted by simple canopy structure measures, and more elaborate models of throughfall fluxes have to be adopted. The magnitude of water and nutrient fluxes inside the canopy, however, is also affected by non-vascular plants (mosses, liverworts and lichens) since they may account for a large part of the vegetation's aboveground biomass, particularly in montane rainforests (Hölscher, Köhler et al. 2004). In the Esquinas rainforest year-round high humidity results in dense epiphyte colonisation of ravine but not ridge forests (PRa>PRi) while after 25-years of succession epiphytes in SRa were nearly missing (Albert, data not shown). Especially during increased rainfall intensity an increase of the spatial variability of throughfall was observed beneath an old-growth tropical forest, because tropical forest canopies are highly diverse and geometrically complex and therefore have a great number of potential drip points (Loescher, Powers et al. 2002).

3.3 Species composition of forest sites

ANOSIM and SIMPER analysis revealed significant differences in tree species composition between forest sites due to distinct stages of succession and different topography (Table 7). Tree species composition was shown to significantly affect the hydrology and fluxes of nutrients and thus contribute to spatial variability of TF fluxes (Schroth, da Silva et al. 1999). Especially in species-poor tree-based land use systems TF inputs differed significantly between *Bactris gasipaes* (peach palm fruit) and *Bertholletia excelsa* (Brazil nut) within a multistratum agroforestry system (Schroth, da Silva et al. 1999). For NTF, however, results investigated by Spearman matrix rank correlation are contradictory to this since species composition exerted no significant influence on nutrient deposition between primary and secondary forest stands and between ravine and ridge forests in this study. This may probably be the effect of high species diversity in the exceptional species rich tropical lowland rainforest (160 species on 0.36 hectare total surveyed site) that seems to overrule the impact of certain tree species in terms of nutrient deposition.

3.4.1 Effects of season

Especially in the tropics the influence of seasonal climate variations on deposition of nutrients resulting from differences in litterfall patterns and precipitation amounts can be attributed to distinct wet and dry seasons. Litterfall correlated negatively with rainfall, but correlations were not as significant as reported for other tropical forests (Drage 2007 unpublished data). Season also markedly affected throughfall fluxes, being higher for Cl, NO_3, SO_4, PO_4 and DOC during the dry season and for NH_4, Mg and Ca during the wet season. This was in part due to higher VWM concentrations of almost all solutes (except NH_4, Ca) during the dry season, probably due to higher aerosol load in air that is washed out during precipitation events, and due to higher rainfall volumes in the wet season for NH_4, Mg and Ca.

A multiple regression model to determine the relative importance of CE and DD on nutrient deposition in a Brazilian forest archipelago (Filoso et al. 1999) revealed a clear pattern of seasonality in controls of NTF. In the rainy season the contribution of CE to NTF was significant for all ions except Na, whilst DD significantly contributed to Cl only. During the dry season DD affected NTF of most ions (except Cl, PO3 and H), whereas CE showed to have an effect on all ions except Ca and NH_4. The variations in VWM concentration and deposition of solutes between wet and dry season were designated to the large seasonal variations in rainfall depth and biogenic emissions (Filoso, Williams et al. 1999).

3.4.2 Effects of topography and stage of succession

Topography is strongly correlated with (i) altitude and exposure to wind, precipitation and aerosols and (ii) with erosion and nutrient transfers from uphill to downslope. While the first factor affects microclimate and deposition velocity, the second effectively controls soil fertility across topographic gradients. Topography may therefore increase DD by exposure to aerosol laden air masses and CE by increasing soil fertility in down slope areas. We found clear evidence for increased DD to the ridge forest (PRi) where NTF of Na was significantly higher than at the ravine site (PRa). Moreover, factor 2 from PCA analysis of NTF which was comprised by sea salt ions (Na, Cl, Mg, SO_4) and NO_3 was significantly higher at the PRi site (compared to PRa) which was situated at a site of higher elevation and thus was most exposed to deposition of aerosols (Eklund, McDowell et al. 1997). The contribution of NO_3 to PCA factor 2 can be explained by greater deposition of aerosols from biogenic origin or from biomass burning to the higher elevation site. A significant effect of soil fertility and foliar nutrient concentration on NTF has been previously reported by Filoso et al (1999) and Tobon et al. (2004). Higher nutrient availability at the ravine site was supported by 12-fold higher soil water NO_3 and 5-fold higher soil water PO_4 concentrations in PRa compared to PRi. This actually translated into higher NTF of PO_4 at the PRa site, and showed up in significantly higher factor values for PCA factor 3, which was determined by PO_4 and NO_3. Greater NTF of PO_4 can be attributed to higher soil fertility and lower NUE mirroring less nutrient limitation of the ravine site. Also litter nitrogen content was highest in the primary ravine forest, the site which turned out to be the most nutrient rich with fastest nutrient cycling rates (Drage 2007 unpublished data). Topography therefore had a significant effect on NTF in the Esquinas forest. Similarly throughfall fluxes of K, P and Mg were found to be higher at lower elevation than at higher elevation sites in tropical forest sites in Mexico and Colombia, suggesting that lowland sites have a decreased tendency to cycle nutrients as efficiently as sites at higher elevations (Grubb 1977; Vitousek 1984; Vitousek & Sanford 1986). Thus low net throughfall fluxes of N and P may be associated with an economic use of these elements by trees and epiphytes, which would be in accordance with the conclusions of (Veneklaas 1990), suggesting limited availability and efficient use of N and P in tropical forests situated at higher altitudes (Clark, Nadkarni et al. 1998). Microclimate and soil fertility are also key determinants of vegetation composition and structure, which also differed significantly between PRa and PRi, however had no effect (tree species composition) or little effect (vegetation structure) on NTF differences between PRa and PRi sites. On the other hand, we found no significant differences in relative TF or SF volume between the three study sites. This is probably the result of the negligible influence of topography on hydrologic distribution and the greater impact of the local climatic characteristics deriving from the Golfo Dulce sea basin.

Disturbance and initiation of secondary forest succession has a strong impact on tree species composition, vegetation structure, and biomass and nutrient distribution. The large demand for nutrients to allow regrowth and biomass accrual of secondary forests commonly leads to an intermittent decrease in soil nutrient availability. Comparing primary ravine forest (PRa) and secondary ravine forest (SRa) nutrient depletion becomes clear since in soil water NO_3 and PO_4 concentrations were 36- and 1.7-fold lower in the secondary forest. Decreases in soil fertility at the SRa site also corresponded to significantly lower NTF of PO_4 and NO_3. However, identification of sources of nutrients in NTF conducted by a PCA and further ANOVA for differences between forest sites revealed that factor 1 accounting for solutes that derived mainly from canopy exchange processes (K, Mg, Ca, DON and DOC) showed highest values at the SRa site. This result was attributed to the characteristics of plant species in the secondary ravine forest in a relatively young stage of succession (Drage 2007 unpublished data). Forests in different stages of succession exhibit differences in nutrient incorporation rates because of different growth rates and life form strategies of characteristic species. Leaves of fast growing early successional species have a shorter leaf life time, are less sclerotic but are more nutrient rich; the present tree species at SRa are therefore more likely to leach readily soluble elements (Tukey 1970). Moreover, tree species composition and vegetation structure were significantly affected by successional stage but had little or no effect on NTF in secondary and primary ravine forests.

Conclusions

Based on a multiple regression model to estimate dry deposition, we showed that former estimates based on bulk precipitation only strongly underestimated the external inputs of nutrients to tropical rainforests. Further, we here demonstrated that dry deposition and canopy exchange control net throughfall fluxes (NTF), and factors affecting the amount and ratio of dry deposition and canopy exchange therefore directly affect NTF. Whereas NTF of K, Mg, Ca, DOC, DON and PO_4 derived from canopy leaching, Na, Cl, NH_4, NO_3 and SO_4 where taken up within the forest canopy. The tree species composition did not account for the differences found in NTF between forest sites, and vegetation structure had no (canopy closure, tree height) or little effect (LAI) on NTF. Topography significantly affected NTF via dry deposition to higher elevation sites and via soil fertility and canopy exchange at down slope sites. Secondary succession affected NTF through reduced soil fertility and changes in leaf composition and life time, decreasing the leaching of N and P but increasing the canopy exchange of highly leachable solutes.

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Figure 1: Study area, showing the tropical research station La Gamba (TRSLG) and the forest sites: secondary ravine (SRa), primary ravine (PRa) and primary ridge (PRi) forest in the Esquinas forest (Piedras Blancas National Park) in south-western Costa Rica.

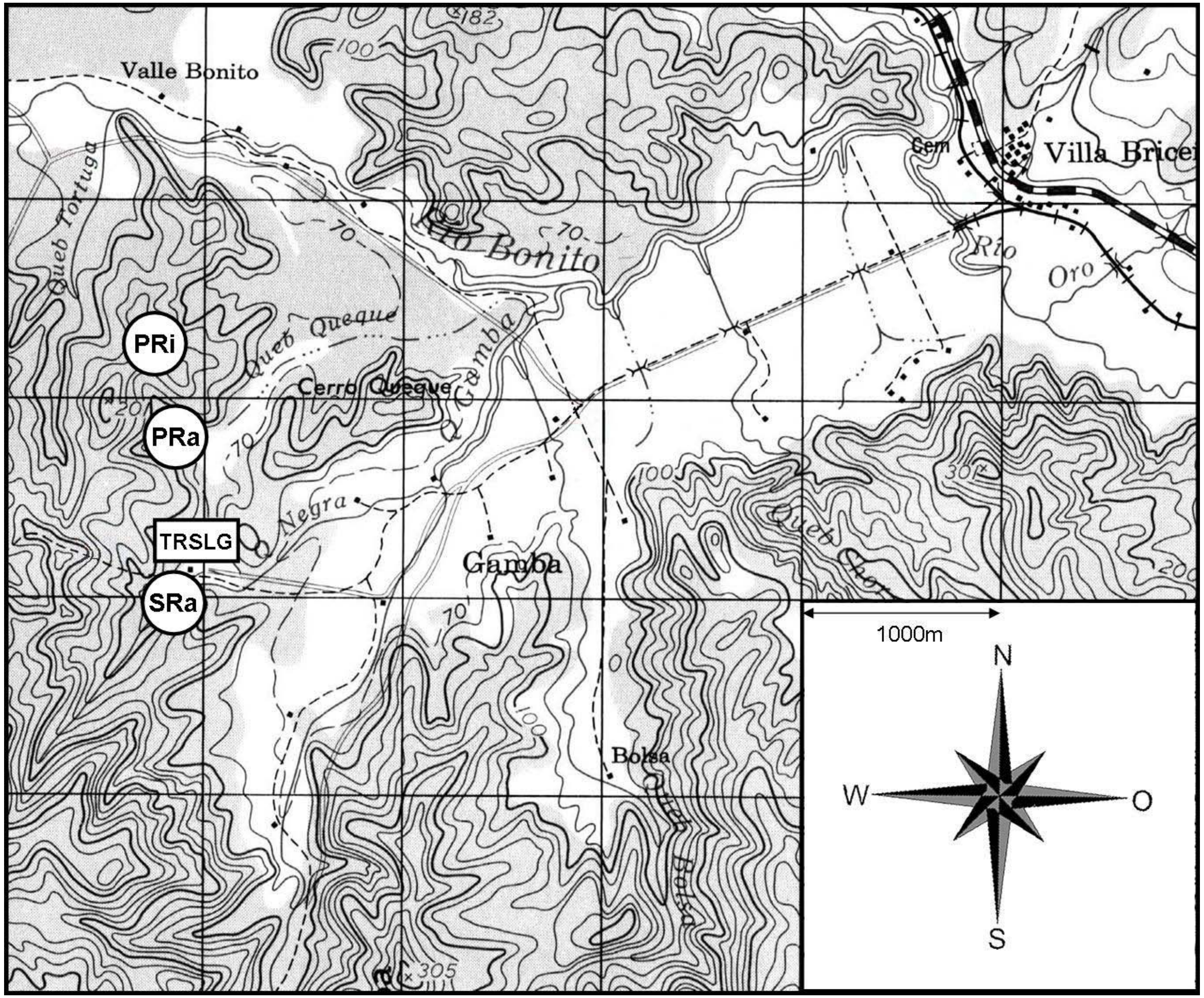


Figure 2: Climate diagram of La Gamba, Golfito, Costa Rica. Dark area represents monthly mean precipitation (MAP 5769mm). Hatched area represents monthly mean temperature (MAT 28.1°C).

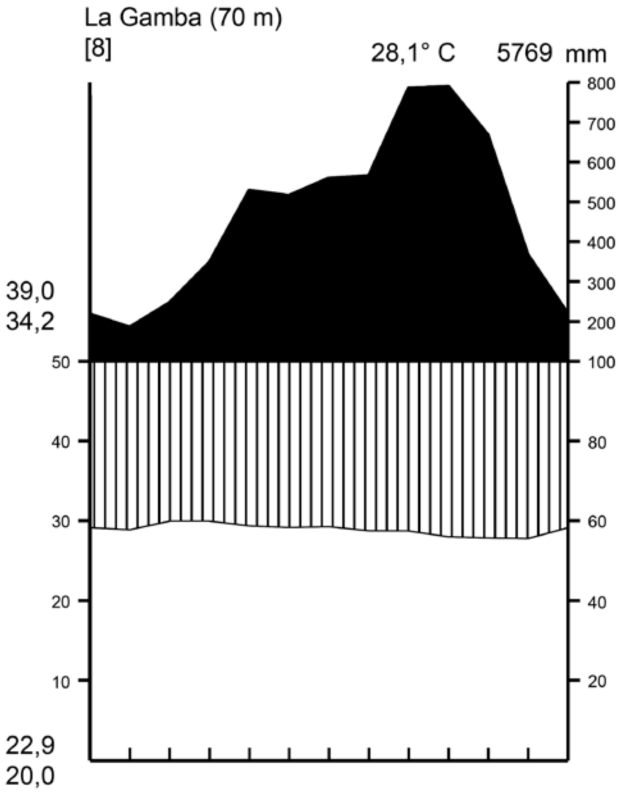


Table 1: Volume-weighted mean concentrations per sites of solutes in bulk precipitation (BP, n=3), throughfall (TF, n=15), stemflow (SF, n=12), litter percolate (LP, n=6) and soil water (SW, n=6). Data are means ± standard error and are given in µmol per litre for the respective forest sites, secondary ravine (SRa), primary ravine (PRa) and primary ridge (PRi) forest in the Esquinas forest (Piedras Blancas National Park) in south-western Costa Rica. DON concentration in SF at PRi was not detectable (n.d.). Results of One-way ANOVA (F(Df) and p-value) showing significant differences between the sample categories: BP, TF, SF, LP and SW are presented combined for all sites. Differences between sites are presented in the text.

Fraction	Site	H	Na	NH_4	K	Mg	Ca	Cl	NO_3	SO_4	PO_4	DOC	DON	TDN
BP (n=3)	TRSLG	25,2 ± 2,9	7,4 ± 0,6	6,9 ± 0,8	4,1 ± 0,8	3,2 ± 0,5	7,4 ± 0,9	4,2 ± 0,6	3,1 ± 0,3	2,5 ± 0,2	0,2 ± 0,1	51,9 ± 4,6	2,4 ± 1,4	12,4±2,5
TF (n=45)	SRa	7,8 ± 2,3	5,5 ± 0,4	7,8 ± 1,7	24,2 ± 3,0	5,6 ± 0,4	11,2 ± 0,7	7,5 ± 0,4	0,9 ± 0,1	2,9 ± 0,2	0,5 ± 0,1	129 ± 11,6	8,0 ± 1,1	16,7±2,4
	PRa	4,2 ± 1,7	5,7 ± 0,4	6,9 ± 0,7	37,9 ± 13,1	7,3 ± 1,1	12,1 ± 1,0	10,6 ± 1,9	1,4 ± 0,1	3,3 ± 0,3	1,0 ± 0,3	142 ± 33,4	8,6 ± 1,8	16,9±1,7
	PRi	8,1 ± 2,8	8,6 ± 1,1	4,8 ± 0,4	17,9 ± 2,1	5,3 ± 0,4	8,9 ± 0,5	10,2 ± 1,3	1,2 ± 0,1	3,8 ± 0,5	0,3 ± 0,1	106 ± 12,2	6,7 ± 1,3	12,8±1,3
SF (n=36)	SRa	31,2 ± 0,8	33,7 ± 8,0	70,4 ± 17,8	232 ± 72,6	69,4 ± 11,0	84,8 ± 14,5	77,1 ± 8,0	0,5 ± 0,2	5,9 ± 0,2	1,4 ± 0,8	2140 ± 252	15,9 ± 8,4	86,8±19,4
	PRa	20,5 ± 2,8	35,1 ± 4,6	42,9 ± 2,7	328 ± 118	33,6 ± 7,8	88,6 ± 17,4	89,0 ± 40,5	6,2 ± 4,6	7,6 ± 2,3	2,8 ± 0,9	1359 ± 347	65,4 ± 21,8	114,4±21,5
	PRi	155 ± 134	61,9 ± 18,4	42,2 ± 11,0	541 ± 146	103 ± 12,0	148 ± 58,9	1800 ± 680	235 ± 234	65,7 ± 31,6	2,1 ± 0,6	3367 ± 1196	n.d.	139,2±44,2
LP (n=6)	SRa	3,0 ± 0,6	6,7 ± 1,6	4,2 ± 1,1	67,7 ± 32,7	11,5 ± 2,4	26,6 ± 4,1	23,5 ± 11,3	0,4 ± 0,3	4,1 ± 1,4	0,2 ± 0,1	217 ± 57,2	4,8 ± 1,1	9,4±1,3
	PRa	2,3 ± 0,3	6,5 ± 3,1	7,4 ± 2,9	60,8 ± 13,6	13,3 ± 3,0	29,2 ± 11,9	18,3 ± 11,1	4,3 ± 1,7	2,4 ± 1,0	0,2 ± 0,0	109 ± 18,4	7,6 ± 1,2	19,3±5,6
	PRi	12,1 ± 9,0	9,9 ± 3,3	10,2 ± 1,9	38,6 ± 12,8	11,3 ± 1,2	24,7 ± 3,6	19,9 ± 12,3	1,0 ± 0,6	4,2 ± 0,6	0,8 ± 0,8	216 ± 81,8	7,3 ± 7,7	18,4±9,0
SW (n=6)	SRa	3,2 ± 0,9	23,7 ± 1,6	4,7 ± 0,4	40,8 ± 9,6	16,4 ± 2,9	27,4 ± 3,7	29,8 ± 6,9	0,6 ± 0,2	4,7 ± 1,9	0,3 ± 0,1	246 ± 76,9	8,2 ± 0,4	13,4±0,9
	PRa	3,5 ± 2,1	25,6 ± 9,2	3,6 ± 0,4	39,1 ± 10,6	20,5 ± 4,7	34,8 ± 6,0	25,0 ± 7,5	21,7 ± 13,6	6,1 ± 2,6	0,5 ± 0,3	137 ± 50,2	10,5 ± 3,7	35,8±10,7
	PRi	3,5 ± 1,0	21,5 ± 5,0	10,1 ± 3,2	28,5 ± 2,6	15,4 ± 0,9	21,6 ± 2,1	35,0 ± 9,9	1,8 ± 0,5	6,2 ± 2,7	0,1 ± 0,0	162 ± 33,2	1,9 ± 5,6	13,8±2,9
ANOVA	F (38)	16,1	28,7	31,7	45,0	59,0	63,8	18,1	0,9	6,1	10,1	53,6	9,7	30,0
	p-value	**<0,001**	**<0,001**	**<0,001**	**<0,001**	**<0,001**	**<0,001**	**<0,001**	0,36	**<0,001**	**<0,001**	**<0,001**	**<0,001**	**<0,001**

Table 2: Annual solute fluxes in bulk precipitation (BP), throughfall (TF) and stemflow (SF) values are means ± standard error given in kg per ha and year. Results of One-way ANOVA (F(Df) and p-value) showing significant differences in annual TF & SF fluxes between forest sites are presented for secondary ravine (SRa), primary ravine (PRa) and primary ridge (PRi) forest in the Esquinas forest (Piedras Blancas National Park) in south-western Costa Rica. Different letters indicate significant differences between sites.

Site	H	Na	NH_4	K	Mg	Ca	Cl	NO_3	SO_4	PO_4	DOC	DON	TDN
Bulk precipitation	1,4 ± 0,1	10,0 ± 1,4	5,6 ± 0,4	9,3 ± 2,5	4,5 ± 0,5	17,3 ± 1,3	8,6 ± 1,3	2,5 ± 0,2	4,7 ± 0,4	0,4 ± 0,1	36,1 ± 3,1	1,9 ± 0,3	10,0 ± 0,7
Throughfall													
SRa	0,5 ± 0,1	4,8 ± 0,5 **a**	4,1 ± 1,0	35,7 ± 4,9	5,1 ± 0,3	16,7 ± 1,0	9,2 ± 0,5	0,4 ± 0,0 **a**	3,2 ± 0,2	0,5 ± 0,1 **a**	49,8 ± 4,4	3,0 ± 0,4	7,5 ± 1,1
PRa	0,3 ± 0,1	5,1 ± 0,5 **a**	3,8 ± 0,5	49,9 ± 14,0	6,7 ± 0,8	18,6 ± 1,6	12,2 ± 1,6	0,7 ± 0,1 **b**	3,6 ± 0,3	1,1 ± 0,3 **b**	54,1 ± 10,8	3,9 ± 0,9	7,9 ± 0,7
PRi	0,6 ± 0,2	7,9 ± 1,3 **b**	2,6 ± 0,3	26,4 ± 3,2	5,0 ± 0,4	14,4 ± 1,7	13,1 ± 2,1	0,6 ± 0,0 **b**	4,1 ± 0,3	0,3 ± 0,1 **a**	42,6 ± 5,5	2,7 ± 0,8	6,0 ± 0,7
Stemflow													
SRa	<0,01 ± 0,00	0,07 ± 0,01	0,11 ± 0,02	1,16 ± 0,17	0,17 ± 0,07	0,29 ± 0,08	0,29 ± 0,05 **a**	<0,01 ± 0,00	0,03 ± 0,01 **a**	<0,01 ± 0,00	2,33 ± 0,65	0,03 ± 0,02	0,14 ± 0,01
PRa	<0,01 ± 0,00	0,08 ± 0,02	0,05 ± 0,01	1,13 ± 0,15	0,08 ± 0,01	0,42 ± 0,17	0,29 ± 0,08 **a**	0,01 ± 0,00	0,03 ± 0,00 **a**	0,01 ± 0,00	1,77 ± 0,29	0,11 ± 0,03	0,17 ± 0,05
PRi	0,01 ± 0,01	0,20 ± 0,11	0,08 ± 0,03	1,55 ± 0,60	0,30 ± 0,15	0,48 ± 0,15	11,20 ± 7,46 **b**	0,03 ± 0,03	0,13 ± 0,06 **b**	<0,01 ± 0,00	4,58 ± 2,01	0,12 ± 0,11	0,23 ± 0,12
ANOVA (TF)													
F (41)	1,80	4,73	1,83	2,69	1,74	2,49	1,65	5,79	2,40	7,32	0,67	2,12	2,06
P	0,18	**0,01**	0,17	0,08	0,19	0,10	0,21	**0,01**	0,11	**0,002**	0,52	0,13	0,14
ANOVA (SF)													
F (28)	1,46	1,33	0,37	2,88	2,38	1,25	6,67	1,88	3,97	1,72	3,14	1,66	1,12
p	0,25	0,28	0,69	0,07	0,11	0,30	**0,004**	0,17	**0,03**	0,20	0,06	0,21	0,34

Figure 3: Net-Fluxes of solutes in throughfall (NTF) secondary ravine (SRa, black bars), primary ravine (PRa, white bars) and primary ridge (PRi, grey bars) forest sites, respectively. Values represent means ± standard errors of NTF in kg per square meter and year (n=15 collectors per site).

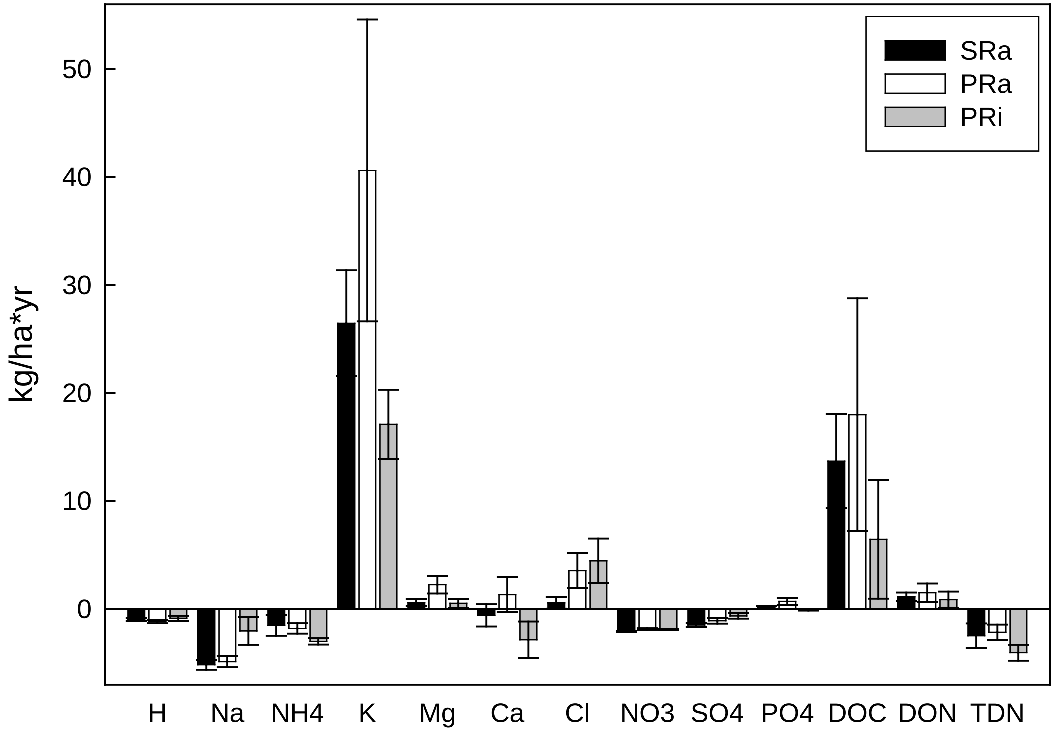


Figure 4: Contribution of canopy exchange (CE, black bars) & dry deposition (DD, white bars) to annual net throughfall flux in the Esquinas rainforest, Costa Rica. Data were analysed combined for the three forest sites. Bars indicate means ± standard errors in kg per ha and year (n=30 precipitation events) and were calculated based on the multiple regression model by Lovett et al (1984).

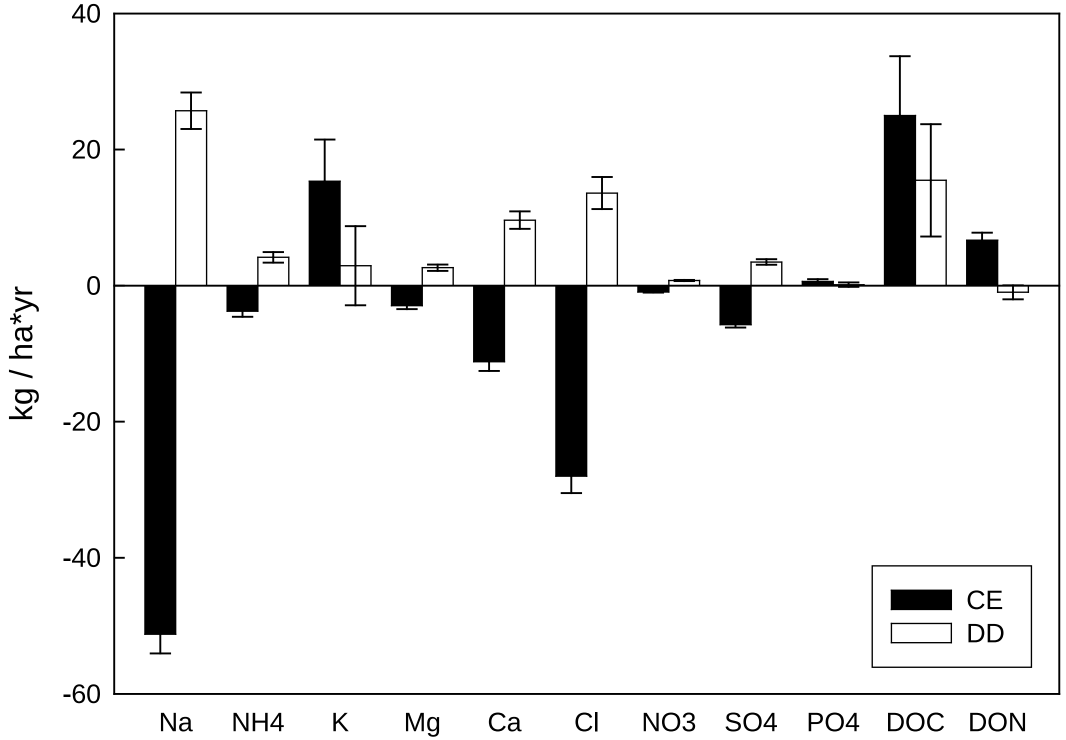


Table 3: Results of the multiple regression model (Lovett et al. 1984) of event NTF against rain volume and number of antecedent dry days for canopy exchange (CE) constant (UNIT) and dry deposition (DD) constant (UNIT). Adjusted R square and p-values from multiple regression are given.

Variables	H	Na	NH_4	K	Mg	Ca	Cl	NO_3	SO_4	PO_4	DOC	DON
CE	-6,31 ± 2,05	-38,14 ± 2,11	-4,59 ± 1,01	6,72 ± 2,69	-2,08 ± 0,35	-4,78 ± 0,58	-13,51 ± 1,20	-1,14 ± 0,11	-3,06 ± 0,24	0,34 ± 0,19	35,66 ± 12,45	8,18 ± 1,32
DD		1398 ± 146	371 ± 70	93,8 ± 186	136 ± 24	300 ± 40,2	479 ± 83	67,7 ± 7,5	135 ± 16,3	5,67 ± 12,9	1612 ± 860	-87,3 ± 91,4
R^2 adj.	0,05	0,47	0,09	0,01	0,12	0,20	0,25	0,28	0,33	0,01	0,03	0,08
p-value	**<0,01**	**<0,01**	**<0,01**	**<0,05**	**<0,01**	**<0,01**	**<0,01**	**<0,01**	**<0,01**	0,12	**<0,01**	**<0,01**

Figure 5: Throughfall (TF) and stemflow (SF) volumes in forests of secondary ravine (SRa, black bars), primary ravine (PRa, white bars) and primary ridge (PRi, grey bars) sites in the Esquinas forest (Piedras Blancas National Park) in south-western Costa Rica. Mean ± SE of TF & SF volumes are given in percent of BP (30 rain events during survey period 23.02.2005-22.02.2006; 5840.5mm; 80 days without rain). Bars give means and error bars show standard errors of the mean.

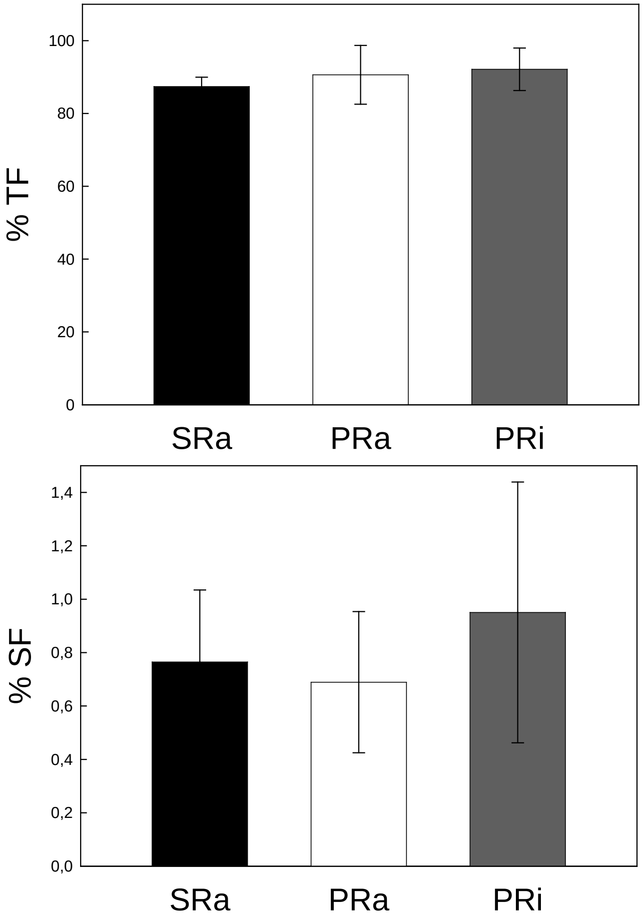


Table 4: Principal component analysis of annual NTF solutes from single throughfall collectors. Loadings on factors, eigenvalues and percent variances of variables from net throughfall (NTF) of simple collector annual fluxes within sampled precipitation events (n=30).

Variables	Factor 1	Factor 2	Factor 3	Factor 4
H	-0,03	-0,01	-0,11	**-0,81**
Na	0,05	**0,81**	0,03	-0,26
NH_4	0,09	0,08	**0,88**	-0,10
K	**0,55**	0,26	-0,01	**0,64**
Mg	**0,58**	**0,56**	0,00	0,38
Ca	**0,67**	0,45	0,18	0,05
Cl	0,38	**0,66**	-0,11	0,39
NO_3	-0,33	**0,59**	0,47	0,06
SO_4	0,22	**0,74**	0,04	0,24
PO_4	0,11	-0,05	**0,74**	0,47
DOC	**0,86**	0,22	-0,08	0,20
DON	**0,79**	-0,13	0,12	-0,01
Eigenvalues	4,46	1,75	1,56	1,06
% Variance explained	37,19	14,58	12,99	8,79

Figure 6: One-way ANOVA of PCA factor values as presented in table 4, showing significant differences between sites of secondary ravine (SRa), primary ravine (PRa) and primary ridge (PRi) forest in the Esquinas forest (Piedras Blancas National Park) in south-western Costa Rica, respectively.

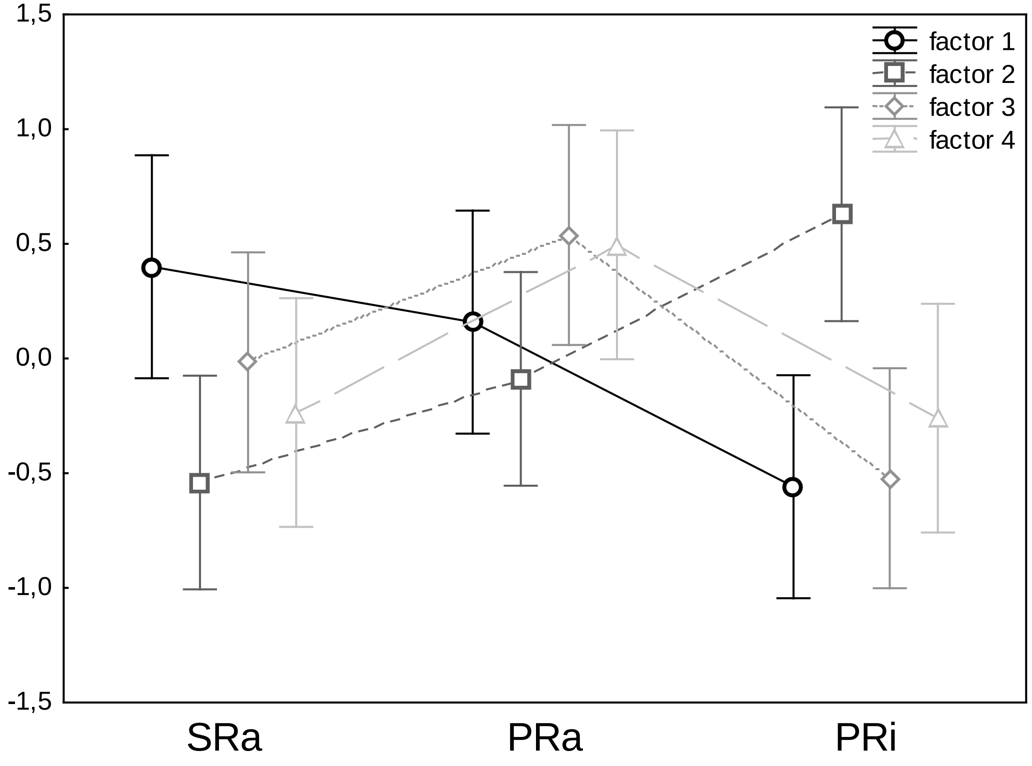


Table 5: Vegetation characteristics of secondary ravine (SRa), primary ravine (PRa) and primary ridge (PRi) forest in the Esquinas forest (Piedras Blancas National Park) in south-western Costa Rica. Total species and total individual numbers of tree species below and above 10 cm in diameter at breast height (dbh) are presented. Fisher's alpha index is given as an indicator of species diversity. Means and coefficient of variation (CV%) are given for parameters of vegetation structure: height of trees; leaf area index (LAI) determined by Sundata & Hemiview of respective forest sites.

	Trees 2,5-10cm dbh (0.03ha)			Trees >10cm dbh (0.12ha)			Treeheight (>10cm dbh)		LAI Sundata		LAI Hemiview	
Site	Total species	Total individuals	Fisher's alpha	Total species	Total individuals	Fisher's alpha	Mean	CV%	Mean	CV%	Mean	CV%
SRa	29	65	20	15	31	11	21,51	41,03	6,94	16,71	2,80	20,76
PRa	18	28	22	21	29	34	17,40	43,24	8,33	23,37	3,18	25,31
PRi	52	167	26	25	29	86	16,60	38,81	7,13	18,16	2,94	9,00

Table 6: Spearman-Matrix-Rank Correlation relating canopy cover above throughfall collectors and ionic composition (NTF). Rho values indicate strength of correlation; p-values give significance of correlation.

Variables	Rho	p-value
H	-0,04	0,79
Na	0,11	0,45
NH_4	0,10	0,51
K	-0,19	0,22
Mg	0,05	0,76
Ca	-0,20	0,18
Cl	-0,24	0,12
NO_3	-0,15	0,32
SO_4	-0,12	0,43
PO_4	-0,17	0,27
DOC	-0,19	0,22
DON	-0,21	0,17
TDN	-0,16	0,30

Table 7: Analysis of similarity percentages (SIMPER) testing for similarity and dissimilarity of tree species above and below 10cm in diameter at breast height (dbh) between respective forest sites: secondary ravine (SRa), primary ravine (PRa) and primary ridge (PRi). Values presented are average similarity (Av.Sim), average dissimilarity (Av.Diss), percent of contribution (Contrib%) and cumulative percent (Cum%) to total diversity of tree species at the respective forest site.

Trees 2,5-10cm dbh			
Similarity			
Species	Av.Sim	Contrib%	Cum.%
Group SRa	26,7		
Psychotria elata		56,5	56,5
Guatteria chiriquiensis		10,7	67,2
Tetrathylacium macrophyllum		9,3	76,5
Group PRa	9,2		
Lozania pittieri		51,5	51,5
Siparuna andina		48,5	100,0
Group PRi	34,2		
Vochysia ferruginea		33,1	33,1
Croton cf schiedeanus		25,6	58,6
Mabea cf occidenta		11,0	69,6

Trees >10cm dbh			
Similarity			
Species	Av.Sim	Contrib%	Cum.%
Group SRa	11,5		
Vochysia ferruginea		86,3	86,3
Guarea grandifolia		5,3	91,6
Group PRa	5,2		
Cecropia obtusifolia		39,0	39,0
Iriartea deltoidea		35,4	74,4
Trichospermum grewiifolium		15,7	90,1
Group PRi	2,7		
Qualea paraensis		40,7	40,7
Marila laxiflora		23,2	63,9
Protium ravenii		18,1	81,9

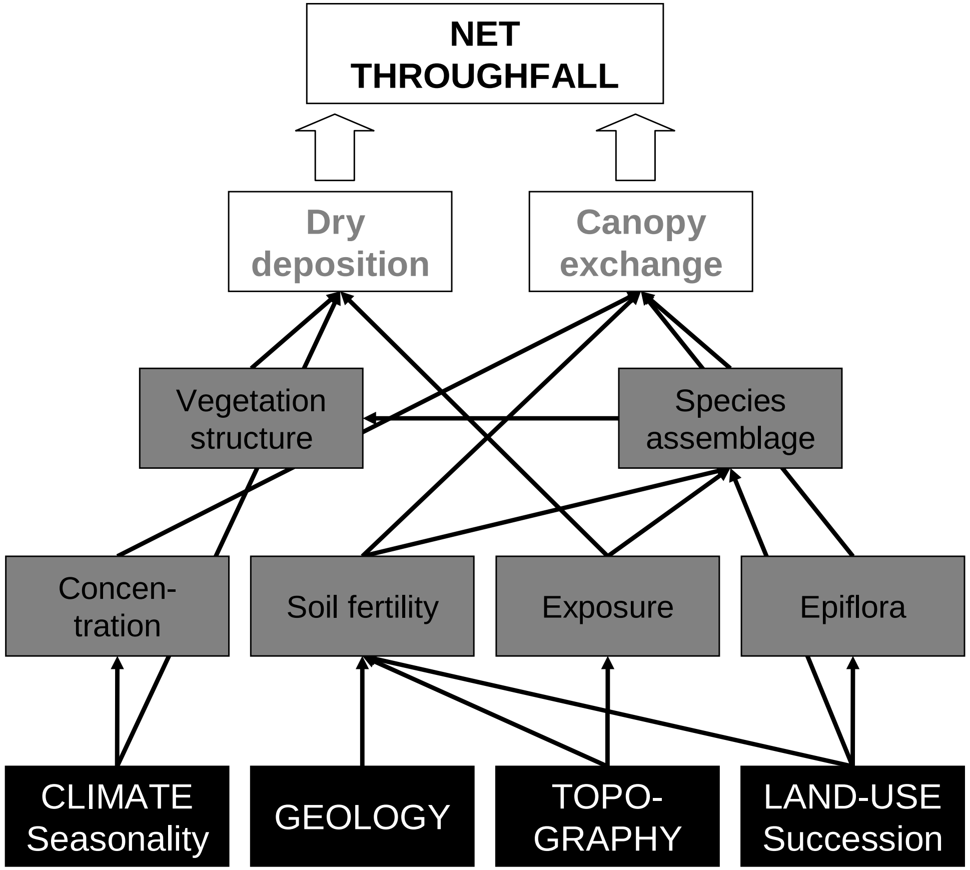
Dissimilarity			
Species	Av.Diss	Contrib%	Cum.%
Groups SRa & PRa	98,3		
Psychotria elata		12,7	12,7
Tetrathylacium macrophyllum		4,3	17,1
Siparuna andina		4,2	21,2
Groups SRa & PRi	92,1		
Vochysia ferruginea		10,2	10,2
Croton cf schiedeanus		6,9	17,1
Psychotria elata		5,8	22,8
Groups SRa & PRi	100		
Vochysia ferruginea		13,0	13,0
Croton cf schiedeanus		7,7	20,7
Mabea cf occidenta		3,8	24,5

Dissimilarity			
Species	Av.Diss	Contrib%	Cum.%
Groups SRa & PRa	96,7		
Vochysia ferruginea		16,4	16,4
Cecropia obtusifolia		8,0	24,3
Iriartea deltoidea		5,9	30,2
Groups SRa & PRi	97,9		
Vochysia ferruginea		14,6	14,6
Qualea paraensis		5,3	19,9
Guatteria amplifolia		4,9	24,8
Groups SRa & PRi	99,5		
Cecropia obtusifolia		5,4	5,4
Iriartea deltoidea		4,9	10,3
Qualea paraensis		4,7	15,0

Tables 8: Spearman-matrix-rank correlation of ionic composition (NTF) and species assemblages of sites. Rho values indicate strength of correlation; p-values give significance of correlation.

Variables	Rho	p-value
H	-0,029	0,667
Na	0,059	0,182
NH_4	0,008	0,458
K	-0,028	0,659
Mg	0,003	0,481
Ca	0,073	0,104
Cl	-0,028	0,670
NO_3	0,032	0,292
SO_4	0,014	0,394
PO_4	-0,006	0,513
DOC	0,034	0,296
DON	0,032	0,300
TDN	0,01	0,397

Figure 7: Conceptional model of factors controlling net throughfall flux via canopy exchange and dry deposition. Secondary controls (grey boxes) are altered by the primary controls (dark boxes) situated at the lower end which together impact nutrient composition in NTF via DD and CE (white boxes).



Zusammenfassung

Tropische Regenwälder könnten eine große Rolle in der globalen Kohlenstoffbilanz spielen, da sie als eine der größten terrestrischen C-Senken angesehen werden. Anhand vieler Studien wird deshalb versucht den Beitrag und die Verteilung von Nährstoffflüssen in Ökosystemen zu quantifizieren. Wüsste man erst einmal über momentane Umsatzraten bescheid, könnte man vorhersehen wie sich Veränderungen der Nährstoffzusammensetzung in Zukunft auf ein Ökosystem auswirken. Derzeit besteht die Möglichkeit dass sich der Status der tropischen Regenwälder als C-Senken aufgrund von anthropogenen Eingriffen (Abholzung von Regenwäldern, Landwirtschaft und vermehrter Düngereintrag) insofern umkehren könnte, als dass sie letztendlich zu C-Quellen werden könnten.

Im Zuge dieser Diplomarbeit in einem tropischen Tieflandregenwald in Costa Rica wurde in mehreren Arbeitsgruppen versucht die Dynamik und Stoffflüsse des außerordentlich diversen Ökosystems zu quantifizieren. Die Datenerhebung umfasste zahlreiche Aufnahmen: Angefangen von der Ausweisung der vorgesehenen Untersuchungsflächen, Messung des pflanzlichen Biomasse-Zuwachs mittels Dendrometerbändern, Besammlung von Laubstreu und Charakterisierung des C/N-Verhältnisses, über die Bestimmung der Flussmengen von Kronentrauf, Stammabfluss und des Bodenwassergehalts, bis hin zu Untersuchungen der Nährstoff-turnover Prozesse anhand von pool-dilution Experimenten mittels stabiler Isotope.

Es wurden insbesondere die Stoffflüsse und Quellen der häufigsten Nährstoffe, in Form von DOC, DON und der An- und Kationen Cl^-, NO_3^-, SO_4^{2-}, PO_4^{3-} und Na^+, K^+, NH_4^+, Mg^{2+} und Ca^{2+} untersucht und deren Herkunft und Verteilung in einem tropischen Waldökosystem beschrieben. Dazu wurden Proben von Laubstreu, Regenwasser, Kronentrauf, Stammabfluss und Bodenwasser zur Beantwortung der Fragestellungen betreffend der Dekomposition, nutrient use efficiency (NUE) und turnover Prozesse des Ökosystems Regenwald entnommen und in konservierter Form zur Analyse an das Department überstellt. Die darauf folgende Laborarbeit bezog sich vor allem auf die Quantifizierung des gesammelten Probenmaterials durch Analyse von Bodenextrakten, Blattmaterial, Groblitter und Wasserproben. Für die Bestimmung und Auswertung der Stoffflüsse der Hydrologie wurden Analysen mittels HPLC-Ionenchromatographie, Massenspektrometrie, Photometrie und TOC/TN Analysen verwendet.

Basierend auf einem vorliegenden Modell, zur Quantifizierung der Einflüsse von Niederschlagsmenge und Trockendeposition wurde ein neuer Gesichtspunkt erarbeitet, welcher ergab dass bisherige Studien den Einfluss von Trockendeposition auf den Gesamtnährstoffeintrag massiv unterschätzten obwohl generell Nährstoffflüsse aus Austauschprozessen des Kronendaches überwiegen.

Das Ziel dieser Studie war es die Hauptfaktoren welche den Nährstoffeintrag durch Nährstoffflüsse im Netto-Kronentrauf beeinflussen zu beschreiben.

Zusätzlich habe ich selbständig ein Modell zur Untersuchung der Zusammenhänge zwischen Stoffflüssen und Diversität der erhobenen Pflanzen-Arten entworfen, um der Frage nachzugehen inwiefern die jeweiligen Arten den Nährstoffeintrag in Kronentrauf und Stammabfluss beeinflussen und steuern können. So wurden zum Beispiel die eingetragenen Mengen an Nährstoffen mit dem Blattflächenindex des jeweiligen Standortes und auch den dort vorkommenden Baumarten verschnitten und zwischen den Standorten untereinander verglichen.

Die Verarbeitung der erhobenen Datensätze erfolgte mittels der statistischen Methoden ANOVA, PCA und Multiple Regression in den Programmen Statgraphics und Statistika. Die Erfassung des Einflusses der Arten-Community auf die Nährstoffzusammensetzung wurde mittels dem Programm PRIMER und den Algorithmen ANOSIM, SIMPER und Spearman-Matrix Rang Korrelation bewerkstelligt.

Die Studie ergab im Wesentlichen, dass der Eintrag von Nährstoffen durch Freilandniederschlag, Kronentrauf und Stammabfluss im Zeitraum von einem Jahr extremen Schwankungen unterliegt, welche auf mehrere Faktoren zurückzuführen waren. Hauptsächlich bestimmten die Faktoren: Saisonalität, Topographie, Geologie, Sukzession etc. die Nährstoffverfügbarkeit auf den unterschiedlichen Standorten. Es konnten auch gemeinsame Quellen betreffend der Herkunft von Nährstoffen ausgewiesen werden. So wurden Na, Cl, Mg und SO4 etwa hauptsächlich durch Verdunstungsprozesse an der Meeresoberfläche eingebracht während Stoffflüsse von NO3 und PO4 der besseren Versorgung von Nährstoffen auf unterschiedlich situierten Standorten zugewiesen werden konnten. Obwohl Unterschiede im Diversitäts- und Blattflächenindex zwischen verschiedenen Sukzessionsstadien nachgewiesen werden konnten, war es nicht möglich die Zusammensetzung der Baumarten der einzelnen Standorte mit den Nährstoffflüssen zu korrelieren. Dies mag daran liegen das der ausgesprochene Artenreichtum von über 200 Baumarten in der Region des Esquinas Nationalparks, die unterliegenden Differenzierungen betreffend der Zusammensetzung und Verteilung von Nährstoffen in diesem tropischen Ökosystem überschattet.

Tropische Regenwälder gehören zu den diversesten Ökosystemen der Erde und daher wird es weiterhin eine Herausforderung bleiben darin Stoffflüsse zu messen, zu quantifizieren und zu beschreiben. Diese Studie bietet einen weiteren Einblick in die Funktionen und Mechanismen von Nährstoffflüssen, welche in Zukunft hinsichtlich der Kohlenstoff-Bilanz, besonders in Zeiten globaler Erwärmung, von erhöhter Bedeutung sein könnten.

Curriculum Vitae

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Laborarbeiten, statistische Auswertung und Fertigstellung der Diplomarbeit am Department für Chemische Ökologie und Ökosystemforschung.

Auswertung der Ergebnisse der Studie: „Banderillas: Effects of deforestation on dragonflies (Insecta, Odonata) in the Pacific lowland of Costa Rica“.

Februar 2005 – WS 2007:

Übernahme der Diplomarbeit mit dem Arbeitstitel: „Nährstoffkreisläufe und Rezyklierung in einem tropischen Tiefland-Regenwald (Piedras Blancas, Costa Rica)“.

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SS 2004 – SS 2008:

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Inskription Diplomstudium Biologie, Universität Wien.

Abschluss des 1. Abschnitt im Diplomstudium Biologie (Studienkennzahl A-437).

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Erarbeitung einer Studie hinsichtlich der Auswirkungen der Landnutzungsänderung auf die Libellengemeinschaften des Nationalparks „Piedras Blancas, Costa Rica“ mit dem Titel: „Banderillas: Effects of deforestation on dragonflies (Insecta, Odonata) in the Pacific lowland of Costa Rica“. Daraus resultierte eine Publikation im Werk: „National history of the Golfo Dulce region“. (Hrsg.: Biologiezentrum des oberösterreichischen Landesmuseums, Linz). Erscheinung voraussichtlich August 2008.

WS 2006:
Tutorium des Praktikums: Schlüsseltechniken der Ökologie: Stable Isotope Tracing
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Tutorium des Projektpraktikums: Kohlenstoffkreislauf alpiner Ökosysteme (A. Richter, W. Wanek).

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Absolvierung diverser Praktika am Department: Chemische Ökologie und Ökosystemforschung (Leitung: M. Popp):
Projektpraktikum: Kohlenstoffkreislauf alpiner Ökosysteme (A. Richter, W. Wanek).
Stressanpassung höherer Pflanzen (A. Richter, W. Wanek).
Rhizosphäre: Biodiversität, Stoffwechsel und Interaktionen im Wurzelraum (G. Bachmann, P. Zolda).
Planung und Auswertung multifaktorieller Experimente in der Ökologie (G. Bachmann).
Spezielle chemische Physiologie der Pflanzen I & II (R. Albert, M. Popp, A. Richter).

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Interessen:

März 2007:

Ausbildung zum Ultra-light Piloten für UL-Geräte: „Gyrocopter“ während einer mehrwöchigen Ausbildung in Jerez, Spanien.

Seit 1994:

Sänger in der vierköpfigen Band: „Tomorrow She“. Mehrmals pro Jahr Live-Auftritte und Produktion von 4 CD-Alben während mehrerer Studio-Aufnahmen.

Seit 1992:

Mitglied im Kajak-Verein „Wildalpen“. Jährliche Befahrungen der „Salza“ in Wildalpen, Steiermark.