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# DISSERTATION

Titel der Dissertation

## **Primary production & nutrient cycling in tropical rainforests**

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## WALDEN; OR LIVE IN THE WOODS

*"I went to the woods because I wished to live deliberately, to front only the essential facts of life, and see if I could not learn what it had to teach, and not, when I came to die, discover that I had not lived. I did not wish to live what was not life, living is so dear; nor did I wish to practice resignation, unless it was quite necessary. I wanted to live deep and suck out all the marrow of life, to live so sturdily and Spartan-like as to put to rout all that was not life, to cut a broad swath and shave close, to drive life into a corner, and reduce it to its lowest terms, and, if it proved to be mean, why then to get the whole and genuine meanness of it, and publish its meanness to the world; or if it were sublime, to know it by experience, and be able to give a true account of it in my next excursion."*

HENRY DAVID THOREAU





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## ZUSAMMENFASSUNG

Tropische Regenwälder nehmen eine Schlüsselposition im globalen Kohlenstoff- und Wasserkreislauf ein, da sie 37% des globalen terrestrischen Kohlenstoff-Pools darstellen, ein Drittel der terrestrischen Nettoprimärproduktion ausmachen und mehr als die Hälfte der weltweit vorkommenden Pflanzen- und Tierarten beinhalten. Der Verlust tropischer Waldökosysteme hat daher einen immensen Einfluss auf die globale Biodiversität und das Weltklima.

Darüberhinaus bestimmt der Anteil des in tropischer Baumbiomasse gebundenen Kohlenstoffs die Menge des in der Atmosphäre verbleibenden klimaaktiven Treibhausgases Kohlendioxid und hat daher eine bedeutende Funktion als globale Kohlenstoff-Senke. Trotzdem ist bis dato nicht gänzlich geklärt wie sich die zugrundeliegenden biogeochemischen Prozesse, welche auf die zukünftige Entwicklung tropischer Ökosysteme und deren Funktion als global bedeutender Kohlenstoffspeicher wirken, im Zuge des globalen Wandels entwickeln werden.

In der vorliegenden Doktorarbeit beleuchten wir daher die biogeochemische Funktion tropischer Regenwälder, indem wir die zugrundeliegenden Mechanismen der Kohlenstoff-Alloka-

tion (**Kapitel 1**), sowie des Nährstoffkreislaufs tropischer Waldökosysteme in hydrochemischen Flüssen von Kronentrauf (**Kapitel 2**) und Stammabfluss (**Kapitel 3**) quantifizieren und abschließend die Bedeutung dieser wichtigen Ökosystemprozesse hinsichtlich der Sensibilität tropischer Biomasseproduktion und damit verbundener Kohlenstoffspeicherung in Bezug auf zu erwartende zukünftige Klimaschwankungen diskutieren (**Kapitel 4**).

Die Ergebnisse dieser Studie liefern einen neuartigen Ansatz die Zusammenhänge verschiedener Umweltkontrollen darzustellen, welche die Biomasseproduktion und damit den Kohlenstoffspeicher tropischer Waldökosysteme kontrollieren. Wir zeigen, dass lokale Parameter, wie Wasserverfügbarkeit und Boden-Nährstoffgehalt die biogeochemische Funktion tropischer Waldstandorte drastisch beeinflussen. Daher könnten bereits kleinräumige standortspezifische Unterschiede in topographischer Lage und bodenbedingte Eigenschaften, sowie Sukzession und lokale Artenzusammensetzung die Reaktion tropischer Waldökosysteme auf globale Klimaveränderungen bestimmen.



## SUMMARY

Knowledge of mechanisms controlling primary production and nutrient cycling in tropical rainforests is of major importance due to the crucial role of tropical forests in the coupling of global climate and terrestrial ecosystem processes. Tropical forests are key components of global carbon, water and energy cycles containing 37% of the global terrestrial carbon pool, accounting for one third of terrestrial net primary production of organic material and comprising more than half of the world's plant and animal species. Loss of tropical rainforests therefore has severe impacts on global biodiversity, net primary production and climate.

The proportion of atmospheric carbon dioxide allocated to wood production is an important determinant of the carbon sink strength of tropical forest ecosystems. However, our understanding of the biogeochemical functioning of tropical rainforests, and how they will respond to global drivers such as climate change and increased human pressures, is highly fragmentary.

In this thesis, we therefore explore the biogeochemical functioning of tropical ecosystem processes by identifying the mechanisms dri-

ving carbon allocation in tropical rainforests (**Chapter 1**), as well as investigating hydrological pathways and associated nutrient fluxes in bulk precipitation, throughfall (**Chapter 2**) and stemflow (**Chapter 3**) and finally discuss the impact of these important ecosystem processes that potentially determine the sensitivity of tropical forest aboveground productivity to climate anomalies (**Chapter 4**).

Our study provides a mechanistic understanding on tropical ecosystem processes and proposes a novel framework to disentangle interrelated pathways among environmental drivers controlling the cycling of carbon and nutrients in tropical forest ecosystems. Our results suggest that local characteristics of tropical forest sites potentially determine the biogeochemical functioning of these ecosystems. Therefore, it is likely that site-specific differences in topographic position and edaphic properties, as well as disturbance history and local tree species composition of respective forest sites could determine the response of tropical forest ecosystems to projected global changes.



## THESIS OUTLINE

In this thesis, following a general introduction, we explore the biogeochemical functioning of tropical forest ecosystems. We identify the mechanisms driving carbon allocation in tropical rainforests (Chapter 1), investigate hydrological pathways and associated nutrient fluxes via bulk precipitation, throughfall (Chapter 2) and stemflow (Chapter 3) and eventually consider the significance of local topo-edaphic factors that potentially determine the sensitivity of tropical net primary production to climate anomalies (Chapter 4). We eventually synthesize our findings by giving an outlook on future trends of tropical ecosystem functioning in times of global change.

**Chapter 1** presents *“New insights into mechanisms driving carbon allocation in tropical rainforests”*, recently published in *New Phytologist* (Hofhansl et al., 2014). Based on the available literature we compiled a global data set comprising more than 100 tropical forest sites to examine large-scale and long-term controls of tropical net primary production. The proportion of carbon (C) allocated to wood production is an important determinant of the C sink strength of forest ecosystems. Therefore understanding the mechanisms controlling wood production and its responses to environmental drivers is essential to accurately predict future responses of tropical forest ecosystems in terms of carbon sequestration. We found that wood and canopy production did not respond uniformly to environmental drivers, resulting in increased relative wood production with increasing mean annual temperature and soil phosphorous availability. Our results furthermore highlight that tropical montane and tropical lowland forests will likely respond differently to projected global changes as wood production increased with the amount of precipitation in high productive lowland forests, but with the length of the dry season in low productive montane forests. We conclude that tropical C sequestration will not

respond uniformly to global changes in tropical forests growing on different substrates and at different elevations. Our study provides a novel framework to disentangle interrelated pathways among environmental drivers controlling the C sink strength of tropical forest ecosystems.

**Chapter 2** describes modeling the contributions of dry deposition and canopy exchange to nutrient inputs via bulk precipitation and throughfall in a study entitled *“Topography strongly affects atmospheric deposition and canopy exchange processes in different types of wet lowland rainforest, Southwest Costa Rica”*, published in *Biogeochemistry* (Hofhansl et al., 2011). In this study we highlighted that estimates based on bulk precipitation underestimated total atmospheric deposition to tropical rainforests by up to 10-fold by ignoring the contributions of dry deposition. Canopy exchange contributed most of the aboveground inputs to the forest soil of  $\text{Na}^+$ , about half of  $\text{K}^+$ , 10% of P and  $\text{Mg}^{2+}$  and negligible for N, C and other elements. Tree species composition did not account for the differences found in net throughfall between forest sites, and vegetation structure (plant area index) had only a small effect on net throughfall. However, disturbance history affected net throughfall through reduced soil fertility and differences in leaf traits on secondary forest sites. Eventually we found that topography most significantly affected net throughfall via increased dry deposition at sites of higher elevation and via soil fertility and thus increased canopy exchange at down slope sites.

**Chapter 3** investigates the *“Controls of hydro-chemical fluxes via stemflow in tropical lowland rainforests: effects of meteorology and vegetation characteristics”*, published in *Journal of Hydrology* (Hofhansl et al., 2012). In this study we measured stemflow hydrology and biogeochemistry in two primary forests in ridge and ravine position, as well as a secondary forest located in south-western Costa Rica. Besides major

nutrient inputs via litterfall and throughfall we found that, in terms of nutrient cycling, stemflow constitutes an important pathway for the localized input of highly enriched solutes to the forest floor. In general, stemflow hydrochemistry was mainly controlled by meteorology (precipitation magnitude and duration), ecosystem characteristics (topography and plant area index) and species-specific traits (stem diameter and tree height). Stemflow was highly enriched in nutrients compared to bulk precipitation and most solutes (especially DOC and  $K^+$ ) were leached, while inorganic nitrogen and phosphorus (i.e.  $NO_3^-$  and  $PO_4^{3-}$ ) were retained along the stemflow pathway. We elaborated a multiple regression model dissecting the contributions of canopy exchange and dry deposition processes and found that canopy exchange rather than dry deposition dominated the accumulation of nutrients in net stemflow. We finally calculated that stemflow comprised 1–10% of dissolved internal recycling of nutrients, but together with throughfall made up to 50% of total aboveground nutrient returns (including litterfall), demonstrating that total dissolved returns of nutrients represent a pivotal portion of the internal nutrient cycle of tropical rainforests.

Chapter 4 evaluates the “Sensitivity of tropical forest aboveground productivity to climate anomalies”, submitted to *Global Biogeochemical Cycles* (Hofhansl et al., 2014) by determining the response of tropical lowland forest sites to a recent El Niño Southern Oscillation (ENSO) anomaly at forest sites differing in topographic position and disturbance history located in south-western Costa Rica. During seven consecutive years of monthly-recorded data on tropical forest aboveground net primary production (ANPP) in this study, we found that a recent ENSO transition (2009–2011) reduced ANPP by -20% in response to increased drought (-780 mm MAP) and maximum temperatures (+3°C

MATmax) during the El Niño drought period. However, subsequently ANPP recovered by +24% due to a lagged growth response after the La Niña wet period, such that drought-induced reductions were overcompensated. Interestingly, this growth response was largely due to variations in woody biomass production rather than leaf production. Our results indicate that wood production rather than canopy production accounts for drought-induced reductions of tropical forest ANPP in response to interannual climate anomalies and thus highlight the importance of wood production in terms of the C sequestration potential of tropical forest ecosystems. Most strikingly, we found a pattern indicating the importance of local site characteristics in determining the responses of tropical forest aboveground productivity to large-scale climate anomalies, as growth reductions were most prominent at the exposed primary ridge forest site (PRi; -35%) but less intense at the primary ravine forest site (PRa; -26%) and the downslope secondary re-growth forest site (SRa; -26%). This site-specific climate sensitivity was due to topographic differences in soil type and soil depth and thus water availability as was indicated by differences in soil bulk density and soil moisture between the respective study sites. It is therefore plausible that during the El Niño dry-period increased maximum temperatures and decreased precipitation inputs triggered drought stress of trees at the more exposed ridge forest and secondary regrowth forest site but did not significantly affect wood production at the moist ravine forest site. Our results indicate that site-specific characteristics, such as local topographic position and edaphic properties as well as disturbance history and local species composition of nearby tropical lowland forest sites, determine the response of tropical forest aboveground productivity to climate anomalies.







## GENERAL INTRODUCTION

Tropical rainforests are key components of global carbon, water and energy cycles, containing about 40% of the global terrestrial carbon pool (Dixon et al., 1994), accounting for one third of terrestrial net primary production of organic material (Field, 1998) and comprising more than half of the world's plant and animal species (Myers et al., 2000). Moreover, tropical rainforests serve important ecosystem functions such as water recharge and erosion control, as well as timber and food production. Loss of tropical rainforests therefore has major impacts on global biodiversity, net primary production and climate. However, our mechanistic understanding of the biogeochemical functioning and knowledge on future responses of tropical rainforests to global climate change and increased human pressures is highly fragmentary (Sala et al., 2000; Clark et al., 2001b; Wright, 2001; Malhi & Phillips, 2004).

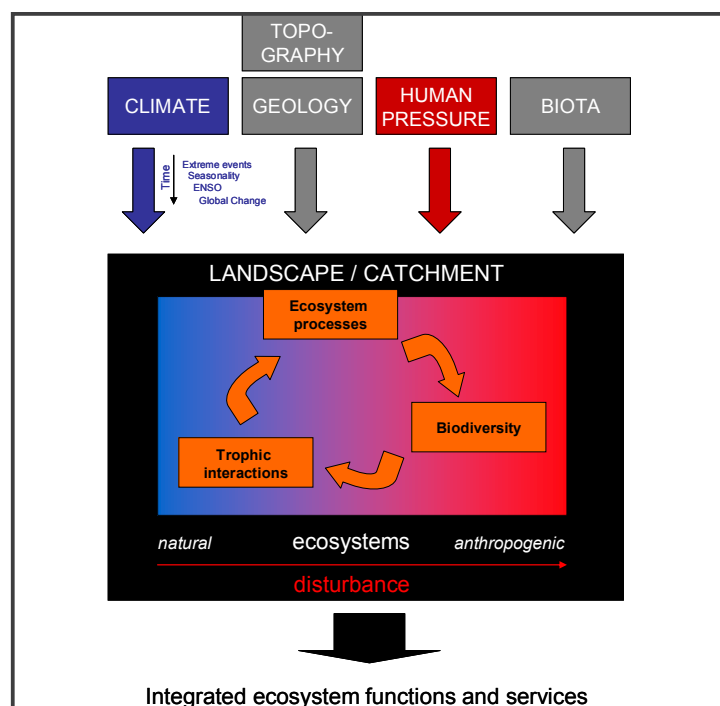
In general, (1) climate, (2) edaphic factors (soil fertility, topography) and (3) disturbance history represent the key factors determining species richness, forest biomass and net primary production in tropical forest ecosystems (Fig. 1).

Net primary production (NPP) is defined as the biochemical construction of new organic material over a specified time interval, or gross primary production (GPP) less autotrophic respiration ( $R_{\text{aut}}$ ). Thus NPP of an ecosystem controls net ecosystem production by sequestering atmospheric  $\text{CO}_2$  and supplies organic material for heterotrophic respiration ( $R_{\text{het}}$ ; Fig. 2).

To measure NPP, the production of new organic matter over a specified time interval is quantified. Net increases in wood of stems and branches, fine and coarse litterfall, and net root increment generally comprise more than 80% of NPP and are therefore most often studied (Clark et al., 2001a). Due to the difficulty in estimation of belowground NPP (BNPP), aboveground NPP (ANPP) is most frequently studied and quantified as the sum of stand increment and litterfall rates, although other loss processes such as herbivory (Metcalf et al., 2014) and the volatilization of organic molecules also factor in NPP estimates (Clark et al., 2001a), thus resulting in underestimation of ANPP due to structural losses (Chambers et al., 2001).

Litterfall and wood increment comprise

FIGURE 1:  
DRIVERS OF  
BIODIVERSITY  
AND  
ECOSYSTEM  
PROCESSES  
IN TROPICAL  
ECOSYSTEMS.  
(SOURCE:  
[HTTP://WWW.  
UNIVIE.AC.AT/  
BDEF](http://www.univie.ac.at/BDEF)).



about 90% of ANPP in tropical forests (Aragao et al., 2009), with average contributions of  $53 \pm 14\%$  for wood increment and  $47 \pm 8\%$  for litterfall (Malhi et al., 2011). These contributions vary between sites but the environmental determinants of this variability are largely unknown (Malhi et al., 2011). Recent studies proposed that there exists no simple relationship between aboveground tree growth and fine-litter production (Shoo & VanDerWal, 2008). The lack of a simple relationship between the two components was therefore suggested to likely result from underlying mechanistic processes.

In this regard, phenotypic or interspecific traits such as growth form or allocation of biomass to foliage and wood in response to selective pressures such as climatic conditions, soil types (Brown & Lugo, 1982; Herbert & Fownes, 1999; Harrington et al., 2001; Paoli et al., 2005) or a combination of both (Kitayama & Aiba, 2002) could determine the pattern of biomass allocation in tropical trees.

The allocation of biomass to canopy vs. wood material has important implications for tropical biogeochemistry since short-lived canopy components and long-lived wood exhibit distinct differences in nutrient content, decomposition and turnover rate. Hence, in biogeochemical terms wood production represents an important component of ecosystem C sequestration, whereas canopy production and subsequent fine litterfall represent an important nutrient recycling process (Vitousek, 1984). However, leaf and wood production show asynchronous seasonal patterns since leaf production peaks at the beginning of the dry season and wood production during the onset of the rainy season (Wagner et al., 2013). Moreover, trees invest more in biomass production in the cooler season with lower solar radiation and more in maintenance during the warmer high radiation period (Girardin et al., 2013). As a result, the allocation of biomass between long-lived wood and comparatively short-lived leaves and fine roots could represent an important feature determining the C sink-strength of tropical forests (Doughty et al., 2014).

#### LARGE-SCALE DETERMINANTS AFFECTING THE C SINK STRENGTH OF TROPICAL FORESTS

The C sink strength of tropical forests is controlled by several factors whereof soil fertility,

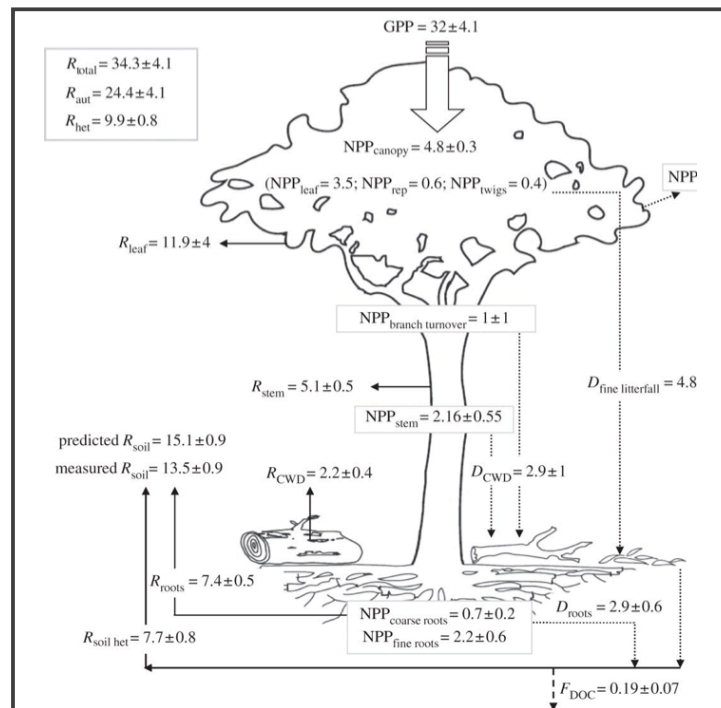


FIGURE 2: PATHWAYS AND FLUXES OF CARBON IN COMPONENTS OF TROPICAL PRIMARY PRODUCTION. (SOURCE: MALHI ET AL., 2011).

air temperature and precipitation are the most prominent ones (Vitousek, 1984; Schuur, 2003; Cleveland et al., 2011). There has been considerable controversy about the effects of increasing  $\text{CO}_2$  and climate change on the productivity and C cycling in tropical forests (Körner, 2004). Whereas short-term effects of increased temperature and decreased precipitation resulted in increased mortality of tropical trees (Phillips et al., 2009), Amazonian long-term forest inventory plots reported increasing trends in tree recruitment, coupled with increasing tree biomass over the past 50 years (Phillips, 1998). Over the past century atmospheric  $\text{CO}_2$  concentrations have doubled and mean annual temperatures have shown a strong warming trend (Hulme et al., 2001; Malhi & Wright, 2004). Over the next century, mean annual temperature is predicted to increase  $1\text{--}5^\circ\text{C}$  in tropical regions (Cramer et al., 2004; Solomon, 2007). Concomitant changes in precipitation that lead to increased drought (or soil saturation) could likely have a significant impact on fundamental tropical ecosystem functions as processes like litterfall, decomposition and nutrient uptake are synchronized with

the seasonal variation of rainfall between dry and wet season in tropical forest ecosystems. Both drought and excess water availability impair the mineral nutrition of trees by influencing, on the one hand the nutrient availability in the soil, and on the other hand the physiology of the uptake systems, mainly of the mycorrhizal tree roots. Extreme water regimes also change interaction patterns among plants and between plants and microorganisms, and alter the C balance of trees and ecosystems (Kreuzwieser & Gessler, 2010). Therefore, projected changes in the frequency and severity of climate anomalies will likely feed back on the amount and distribution of C stored in tropical forests via alterations of decomposition and mineralization processes and the partitioning of NPP to aboveground and belowground components (Goldammer, & Seibert 1990).

#### PRIMARY PRODUCTION & CLIMATE CHANGE IN TROPICAL FORESTS

What determines the seasonal and interannual variation of tropical NPP has become a hotly debated subject in studies investigating tropical ecosystem processes (Rowland et al., 2013; Huasco et al., 2013; Doughty et al., 2014). So far, it remains unknown whether direct effects of climate on tropical NPP or rather inherent phenological rhythms in growth allocation dominate the growth response of tropical forest ecosystems to climatic signals. In this regard, it has been suggested that changing tree growth rates could reflect shifts in NPP partitioning between wood and canopy (or wood and fine root) components rather than changes in overall productivity (Doughty et al., 2014) due to a substantial decoupling between irradiance driven leaf renewal and water driven wood production (Wagner et al., 2013). Furthermore, it has been shown that climate-induced NPP variation was largely due to a response in wood production

rather than litterfall (Vasconcelos et al., 2012). Whereas short-lived components (leaf, twig and reproductive litterfall) were not significantly related to interannual climate variation, the production of long-lived tissues (wood production) was negatively affected by water limitation and higher temperatures (Clark et al., 2013). As a result, projected increases in maximum temperatures and concomitant decreases in precipitation could trigger drought-induced reductions in wood production and thus negatively affect the C sequestration potential of tropical forest ecosystems.

To better understand future responses of tropical C sequestration, several approaches have been followed, including ecosystem manipulation studies, observational studies of the effects of inter-annual climate fluctuations and large transect studies. Nonetheless, the number of plot-scale ecosystem manipulation experiments in tropical forests is limited to a few throughfall exclusion (Nepstad, 2002; Brando et al., 2008; Moser et al., 2014), litter manipulation (Wood et al., 2009; Townsend et al., 2011) and nutrient addition experiments (Giardina et al., 2003; Kaspari et al., 2008; Homeier et al., 2012; Fisher et al., 2013), while CO<sub>2</sub> or warming manipulations have yet to be undertaken. Therefore, latitudinal or elevational gradients in climate have been used as a proxy for future climate change effects on long-term responses of tropical forest ecosystem processes. Although these approaches offer valuable insights into future impacts on tropical forests, such extrapolations often confound interacting effects of fundamental mechanisms underlying ecosystem responses and feedbacks to climatic and anthropogenic changes (see: Zuidema et al., 2013; Zhou et al., 2013). In order to disentangle the effects of interrelated environmental controls on tropical forest C sequestration long-term and high-resolution records on climate and primary production are essential

(Clark et al., 2013; Zuidema et al., 2013; Zhou et al., 2013). Evaluation of simple climate metrics, such as mean annual temperature (MAT) and precipitation (MAP), is likely to be insufficient to capture the effects of seasonal and interannual climate variations, which are expected to be strongly affected by future climate change (Cleveland 2011). For instance, periodic climate fluctuations such as those triggered by El Niño Southern Oscillation (ENSO) can be used to investigate the effects of climatic excursions on tropical forest productivity. In Central America the ENSO transition is associated with two phases; the warm and dry El Niño phase characterized by less annual precipitation and higher annual temperatures (Clark et al., 2003; Phillips et al., 2009; Clark et al., 2010), opposite to the cold and wet La Niña phase (McPhaden et al., 2006). Therefore, the observation of tropical ecosystem processes such as litterfall and wood increment observed during an ENSO transition provides reliable information on the response of tropical ecosystem processes to anomalous climate extremes and can therefore serve as useful proxy for potential future climate change scenarios.

Recent studies have addressed this issue by investigating which factors control seasonal and interannual changes in tropical tree growth (Gliniars et al., 2013; Rowland et al., 2014; Mendivelso et al., 2014). In general, precipitation and solar radiation were the main seasonal drivers of tropical tree growth (Wagner et al., 2014), while maximum temperatures (Gliniars et al., 2013) and increasing drought periods reduced tree growth (Mendivelso et al., 2014). Furthermore, Rowland et al. (2014) demonstrated significant differences between tree functional properties and the degree of seasonality of tree growth, consistent with a hypothesized trade-off between maximum potential growth rate and hydraulic safety of tropical trees. Therefore fast-growing, low wood density, tall and broad

stemmed trees experienced greater reductions in dry season increment than slower-growing trees with higher wood density, indicating that the functional composition of tropical forests is an important determinant of annual patterns of biomass accumulation (Rowland et al., 2014). On the one hand, this suggests that long-term changes in climate variables might trigger shifts in species composition in favor of slow-growing, drought-tolerant species in conjunction with an increase in forest biomass (Fauset et al., 2012). On the other hand, more frequent short-term disturbances such as those linked to ENSO events typically increase the mortality of large trees (Phillips et al., 2010) and thus may trigger a decrease in stand-level biomass. Hence, projected increases in short-term climate anomalies could possibly counteract the long-term effects of increasing biomass due to shifts in species composition, and thus negatively affect the C sequestration potential of tropical forests.

Despite the fact that temperature was reported the most important predictor of tropical forest productivity (Raich et al., 2006), this relationship was recently found to be driven by distinct temperature differences between low productive montane and high productive lowland forests, such that within tropical lowland forests soil-based measures of phosphorus explained a significant proportion of variation in aboveground NPP (Cleveland et al., 2011). In addition, limitations of soil water and nutrient availability are lower in highly productive lowland forests stocking on soils rich in nutrients and moisture and thus decreasing the relative investment into belowground NPP components. As a result, these forests were found to allocate a greater proportion of NPP into aboveground structures, mainly wood production (McMurtrie & Dewar, 2013). Accordingly, the biomass production efficiency, i.e. the fraction of C allocated to wood production, increased three-fold with increa-



sing nutrient availability, whereas foliage and root production remained unchanged (Vicca et al., 2012). This suggests that in more productive forests with high nutrient and water availability and higher annual temperature a greater proportion of NPP is allocated to wood production, therefore increasing aboveground C storage. Hence, this underlines the importance of local topo-edaphic factors, which affect soil water and nutrient availability and in turn determine the amount of C stored in aboveground tree biomass and thus the C sink strength of tropical forests.

### NUTRIENT CYCLING & CLIMATE CHANGE IN TROPICAL FORESTS

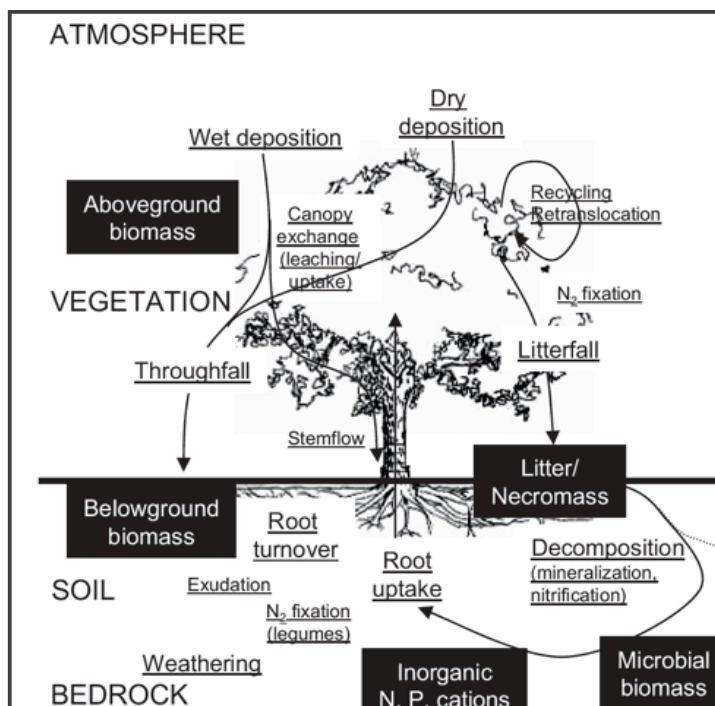
Nutrient cycling - the cycling of elements in ecosystems - describes fluxes of nutrients between pools in soils, plants, animals and decomposer microorganisms (Fig. 3).

In tropical forests, in contrast to most other ecosystems, the greatest amount of organic matter and nutrients is stored in living biomass rather than the soil matrix (Whitmore, 1998). However, up to 30% of the overall carbon flux

may be transferred into the belowground rooting zone from trees to mycorrhizal symbionts (Vicca et al., 2012). Moreover, this carbon transfer is inversely related to nutrient availability, such that mycorrhizal abundance declines in response to nitrogen and phosphorous availability (Högberg et al., 2003; Treseder, 2004). Hence, forests with high nutrient availability do not need to invest photosynthates into the root system to gather limiting resources and were reported to produce aboveground biomass more efficiently (Vicca et al., 2012). This suggests that the nutrient status of a tropical rainforest affects the relative investment into belowground biomass, which in turn determines the amount of photosynthates (mostly carbon) available for investment into aboveground biomass (mainly tree growth) and thus the C sink strength of tropical forest ecosystems.

Over the long term, the nutrient status of a tropical rainforest is controlled by the balance between processes governing nutrient inputs (dry and wet deposition, weathering and nitrogen fixation) and nutrient outputs (soil leaching and volatilization). While processes such as nu-

FIGURE 3:  
POOLS AND  
FLUXES OF  
CARBON AND  
NUTRIENTS  
IN TROPICAL  
RAINFORESTS.  
(SOURCE: W-  
NEK ET AL.,  
2008).



trient uptake and release by plants and microorganisms are mostly governed by the same factors, inputs and losses occur along different pathways. The consequences are differences in the “openness” and “buffering capacity” of the main cycles of carbon, water, nitrogen and phosphorus (Chapin et al., 2011). While the carbon cycle is highly open and well buffered through the exchange of CO<sub>2</sub> with the atmosphere, the water cycle lacks notable storage capacity and thus organisms strongly depend on water inputs from precipitation.

In tropical rainforests, nutrient

cycles are relatively more closed than in other terrestrial ecosystems, and characterized by intensive internal cycling compared to relatively low inputs and losses (McDowell, 1998). Nitrogen is especially limited as bedrock is virtually N free and N is therefore introduced into soils and ecosystems by biological N fixation. Therefore, developing ecosystems are rather N limited but relatively rich in P and other rock-derived elements (Harrington et al., 2001). However, with soil age weathering and leaching processes result in cation and P depletion, while N accumulates in soils and vegetation, leading to P limitation of the productivity of old tropical forest ecosystems (Herbert & Fownes, 1995; Vitousek & Farrington, 1997). In addition, in highly weathered tropical soils P is often occluded in secondary minerals and highly resistant organic compounds, which further contributes to P limitation of tropical primary productivity. However, atmospheric deposition of  $K^+$ ,  $Na^+$ , N,  $Cl^-$  and  $SO_4^{2-}$  in dust, aerosols and precipitation represents a major source of elements sustaining primary production in forests that stock on highly nutrient depleted tropical soils (Chadwick et al., 1999). Moreover, erosion and tectonic uplift can counteract the depletion of primary minerals in geologic active tropical regions (Porder et al., 2006). Hence, to maintain forest biomass and production at high levels, the nutrient demands and ecosystem losses must be met by internal recycling through nutrient release from decomposing fine litter, dead wood and roots, as well as from weathering and smaller inputs by wet and dry deposition and nitrogen fixation.

Whereas aboveground biomass represents the biggest portion of ecosystem C stocks, the

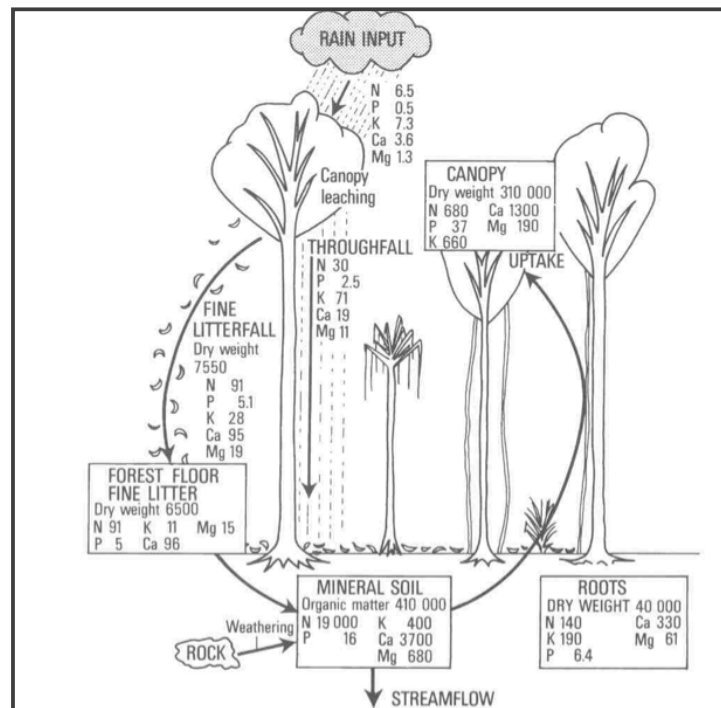


FIGURE 4:  
PATHWAYS  
OF NUTRI-  
ENT CYCLING  
IN TROPICAL  
RAINFORESTS.  
(SOURCE: JOR-  
DAN, 1985).

major sources of nutrients for internal nutrient cycling include litterfall and litter decomposition processes as well as the input of canopy leachates via throughfall and stemflow. Litterfall provides the central source for nutrient cycling of N, P and  $Ca^{2+}$  (Martius & Bandeira, 1998) and throughfall and stemflow contribute significantly to nutrient cycles of  $K^+$  and  $Mg^{2+}$  (Chuyong et al., 2003; Tobon et al., 2004) in tropical rainforests (Fig. 4).

Litterfall and subsequent litter decomposition are key processes in terrestrial nutrient cycling producing nutrients in available forms for plant and microbial production via the breakdown of organic matter. The rate of decomposition is determined by litter quality and the physical environment (Austin & Vitousek, 2000). In general, more nutrient rich "high quality" litter decomposes more rapidly than "low quality" litter that is low in nutrients. Therefore forest sites with low decomposition rates have to cycle nutrients more efficiently and thus high stand level nutrient use efficiency often points to nutrient limitation (Santiago & Mulkey, 2005). Nutrient limitation affects forest productivity in multi-



le ways, e.g. by reducing leaf area index (LAI), photosynthetic capacity, or both (Harrington et al., 2001). High NPP in tropical rainforests therefore indicates that the nutrient use by tropical forests is enhanced by several nutrient conserving mechanisms, increasing the retention of nutrients in the living or dead biomass pool (e.g. higher fraction of nutrient re-translocation, increased life span of leaves, fine roots and mycorrhizal association). Therefore, vegetation and soil microbes play a key role in retaining and recycling essential nutrients through production and decomposition of plant biomass. In turn, factors affecting rates of production and decomposition can feedback on nutrient cycling both directly through mineralization of organically bound nutrients, and indirectly through changes in nutrient retention and storage associated with plant biomass and soil organic matter (McGroddy & Silver, 2011).

For instance, climate change impacts on litter production may result from shifts in the timing and amount of rainfall since litterfall and nutrient uptake are synchronized to seasonal patterns of precipitation (McGroddy & Silver, 2011). It has been shown that seasonality of litterfall was negatively correlated to mean annual precipitation (Santiago & Mulkey, 2005) and positively to the seasonality of rainfall (Chave et al., 2010). Hence, alterations in the amount and timing of rainfall may significantly affect nutrient cycling via litter production, as leaf litter nutrient concentrations are related to rainfall seasonality in moist and dry tropical forests (Read & Lawrence, 2003; Wood et al., 2005). Unlike for N, leaf litter P concentrations are positively correlated with antecedent rainfall, and cations are mainly leached from live leaf tissue (Wood et al., 2005). The latter process further highlights the importance of nutrient inputs derived from canopy leaching and atmospheric deposition, which are transported via hydrological pathways by throughfall and

stemflow to the forest floor. However, as climate change likely leads to alterations in patterns of precipitation, shifts in the length of intermittent dry season may lead to temporal separation of plant demands and nutrient availability (Silver, 1998). Although it has been shown that plant species can respond flexibly to changing nutrient availabilities by increasing nutrient re-translocation from senescent plant tissues (Herbert & Fownes, 1999; Harrington et al., 2001), over the long-term a shift to significantly wetter or drier environments could trigger shifts in species composition with associated changes in both litter quality and quantity (Condit, 1998; Santiago et al., 2005), in turn affecting decomposition and nutrient cycling. As a result, nutrient cycling in tropical forests is likely to be sensitive to global changes, due to alterations in the amount and distribution of precipitation affecting plant litter dynamics, and decomposition processes via shifts in tree species composition.

#### **LOCAL-SCALE & SPECIES-SPECIFIC DETERMINANTS AFFECTING THE C SINK STRENGTH OF TROPICAL FORESTS**

Besides the large-scale determinants of tropical forest productivity discussed in the previous sections, local topo-edaphic factors affecting soil water and nutrient availability will likely determine the sensitivity of tropical tree species to climatic and anthropogenic changes. For instance, topographic variation in water availability coupled with differential drought sensitivity of tropical tree species was found to shape species distribution in tropical forests (Engelbrecht et al., 2007). In accordance, Comita et al. (2009) found that differential patterns of seedling mortality among species contribute to species topographic habitat associations and thus contribute to niche differentiation in tropical forest communities. Therefore, changes in water availability due to more frequent severe drought periods

may significantly affect population dynamics with potential long-term consequences for species abundance and distribution (Condit, 1998; Condit et al., 2004; Condit et al., 2013). Furthermore, such drought-induced shifts in species composition were found in association with alterations in aboveground tree biomass (Fauset et al., 2012) and thus could affect aboveground C storage in tropical forests.

It has been shown that the drought sensitivity of tropical tree growth differed among Neotropical tree species, such that diverse growth responses among coexisting tree species were related to species-specific responses of wood formation to water availability (Mendivelso et al., 2014). Therefore, more sensitive species require more water and more efficient water transport for growth than less sensitive species and thus drought sensitivity is related to different life-history strategies of drought-tolerant versus fast-growing opportunistic species that determine water use and storage (Markesteijn et al., 2011). Consistently, the sensitivity of tropical tree growth to climate variations was found to be associated to functional trade-offs between early and late-successional species in Amazonian lowland rainforests (Rowland et al., 2014). In general, early successional tree species with low wood density rather invest into rapid growth to prevent shading, whereas late-successional climax species tend to be shade-tolerant but slow growing to reduce mortality risks (Rowland et al., 2014). As a result, short-term drought anomalies could have the potential to kill trees selectively since fast-growing, light-wooded trees might be especially vulnerable to drought by cavitation or carbon starvation (Condit et al., 1996; McDowell et al., 2008). In accordance, Phillips et al. (2009) found that Amazonian tree species dying during a recent El Niño drought period had lower wood densities than those dying before. Therefore, species with denser

wood were less vulnerable to drought and thus could become dominant after longer periods of water deficit (Phillips et al., 2010).

A recent study modeling the effects of non-random species loss on aboveground carbon storage found that the extinction of fast-growing species with the lowest wood density increased C storage by 10%, whereas the loss of high statured drought-tolerant species resulted in a strong decline in C stocks by over 30% (Bunker, 2005). In accordance, during the 2009 El Niño drought period occurring throughout the Amazon the biomass carbon sink was reversed due to increased tree mortality (Phillips et al., 2009). However, during recent decades forests aboveground biomass increased significantly by 0.6 Mg carbon per hectare and year among 59 plots monitored in old-growth Amazon (Phillips, 1998; Baker et al., 2004a). In fact, besides tree growth and stem recruitment also tree mortality and turnover rates have increased substantially (Lewis et al., 2004), suggesting an increase in the frequency of tree-fall gap formations (Phillips & Gentry, 1994). This would indicate an advantage of light-demanding species with higher growth rates at the expense of slow growing shade-tolerant species (Körner, 2004) in association with a community wide decrease in carbon content (West et al., 1999) and thus C storage. A resulting Amazon-wide decrease in mean wood specific gravity of just below 0.5% would cancel out the C sink effect apparently caused by accelerated plant productivity (Phillips et al., 2011).

Nonetheless, it was reported that there exist two groups of forest sites across the Amazon: the more dynamic and faster growing sites in the western Amazon, and less dynamic and slower growing sites in the eastern and central Amazon (Lewis et al., 2004). These results are generally consistent with the 'positive feedback hypothesis' (Quesada et al., 2009), which contrasts rich soils with high turnover that support

fast-growing species with smaller maximum sizes and lower wood density, vs. less fertile soils with lower turnover that support the accumulation of many, larger trees with high wood density (Baraloto et al., 2011). According to the assumptions, soil physical and chemical conditions trigger positive feedback mechanisms that maintain the large-scale patterns of slow growth and long residence times in the eastern and central areas of the Amazon Basin, as well as a dominance of fast-growing, light-demanding species in the western and southern parts (Quesada et al., 2012). In the eastern forests low disturbance leads to shade environments and together with limited nutrient supply favors tree species with a slow growth strategy, thus increasing wood density and carbon residence times. In the western forests greater nutrient availability favors fast-growing tree species with a lower investment into woody structures, thus reducing mean tree life times, increasing turnover rates and disturbance frequencies (Quesada et al., 2012). Overall, this indicates that soil physical conditions and associated soil nutrient availability potentially determine forest disturbance levels and tree turnover rates, and thereby directly influence stand level wood density and carbon storage in tropical forest ecosystems.

#### **TROPICAL DEFORESTATION, SECONDARY RE-GROWTH & LAND-USE CHANGE IN TROPICAL FORESTS**

Tropical deforestation and land use change have a significant impact on the global carbon cycle through increased rates of carbon emissions to the atmosphere and the loss of aboveground and belowground carbon accumulation and storage capacity (Silver et al., 2001). In general, tropical carbon storage is under major threat due to ongoing deforestation and conversion of pristine forest to pasture and agricultural land, further increasing rates of carbon

emissions to the atmosphere (Silver et al., 2001). Hence, in many tropical areas, such as the Brazilian Amazon, an increase in secondary forest cover is still directly related to loss of C stocks at the landscape scale (Houghton et al., 1991). However, despite the fact that about half of secondary forests in tropical America are adopted from previously undisturbed primary forest (Brown & Lugo, 1990) in many tropical regions reforestation occurs in the form of agroforestry systems and plantations, thus an increase in secondary forest cover on formerly cleared lands typically represents an increase in forest biomass and associated C stocks. Approximately half of the tropical biome is in some stage of recovery from past human disturbance, due to secondary forest re-growth on abandoned agricultural or pasture lands (Silver et al., 2001). Secondary forests store approximately 40% of tropical biomass C and annually grow by about 9 million hectares per year (Brown & Lugo 1990). Therefore, secondary forests are becoming an increasingly important component of tropical landscapes with the potential to restore tropical C storage after substantial losses of soil carbon due to deforestation (Schedlbauer & Kavanagh, 2008). However, although restored forests could improve ecosystem services and enhance biodiversity conservation, their species composition and structure will not match the original forest cover (Chazdon, 2008). These shifts in life-form and species composition along successional gradients of regeneration potentially affect the aboveground structure and biomass as the forests age. Hence, which species predominate during secondary succession may have a large effect on the C storage of tropical landscapes. For instance, it was proposed that future aboveground C storage could vary by several hundred percent, depending on species composition scenarios for a Panamanian tropical lowland rainforest (Bunker et al., 2005). Such documented relationships

between biodiversity and C storage, as well as recent indications of positive biodiversity-ecosystem functioning relationships in these hyper-diverse systems (Cavanaugh et al., 2014), highlight the importance of conservation and management of the biological richest ecosystems on the planet.

Since carbon gain or release at the landscape scale is usually estimated as the change in C content due to changes in biomass of the vegetative cover, this estimate is affected by a suite of environmental and ecological factors. To that end, a recent literature evaluation aimed at investigating the effects of tropical forest succession on tropical C stocks and found that while aboveground C accumulation was affected by time of abandonment, past land-use and land cover type, such that aboveground biomass C accumulated during secondary succession, soil C stocks changed very little with time since abandonment (Spiotta et al., 2008). Therefore, soil carbon storage did not increase with secondary forest age and was unrelated to increases in aboveground carbon storage (Schedlbauer & Kavanagh, 2008). As a result, in contrast to aboveground biomass C, soil C stocks were reported similar between tropical secondary forests, tree plantations and reference forests at the pantropical scale (Spiotta & Sharma, 2013). Forest age was generally reported a poor predictor of soil C stocks, however, it was suggested that environmental variables (rainfall, temperature, soil type) are more important determinants for soil C stocks on high productive sites, while human management factors (land cover type, prior land use) show stronger effects on low productive sites (Spiotta & Sharma, 2013). This suggests that differences in the turnover and nutrient dynamics between forest sites could determine the rate of recovery (resilience) of the carbon stock after disturbance. While in high productive and nutrient-rich systems rapid turnover of

aboveground biomass and comparatively high litter inputs rapidly replenish soil C stocks after disturbance, this process is delayed on nutrient-impoverished soils. Therefore, such high rates of productivity are often associated with low nutrient use efficiency and high leaching rates, whereas low productive systems exhibit high nutrient conservancy, such that overall soil C stocks are comparable between both systems.

Nonetheless, soil fertility can be an important factor determining the regeneration of tropical forests, as prior land-use such as repeated fire and long-term pasture use may have caused substantial losses of nutrients from agricultural soils. Nutrient fertilization experiments on abandoned pastures found that tropical tree species during early succession responded positively to nitrogen (Davidson, 2004), whereas secondary succession responded most to phosphorous addition (Gehring, 1999). In addition, a recent study investigating nutrient dynamics during succession in dry tropical forests found that forest structure and litter nutrient concentrations are strongly influenced by water and nutrient availability (especially P), as well as land-use history (Read & Lawrence, 2003). Whereas P nutrient use efficiency was lowest at sites of highest productivity, litter resorption proficiency was highest at low productive sites. This suggests that stand-level nutrient use efficiency tends to diminish with increasing productivity and nutrient availability. Therefore, water and nutrient limitation not only represent important controls on primary production and nutrient cycling but also constitute significant factors determining the recovery and regeneration of tropical forest ecosystems (Read & Lawrence, 2003).

In summary, this highlights the complicated nature of carbon, water and nutrient cycles that eventually determine the productivity and carbon storage of tropical forests. As a result,



both large-scale environmental drivers, as well as local-scale topo-edaphic factors that affect water and nutrient availability and thus shape niche differentiation of tropical tree species will likely affect the C storage capacity in tropical forest ecosystems. Therefore, spatial differences in soil type, hydrology and soil fertility, as well as successional stage and tree species composition between respective forest sites could represent key factors determining the response of tropical aboveground net primary production to projected global changes and thus affecting the C sink strength of tropical forest ecosystems.

### STUDY AIMS

Tropical forests are of global significance to climate because of their ability to alter the global water and carbon cycles through the exchange of energy, water and trace gases. Due to the linkage of global carbon and nutrient cycles with climatic variables tropical forests are evidently sensitive to global changes in resource levels and may show large structural and dynamic changes in the future. Understanding the mechanisms controlling carbon storage and nutrient

cycles of tropical forests and its responses to environmental drivers is therefore of paramount importance to accurately predict future responses of tropical forest C sequestration to projected global changes.

In this thesis we therefore evaluate the climate sensitivity of tropical aboveground net primary production by investigating seven consecutive years of monthly censuses ( $n=84$ ) on aboveground biomass increment of 379 tropical trees as well as associated nutrient inputs via litterfall, throughfall, stemflow and bulk precipitation at three forest sites differing in topography and disturbance history located in southwestern Costa Rica. Among the investigated environmental drivers, climate (temperature, precipitation, dry season length) and edaphic factors (soil fertility, topography) constituted the major controls on primary production and nutrient cycling in tropical lowland rainforests. Moreover the highly diverse tree vegetation (approx. 200 species per hectare) showed the highest wood increments and among the highest litterfall rates published to date and thus highlights the exceptional position of the high productive lowland

rainforests located in southwestern Costa Rica.

We focus on the effects of topography and anthropogenic disturbance on forest primary production (wood increment, litterfall, and fine root production) and nutrient cycling (atmospheric deposition, canopy exchange, throughfall, stemflow, litter decomposition, and soil nutrient contents) at different spatial and temporal scales; (i) globally across wide climatic gradients based on a literature compilation of pantropical forest sites, as well as locally over (ii) interannual and (iii) seasonal time scales, at three lowland forest sites

FIGURE 5:  
STUDY SITES  
DIFFERING  
IN TOPOG-  
RAPHY AND  
DISTURBANCE  
HISTORY IN  
SOUTHWES-  
TERN COSTA  
RICA. (SOUR-  
CE: [HTTP://  
WWW.UNIVIE.  
AC.AT/BDEF](http://www.univie.ac.at/BDEF)).



differing in topography and disturbance history in southwestern Costa Rica (Fig. 5).

### STUDY DESIGN

To study the response of tropical ecosystem processes in relation to (1) climate anomalies i.e. El Niño Southern Oscillation (ENSO), as well as local site characteristics such as (2) topographic position and (3) disturbance history we established monitoring sites in the vicinity of the Tropical Research Station La Gamba, Piedras Blancas National Park (“Regenwald der Österreicher”), Costa Rica. The study sites are located at the Southern Pacific slope of Costa Rica, with a mean annual temperature (MAT) of 28° C and a mean annual precipitation (MAP) of 6000 mm (Weber et al., 2001; Wanek et al., 2008; Weissenhofer et al., 2008). The Golfo Dulce region is outstanding in terms of extraordinary high MAP and MAT, plant species diversity and productivity and therefore represents an exceptional habitat to study the effects of climatic variations on tropical ecosystem processes.

Based on recent remote sensing data forest plots were established in the following ecosystems: primary undisturbed rainforests situated in (1) hilltop and (2) valley bottom positions, as well as (3) secondary forests aged about 15-25 years and stocking on abandoned pasture or agricultural land. In each of the study sites monitoring plots were set up in triplicate (each 400 m<sup>2</sup>), so that each forest type was covered by 0.12 hectare of survey area.

Ecosystem monitoring included data on climate variation (i.e. daily precipitation as well as daily mean, minimum and maximum temperature), topography (i.e. elevation, aspect, and slope), edaphic characteristics (microclimate,



**FIGURE 6:**  
MEASUREMENT OF ABOVEGROUND BIOMASS INCREMENT AS A SURROGATE OF WOOD PRODUCTION. (SOURCE: [HTTP://WWW.UNIVIE.AC.AT/BDEF](http://www.univie.ac.at/bdef)).

soil physics and chemistry), biodiversity (tree species composition), as well as ecosystem processes (aboveground net primary production, wood increment, litterfall, throughfall, stem-flow and associated nutrient fluxes).

In this thesis we opted to investigate the seasonal variation of aboveground net primary production (ANPP) and therefore used wood increment as indicator of wood production (Fig. 6), as well as total fine litterfall corrected for changes in leaf area as surrogate for canopy production (Fig. 7), at monthly time resolution.

Wood production (WP) was estimated by repeatedly measuring the diameters at breast height (DBH) of all trees approx. 1.30 m aboveground or above buttresses or other irregularities according to standard best-practice techniques (Clark et al., 2001a; Baker et al., 2004b). Trees above 10 cm DBH were equipped with dendrometer bands (Fig. 6). Trees below 10 cm DBH were measured using sliding calipers. Measurements were repeatedly performed every month for trees above 10 cm DBH and every 3 months for trees below 10 cm in diameter throughout the study period between 2006 and 2013. Tree height

was estimated for all trees of this study ( $n=349$ ) using inclinometers (Suunto PM-5/360 PC clinometer, Valimoti, Finland) and wood density ( $\rho$ ) was measured for 13 out of 61 tree species in this study for which data were not available in the literature. For the remaining species data on wood density was retrieved from the global wood density database (Zanne et al., 2009). We then used the allometric equation for wet forest stands ( $AGB = \exp(-2.557 + 0.940 \ln(\rho D^2 H))$ ) published by Chave et al. (2005) to calculate WP in  $Mg\ ha^{-1}\ yr^{-1}$  (Keeland & Sharitz, 1993; Clark & Clark, 2000).

Canopy production (CP) was estimated by collecting litterfall in litter traps (50 cm in diameter) fixed 100 cm above soil level. Traps were made of bottom cut PVC tubing, covered by a 1x1 mm nylon mesh, and positioned in the center of ten subplots in each of the three forest sites (Fig. 7). Samples have been taken in intervals ranging from 2 to 4 weeks between February 2005 and April 2013. Litter samples were divided into two fractions: fine leaf litter (consisting of leaves only) and residual litter (consisting of twigs, reproductive material and fine unidenti-

fiable material), oven dried and weighed to calculate canopy production in mega gram carbon per hectare and year (Drage, 2007). The sum of these fractions was used to calculate total fine litterfall in  $Mg\ ha^{-1}\ yr^{-1}$  (but see: Clark et al., 2001a). We furthermore calculated canopy production (CP in  $g\ m^{-2}$ ) from litterfall (LF in  $g\ m^{-2}$ ) corrected for changes in leaf area index (LAI in  $m^2\ m^{-2}$ ) times leaf mass area (LMA in  $g\ m^{-2}$ ) following the equation:  $CP = LF + (LAI_t - LAI_{t-1}) * LMA$  and then converted CP to  $Mg\ ha^{-1}\ yr^{-1}$ .

We finally calculated aboveground net primary production (ANPP) as the sum of wood production (WP) and canopy production (CP). This estimate of ecosystem productivity was then used to analyze the relationship between climate variables (i.e. bulk precipitation, number of dry days, maximum and minimum temperatures) and productivity parameters (i.e. ANPP, WP, CP) concerning the response of tropical ecosystem processes to climate anomalies.

FIGURE 7:  
MEASUREMENT OF LITTERFALL AS A SURROGATE OF CANOPY PRODUCTION. (SOURCE: [HTTP://WWW.UNIVIE.AC.AT/BDEF](http://www.univie.ac.at/BDEF)).





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## NEW INSIGHTS INTO MECHANISMS DRIVING CARBON ALLOCATION IN TROPICAL FORESTS





# New insights into mechanisms driving carbon allocation in tropical rainforests

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## Summary

- The proportion of carbon allocated to wood production is an important determinant of the carbon sink strength of global forest ecosystems. Understanding the mechanisms controlling wood production and its responses to environmental drivers is essential for parameterization of global vegetation models and to accurately predict future responses of tropical forests in terms of carbon sequestration.
- Here, we synthesize data from 105 pantropical old-growth rainforests to investigate environmental controls on the partitioning of net primary production to wood production (%WP) using structural equation modeling.
- Our results reveal that %WP is governed by two independent pathways of direct and indirect environmental controls. While temperature and soil phosphorus availability indirectly affected %WP via increasing productivity, precipitation and dry season length both directly increased %WP via tradeoffs along the plant economics spectrum.
- We provide new insights into the mechanisms driving %WP, allowing us to conclude that projected climate change could enhance %WP in less productive tropical forests, thus increasing carbon sequestration in montane forests, but adversely affecting lowland forests.

## Introduction


The allocation of gross primary production (GPP) to net biomass production (NPP) as opposed to losses through respiration determines the residence time and sink strength of carbon (C) in terrestrial ecosystems (Chen *et al.*, 2013; Galbraith *et al.*, 2013). As terrestrial NPP is controlled by temperature, water, and nutrient availability, global change probably affects terrestrial C allocation and hence the terrestrial C sink strength, in turn triggering feedback mechanisms on climate (Clark *et al.*, 2001b). Tropical forests contribute substantially to the terrestrial C sink (Stephens *et al.*, 2007) and thereby play important roles in global climate regulation, but they also respond sensitively to global changes (Clark *et al.*, 2003). Understanding the mechanisms of tropical forest C allocation and its response to environmental drivers is therefore of paramount importance for parameterization of global vegetation models and to accurately predict future responses of tropical C sequestration to global changes (Litton *et al.*, 2007; Chen *et al.*, 2013; McMurtrie & Dewar, 2013).

The available empirical data have so far not resulted in an unequivocal pattern of forest C allocation at larger scales. A recent synthesis of carbon allocation across global forest ecosystems could not identify priorities for the products of photosynthesis, as fluxes to all components of GPP increased with productivity (Litton *et al.*, 2007). However, the authors reported that increased resource supply resulted in increased productivity,

followed by increased allocation to above-ground wood production, while the allocation to foliage and autotrophic respiration was more conservative and that to roots decreased with productivity (Litton *et al.*, 2007). In agreement with this, Vicca *et al.* (2012) demonstrated that fertile forests exert higher biomass production efficiency, such that the fraction of C allocated to above-ground wood production increased with nutrient availability.

However, knowledge of the mechanisms controlling C allocation remains especially scarce for tropical forests, as GPP and NPP data are available for only a few sites, causing these ecosystems to be underrepresented in global syntheses (Malhi *et al.*, 2011; Chen *et al.*, 2013; Clark *et al.*, 2013; Zhou *et al.*, 2013; Zuidema *et al.*, 2013). This is even more valid for environmental controls on tropical forest C allocation.

Across the tropical forest biome, temperature was reported as the strongest predictor of tropical forest NPP, such that all components of NPP increased in response to temperature with no effect on wood relative to canopy production (Raich *et al.*, 2006), although, globally, allocation to wood production increased with productivity (Litton *et al.*, 2007). However, just recently, Cleveland *et al.* (2011) found that the strong positive relationship between temperature and tropical forest productivity was driven by distinct differences in NPP between cool montane and warm lowland forests, caused by differences in proximal drivers of NPP in these forest types. By contrast, for lowland tropical rainforests, small increases in night-time temperature associated with El Niño

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phenomena were shown to strongly depress wood production while canopy production was relatively unaffected (Clark *et al.*, 2013), indicating that these forests thrive close to their thermal optimum (Corlett, 2011). Moreover, the productivity of tropical rainforests was reported to decline at the highest amounts of mean annual precipitation, caused by reduced decomposition and nutrient availability in the long term (Schuur, 2003; Powers *et al.*, 2009). However, this negative effect could also result from indirect effects of reduced light availability as a result of increased cloud cover during precipitation events (Graham, 2003; Pau *et al.*, 2013), rather than being a direct consequence of water availability (Wagner *et al.*, 2012, 2014). On the other hand, wood production was found to respond more sensitively to drought in throughfall exclusion experiments than canopy production and litterfall (Brando *et al.*, 2008; Moser *et al.*, 2014), suggesting that allocation tradeoffs among NPP components dominate the response of tropical forest growth to seasonal and interannual drought (Doughty *et al.*, 2014). Overall, these opposing trends therefore point to strong differences in spatial (montane vs lowland) as well as temporal (long-term vs short-term) responses of tropical NPP components, forest C allocation and eventually C sequestration to environmental drivers, such as changing climate and atmospheric deposition.

Short-term and long-term responses may differ markedly, as short-term environmental changes act on the present tree community, whereas long-term responses affect species turnover, triggering changes in tropical forest community composition. Alterations in the composition of tropical tree communities in response to environmental change could trigger community-wide shifts in plant functional traits that affect the performance and life-history strategy of tropical trees (Poorter *et al.*, 2009).

Many important plant functional traits covary or are negatively related as a result of opposing investment strategies along the plant economics spectrum (Baraloto *et al.*, 2010). For instance, opportunistic species are characterized by fast growth and high hydraulic conductivity, whereas drought-tolerant species grow more slowly but maximize plant hydraulic safety (Poorter & Bongers, 2006). Hence, plant functional traits such as those associated with slow vs fast plant growth (Reich, 2014) can determine the resistance and resilience of trees to periodic disturbances and cause drought-induced shifts in the functional composition of tropical rainforest trees in the long term (Fauset *et al.*, 2012). Concomitant shifts along the plant economics spectrum resulting from species turnover could thus lead to changes in stand-level measures of C allocation, as, for instance, a shift towards greater plant hydraulic safety associated with higher wood density and lower leaf area : sapwood area ratios could result in increased C allocation to wood production and decreased allocation to canopy production.

The current knowledge suggests that projected changes in environmental drivers such as elevated temperature, increasing length of drought periods and increasing nutrient deposition could result in alterations of long-term woody biomass C sequestration in tropical old-growth forests (Phillips *et al.*, 2010; Fauset *et al.*, 2012; Doughty *et al.*, 2014). So far, however, the relationships and interactions among multiple environmental drivers and

tropical forest wood allocation remain poorly resolved. Hence, in this study we aimed to elucidate the underlying mechanisms and pathways among environmental drivers of C allocation to wood production in tropical rainforests. To that end, we compiled a pantropical database of > 100 old-growth forests for which data on wood and canopy (and fine root) production were reported. We applied structural equation modeling to resolve the relative importance of environmental controls (i.e. mean annual temperature (MAT), mean annual precipitation (MAP), dry season length (DSL) and cloud cover (CLD), as well as leaf, litter and soil N : P ratios) on the partitioning of NPP to wood production (%WP).

We hypothesized that %WP increases with environmental factors that promote overall forest productivity, and thus cause light limitation and enhanced stem height growth; that %WP increases as a result of drought-induced changes in investment strategies along the plant economics spectrum, causing coordinated tradeoffs among plant functional traits which promote % WP; and, finally, that projected global changes might affect the C sequestration potential of tropical tree species in montane and lowland regions differently, based on shifts in major environmental constraints on NPP and %WP across altitudinal gradients.

## Materials and Methods

## Study design and site characterization

To identify relationships between environmental factors and mechanisms driving C allocation in tropical forests, we compiled a database of 105 pantropical forest sites using the ISI Web of Knowledge search engine and other online resources, searching for the following terms and combinations thereof: tropical, forest, litterfall, canopy production, tree increment, wood production, root production, root turnover, net primary production, gross primary production and carbon allocation (see Supporting Information Table S1 for database). Annual fluxes of dry mass as presented by some studies were converted to mass C by assuming that C concentration of vegetation was, on average, 50% (Clark *et al.*, 2001b). We incorporated only data from old-growth wet and moist evergreen tropical forests without recent disturbance for which both plot-based litterfall (as surrogate for canopy production) and above-ground biomass increment (as surrogate for wood production) were reported. Mangrove forests, dry tropical forests, tropical deciduous forests and secondary tropical forests, which together comprise c. 50% of total tropical forest land area (<http://www.fao.org/docrep/k0050e/k0050e03.htm>), were excluded from this analysis.

Litterfall comprises the largest portion of canopy production, which is sampled by litterfall traps and transects; only studies extending over at least 1 yr with at least monthly collection intervals were included in our database. Large leaves (> 50 cm in length) and branches (coarse litterfall > 2 cm in diameter) are rarely measured and therefore were not included here. Fine litterfall (< 2 cm in diameter) generally comprises leaves, reproductive structures, small twigs and other fine materials (Clark *et al.*, 2001a). Other components of canopy production are rarely

studied, including branch production, losses to herbivores, volatile organic compounds and decomposition of litter trapped in the canopy or in litterfall traps. The contribution of these components is usually small, with the exception of branch production and branchfall, but given the scarcity of branchfall data, we did not correct for this.

Wood production is assessed as tree girth increment at breast height (*c.* 1.3 m) measured over intervals ranging from monthly to 5-yearly using tree girth tapes or with dendrometer bands. Allometric equations were applied to relate the increment in diameter at breast height (DBH), tree height (*H*) and wood density (WD) to above-ground biomass increment. A range of different allometric equations were used by the compiled studies, based on  $DBH^2$ ,  $DBH^2 \times H$ ,  $DBH^2 \times WD$  or  $DBH^2 \times H \times WD$ . We did not correct for these differences in allometric equations used for the 105 study sites, as raw data for individual trees (species, DBH, *H*, WD) are commonly not reported or available.

The final dataset comprised 43 montane and 62 lowland forests (Fig. 1; Table S1) according to a threshold elevation of 1000 m above sea level (asl) (*sensu* Holdridge *et al.*, 1971). The geographical coverage by continent was highest for South and Central America (62 sites), and decreased towards South and East Asia (26), Hawaii (12), Africa (3) and Australia (2). Climate data (i.e., MAT, MAP, DSL) were derived from the respective papers or, if not presented, from online resources such as the Climatic Research Unit databases (<http://www.cru.uea.ac.uk>) and WorldClim global climate data (<http://www.worldclim.org>). DSL is defined as the number of months during which rainfall is > 100 mm. CLD was retrieved from the IPCC-data distribution center using 0.5° resolution datasets during the period 1961–1990 (CRU TS2.1) provided by the Climatic Research Unit (CRU; <http://www.cru.uea.ac.uk/>).

Moreover, we searched for site-matched data on soil total N and P, litter N and P and foliar N and P to compute respective N : P ratios for soil (soil N : P), litter (litter N : P) and leaves (foliar N : P). Stand-level data on litter and leaf N : P were either reported, or we calculated this as the mean of species-specific values (usually > 5 to up to > 50 species were reported). Soil data were derived from soil samples taken between 0 and 30 cm excluding surface litter, and where necessary were calculated as a weighted mean for 0–30 cm soil depth. Soil types comprised many organic soils in montane tropical forests and mainly mineral soils in lowland sites (Table S1). Soil total N and P are much higher in organic soils than in mineral soils, and the contribution

of organic horizons to topsoil increases with elevation as a result of decreasing decomposition rates. We therefore refrained from using soil total N or soil P as proxies for N or P availability. Instead, we used soil N : P (litter N : P, foliar N : P) as an indicator of soil P relative to N availability as soil N : P ratios are relatively independent of soil N or P concentration (Xu *et al.*, 2012). High soil N : P ratios as found in highly weathered soils might therefore be used as indicators of P limitation in such environments (Yang & Post, 2011). Final site coverages for climate data were 100% for MAT, MAP and DSL, 96% for CLD, 82% for soil N : P, 68% for litter N : P, and 51% for foliar N : P. Root production data were only available for 40 out of 105 sites.

#### Statistical design and data analysis

All statistical analyses were performed using R (R Development Core Team, 2012). Data distributions were analyzed for normality and nonnormal data were log-transformed or rank-transformed to attain normality. Before further analysis, we removed outliers, defined as data that were beyond three SD of the mean, from the dataset. Residuals of linear regression analyses were analyzed for normality, and data with leverage and influence inconsistent with the full dataset were identified and removed. To describe patterns in the available data and discern potentially responsible drivers, we used three complementary statistical approaches. To investigate drivers of NPP partitioning to WP we used linear regressions as well as partial linear regressions and their residuals. Classification and regression tree (CART) analyses were conducted to indicate the relative importance among environmental controls on %WP. Finally, we computed structural equation models (SEMs) to investigate pathways of interrelated environmental controls on %WP.

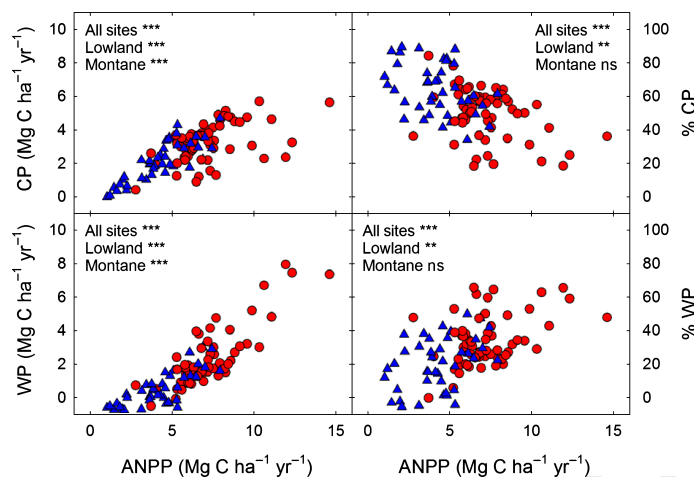
Linear regressions were computed to test for dependencies between NPP components (Fig. S1) as well as above-ground NPP (ANPP) components (Fig. 2), that is, canopy production (CP), wood production (WP), root production (RP) and partitioning to WP (%WP). We moreover used linear regression models to investigate the effects of climatic variables, that is MAT, MAP, DSL and CLD (Fig. 3), as well as the various N : P ratios (Fig. 4), on tropical ANPP, CP, WP and %WP. Climate variables were standardized to allow direct comparison of respective effects on ANPP components and %WP. The standardized variables are dimensionless with a mean of zero and an SD of one. Thus, coefficients in simple and multiple regressions with

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**Fig. 1** Geographic locations of tropical study sites (fully described in Table S1). Blue triangles, montane tropical rainforests (> 1000 m above sea level (asl)); red circles, lowland tropical rainforests (< 1000 m asl).







**Fig. 2** Relationship of canopy production (CP) and wood production (WP), as well as respective partitioning of above-ground net primary production (ANPP) to canopy production (%CP) and wood production (%WP) in relation to ANPP. Blue triangles, montane tropical rainforests (> 1000 m above sea level (asl)); red circles, lowland tropical rainforests (< 1000 m asl). Corresponding regression significance levels are indicated by asterisks (\*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; \*,  $P < 0.05$ ; ns, not significant).

standardized variables indicate the respective contributions to the variation in ANPP and %WP in terms of a relative unit change. Residuals of the most significant predictor in multiple regressions were used to test for independent effects of interrelated significant variables on %WP (Table S2).

Classification and regression tree (CART) analysis was used to determine the relative importance of predictors in explaining variation in the response variable. This method is especially suited for handling unbalanced data, including missing values (De'ath & Fabricius, 2000). Moreover, CART is capable of handling higher-order interactions among variables such as effects of nutrient–climate interactions (Townsend *et al.*, 2011). Based on the assumptions by Cleveland *et al.* (2011) and given that across the whole data set MAT had the strongest effect on tropical forest production, we used CART to dissect the pantropical data set into lowland and montane forest sites and investigated the environmental factors controlling ANPP and %WP in both forest types (Fig. 5).

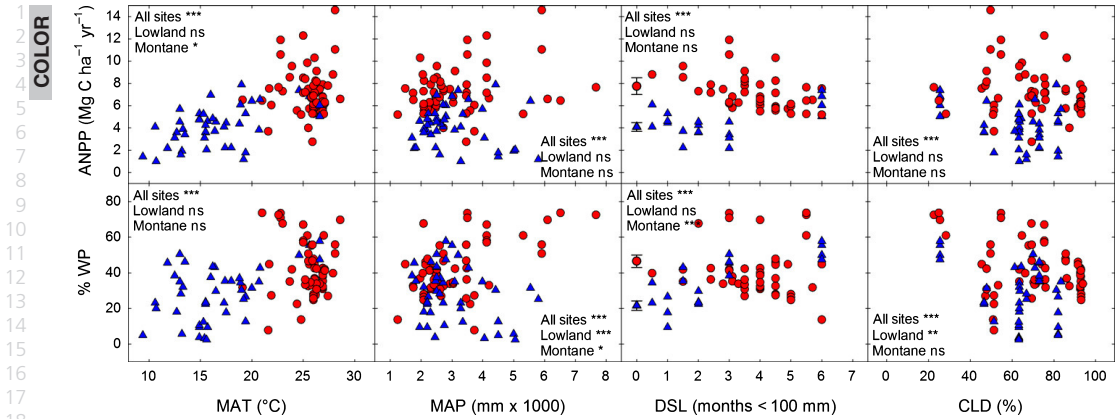
Structural equation modeling is a multivariate statistical tool using the covariance among variables to build and test models with specific multistep pathways of influence on one or more final response variables. This technique goes beyond standard multiple regression approaches by elucidating the interaction of variables related to the process of interest (Fox, 2006). As a first step, we developed a conceptual base model (Fig. S2) involving all variables that might be causally related to one another and to the response variables. For this, we included the climate variables MAT, MAP, DSL and CLD as exogenous factors, as well as ratios of soil N : P, litter N : P and foliar N : P as endogenous factors; both sets of variables were reasoned to directly and indirectly affect the response variables ANPP and %WP. To cope with missing values and thus changing total numbers of observations in the full pantropical data set (Table S1), we had to evaluate different base models. The full model, including all environmental variables, had the lowest number of observations ( $n = 38$ ). The

climate-only model, including the variables MAP, MAT, DSL and CLD, was based on the largest data set ( $n = 101$ ). The graphical model representations show the respective variables (boxes), with respective causal and directional connections between variables (arrows). Arrow length does not indicate the strength of the connection, but each path has a (standardized) path coefficient, which represents the slope of that relationship in a multivariate context. The overall goodness of fit is indicated by a  $\chi^2$  statistic and corresponding  $P$ -values, where a high  $P$ -value represents a good fit between the model and the data. Model optimization was an iterative process analogous to stepwise multiple regression. Insignificant paths were removed from the base model in a stepwise manner, aiming at improvement of the overall model fit (see Colman & Schimel, 2013). To compare alternative models and determine the most parsimonious model, we used Akaike's information criterion (AIC; Burnham *et al.*, 2011), arriving at a final model including the variables MAP, MAT, DSL, and soil N : P ratio ( $n = 86$ ; Fig. 6).

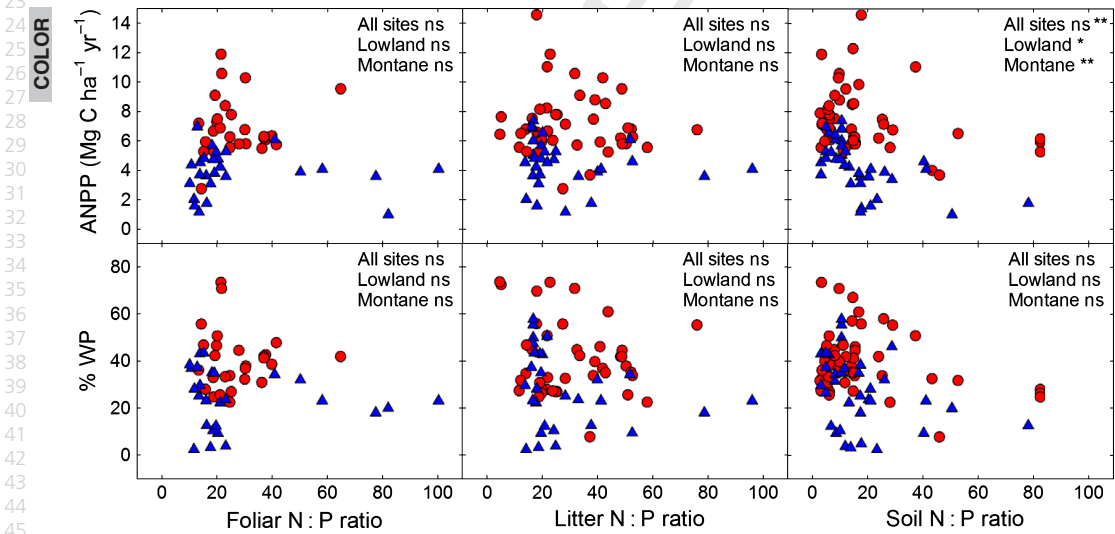
#### Uncertainty and robustness of the environment–ANPP relationships

We expect relatively low uncertainty in the litterfall data, as very similar methodology was used at all sites (litter traps had 0.25–1 m<sup>2</sup> area, were replicated five to 20 times in each forest type/site, with collection intervals of 2–4 wk over at least 1 yr). Measurements of tree girth and increment are also not expected to cause large uncertainty; however, the use of different allometric models (most studies used DBH-only based models, some DBH  $\times$  WD, the fewest DBH  $\times$  H  $\times$  WD) adds the highest degree of bias and uncertainty in studies of forest biomass and wood production (see Chave *et al.*, 2005). The use of a recently published pantropical allometric model (Chave *et al.*, 2014) could greatly narrow this uncertainty, but inaccessibility of the raw data on species affiliations, DBH, H and WD, obviated this approach. Another





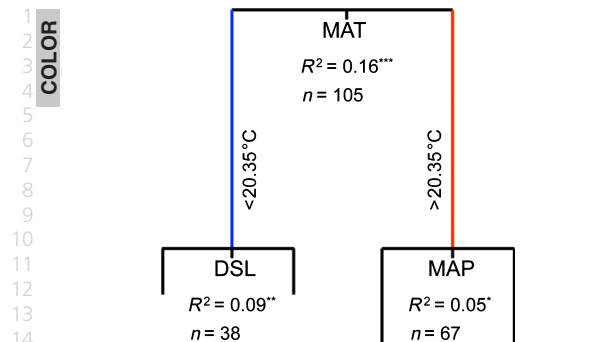
**Fig. 3** Relationships of above-ground net primary production (ANPP) and ANPP partitioning to wood production (%WP, as a percentage of ANPP) to major climatic drivers, that is, mean annual temperature (MAT), mean annual precipitation (MAP), dry season length (DSL) and cloud cover (CLD). Blue triangles, montane tropical rainforests (> 1000 m above sea level (asl)); red circles, lowland tropical rainforests (< 1000 m asl). Corresponding regression significance levels are indicated by asterisks (\*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; \*,  $P < 0.05$ ; ns, not significant). See Table S1 for details on respective study sites.



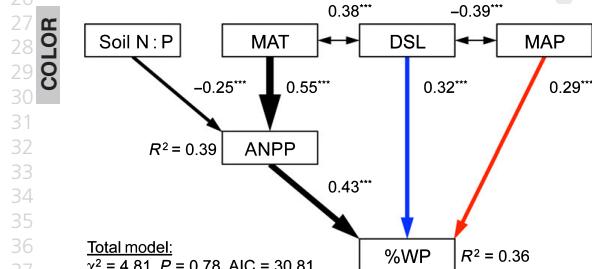
**Fig. 4** Relationships of above-ground net primary production (ANPP) and ANPP partitioning to wood production (%WP, as a percentage of ANPP) to nitrogen : phosphorus (N : P) ratios of leaves (foliar N : P), litter (litter N : P), and soil (soil N : P). Blue triangles, montane tropical rainforests (> 1000 m above sea level (asl)); red circles, lowland tropical rainforests (< 1000 m asl). Corresponding regression significance levels are indicated by asterisks (\*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; \*,  $P < 0.05$ ; ns, not significant). See Table S1 for details on respective study sites.

uncertainty in the pantropical dataset derives from the fact that in some tropical forests litterfall and wood increment were not measured over the same period of time, and for some sites measurements differed by up to 10 yr. Taken together, these errors cause a substantial increase in the uncertainty of data on wood increment relative to litterfall data; we suggest therefore that any uncovered significant environment–productivity relationship

across tropical forest sites can be considered robust. Moreover, we want to point out that environment–ANPP and environment–%WP relationships as reported here, based on sites where both litterfall and wood increment were reported, can be expected to be more reliable compared with the many studies where only one component of ANPP was measured and missing components were extrapolated from mathematical



**Fig. 5** Classification and regression tree (CART) analysis indicating how the major environmental controls, mean annual temperature (MAT), mean annual precipitation (MAP), and dry season length (DSL), explain variance in above-ground net primary production partitioning to wood production (%WP) in tropical rainforests. Predictor variables are depicted at each branch and coefficients of determination and corresponding significance levels are indicated by asterisks (\*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; \*,  $P < 0.05$ ; ns, not significant) as well as the number of observations reported below. MAT was the most important predictor of %WP, followed by DSL in montane sites (MAT  $< 20.4^{\circ}\text{C}$ ,  $n = 38$ ; blue branch) and MAP in lowland sites (MAT  $> 20.4^{\circ}\text{C}$ ,  $n = 67$ ; red branch). See Table S1 for details of respective study site.



**Fig. 6** Structural equation model (SEM) indicating pathways of influence among environmental drivers (mean annual temperature (MAT), mean annual precipitation (MAP), dry season length (DSL) and soil nitrogen : phosphorus (N : P) ratio) on above-ground net primary production (ANPP) and ANPP partitioning to wood production (%WP) in tropical rainforests. Arrow width indicates effect strength, and numbers are standardized path coefficients with corresponding significance levels indicated by asterisks (\*\*\*,  $P < 0.001$ ). The overall goodness of fit of the model is indicated by the  $\chi^2$  statistic and corresponding  $P$ -values, where a high  $P$ -value ( $P > 0.05$ ) represents little difference between the model and the data. Akaike's information criterion (AIC) was used to compare alternative models and determine the most parsimonious model.

relationships to the measured component (see Shoo & VanDerWal, 2008).

## Results

We found that in the full dataset ( $n = 105$ ) both components of ANPP (i.e., CP and WP) increased with ANPP (Fig. 2). However, compared with CP, WP showed a steeper increase with

ANPP, such that ANPP partitioning to WP (%WP) increased while that to CP (%CP) decreased with productivity (Fig. 2).

We further analyzed a subset ( $n = 40$ ) of tropical forest sites, where data on ANPP and root production (RP) were available, to evaluate the partitioning of NPP to canopy, wood and root production, and similarly found that all components of NPP (i.e., CP, WP, and RP) increased with productivity (Fig. S1). However, NPP partitioning to CP (%CP), WP (%WP) and RP (%RP) showed no significant relationship with productivity; that is, we found no evidence of changes in NPP partitioning with increasing productivity in the smaller dataset (Fig. S1). In the smaller dataset, we also did not observe the increase in %WP with ANPP that we found in the large dataset (data not shown).

## Mechanisms driving ANPP partitioning to WP in tropical forests

Testing predictors of ANPP revealed that MAT most strongly affected ANPP ( $R^2 = 0.35$ ,  $P < 0.001$ ) followed by soil N : P ( $R^2 = 0.11$ ,  $P < 0.01$ ) and DSL ( $R^2 = 0.04$ ,  $P < 0.05$ ) (Table S2). Testing predictors of ANPP partitioning showed that %WP was affected by ANPP ( $R^2 = 0.28$ ,  $P < 0.001$ ), as well as by MAT ( $R^2 = 0.16$ ,  $P < 0.001$ ), DSL ( $R^2 = 0.09$ ,  $P < 0.01$ ), MAP ( $R^2 = 0.05$ ,  $P < 0.05$ ) and nearly so by soil N : P ( $R^2 = 0.04$ ,  $P = 0.052$ ). Furthermore, we found significant effects of MAP ( $R^2 = 0.05$ ,  $P < 0.05$ ) and DSL ( $R^2 = 0.05$ ,  $P < 0.05$ ) on the residuals of the ANPP-%WP relationship, which are therefore independent of ANPP effects on %WP. In turn, we found significant effects of ANPP on the residuals of the environment-%WP relationships ( $R^2 = 0.10$ – $0.32$ ,  $P < 0.001$ ), including MAT, MAP, DSL and soil N : P, which are therefore independent of environmental effects on %WP (Table S2). Overall, this indicated that there must exist multiple independent but parallel pathways of control on the partitioning of ANPP to WP.

We therefore computed a CART analysis to determine the relative importance of the predictors (MAT, MAP, DSL, CLD and soil N : P ratio) in explaining the variation in the response variable (%WP; Fig. 5). We found that MAT was the most important predictor ( $R^2 = 0.16$ ,  $P < 0.001$ ), followed by DSL ( $R^2 = 0.09$ ,  $P < 0.01$ ) in tropical rainforests with MAT  $< 20.4^{\circ}\text{C}$ , and MAP ( $R^2 = 0.05$ ,  $P < 0.05$ ) in tropical rainforests with MAT  $> 20.4^{\circ}\text{C}$ . CART therefore dissected the data set into cool ( $< 20.4^{\circ}\text{C}$ ) and warm ( $> 20.4^{\circ}\text{C}$ ) tropical forest sites. This dissection is in good agreement with the classification threshold of lowland forests ( $< 1000$  m asl,  $n = 62$ ) and montane forests ( $> 1000$  m asl,  $n = 43$ ), with a misclassification of only five out of 105 ( $< 5\%$ ) tropical forest sites (Table S1). Furthermore, this indicated that %WP was affected by MAT, MAP, and DSL (Fig. 3; Table S2). While MAT increased %WP across all forest sites, MAP increased %WP in lowland but not montane sites, and DSL increased %WP in montane but not lowland sites (Fig. 5).

Computation of a series of SEMs finally provided an insight into the effects of simultaneous and interactive environmental drivers on the partitioning of ANPP to WP (Fig. 6). The most parsimonious model ( $\text{AIC} = 30.81$ ,  $\chi^2 = 4.81$ ,  $P = 0.78$ ) revealed two pathways of control on %WP ( $R^2 = 0.36$ ,  $P < 0.001$ ). First,

MAT and soil N:P positively affected %WP but indirectly through stimulating ANPP ( $r=0.43$ ,  $P<0.001$ ), such that %WP increased with productivity. MAT most strongly increased ANPP ( $r=0.55$ ,  $P<0.001$ ), while soil N:P negatively affected ANPP ( $r=-0.25$ ,  $P<0.001$ ), indicating a positive effect of soil phosphorus relative to nitrogen content on forest productivity and %WP. Secondly, DSL and MAP did not affect ANPP but showed a direct positive effect on the partitioning of ANPP to WP ( $r=0.29-0.32$ ,  $P<0.001$ ), indicating an independent and direct pathway driving %WP in response to DSL and MAP. The fact that the coefficients of determination were almost identical for the indirect ( $R^2=0.19$ ,  $P<0.001$ ) as well as the direct pathway ( $R^2=0.19$ ,  $P<0.001$ ) furthermore highlights that both mechanisms contribute similarly (Fig. 6).

## Discussion

Based on an SEM investigating 105 pantropical old-growth forests, we show that carbon allocation is controlled by two independent pathways involving multiple environmental variables. While in our model, the first pathway represents indirect environmental controls on the partitioning of ANPP to WP (%WP), the second pathway represents direct environmental controls on %WP. Our results for tropical forests are in line with theoretical C allocation strategies (Franklin *et al.*, 2012) and a recently proposed C allocation scheme for global forests (Chen *et al.*, 2013). The novelty of our approach, however, is that it clearly differentiates between direct and indirect environmental controls on %WP. In the following sections we therefore differentiate between these independent mechanisms, discuss each with regard to respective environmental drivers and conclude with implications of our findings for tropical C sequestration.

### Environmental controls on wood partitioning in tropical forests

Given the few data available on tropical forest GPP ( $n=10$ ; Chen *et al.*, 2013) and the limited number of tropical forest sites for which data on ANPP and below-ground production are available, we investigated the environmental controls on %WP at two levels: on the basis of NPP data ( $n=40$ ) as well as ANPP data ( $n=105$ ).

In the smaller data set on tropical forest NPP, we found strong allometric constraints on component NPP fluxes (i.e. CP, WP, and RP increased with NPP). However, we did not find tradeoffs in the partitioning among NPP components; that is, %WP, %CP and %RP did not change with NPP and %WP did not increase with ANPP in this dataset (Fig. S1).

In the larger dataset on tropical ANPP, we did identify a trade-off between ANPP components, such that along the pantropical gradient of productivity, the partitioning to wood biomass (%WP) increased with ANPP (Fig. 2), similar to what was shown for global forests (Litton *et al.*, 2007). In agreement with this, a recent study investigating the biomass production efficiency of global forests reported that the fraction of carbon allocated to wood production increased threefold with increasing nutrient

availability, while foliage and root production remained unchanged (Vicca *et al.*, 2012). This suggests that in more productive forests with high nutrient and water availability and high MAT, a greater proportion of NPP (and ANPP) is allocated to wood production, reflecting our findings of increased %WP in lowland than in montane forests (Fig. 2).

This result was mirrored by the first pathway of the SEM that indicated indirect environmental controls of MAT and soil N:P on %WP by promoting ANPP (Fig. 6). While MAT was reported as the strongest predictor of NPP across tropical rainforests (Raich *et al.*, 2006), a recent synthesis indicated that this relationship was driven by distinct temperature differences between low productive montane and high productive lowland forests (Cleveland *et al.*, 2011). However, within tropical lowland forests, soil-based measures of phosphorus were the only variables explaining a significant proportion of the variation in ANPP (Cleveland *et al.*, 2011). In agreement with this, the SEM in this study indicated positive effects of MAT and relative soil P availability (i.e. the inverse of soil N:P ratio) on ANPP along the pantropical gradient in forest productivity (Fig. 6). It is, however, likely that increased vegetation density in high productive forests triggers increased competition for limiting resources. For instance, it was shown that crowded plants adapt their growth strategy by allocating a greater proportion of biomass to competitive structures such as stems as a consequence of light limitation (Weiner, 2004). This has also been termed the 'race for light' in forests (Wolf *et al.*, 2011), driving NPP allocation towards stem height growth (instead of leaf area production) to maximize exposure of the leaf area to more favorable light conditions. Moreover, limitations by soil water and/or nutrient availability were reported to be lower in highly productive forests, stocking on soils rich in nutrients and moisture, thus essentially decreasing relative investments into roots to capture below-ground resources (McMurtree & Dewar, 2013). As a result of the fact that plants will allocate relatively more biomass in response to the most limiting factor for growth, this would be seen as increased relative investment into above-ground structures, mainly woody biomass (Poorter *et al.*, 2011). Hence, we suggest that the pattern of indirect controls on %WP identified in the SEM could result from the observation that increasing forest productivity simultaneously increases competition for light, causing tree height and tree diameter growth and therefore %WP to increase (Lewis & Tanner, 2000).

The second, direct pathway of environmental controls on %WP, through MAP and DSL, points to direct tradeoffs between WP and CP (or between WP and RP) in response to proximate environmental drivers, independent of constraints by forest productivity (Fig. 6). Although both MAP and DSL represent measures of forest water availability, which are commonly inversely related, our model indicated that both MAP and DSL had a positive effect on %WP (see SEM analysis in Fig. 6). This was because, in lowland forests, %WP increased with MAP, while in montane forests, %WP increased with DSL (see CART analysis in Fig. 5; Table S2), explaining that DSL and MAP, though acting adversely on forest water relations, both had positive effects on %WP across all forest sites in the SEM analysis. We suggest

that this direct pathway of environmental controls on %WP could be associated with tradeoffs along the plant economics spectrum and thus relates to the cost-effectiveness of investments into stem, leaf and root tissues, independent of productivity.

Leaf investment strategies were shown to vary from cheap, short-lived to well protected, long-lived leaves, trading off carbon gain against leaf persistence (Poorter & Bongers, 2006). In general, increasing MAP should increase stand-level leaf longevity as a result of decreasing prominence of deciduous tree species, in turn promoting evergreen broadleaved tropical trees. Furthermore, it was shown that increasing MAP triggered coordinated changes in physiological traits of tropical canopy trees, such that the longevity of leaves increased in lowland tropical rainforests (Santiago *et al.*, 2004). Given that the leaf area index of tropical lowland rainforests does not change significantly with MAP (Asner *et al.*, 2003), greater leaf longevity translates into smaller investments into canopy production relative to wood production and therefore into an increase in %WP, although this might be offset by greater leaf mass per area in long-lived leaves. Our finding of increasing %WP with MAP in lowland forests therefore points to a tradeoff between CP and WP mediated by concerted changes along community-wide means of the leaf economics spectrum.

Wood investment strategies are also expected to change along the plant economics spectrum in order to maximize plant hydraulic safety with increasing drought frequency and intensity. Wood traits affect the hydraulic conductance and thus represent important components affecting the performance and life-history strategy of tropical trees (Poorter *et al.*, 2009). For instance, opportunistic species are characterized by low wood density, reduced leaf dry mass per area, and high hydraulic conductivity in order to maintain high photosynthetic rates that enhance carbon gain and boost vertical growth (Poorter & Bongers, 2006). However, such cheap volumetric stem construction represents less structural support, and thus low wood density is often associated with higher mortality rates (Chave *et al.*, 2009). As a result, drought-intolerant species, because of high hydraulic efficiency but low hydraulic safety, are restricted to habitats that have high water availability, whereas drought-tolerant species, because of high hydraulic safety, are better competitors in drier habitats (Markesteijn *et al.*, 2011). In reverse, increased hydraulic safety is associated with higher wood density, lower hydraulic conductivity and therefore less leaf area per area of stem conducting tissue (Markesteijn *et al.*, 2011). All these trends cause %WP to increase and %CP to decrease when increasing DSL enhances community-wide degrees of hydraulic safety. A recent synthesis of an African long-term forest inventory indicated the importance of species composition in determining the response of tropical forests to long-term droughts (Fauset *et al.*, 2012). In the two decades of drought, species increasing in abundance showed significant differences in traits compared with those decreasing in abundance, such that a shift in community composition in favor of drought-tolerant species was in conjunction with an increase in forest biomass, pointing to increased C allocation to wood production. Our finding of increasing %WP with DSL in montane forests therefore points to a tradeoff between plant traits that

maximize water conservation and hydraulic safety along community-wide means of the stem (plant) economics spectrum. Overall, the effects of MAP and DSL on %WP, driving changes in the relative investments into leaves, stems or roots, may therefore be reconciled on the basis of community-wide shifts along the plant (leaf, stem, and root) economics spectrum in the long run.

#### Implications for tropical biogeochemistry and ecosystem functioning

Our analysis provided new insights into patterns and mechanisms driving C allocation in tropical rainforests by identifying independent pathways of environmental controls on %WP. The expression of the different pathways will, however, strongly depend on the functional plasticity of the present species in the short term as well as on species turnover, depending on species migration and dispersal abilities in the long term. Understanding the patterns and mechanisms driving C allocation are key for the parameterization of global vegetation models in order to accurately predict changes in C sequestration of tropical and global forests in response to environmental change.

The pattern of enhanced %WP along tropical gradients in forest productivity that we found in this study supports the global relationship reported by Litton *et al.* (2007) and suggests greater C sequestration in wood biomass in more productive lowland than in montane tropical rainforests. Our results further imply that predicted increases in temperature and dry season length could potentially increase %WP and thus C sequestration in montane tropical forests. By contrast, in lowland tropical forests that were reported to thrive close to their thermal optimum (Doughty & Goulden, 2008; Corlett, 2011; Clark *et al.*, 2013), %WP is more likely to respond neutrally or negatively to increasing temperatures. Decreases in annual precipitation (or increases in heavy precipitation with prolonged intermittent dry periods) could therefore decrease %WP in lowland rainforests, causing C sequestration to decrease. However, this effect could be partially alleviated by drought-induced shifts in the functional composition of tropical rainforest trees, favoring drought-tolerant species over less competitive opportunistic species in conjunction with a shift in community-wide functional traits that promote %WP and thus C sequestration.

In conclusion, our analysis demonstrated the complex interplay of direct and indirect environmental drivers controlling tropical C allocation that eventually determine the potential responses of tropical forest C sequestration to environmental changes. Albeit that further long-term and local measurements of forest productivity as well as manipulative experiments are urgently needed to allow implementation of the right causalities (Fatichi *et al.*, 2013), our study provides a novel framework to disentangle interrelated pathways among environmental drivers controlling the C sink strength of tropical forest ecosystems.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Relationships of canopy production (CP), wood production (WP) and root production (RP), as well as respective relative partitioning to net primary production (NPP).

**Fig. S2** Structural equation base model indicating pathways of influence among environmental drivers on ANPP partitioning to wood production (%WP).

**Table S1** Literature compilation of pantropical study sites ( $n = 105$ )

**Table S2** Results of partial linear regressions indicating the relative importance of direct and indirect environmental controls on ANPP partitioning to wood production (%WP)

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**TOPOGRAPHY STRONGLY AFFECTS ATMOSPHERIC DEPOSITION AND CANOPY EXCHANGE PROCESSES IN DIFFERENT TYPES OF WET LOWLAND FOREST, SOUTHWEST COSTA RICA**





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## Topography strongly affects atmospheric deposition and canopy exchange processes in different types of wet lowland rainforest, Southwest Costa Rica

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**Abstract** Bulk precipitation and throughfall were collected in a wet lowland rainforest in SW Costa Rica on an event basis to allow modelling the contributions of dry deposition and canopy exchange to nutrient inputs and internal cycling of nutrients. Estimates based on bulk precipitation underestimated total atmospheric deposition to tropical rainforests by up to 10-fold ignoring the contributions of dry deposition. Canopy exchange contributed most of the aboveground inputs to the forest soil of  $\text{Na}^+$ , about half for  $\text{K}^+$ , 10% for P and  $\text{Mg}^{2+}$  and negligible for N, C and other elements. Tree species composition did not account for the differences found in net throughfall between forest sites, and vegetation structure (plant area index) had only a small effect on net throughfall. Forest regrowth affected net throughfall through reduced soil fertility and differences in leaf traits. Topography most significantly affected net throughfall via increased dry deposition at sites of

higher elevation and via soil fertility and increased canopy exchange at down slope sites.

**Keywords** Canopy exchange · Dry deposition · Nutrient cycling · Secondary succession · Topography

### Introduction

Tropical forests are of global significance to climate because of their ability to alter the global water and carbon cycles through the exchange of energy, water and trace gases (Beringer et al. 2002; Fisch et al. 2004). They contribute significantly to the world's carbon budget (Clark et al. 2001a), accounting for 32–36% of terrestrial net primary production (Field et al. 1998; Melillo et al. 1993), and about 59% of the global carbon pool in forests is stored in tropical regions (Dixon 1994). Net primary production (NPP) of tropical forests is strongly controlled by climate (temperature, precipitation) (Schoor 2003). This general pattern is modified by two other factors, soil fertility and dry season length. Both have been shown to affect tree species composition, aboveground biomass and wood density across regional scales, e.g. across the Amazon basin, while NPP was only related to soil nutrient availability (Baker et al. 2004a, b; Malhi et al. 2004; ter Steege et al. 2006). Moreover, nutrient limitation of forest NPP has been conclusively demonstrated in Hawaii across wide

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climatic gradients (precipitation, altitude and/or temperature) but also along substrate age gradients ranging from 100s to millions of years (Harrington et al. 2001; Martinelli 2004; Vitousek 2004). Nutrients are therefore a key determinant of forest productivity and of the functioning of tropical rainforests in the 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 quantified and understood.

In order to sustain high NPP there must be a relatively closed cycling of nutrients, since tropical soils are often highly weathered and thus are poor in nutrients. Continuous losses of nutrients from the system would lead to further nutrient depletion if not replenished by atmospheric deposition, weathering and N fixation (Vitousek 1984). While atmospheric deposition represents the sum of wet and dry deposition (and occult deposition from fog and clouds), most if not all studies in tropical forests have assessed atmospheric nutrient inputs only via bulk precipitation—the inputs by dry deposition being largely unknown. Nutrients are recycled via production and decomposition of dead plant material in litterfall and root turnover and through dissolution of elements in throughfall and stemflow. The contribution of root turnover and decay to internal nutrient cycling is almost unknown in tropical rainforests (Tobón et al. 2004a). In contrast, nutrient fluxes in litterfall and throughfall are relatively easy to measure and studies have produced a good general understanding of the relative roles of litterfall and throughfall. For instance, it was shown that the production of fine (and coarse) litter represents the major source of aboveground input of nutrients (e.g. N, P,  $\text{Ca}^{2+}$ ) in tropical forests, while throughfall can account for up to 50% of the input of  $\text{K}^+$  and other elements to the forest floor. Throughfall may therefore potentially comprise an important pathway for the internal recycling of nutrients aboveground (Chuyong et al. 2004; Schroth et al. 2001; Tobón et al. 2004b). It is, however, highly problematic to compare litterfall and throughfall directly in terms of internal nutrient cycling processes since external inputs and internal recycling processes contribute to throughfall fluxes. Elements in throughfall derive from three processes (Chapin et al. 2002; Hansen et al. 1994; Lovett and Lindberg 1984; Lovett et al. 1996; Parker 1983):

- (1) Passage of incident precipitation through the canopy (wet or bulk precipitation),
- (2) Wash-off of dry deposited materials such as particles and adsorbed gases (“dry deposition”), and
- (3) Solute exchange between intercepted rainfall and canopy surfaces like foliage, woody parts, epiphytes and microorganisms (“canopy exchange”).

Net throughfall corrects for bulk precipitation, but represents a mixture of dry deposition (2) and canopy exchange (3). It is therefore of great importance to differentiate their contributions to throughfall to allow comparisons between litterfall and canopy exchange as internal recycling processes, to investigate landscape scale controls on canopy exchange and dry deposition and to assess the significance of dry deposition for atmospheric deposition in tropical forests.

There have been several attempts to dissect the contribution of dry deposition and canopy exchange to throughfall chemistry, most thereof based on the canopy budget model (Staelens et al. 2008) and the multiple regression model (Lovett and Lindberg 1984; Lovett et al. 1996). In the canopy budget model dry deposition of base cations is estimated by a ‘filtering approach’ which is based on the assumption that aerosols containing  $\text{K}^+$ ,  $\text{Ca}^{2+}$ , and  $\text{Mg}^{2+}$  are deposited equally onto the forest canopy as particles containing a tracer ion. Generally,  $\text{Na}^+$  is used as a tracer ion because it is only deposited by particles and is assumed not to be affected by canopy exchange processes. However,  $\text{Na}^+$  has been shown to be leached from mangrove canopies (Wanek et al. 2007) or to be taken up in canopies of tropical lowland rainforests (Tobón et al. 2004b). Moreover, several assumptions with unconstrained parameters are necessary to compute canopy exchange and dry deposition of  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and  $\text{H}^+$  (Staelens et al. 2008). The multiple regression model is based on the finding that net throughfall fluxes of dissolved nutrients are highly correlated with (i) the amount, duration and intensity of precipitation penetrating the canopy (positively related to canopy exchange) and (ii) the length of antecedent dry period being positively related to dry deposition (Lovett and Lindberg 1984; Lovett et al. 1996). A bias in this multiple regression model may arise as dry deposition can be



underestimated due to incomplete wash-off from canopy surfaces or overestimated through accumulated material in throughfall samplers during dry periods.

For temperate and boreal forests it was shown that throughfall chemistry mainly depends on factors like latitude, elevation, seasonality, proximity to the sea, species composition, forest age and local land use (Levia and Frost 2006; Parker 1983). In tropical rainforests the mechanistic understanding of throughfall hydrochemistry is much less developed, though effects of season, soil fertility, vegetation cover, tree species and vicinity to the sea were reported to affect dry deposition and canopy exchange of elements (Filoso et al. 1999; Schroth et al. 2001; Tobón et al. 2004b; Wanek et al. 2007, 2008).

Therefore this study investigated the following research questions:

- (1) What are the major landscape scale controls of nutrient fluxes via net throughfall?
  - a. season, topography and stage of succession
  - b. plant (leaf) area index and tree species composition
- (2) What is the magnitude of internal nutrient cycling via litterfall and canopy exchange?
- (3) What is the contribution of dry deposition to external nutrient inputs by atmospheric deposition?

There is a particular gap in studies of net primary production and nutrient cycling (litterfall and throughfall) in areas of high precipitation and temperature, where forest net primary production was reported to decline (Schuur 2003). Moreover, most studies in high rainfall tropical rainforests were performed on nutrient poor Oxisols not on more fertile soils such as Inceptisols and Ultisols. This study was carried out in the Esquinas forest, Parque Nacional Piedras Blancas, in SW Costa Rica. The study site is of particular interest for investigations on biogeochemistry, because forests are growing on nutrient rich Ultisols and Inceptisols due to ongoing tectonic land lift and moderate erosion (Gardner et al. 1992; Weissenhofer et al. 2008), tree diversity is high (140–210 spp. >10 cm dbh per hectare), mean annual precipitation (MAP) is >5800 mm and mean annual temperature (MAT) is about 28°C, representing a tropical wet lowland rainforest climate.

## Material and methods

### Study area

The study was conducted at the Tropical Research Station La Gamba (TRSLG; 8°42'03" N, 83°12'06" W, 70 m.a.s.l.) situated at the borders of the Piedras Blancas National Park, covering an area of approximately 148 km<sup>2</sup>, reaching from the Golfo Dulce's seashore to the village of La Gamba, in the province Puntarenas in the Southwest of Costa Rica. The vegetation is characterized by wet tropical lowland rainforest (Holdridge 1967) extending from sea level up to 580 m 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 on lower slopes and ravines (Pamperl 2001).

Mean annual temperature was 28.1°C and ranged from 22.9 to 34.2°C on monthly average (Weber 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 5810 ± 430 mm (1998–2007, Tropical Field Station La Gamba) with a short dry season from January to March (monthly mean precipitation approx. 180 mm), and a pronounced wet season from September to November (monthly mean precipitation about 800 mm).

### Study design

Study plots were randomly established in three different forest types: primary ridge (PRi; 8°42'16" N, 83°12'20" W, 120 m.a.s.l.), primary ravine (PRa; 8°42'16" N, 83°12'15" W, 80 m.a.s.l.) and secondary ravine (SRa; 8°42'01" N, 83°12'09" W, 80 m.a.s.l.) forest. Secondary stands were formerly used as cacao plantations and for tree logging but have remained undisturbed for over 20 years. Plots were set up in triplicate either as squares of 20 × 20 m, separated by a distance of >10 m and divided into subplots of 10 × 10 m each, or as rectangles of 10 × 40 m subdivided into subplots of 10 × 10 m and separated by 10–30 m due to spatial restriction at the ridge site. Distance

between sites was approximately 1.5 km and each forest type was covered by 0.12 ha of survey area. Inside these subplots all trees above 10 cm diameter at breast height (dbh) were 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 photo-herbarium is available at the TRSLG.

The plant (leaf) area index (PAI) was estimated by two techniques. (1) PAI within  $\pm 30^\circ$  zenith angle (total  $60^\circ$ ) above each throughfall collector was estimated by taking hemispherical photographs on days of uniform overcast skies. A digital camera (Nikon Coolpix 8100 with FC-E9 fisheye adaptor lens  $183^\circ$ ) was balanced horizontally and directed to the geographic north. For evaluation of PAI we employed the software Hemiview (Delta-T-Devices 1999) and Sidelook (Nobis 2005) using the following parameters: solar transmission coefficients: transmissivity 0.4, diffuse proportion 0.45, external solar flux  $1370 \text{ W/m}^2$ ; diffuse distribution: standard overcast sky; picture settings: threshold 182, radiant 911, rotation 0.0 (north) and magnetic declination 0.5 east. (2) PAI was estimated by light absorbance through the canopy using a SunScan probe v1.05 and the Sunshine Sensor BF3 (Delta-T Ltd, U.K.).

#### Sampling design

Soil samples were taken in triplicate from  $5 \times 5 \text{ m}$  subplots situated in each plot. Samples were taken with a soil corer (8 cm diameter) to a depth of 5 cm after removal of the litter layer. Soils were sieved through a 2 mm sieve. Soil water content was measured by oven drying 5 g fresh weight of each sample at  $80^\circ\text{C}$  for 48 h. Nutrients were extracted from soil (2 g fresh weight) by adding 15 ml 10 mM  $\text{CaCl}_2$ , shaking for 1 h and filtering through ash-free filter paper (Whatman ashless, Grade 40: 8  $\mu\text{m}$  pore size, Whatman International Ltd, Maidstone, England). Extracts were stabilized against microbial transformations by addition of phenyl mercuric acetate to 50  $\mu\text{M}$ , and kept frozen until transported to our laboratory in Vienna. Soil bulk density was determined by measuring the dry weights of three replicates of  $10 \times 10 \times 10 \text{ cm}$  soil cubes from each plot.

Plots were equipped with collectors for litterfall (10 per forest type), throughfall (15 per forest type), stemflow (12 per forest type) and soil water (6 per forest type). Litterfall samplers were made from fine-mesh nylon (1 mm mesh size) mounted on  $0.5 \times 0.5 \text{ m}$  PVC frames at 1 m height aboveground and placed in ten of twelve subplots per forest site to reduce sampling effort. Sampling of litterfall was done every 2 weeks throughout the study period. Litter samples were divided into two fractions: fine leaf litter and residual litter (consisting of twigs, reproductive material and fine unidentifiable material). Sampling for hydrochemistry was performed on an event basis ( $n = 30$ ) from February to April and August to October 2005 after every rainstorm. Precipitation events below 5 mm were discarded in consideration of minimum canopy interception storage. Of the total 30 precipitation events collected, 12 were studied for solute concentrations and analyzed by multiple regression model and canopy budget model, and six were statistically investigated for hydrochemical differences between rainy and dry season. In this study we individually analyzed single collector samples to assess the heterogeneity of throughfall fluxes and its controls, and therefore did not combine them to compound samples for each event and plot. Bulk deposition samplers ( $n = 2$ ) were placed in an open area surrounding the TRSLG to quantify the amount and chemistry of open precipitation. They consisted of plastic (PVC) tubes of 20.5 cm diameter and 100 cm length that were fixed 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, and the first sampling event after renewal was discarded. Generally bulk deposition includes a small fraction of dry deposition. In this study the closure of bulk precipitation samplers between sampling periods reduced this small contribution of dry deposition to bulk deposition samplers and bulk deposition therefore largely represents wet deposition. To avoid contamination during and between sampling intervals collectors for throughfall were covered with a wire net (mesh width 10 mm) 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, accumulation of dry deposits and any contamination when no samples were taken. Collectors were opened every 3–7 days until a rainfall event occurred and was collected. Otherwise the collectors were kept closed. Throughfall collectors ( $n = 45$ ) were set up according to the design described for bulk deposition collectors. Throughfall was sampled by placing the collectors in the middle of every subplot and also in the middle of each plot, so that every plot was equipped with five traps. After each rainfall event the total amount of water per collector was determined volumetrically using measuring cylinders. Two types of stemflow collectors ( $n = 36$ ) were used for trees with diameter at breast height (dbh) greater and smaller than 10 cm. For trees <10 cm dbh 0.5 l polyethylene bottles were longitudinally cut on one side and mounted upside down around the stems. Bottles were sealed to the stem by sanitary silicone and connected to collection bottles (1–5 l, PE) using silicone tubing. Trees with a diameter >10 cm dbh were equipped with a flexible tubing (garden hose) 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 stemflow losses. Collection vessels (allowing up to 25 l of stemflow sampling from large trees above 30 cm dbh) were connected to the flexible tubes when sampling was performed or disconnected between sampling events. The first event of stemflow collection was discarded to avoid contamination from injured bark and sanitary silicone. After each rainfall event total amount of water per collector was determined volumetrically using measuring cylinders. Soil water samples ( $n = 9$ ) were 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 were evacuated with a hand operated vacuum pump to a pressure of 40 kPa.

Directly after sample collection the pH was measured in all water fractions at TRSLG using a Sentron ArgusX pH meter (Sentron, Roden, Netherlands). Due to technical problems only four rainfall events were measured for pH. From each collector two sample aliquots (15 ml) were then transferred into 20 ml HDPE vials and stabilized against

microbial transformation by addition of  $\text{HgCl}_2$  (30  $\mu\text{M}$  end concentration, for TOC/TN analysis) or Hg-Phenyl acetate (30  $\mu\text{M}$  end concentration, for ion chromatography) and stored at  $-20^\circ\text{C}$  immediately after collection.

#### Chemical analyses

The following chemical analyses were performed at the Department of Chemical Ecology and Ecosystem Research, University of Vienna, Austria: Inorganic anions ( $\text{Cl}^-$ ,  $\text{NO}_3^-$ ,  $\text{SO}_4^{2-}$ ,  $\text{HPO}_4^{2-}$ ) and cations ( $\text{Na}^+$ ,  $\text{NH}_4^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ) 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,  $4 \times 250$  mm, Dionex) using a linear KOH gradient (2–30 mM in 6 min, total run time 10 min). Cations were separated on a cation exchange column (CS16,  $5 \times 250$  mm, Dionex) by an isocratic method with methanesulfonic acid as eluent (30 mM methanesulfonic acid for 26 min and  $40^\circ\text{C}$ ). Data analysis was conducted with Chromeleon Version 6.70 Build 1820. NPOC (non-purgeable organic carbon) and TDN (total dissolved nitrogen) content of samples were determined using a TOC- $\text{V}_{\text{CPH/CPN/TNM-1}}$  analyzer (Shimadzu, Japan). DON was calculated by subtracting DIN (dissolved nitrate and ammonium) from measured TDN. The respective details on analytical performance (e.g. linearity, limit of quantification, precision) are presented in Supplementary Table 1.

Dried soil and litter samples were homogenized in a ball mill (Retsch MM2000) and aliquots (1.5–2.0 mg) were weighed into tin capsules for analysis of total carbon and nitrogen content by elemental analysis (EA 1110, CE Instruments). For phosphorus and cation analysis litter samples were first acid digested. Approximately 100 mg dried samples were wet digested with 5 ml nitric acid-perchloric acid mixture ( $\text{HNO}_3:\text{HClO}_4$  4:1) (Kolmer et al. 1951) in 25 ml glass flasks on a heating plate where the temperature was increased stepwise to  $250^\circ\text{C}$  and the final temperature held until a small residual volume was left in the glass flask. Samples were cooled to room temperature, and filled to 25 ml with high purity water. The digests were filtered and total phosphorus measured by colorimetric analysis using the phosphomolybdate blue method (Schinner

et al. 1996) and cations ( $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ) by atomic absorption spectrometry.

#### Calculations

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

$$\text{VWM} = \frac{\sum_{i=1}^n (C_i * V_i)}{\sum_{i=1}^n V_i} \quad (1)$$

Annual nutrient fluxes were calculated by multiplication of volume weighted mean values per trap with the ratio of throughfall volume: bulk precipitation volume of the respective trap during the sampling period times annual precipitation volume. Throughfall (Eq. 2) 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 canopy exchange (CE) and dry deposition (DD):

$$\text{TF} = \text{BP} + \text{CE} + \text{DD} \quad (2)$$

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

$$\text{NTF} = \text{TF} - \text{BP} = \text{CE} + \text{DD} \quad (3)$$

To calculate the contribution of canopy exchange and dry deposition to annual net throughfall fluxes we computed and compared two different approaches i.e. the multiple regression model (Lovett and Lindberg 1984) and the canopy budget model (Ulrich 1983).

#### Multiple regression model

The multiple regression model was proposed by (Lovett and Lindberg 1984) for the separation of canopy exchange and dry deposition components of net throughfall based on event sampling (Eq. 4):

$$\text{NTF}_x = a + b1 * A + b2 * P \quad (4)$$

In this regression equation factors b1 (dry period constant) and b2 (bulk precipitation constant) represent coefficients of the calculated linear model for A (antecedent dry period; in days) and P (magnitude of

precipitation; in mm) and a is the intercept term. A negative canopy exchange coefficient (b2) indicates uptake of the solute during a rain event, while a positive coefficient points to canopy leaching of the solute. For a given precipitation event DD is the product of the dry deposition coefficient (b1) and the antecedent dry period (A), while CE is the product of the canopy exchange coefficient (b2) times the amount of precipitation (P). Multiple regression model calculations were performed with the mean net throughfall fluxes of all collectors of a forest type per event. With this model it is possible to investigate whether a certain element rather derives from dry deposition or canopy exchange processes and therefore originates from external or internal sources in terms of nutrient cycling (Filoso et al. 1999; Lovett et al. 1996; Veneklaas 1990). By multiplying the values for b1 by annual number of dry days (80 days during the study year) and b2 by the annual amount of precipitation (5720 mm during the study year) it is possible to estimate the annual fluxes of dry deposition and canopy retention or leaching.

Moreover, the calculation of annual dry deposition allows studying the uncertainty of atmospheric deposition estimates based on bulk deposition only or based on combined bulk plus dry deposition (total deposition), by calculating the relative contribution of dry deposition to total atmospheric deposition (Eq. 5):

$$\text{relDD}(\%) = \text{DD} / (\text{DD} + \text{BP}) * 100 \quad (5)$$

#### Canopy budget model

The canopy budget model simulates the interaction of substances within forest canopies based on measurements of throughfall and precipitation and therefore is applicable to distinguish the relative importance of dry deposition and canopy exchange to net throughfall fluxes. The model has been used to estimate dry deposition and canopy exchange fluxes in a wide range of forest ecosystems, and different approaches have been reported (Staelens et al. 2008). Canopy budget model calculations are commonly based on mean (semi)annual fluxes in throughfall per forest site. We here compare three different approaches considering the application of a tracer ion only (filtering approach), the reference approach and the weak acid approach on an annual time step basis:

**Filtering approach** The filtering approach (Ulrich 1983) is used to estimate dry deposition of base cations ( $K^+$ ,  $Ca^{2+}$ , and  $Mg^{2+}$ ). In this approach aerosols containing base cations are assumed to be deposited with equal efficiency onto the forest canopy as particles containing an inert tracer ion. Sodium is often used as a tracer ion because it is assumed not to be influenced by canopy exchange processes (Staelens et al. 2008). Dry deposition of a certain element X ( $DD_X$ ) is calculated as the product of the dry deposition factor (DDF) of the tracer ion (here:  $Na^+$ ), which is the NTF to BP ratio of  $Na^+$ , times the bulk precipitation of element X (Eq. 6):

$$DD_X = \frac{(TF - BP)_{Na}}{BP_{Na}} * BP_X \quad (6)$$

Canopy exchange viz. canopy leaching (CL) of base cations is then determined by subtracting dry deposition from NTF (Eq. 3). This approach has also been applied to solutes other than base cations (Kopacek et al. 2009).

**Reference approach** Considering ion exchange processes within a tree canopy, it is assumed that the canopy uptake (CU) of  $NH_4^+$  and  $H^+$  is counterbalanced by an equivalent release of base cations (Cronan and Reiners 1983). In this reference approach only the flux balance between canopy uptake of  $H^+$  and  $NH_4^+$  and canopy leaching of base cations ( $K^+$ ,  $Ca^{2+}$ , and  $Mg^{2+}$ ) is considered, which due to the ion charge balance of the canopy is assumed to be equal (Eq. 7):

$$CU_{NH_4+H} = CL_{BC} \quad (7)$$

To partition the ion uptake between  $H^+$  and  $NH_4^+$  (Eq. 8a) the relative uptake efficiency factor  $xH$  is applied assuming that the exchange capacity of  $H^+$  per mol is six times greater than that of  $NH_4^+$  ( $xH = 6$ ). Dry deposition of  $H^+$  and  $NH_4^+$  is then calculated based on Eq. 3. Canopy uptake of  $NO_3^-$  is calculated based on preferential uptake of  $NH_4^+$  compared to  $NO_3^-$ , using an efficiency factor of  $NH_4^+$  versus  $NO_3^-$  uptake ( $xNH_4$ ) with a proposed value of 6 (Eq. 8b).  $xNH_4$  has been found to be very close to this assumed value, being 6.4 for detached tree branches at the same forest site (Hinko-Najera Umana and Wanek 2010) as evaluated by  $^{15}NH_4^+$  versus  $^{15}NO_3^-$  retention rates. Dry deposition of  $NO_3^-$  is again calculated by Eq. 3.

$$CU_{NH_4} = \frac{(TF)_{NH_4}}{(TF)_{NH_4} + xH * (TF)_H} * CL_{BC} \quad (8a)$$

$$CU_{NO_3+NH_4} = \frac{xNH_4 * (TF)_{NH_4} + (TF)_{NO_3}}{xNH_4 * (TF)_{NH_4}} * CU_{NH_4} \quad (8b)$$

**Canopy leaching of weak acids** When weak acid (WA) leaching is included in the canopy budget model, it is assumed that canopy leaching of base cations ( $K^+$ ,  $Ca^{2+}$ , and  $Mg^{2+}$ ) is due to canopy uptake of  $H^+$  +  $NH_4^+$  and canopy leaching of WA (Eq. 9).

$$CU_{NH_4+H} = CL_{BC} - CL_{WA} \quad (9)$$

$CL_{WA}$  is calculated by subtracting TD (=WD + DD) from TF of WA. To estimate the concentration of WA in water samples organic anion concentrations are estimated from DOC concentrations and corresponding pH values using a model proposed by (Oliver et al. 1983) so that the dissociation ( $HA = H^+ + A^-$ ) can be estimated by Eq. 10:

$$A^- = \frac{K[DOC]}{K + [H^+]} \quad (10)$$

where  $A^-$  is the organic anion concentration, DOC is the organic carbon concentration and K is the mass action quotient estimated from sample pH using Eq. 11:

$$pK = 0.96 + 0.90pH - 0.039(pH)^2 \quad (11)$$

Statistical analyses

Statistical analyses such as one-way analysis of variance (ANOVA), multiple regression analysis and principle component analysis (PCA) were computed with STATISTICA for Windows 7.5 (STATSOFT 2005). Differences in 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 (with/without log-transformation of data). 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 did not meet homogeneity of variances and normality after log-transformation.

Principle component analysis was applied as a factor analytical technique to reduce the number of

variables and to detect structure in the relationships between variables that is to classify variables (event-based NTF of different solutes, based on single trap results) and compare the forest sites. In compliance with the Scree Test and the Kaiser Criterion (Eigen values > 1) four principle components were extracted and subsequent Varimax Rotation (orthogonal arrangement of factors) was used to allow specific interpretation of data.

Statistical analysis investigating species assemblages were computed with PRIMER 6.0 (Clarke and Gorley 2006). Fisher's alpha index, fitting best for species-rich areas as it accounts especially for rare single species (singletons), was computed to test for 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 type. 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 were related by Spearman matrix rank correlation to test for significant relationships between nutrient fluxes and tree species assemblages on the respective forest site. Another Spearman rank correlation, analysing non-parametric data by the formation of ranks, investigated the relationship between ion fluxes and plant area index above a given throughfall trap.

## Results

### Soils

Bulk densities ranged from  $0.41 \text{ g cm}^{-3}$  (at site PRi) to  $0.61 \text{ g cm}^{-3}$  (at site PRa) (Table 1). Soil pH ( $\text{CaCl}_2$ ) ranged between 3.28 and 3.68 and was lowest at site PRi. Soil  $C_{\text{tot}}$  and  $N_{\text{tot}}$  concentrations were high for the topsoil (0–5 cm, after removal of organic horizon), ranging between 4.8 and 8.6% for C and between 0.37 and 0.64% for N, and were lowest at site SRa (Table 1). Similar to soil solutions, extractable soil  $\text{NO}_3^-$  was highest at site PRa, while  $\text{NH}_4^+$  was highest at site PRi. Extractable  $\text{K}^+$  and  $\text{HPO}_4^{2-}$  did not differ between sites, but  $\text{HPO}_4^{2-}$

**Table 1** Soil characteristics (pH; bulk density, BD, in  $\text{g cm}^{-3}$ ) and concentrations of  $\text{CaCl}_2$  (10 mM)-extractable soil nutrients (0–5 cm, in  $\text{mg kg}^{-1}$ ;  $\text{g kg}^{-1}$  for  $C_{\text{tot}}$  and  $N_{\text{tot}}$ )

	pH ( $\text{CaCl}_2$ )	BD	$\text{Na}^+$	$\text{NH}_4^+$	$\text{K}^+$	$\text{Mg}^{2+}$	$\text{NO}_3^-$	$\text{SO}_4^{2-}$	$\text{HPO}_4^{2-}$	$C_{\text{tot}}$	$N_{\text{tot}}$
PRi	$3.28 \pm 0.02$ a	0.41	$29.3 \pm 12.1$	$24.4 \pm 3.8$ b	$173 \pm 79.8$	$225 \pm 31.3$	$18.8 \pm 4.0$ a	$11.4 \pm 3.8$	$0.7 \pm 0.0$	$85.9 \pm 8.1$	$6.2 \pm 0.3$
PRa	$3.68 \pm 0.04$ b	0.61	$25.9 \pm 4.9$	$11.5 \pm 1.7$ a	$122 \pm 17.2$	$250 \pm 37.0$	$49.6 \pm 7.6$ b	$9.3 \pm 1.3$	$2.1 \pm 0.4$	$77.8 \pm 4.6$	$6.4 \pm 0.3$
SRa	$3.56 \pm 0.04$ b	0.49	$17.3 \pm 3.5$	$6.9 \pm 0.8$ a	$200 \pm 51.8$	$147 \pm 21.5$	$9.0 \pm 1.3$ a	$8.6 \pm 0.9$	$4.8 \pm 2.3$	$48.0 \pm 4.5$	$3.7 \pm 0.2$

Data are means  $\pm 1$  standard error for the respective forest sites, i.e. primary ridge (PRi), primary ravine (PRa) and secondary ravine (SRa) forest (Piedras Blancas National Park, SW Costa Rica). Significant differences between forest sites are indicated by different letters (one-way ANOVA,  $p < 0.05$ )



showed a trend towards greater availability in soil solution at site PRa (and site SRa) compared to site PRi ( $p < 0.10$ ). Concentrations of  $K^+$ ,  $Mg^{2+}$  and  $Ca^{2+}$  in soil solution did not differ significantly between sites (Table 2).

### Throughfall hydrochemistry

One-way ANOVA showed no statistically significant differences in throughfall volumes between forest sites, for rainfall events ranging from 5 to 168 mm. Throughfall comprised between 87% (SRa), 90% (PRa) and 92% (PRi) of bulk precipitation volume, on an annual basis. Annual precipitation during the study year was 5720 mm.

Generally variations in nutrient concentration between collectors within each forest type were relatively high, with CVs ranging between 8–26% for bulk precipitation and 20–160% for throughfall. Due to this high spatial variability few significant differences were found in nutrient concentrations between forest types (Table 2). Statistical analysis of volume weighted mean concentrations and net throughfall fluxes of solutes produced the same significant differences between sites as they are mathematically related i.e. multiplication of volume weighted mean concentration times volume of annual throughfall gives net throughfall flux. Statistical analysis of volume weighted mean concentrations produced the same significant differences as that of throughfall fluxes, which were calculated by multiplying volume weighted mean concentrations times volume of annual throughfall (see results below). Sodium concentrations in throughfall were highest at PRi,  $HPO_4^{2-}$  highest in throughfall at PRa and  $NO_3^-$  lowest in throughfall at SRa (Table 2).

### Nutrient fluxes and throughfall modelling

In the Esquinas forest stemflow contributed <1% to hydrological fluxes and nutrient fluxes in stemflow were well below 5% of that in throughfall at all sites (data not shown), similar to values reported previously (Herwitz and Levia 1997). Stemflow was therefore excluded from further discussion and will be presented in a separate paper.

Bulk precipitation inputs of dissolved ions ranged from 0.4 ( $HPO_4^{2-}$ ) to 20.0 kg ha<sup>-1</sup> year<sup>-1</sup> ( $Ca^{2+}$ ). Inputs for dissolved organic carbon (DOC) and total

**Table 2** Solute concentrations ( $\mu\text{g l}^{-1}$ ) in bulk precipitation and throughfall (volume weighted means) and in soil water

	H <sup>+</sup>	Na <sup>+</sup>	NH <sub>4</sub> <sup>+</sup>	K <sup>+</sup>	Mg <sup>2+</sup>	Ca <sup>2+</sup>	Cl <sup>-</sup>	NO <sub>3</sub> <sup>-</sup>	SO <sub>4</sub> <sup>2-</sup>	HPO <sub>4</sub> <sup>-</sup>	DOC	DON	TDN
Bulk precipitation	25.2 ± 2.9	170 ± 13.8	96.6 ± 11.2	160 ± 31.3	77.8 ± 12.2	297 ± 36.1	149 ± 21.3	43.4 ± 4.2	80.3 ± 6.4	6.2 ± 3.1	623 ± 55.2	33.6 ± 19.6	173 ± 11.1
Throughfall													
PRi	8.1 ± 2.8	198 ± 25.3 b	67.2 ± 5.6	700 ± 82.1	129 ± 9.7	357 ± 20.0	362 ± 46.2	16.8 ± 1.4 b	122 ± 16.1	9.3 ± 3.1 a	1272 ± 146	93.8 ± 18.2	178 ± 11.9
PRa	4.2 ± 1.7	131 ± 9.2 a	96.6 ± 9.8	1482 ± 512	177 ± 26.7	485 ± 40.1	376 ± 67.5	19.6 ± 1.4 b	106 ± 9.6	31.0 ± 9.3 b	1704 ± 401	120 ± 25.2	236 ± 16.9
SRa	7.8 ± 2.3	127 ± 9.2 a	109 ± 23.8	946 ± 117	136 ± 9.7	449 ± 28.1	266 ± 14.2	12.6 ± 1.4 a	93.1 ± 6.4	15.5 ± 3.1 a	1548 ± 139	112 ± 15.4	234 ± 18.6
Soil water													
PRi	3.5 ± 1.0	495 ± 115	141 ± 44.8 b	1114 ± 102	374 ± 21.9	866 ± 84	1243 ± 351	25.2 ± 7.0 a	199 ± 86.7	3.1 ± 0.0	1944 ± 398	26.6 ± 78.4	193 ± 44.5
PRa	3.5 ± 2.1	589 ± 212	50.4 ± 5.6 a	1529 ± 414	498 ± 114	1395 ± 240	888 ± 266	304 ± 190 b	196 ± 83.5	15.5 ± 9.3	1644 ± 602	147 ± 51.8	501 ± 131
SRa	3.2 ± 0.9	545 ± 36.8	65.8 ± 5.6 ab	1595 ± 375	399 ± 70.5	1098 ± 148	1058 ± 245	8.4 ± 2.8 a	151 ± 61.0	9.3 ± 3.1	2952 ± 923	115 ± 5.6	193 ± 5.4

Data are means ± 1 standard error for the respective forest sites, i.e. primary ridge (PRi), primary ravine (PRa) and secondary ravine (SRa) forest (Piedras Blancas National Park, SW Costa Rica). Significant differences between forest sites are indicated by different letters (one-way ANOVA,  $p < 0.05$ ). n.d. not determined

dissolved nitrogen (TDN) were 30.9 and 7.7 kg ha<sup>-1</sup> year<sup>-1</sup>, respectively. Throughfall fluxes of dissolved ions ranged from 0.4 (HPO<sub>4</sub><sup>2-</sup>) to 80.4 kg ha<sup>-1</sup> year<sup>-1</sup> (K<sup>+</sup>). Fluxes of DOC and TDN were found as high as 94.9 and 13.8 kg ha<sup>-1</sup> year<sup>-1</sup> in throughfall, respectively (Table 3). We found significant differences in solute fluxes between bulk precipitation and throughfall (full model:  $F_{(39)} = 3.9$ ,  $p < 0.001$ ). Compared to throughfall, bulk precipitation (BP) showed higher annual fluxes of H<sup>+</sup> (BP > PRa) and NO<sub>3</sub><sup>-</sup> (BP > PRi) and lower fluxes of Na<sup>+</sup> (BP < PRi), K<sup>+</sup> (BP < PRa), Cl<sup>-</sup> (BP < PRi) and SO<sub>4</sub><sup>2-</sup> (BP < PRi). However the greatest differences were found in fluxes of K<sup>+</sup> and NO<sub>3</sub><sup>-</sup>, where fluxes of NO<sub>3</sub><sup>-</sup> were higher and K<sup>+</sup> lower in bulk precipitation compared to throughfall at all sites. Between forest sites we found significant differences in throughfall fluxes for Na<sup>+</sup> (one-way ANOVA,  $p = 0.01$ ) being highest at PRi, NO<sub>3</sub><sup>-</sup> ( $p = 0.01$ ) being lowest at Sra and HPO<sub>4</sub><sup>2-</sup> ( $p = 0.002$ ) being highest at PRa (Table 3). Positive net throughfall fluxes indicated pronounced net increases of K<sup>+</sup> and DOC, with lower enrichments found for Cl<sup>-</sup>, TDN, DON, Ca<sup>2+</sup>, Mg<sup>2+</sup>, Na<sup>+</sup>, SO<sub>4</sub><sup>2-</sup> and HPO<sub>4</sub><sup>2-</sup> (in decreasing order, Fig. 1). In contrast negative values of net throughfall fluxes pointed to marked net retention and/or uptake of NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup> and H<sup>+</sup> (Fig. 1). Statistics of site-specific differences in net throughfall fluxes were consistent with that of throughfall fluxes due to their close mathematical relationship (Eq. 3).

The multiple regression model of event-based net throughfall was highly significant for most solutes, except NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup> and HPO<sub>4</sub><sup>2-</sup> (Table 4). As the intercepts of the multiple regression models were not significant (i.e. not significantly different from zero) for any solute and forest type, they were omitted from final multiple regression analyses. However it should be noted that for regressions that are forced through the origin, the properties of the resulting regression line are different than for an unforced regression. As a consequence, residuals of regressions through the origin must be interpreted with care and the sum of the squared residuals may exceed the total sum of squares, so that  $R^2$  has no clear meaning for regressions through the origin (Neter et al. 1996). Application of regression models with and without intercept terms showed that omitting intercept terms in these regressions resulted in more adequate estimates of canopy exchange and dry deposition (NTF = CE + DD) that differed from calculated net

throughfall (NTF = TF - BP) by a factor of only  $0.96 \pm 0.08$  compared to a factor of  $0.78 \pm 0.09$  from regressions comprising intercept terms.

No significant differences in canopy exchange or dry deposition between forest types were evident, considering overlapping confidence intervals (CI) of their estimates for the three forest sites (CI calculated as the product of SE times 1.96; Table 3). Therefore for comparative analyses of canopy exchange versus litterfall fluxes (Fig. 2), and of dry deposition versus total deposition (Fig. 3), results of the multiple regression model combined for all sites were used. Canopy exchange fluxes were positive in most cases, indicating leaching from the forest canopy; exceptions were NH<sub>4</sub><sup>+</sup> (PRi) and NO<sub>3</sub><sup>-</sup> (all sites) showing negative canopy exchange estimates. Dry deposition estimates were in some cases negative i.e. Na<sup>+</sup> (PRi, PRa), NO<sub>3</sub><sup>-</sup> (all sites) and DOC (PRi). Though most multiple regression models were highly significant a large uncertainty in dry deposition coefficients for some solutes (Na<sup>+</sup>, HPO<sub>4</sub><sup>2-</sup>, NO<sub>3</sub><sup>-</sup>, and NH<sub>4</sub><sup>+</sup>) caused dry deposition estimates not to be significantly different from zero. They are still the best estimates of the deposition rate, even if they were not statistically significant from zero. NTF was mostly dominated by canopy exchange compared to dry deposition for Na<sup>+</sup>, K<sup>+</sup>, Mg<sup>2+</sup>, and SO<sub>4</sub><sup>2-</sup> while dry deposition dominated NTF for TDN and DON and both, canopy exchange and dry deposition, contributed equally to NTF of Ca<sup>2+</sup>, Cl<sup>-</sup> and DOC.

Compared to the multiple regression model the canopy budget model (filtering approach) produced markedly higher estimates of dry deposition for most elements (e.g. for Na<sup>+</sup>) and particularly for the exposed PRi forest site. Higher dry deposition estimates were found for Na<sup>+</sup>, NH<sub>4</sub><sup>+</sup>, Mg<sup>2+</sup>, Ca<sup>2+</sup>, and SO<sub>4</sub><sup>2-</sup> in the canopy budget model compared to the multiple regression model, resulting in lower estimates of canopy exchange fluxes i.e. lower canopy leaching or enhanced canopy uptake in the canopy budget model. In contrast, dry deposition calculated by the canopy budget model was lower compared to the multiple regression model for K<sup>+</sup> and DON, resulting in higher estimates of canopy leaching of these solutes. For Cl<sup>-</sup>, DOC and TDN dry deposition estimates varied between both models, and therefore the resulting canopy exchange fluxes differed in their response between sites and models. At PRi Na<sup>+</sup> throughfall fluxes were highest among sites, translating into an

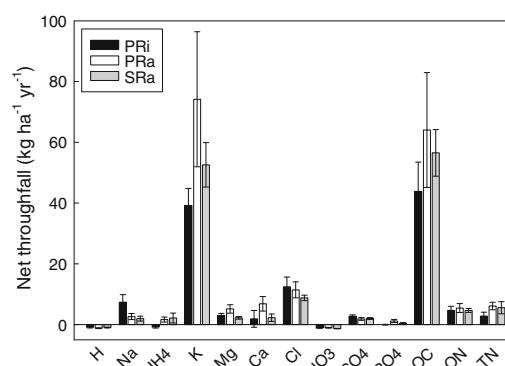
**Table 3** Annual solute fluxes from external sources (atmospheric deposition via bulk and dry deposition), mixed sources (throughfall) and internal sources (litterfall, canopy exchange)

	H <sup>+</sup>	Na <sup>+</sup>	NH <sub>4</sub> <sup>+</sup>	K <sup>+</sup>	Mg <sup>2+</sup>	Ca <sup>2+</sup>	Cl <sup>-</sup>	NO <sub>3</sub> <sup>-</sup>	SO <sub>4</sub> <sup>2-</sup>	HPO <sub>4</sub> <sup>-</sup>	DOC	DON	TDN
Bulk precipitation	1.4 ± 0.1	6.9 ± 1.0	5.1 ± 0.9	6.2 ± 0.4	5.4 ± 0.8	20.0 ± 1.5	6.3 ± 0.4	2.0 ± 0.1	3.3 ± 0.1	0.4 ± 0.1	30.9 ± 1.0	0.6 ± 0.9	7.7 ± 1.9
Throughfall													
PRi	0.6 ± 0.2	14.3 ± 2.5	4.3 ± 0.4	45.5 ± 5.6	8.4 ± 0.7	21.9 ± 2.8	18.7 ± 3.2	0.9 ± 0.1	6.0 ± 0.4	0.4 ± 0.1	74.7 ± 9.7	5.2 ± 1.4	10.5 ± 1.3
PRa	0.3 ± 0.1	9.5 ± 1.0	6.7 ± 0.8	80.4 ± 22.2	10.5 ± 1.4	26.9 ± 2.4	17.7 ± 2.6	1.0 ± 0.1	5.2 ± 0.4	1.6 ± 0.5	94.9 ± 18.9	6.0 ± 1.5	13.8 ± 1.2
SRa	0.5 ± 0.1	8.9 ± 0.8	7.3 ± 1.6	58.8 ± 7.3	7.6 ± 0.4	22.3 ± 1.2	15.1 ± 0.9	0.7 ± 0.1	5.3 ± 0.3	0.8 ± 0.2	87.4 ± 7.7	5.3 ± 0.7	13.2 ± 2.0
Dry deposition													
Multiple regression													
PRi	-0.5 ± 0.8		0.5 ± 0.4	5.1 ± 2.4	0.3 ± 0.4	0.5 ± 0.8	2.9 ± 1.8	-0.2 ± 0.2	0.2 ± 0.3	0.0 ± 0.1	-0.8 ± 19.5	1.2 ± 2.0	1.5 ± 2.6
PRa	-0.1 ± 0.4		0.4 ± 0.5	6.7 ± 4.5	0.5 ± 0.4	1.3 ± 0.9	2.4 ± 1.2	-0.1 ± 0.2	0.2 ± 0.1	0.1 ± 0.2	44.4 ± 12.7	6.6 ± 2.0	7.0 ± 2.7
SRa	0.1 ± 0.4		0.2 ± 0.7	5.5 ± 2.0	0.4 ± 0.4	1.3 ± 0.8	2.5 ± 1.0	-0.2 ± 0.2	0.3 ± 0.1	-0.1 ± 0.1	31.4 ± 14.9	9.1 ± 2.2	9.0 ± 3.2
Filtering app.													
PRi	1.5 ± 0.0	7.4 ± 0.0	5.4 ± 0.0	6.7 ± 0.0	5.8 ± 0.0	21.4 ± 0.0	6.7 ± 0.0	2.2 ± 0.0	3.5 ± 0.0	0.7 ± 0.0	33.1 ± 0.0	0.6 ± 0.0	8.2 ± 0.0
PRa	0.6 ± 0.0	2.6 ± 0.0	2.0 ± 0.0	2.4 ± 0.0	2.1 ± 0.0	7.7 ± 0.0	2.4 ± 0.0	0.8 ± 0.0	1.3 ± 0.0	0.2 ± 0.0	11.9 ± 0.0	0.2 ± 0.0	2.9 ± 0.0
SRa	0.4 ± 0.0	2.0 ± 0.0	1.5 ± 0.0	1.8 ± 0.0	1.5 ± 0.0	5.7 ± 0.0	1.8 ± 0.0	0.6 ± 0.0	0.9 ± 0.0	0.2 ± 0.0	8.8 ± 0.0	0.2 ± 0.0	2.2 ± 0.0
Reference app.													
PRi	-0.4 ± 0.3	7.4 ± 0.0	0.6 ± 0.7	6.7 ± 0.0	5.8 ± 0.0	21.4 ± 0.0	6.7 ± 0.0	-1.1 ± 0.1	3.5 ± 0.0	0.7 ± 0.0	33.1 ± 0.0	0.6 ± 0.0	8.2 ± 0.0
PRa	-0.5 ± 0.2	2.6 ± 0.0	18.5 ± 8.8	2.4 ± 0.0	2.1 ± 0.0	7.7 ± 0.0	2.4 ± 0.0	-0.6 ± 0.2	1.3 ± 0.0	0.2 ± 0.0	11.9 ± 0.0	0.2 ± 0.0	2.9 ± 0.0
SRa	-0.1 ± 0.2	2.0 ± 0.0	7.2 ± 2.2	1.8 ± 0.0	1.5 ± 0.0	5.7 ± 0.0	1.8 ± 0.0	-1.2 ± 0.1	0.9 ± 0.0	0.2 ± 0.0	8.8 ± 0.0	0.2 ± 0.0	2.2 ± 0.0
Weak acid app.													
PRi	0.2 ± 0.5	7.4 ± 0.0	0.6 ± 0.7	6.7 ± 0.0	5.8 ± 0.0	21.4 ± 0.0	6.7 ± 0.0	-1.1 ± 0.1	3.5 ± 0.0	0.7 ± 0.0	33.1 ± 0.0	0.6 ± 0.0	8.2 ± 0.0
PRa	0.5 ± 0.6	2.6 ± 0.0	18.5 ± 8.8	2.4 ± 0.0	2.1 ± 0.0	7.7 ± 0.0	2.4 ± 0.0	-0.6 ± 0.2	1.3 ± 0.0	0.2 ± 0.0	11.9 ± 0.0	0.2 ± 0.0	2.9 ± 0.0
SRa	-0.1 ± 0.2	2.0 ± 0.0	7.2 ± 2.2	1.8 ± 0.0	1.5 ± 0.0	5.7 ± 0.0	1.8 ± 0.0	-1.2 ± 0.1	0.9 ± 0.0	0.2 ± 0.0	8.8 ± 0.0	0.2 ± 0.0	2.2 ± 0.0
Canopy exchange													
Multiple regression													
PRi		8.0 ± 1.7	-0.8 ± 0.8	25.0 ± 4.9	1.6 ± 0.9	1.3 ± 1.7	5.1 ± 2.9	-0.5 ± 0.3	2.1 ± 0.5	0.1 ± 0.1	30.4 ± 10.9	3.2 ± 0.3	2.0 ± 1.4
PRa		3.3 ± 0.7	0.5 ± 1.0	51.4 ± 9.3	3.8 ± 0.7	4.1 ± 1.9	5.4 ± 2.0	-0.4 ± 0.3	1.4 ± 0.2	0.9 ± 0.4	34.8 ± 7.1	1.4 ± 0.2	1.5 ± 1.5
SRa		1.5 ± 0.7	2.0 ± 1.5	34.4 ± 4.2	1.4 ± 0.7	0.7 ± 1.6	2.5 ± 1.6	-0.6 ± 0.3	1.2 ± 0.2	0.4 ± 0.2	25.2 ± 8.4	-0.2 ± 0.0	1.2 ± 1.8
Filtering app.													
PRi	-2.4 ± 0.2	0.0 ± 2.5	-6.2 ± 0.4	32.6 ± 5.6	-2.7 ± 0.7	-19.6 ± 2.8	5.7 ± 3.2	-3.3 ± 0.1	-0.8 ± 0.4	-0.7 ± 0.2	10.8 ± 9.7	4.1 ± 1.4	-5.4 ± 1.3
PRa	-1.7 ± 0.1	0.0 ± 1.0	-0.3 ± 0.8	71.8 ± 22.2	3.1 ± 1.4	-0.8 ± 2.4	9.0 ± 2.6	-1.8 ± 0.1	0.6 ± 0.4	1.5 ± 0.8	52.2 ± 18.9	5.2 ± 1.5	3.2 ± 1.2
SRa	-1.4 ± 0.1	0.0 ± 0.8	0.7 ± 1.6	50.8 ± 7.3	0.7 ± 0.4	-3.5 ± 1.2	7.0 ± 0.9	-1.9 ± 0.1	1.1 ± 0.3	0.4 ± 0.3	47.7 ± 7.7	4.5 ± 0.7	3.4 ± 2.0
Reference app.													
PRi	-0.4 ± 0.2	0.0 ± .5	-1.4 ± 0.5	32.6 ± 5.6	-2.7 ± 0.7	-19.6 ± 2.8	5.7 ± 3.2	0.0 ± 0.0	-0.8 ± 0.4	-0.7 ± 0.2	10.8 ± 9.7	4.1 ± 1.4	-5.4 ± 1.3
PRa	-0.7 ± 0.1	0.0 ± 1.0	-16.8 ± 8.8	71.8 ± 22.2	3.1 ± 1.4	-0.8 ± 2.4	9.0 ± 2.6	-0.4 ± 0.2	0.6 ± 0.4	1.5 ± 0.8	52.2 ± 18.9	5.2 ± 1.5	3.2 ± 1.2
SRa	-0.9 ± 0.2	0.0 ± 0.8	-5.0 ± 1.3	50.8 ± 7.3	0.7 ± 0.4	-3.5 ± 1.2	7.0 ± 0.9	-0.1 ± 0.0	1.1 ± 0.3	0.4 ± 0.3	47.7 ± 7.7	4.5 ± 0.7	3.4 ± 2.0

Table 3 continued

	H <sup>+</sup>	Na <sup>+</sup>	NH <sub>4</sub> <sup>+</sup>	K <sup>+</sup>	Mg <sup>2+</sup>	Ca <sup>2+</sup>	Cl <sup>-</sup>	NO <sub>3</sub> <sup>-</sup>	SO <sub>4</sub> <sup>2-</sup>	HPO <sub>4</sub> <sup>-</sup>	DOC	DON	TDN
<b>Weak acid app.</b>													
PRi	-1.1 ± 0.4	0.0 ± 2.5	-1.4 ± 0.5	32.6 ± 5.6	-2.7 ± 0.7	-19.6 ± 2.8	5.7 ± 3.2	0.0 ± 0.0	-0.8 ± 0.4	-0.7 ± 0.2	10.8 ± 9.7	4.1 ± 1.4	-5.4 ± 1.3
PRa	-1.7 ± 0.6	0.0 ± 1.0	-16.8 ± 8.8	71.8 ± 22.2	3.1 ± 1.4	-0.8 ± 2.4	9.0 ± 2.6	-0.4 ± 0.2	0.6 ± 0.4	1.5 ± 0.8	52.2 ± 18.9	5.2 ± 1.5	3.2 ± 1.2
SRa	-0.8 ± 0.2	0.0 ± 0.8	-5.0 ± 1.3	50.8 ± 7.3	0.7 ± 0.4	-3.5 ± 1.2	7.0 ± 0.9	-0.1 ± 0.0	1.1 ± 0.3	0.4 ± 0.3	47.7 ± 7.7	4.5 ± 0.7	3.4 ± 2.0
<b>Litter fall</b>													
PRi		1.9 ± 0.2		32.7 ± 4.7	16.1 ± 1.9	97.6 ± 9.2			5.2 ± 1.3		4406 ± 467		101 ± 11.1
PRa		2.6 ± 0.3		57.1 ± 6.2	35.1 ± 4.2	200 ± 23.3			10.6 ± 1.4		6232 ± 519		185 ± 15.7
SRa		2.2 ± 0.2		38.9 ± 5.0	18.1 ± 2.6	151 ± 23.1			6.3 ± 0.8		5050 ± 607		116 ± 13.2

Data are means ± 1 standard error (kg ha<sup>-1</sup> year<sup>-1</sup>). Significant differences in annual nutrient fluxes between forest sites i.e. primary ridge (PRi), primary ravine (PRa) and secondary ravine (SRa) forest (Piedras Blancas National Park, SW Costa Rica) are indicated by different letters (one-way ANOVA,  $p < 0.05$ )



**Fig. 1** Net throughfall fluxes (NTF; in kg ha<sup>-1</sup> year<sup>-1</sup>) of solutes in primary ridge (PRi), primary ravine (PRa) and secondary ravine (SRa) forests (Piedras Blancas National Park, SW Costa Rica). Values represent means ± 1 SE ( $n = 15$  collectors per site)

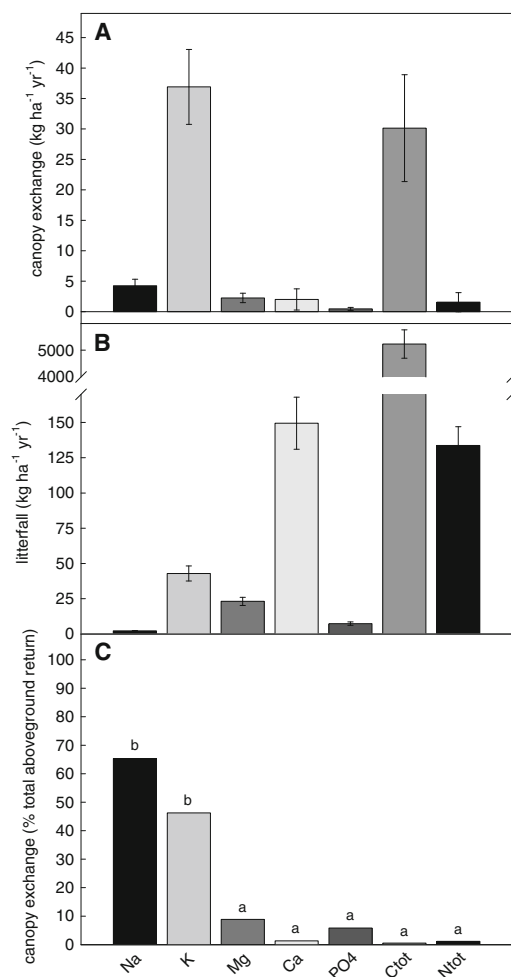
enhanced dry deposition factor and increased dry deposition of many solutes. The reference approach yielded even higher estimates of canopy retention of NH<sub>4</sub><sup>+</sup> and lower estimates for NO<sub>3</sub><sup>-</sup> and H<sup>+</sup>. The application of the weak acid approach slightly affected the H<sup>+</sup> estimates though not those of NH<sub>4</sub><sup>+</sup>.

A detailed investigation of possible model flaws of the multiple regression model and canopy budget model estimates is given in the discussion section. Based on this we used multiple regression model estimates of canopy exchange and dry deposition for evaluation of nutrient budgets. Litterfall represented the major aboveground pathway of internal cycling of elements (i.e. C<sub>tot</sub>, N<sub>tot</sub>, Ca<sup>2+</sup>, K<sup>+</sup>, Mg<sup>2+</sup> and HPO<sub>4</sub><sup>2-</sup>, Fig. 2). Canopy exchange resulted in marked leaching of DOC and K<sup>+</sup> and less so of Cl<sup>-</sup>, Na<sup>+</sup>, Mg<sup>2+</sup>, Ca<sup>2+</sup> and SO<sub>4</sub><sup>2-</sup>. However, contributions by canopy exchange to aboveground cycling were large for Na<sup>+</sup> (69%), K<sup>+</sup> (53%), Mg<sup>2+</sup> (12.3%) and HPO<sub>4</sub><sup>2-</sup> (8.2%), while for Ca<sup>2+</sup>, C<sub>tot</sub> and N<sub>tot</sub> contributions were <2% (full model:  $F_{11,24} = 24.892$ ,  $p < 0.0001$ ). Furthermore, canopy exchange led to significant retention of NO<sub>3</sub><sup>-</sup>, and less so of NH<sub>4</sub><sup>+</sup>, though this was not statistically significant (Fig. 2, Table 3). Dry deposition contributed most to total atmospheric inputs of DON (90%), K<sup>+</sup> (48%), DOC (45%), TDN (43%) and Cl<sup>-</sup> (29%) and to a lesser extent of Ca<sup>2+</sup>, Mg<sup>2+</sup>, SO<sub>4</sub><sup>2-</sup> and NH<sub>4</sub><sup>+</sup> (Fig. 3; full model:  $F_{11,24} = 3.1509$ ,  $p = 0.0091$ ). Bulk deposition estimates therefore would underestimate total atmospheric deposition to this tropical

**Table 4** Results of the multiple regression model (Lovett and Lindberg 1984) of event net throughfall ( $n = 12$ ) against rain volume (mm) and number of antecedent rain free days

	Na <sup>+</sup>	NH <sub>4</sub> <sup>+</sup>	K <sup>+</sup>	Mg <sup>2+</sup>	Ca <sup>2+</sup>	Cl <sup>-</sup>	NO <sub>3</sub> <sup>-</sup>	SO <sub>4</sub> <sup>2-</sup>	HPO <sub>4</sub> <sup>-</sup>	DOC	TDN
<b>PRi</b>											
b2	5.9 ± 1.3	-1.0 ± 1.0	10.9 ± 2.1	1.1 ± 0.6	0.5 ± 0.7	2.5 ± 1.4	-0.6 ± 0.4	1.1 ± 0.3	0.0 ± 0.1	43.4 ± 15.5	2.4 ± 1.8
b1	-27.1 ± 46.0	44.4 ± 36.3	164.6 ± 75.9	17.6 ± 21.4	16.4 ± 25.0	100.9 ± 65.1	-14.3 ± 16.1	7.0 ± 13.2	0.2 ± 3.6	-80.8 ± 2027	133.7 ± 230.3
R <sup>2</sup>	<b>0.70</b>	0.18	<b>0.81</b>	0.35	0.13	0.40	0.29	<b>0.63</b>	0.04	<b>0.50</b>	0.27
p-value	<b>0.004</b>	0.412	<b>0.001</b>	0.140	0.535	0.078	0.182	<b>0.007</b>	0.808	<b>0.044</b>	0.250
<b>PRa</b>											
b2	2.5 ± 0.6	0.6 ± 1.3	22.5 ± 4.1	2.7 ± 0.5	1.8 ± 0.8	2.6 ± 1.0	-0.5 ± 0.4	0.8 ± 0.1	0.5 ± 0.2	49.7 ± 10.1	1.8 ± 1.8
b1	-6.4 ± 19.5	39.3 ± 44.5	215.7 ± 144.7	26.6 ± 18.3	39.4 ± 29.3	85.1 ± 43.8	-11.8 ± 17.4	7.1 ± 3.9	2.8 ± 9.7	462.5 ± 1320	621.0 ± 240.1
R <sup>2</sup>	<b>0.69</b>	0.12	<b>0.81</b>	<b>0.79</b>	0.47	<b>0.58</b>	0.19	<b>0.90</b>	0.36	<b>0.87</b>	<b>0.56</b>
p-value	<b>0.005</b>	0.558	<b>0.001</b>	<b>0.001</b>	0.056	<b>0.013</b>	0.346	<b>&lt;0.001</b>	0.103	<b>&lt;0.001</b>	<b>0.026</b>
<b>SRa</b>											
b2	1.1 ± 0.6	2.4 ± 1.8	15.1 ± 1.8	1.0 ± 0.5	0.3 ± 0.7	1.2 ± 0.8	-0.7 ± 0.4	0.6 ± 0.1	0.2 ± 0.1	35.9 ± 11.9	1.5 ± 2.2
b1	4.7 ± 19.6	14.3 ± 63.5	176.8 ± 65.0	22.1 ± 18.6	40.5 ± 24.9	88.9 ± 34.9	-16.7 ± 18.1	10.4 ± 5.3	-2.7 ± 5.4	3270 ± 1556	807.6 ± 282.4
R <sup>2</sup>	0.33	0.19	<b>0.91</b>	0.41	0.27	<b>0.52</b>	0.32	<b>0.80</b>	0.27	<b>0.70</b>	<b>0.57</b>
p-value	0.161	0.388	<b>&lt;0.001</b>	0.093	0.246	<b>0.026</b>	0.144	<b>&lt;0.001</b>	0.205	<b>0.004</b>	<b>0.023</b>
<b>All sites</b>											
b2	3.2 ± 0.5	0.7 ± 1.2	16.2 ± 2.1	1.6 ± 0.5	0.9 ± 0.4	2.1 ± 0.9	-0.6 ± 0.4	0.8 ± 0.1	0.3 ± 0.1	43.0 ± 7.6	1.9 ± 1.6
b1	-9.6 ± 17.6	32.6 ± 42.2	185.7 ± 75.0	22.1 ± 15.9	32.1 ± 15.5	91.6 ± 40.3	-14.2 ± 16.9	8.2 ± 5.5	0.1 ± 4.7	2605 ± 989	520.8 ± 207.9
R <sup>2</sup>	<b>0.82</b>	0.12	<b>0.90</b>	<b>0.66</b>	<b>0.54</b>	<b>0.57</b>	0.27	<b>0.85</b>	0.38	<b>0.87</b>	<b>0.56</b>
p-value	<b>&lt;0.001</b>	0.574	<b>&lt;0.001</b>	<b>0.008</b>	<b>0.030</b>	<b>0.015</b>	0.200	<b>&lt;0.001</b>	0.089	<b>&lt;0.001</b>	<b>0.024</b>

Multiple regression models showed that intercepts were not significant; data presented here are values from multiple regression models calculated without intercepts. Values are given for bulk precipitation constant (b2), dry period constant (b1), adjusted  $R^2$  square ( $R^2$  adj.) and p-values from primary ridge (PRi), primary ravine (PRa) and secondary ravine (SRa) forests and combined site analysis (Piedras Blancas National Park, SW Costa Rica). Data represent means ± 1 standard error. Bold values indicate statistically significant regressions of NTF of the respective nutrients against precipitation magnitude and number of dry days before the event ( $p < 0.05$ )

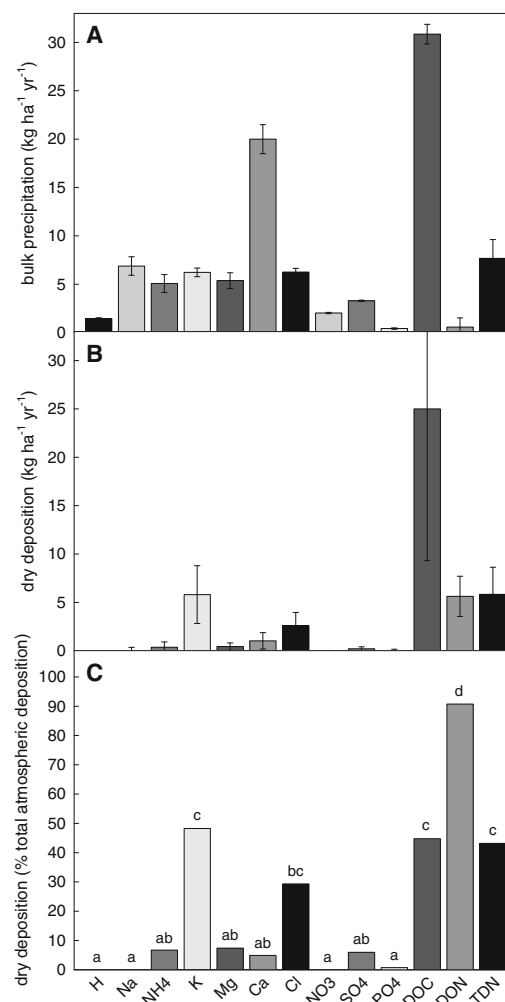


**Fig. 2** Internal nutrient fluxes of **a** canopy exchange (in  $\text{kg ha}^{-1} \text{ year}^{-1}$ ), **b** litterfall and **c** canopy exchange as percentage of aboveground nutrient return to the forest floor i.e. canopy exchange plus litterfall in the Piedras Blancas National Park, SW Costa Rica. Values represent means  $\pm$  1SE of all sites and plots combined. Different letters denote significant differences between solutes (one-way ANOVA, LSD,  $p < 0.05$ )

rainforest by e.g.  $\sim 2$ -fold ( $\text{K}^+$ , DOC, TDN,  $\text{Cl}^-$ ) and 10-fold for DON.

#### Sources of nutrients in net throughfall

In a third approach (besides the multiple regression and the canopy budget model) a principal component analysis was calculated to assess sources of solutes in



**Fig. 3** External nutrient inputs by **a** bulk precipitation (in  $\text{kg ha}^{-1} \text{ year}^{-1}$ ), **b** dry deposition and **c** dry deposition as percentage of total deposition i.e. bulk plus dry deposition in the Piedras Blancas National Park, SW Costa Rica. Values represent means  $\pm$  1SE of all sites and plots combined. Different letters denote significant differences between solutes (one-way ANOVA, LSD,  $p < 0.05$ )

net throughfall fluxes (Table 5). At a threshold of 0.5 for factor loadings, principle component PC 1 (37.2% variance explained) was found to group solutes such as  $\text{K}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Ca}^{2+}$ , DON and DOC i.e. plant nutrients and dissolved organic matter. Principle component PC 2 (14.6% variance explained) showed clustering of typical sea-salt ions ( $\text{Na}^+$ ,  $\text{Cl}^-$ ,  $\text{Mg}^{2+}$ ,  $\text{SO}_4^{2-}$ ) together with  $\text{NO}_3^-$ , while principle



**Table 5** Results of principal component analysis (PCA)

Variables	PC 1	PC 2	PC 3	PC 4
H <sup>+</sup>	−0.03	−0.01	−0.11	<b>−0.81</b>
Na <sup>+</sup>	0.05	<b>0.81</b>	0.03	−0.26
NH <sub>4</sub> <sup>+</sup>	0.09	0.08	<b>0.88</b>	−0.10
K <sup>+</sup>	<b>0.55</b>	0.26	−0.01	<b>0.64</b>
Mg <sup>2+</sup>	<b>0.58</b>	<b>0.56</b>	0.00	0.38
Ca <sup>2+</sup>	<b>0.67</b>	0.45	0.18	0.05
Cl <sup>−</sup>	0.38	<b>0.66</b>	−0.11	0.39
NO <sub>3</sub> <sup>−</sup>	−0.33	<b>0.59</b>	0.47	0.06
SO <sub>4</sub> <sup>2−</sup>	0.22	<b>0.74</b>	0.04	0.24
HPO <sub>4</sub> <sup>−</sup>	0.11	−0.05	<b>0.74</b>	0.47
DOC	<b>0.86</b>	0.22	−0.08	0.20
DON	<b>0.79</b>	−0.13	0.12	−0.01
Eigen values	4.46	1.75	1.56	1.06
% Variance explained	37.19	14.58	12.99	8.79

Bold values indicate factor loadings above 0.5 or below −0.5 and thus common sources of solutes in annual net throughfall of single throughfall collectors. Factor loadings, Eigen values and percentage of variance explained for each principle component (PC 1–4) are given for 12 events for three forest sites (Piedras Blancas National Park, SW Costa Rica)

component PC 3 (13.0% variance explained) was determined by NH<sub>4</sub><sup>+</sup> and HPO<sub>4</sub><sup>2−</sup>. Principle component PC 4 (8.8% variance explained) was determined by solutes H<sup>+</sup> and K<sup>+</sup> which were negatively correlated (Table 5). Together the four components accounted for 73.5% of total variance in net throughfall fluxes. The factor values were then tested by one-way ANOVA for differences between forest sites. PC 1 showed highest values at SRa, differing from PRi. PC 2 was highest at site PRi, differing from SRa. PC 3 was highest at the PRa site and lowest at PRi. For PC 4 no differences between sites were evident (Fig. 4).

Effects of seasonality and vegetation on net throughfall fluxes

In throughfall volume weighted mean concentrations of most solutes (except NH<sub>4</sub><sup>+</sup> and Ca<sup>2+</sup>) were significantly higher in the dry season (events ranging from 5 to 61 mm) than in the wet season (events between 57 and 168 mm) (one way ANOVA,  $p < 0.001$ ). Similarly, seasonality also affected throughfall fluxes, being significantly higher for Cl<sup>−</sup>, NO<sub>3</sub><sup>−</sup>, SO<sub>4</sub><sup>2−</sup>, HPO<sub>4</sub><sup>2−</sup> ( $p < 0.001$ ) and DOC ( $p < 0.01$ ) during the dry season and for NH<sub>4</sub><sup>+</sup> and

Ca<sup>2+</sup> ( $p < 0.001$ ) and Mg<sup>2+</sup> ( $p = 0.01$ ) during the wet season.

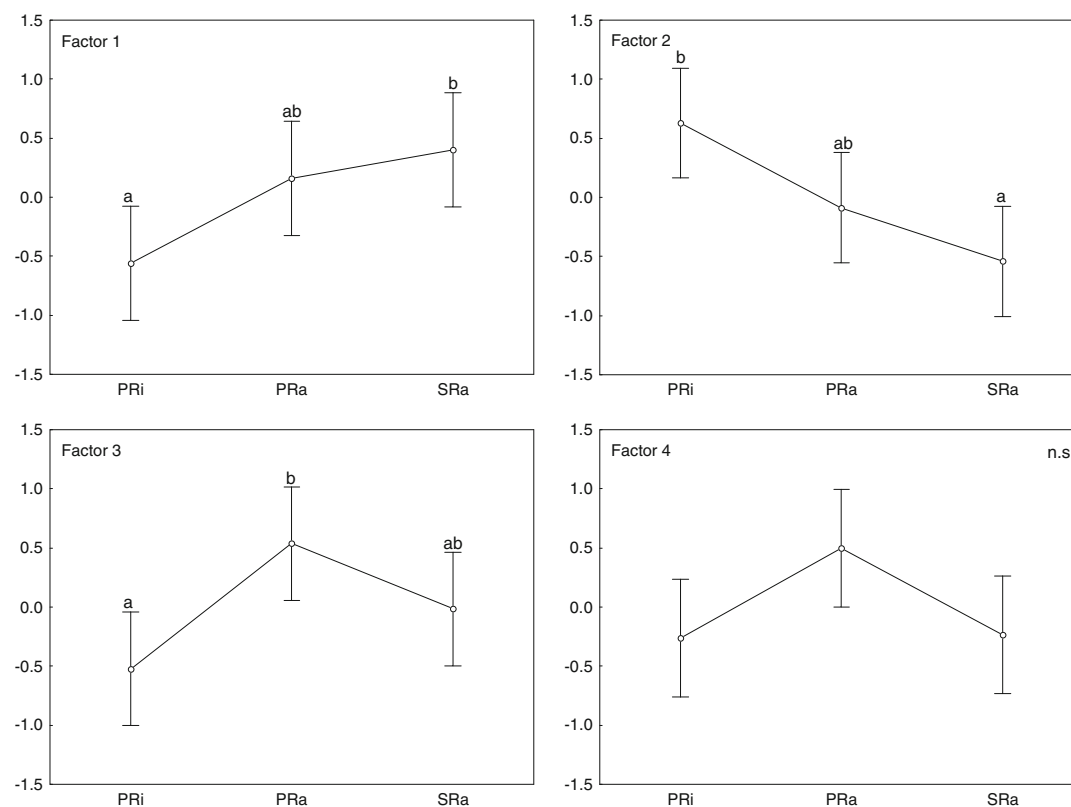
Plant area index (PAI) (Table 6), based on light absorbance by the canopy, was higher for PRa compared to SRa and PRi ( $p < 0.001$ ). Values of PAI calculated by hemispherical photography did not differ between sites but showed the same trend as PAI from light absorbance measurements. The Spearman-Rank correlations between PAI measured above each throughfall collector and NTF of solutes were not significant (Supplementary Table 2).

Fisher's alpha value demonstrated that forest types differed significantly in species diversity for tree species above 10 cm dbh (Fisher's alpha 11–86) while species of trees between 2.5 and 10 cm in diameter at breast height did not (Fisher's alpha 20–26, Table 6). Analysis of similarity (ANOSIM) of species assemblages showed weak differences (high similarity) between forest types for trees between 2.5 and 10 cm dbh (Global Model's  $R = 0.87$ ,  $p = 0.001$ ). PRa differed from PRi and SRa ( $R = 0.79$ – $1.00$ ,  $p = 0.03$ ) whilst SRa and PRi showed no differences in species assemblage ( $R = 0.63$ ,  $p = 0.10$ ). For trees > 10 cm 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 ( $R = 0.01$ ,  $p = 0.003$ – $0.02$ ). Analysis of similarity percentage (SIMPER) confirmed that for trees > 10 cm dbh forests differed most significantly in species composition (average dissimilarity: PRa/PRi: 100%, SRa/PRa: 98.2% and SRa/PRi: 92.1%; Supplementary Table 3). Relating Bray Curtis distance matrices of tree species and ionic composition by Spearman-matrix-rank correlation, however, showed no influence of species composition on throughfall solute fluxes (Supplementary Table 2).

## Discussion

Comparison of the multiple regression and canopy budget model approaches

In comparing the two model approaches to partitioning the contribution of canopy exchange and dry deposition to NTF in forest ecosystems, we found that both the multiple regression model and the canopy budget model involved several caveats that should be considered.



**Fig. 4** Mean values  $\pm$  confidence intervals of the factor loadings of principal components of annual net throughfall fluxes (presented in Table 5). Significant differences between sites i.e. primary ridge (PRi), primary ravine (PRa) and

secondary ravine (SRa) forests (Piedras Blancas National Park, SW Costa Rica) for each factor (1–4) are presented by different letters (one-way ANOVA, LSD,  $p < 0.05$ ). *ns* not significant

**Table 6** Vegetation characteristics of primary ridge (PRi), primary ravine (PRa) and secondary ravine (SRa) forests (Piedras Blancas National Park, SW Costa Rica)

Trees 2.5–10 cm dbh (0.03 ha)				Trees > 10 cm dbh (0.12 ha)			Tree height		PAI (Sundata)		PAI (Hemiview)	
Site	Total species	Total individuals	Fisher's alpha	Total species	Total individuals	Fisher's alpha	Mean	CV%	Mean	CV%	Mean	CV%
PRi	52	167	26	25	29	86	16.6	38.8	7.1	18.2	4.1	14.8
PRa	18	28	22	21	29	34	17.4	43.2	8.3	23.4	4.7	24.4
SRa	29	65	20	15	31	11	21.5	41.0	6.9	16.7	4.1	24.7
Sum	99	260		61	89							

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 coefficients of variation (CV%) are given for height of trees; plant area index (PAI) investigated by Sundata and Hemiview System of the respective forest sites

The multiple regression model was designed for application in temperate regions where the distribution of dry days and precipitation magnitude is more

or less equally throughout the year. The power of multiple regression analysis will be weakened when there is little variation in one of the variables (see

Eq. 4) among events such as here in the length of antecedent dry period that varied only between 0 and 2 days. Therefore the following limitations of the regression model have to be considered: (1) The relationships between (i) precipitation amount and canopy exchange and (ii) antecedent period and dry deposition flux are assumed to be linear. (2) Material accumulated between events is assumed to be washed off the canopy completely and quickly, and the efficiency of this wash-off is assumed to be unrelated to the amount of precipitation (events < 5 mm are excluded from analysis). Dry-deposited material that is retained in the canopy and is not included in NTF and therefore dry deposition may be underestimated for some substances. (3) The dry deposition component includes material that migrates from inside the leaves and branches to surfaces during the antecedent period, and also material accumulating in the TF funnels during the antecedent dry period, such as debris from the canopy, both leading to an overestimation of the dry deposition component. According to these assumptions and limitations the model has proven highly valuable to estimate canopy exchange and dry deposition in areas with convective storms and extended dry weather periods (Lovett et al. 1996; Puckett 1990) but was found less useful in areas characterized by frequent low-intensity rainfall and relatively short dry periods (Draaijers et al. 1994; Lindberg et al. 1990). The high mean annual precipitation of approximately 5800 mm in the study region with an average of 260 rainy days per year (data not shown) therefore indicates unfavourable conditions according to factor (1) but less restrictions by factors (2) and (3) for the application of this approach to correctly estimate the dry deposition component of NTF. For the 30 precipitation events collected the mean number of antecedent dry days was  $\sim 0.5$ , and in the study year only 80 dry days occurred. We therefore anticipate that the local meteorological conditions result in high contributions of canopy exchange to NTF in the study area while contributions of dry deposition to NTF remain sparse and statistically uncertain, as demonstrated.

One more concern with the multiple regressions is the choice of model. Forcing regressions through the origin is commonly not advised and may lead to large uncertainties in calculated dry deposition and canopy exchange rates. However, in this study models without intercepts performed better than those with

intercepts i.e. models with intercepts led to underestimation of measured NTF by  $22 \pm 1\%$  compared to  $4 \pm 1\%$  underestimation by models forced through the origin. The discrepancy mainly derives from the difficulties in interpreting and partitioning the intercept value which neither represents dry deposition nor canopy exchange per se, following the assumptions of the multiple regression model. The intercept value would represent a net throughfall flux per rain event that is not related to precipitation amount (which presumably scales with canopy exchange flux) and to the length of antecedent dry period (which presumably scales with dry deposition flux). The exact nature of this flux remains obscure but in this study was not related to contamination of samples or collectors. The application of multiple regression models computed with intercepts can therefore lead to underestimations of the contributions of canopy exchange and dry deposition to net throughfall flux in tropical rainforests. This finding indicates that the multiple regression model computed without intercept terms (despite legitimate statistical scepticism) constitutes a more adequate instrument for the estimation of canopy exchange and dry deposition fluxes, provided that intercept terms are not significant.

The multiple regression model was not significant for NTF of  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and  $\text{HPO}_4^{2-}$  ions that in tropical rainforest canopies are expected to be highly dynamic, to be exchanged between canopy compartments and to be biochemically transformed (e.g.  $\text{NH}_4^+$  to  $\text{NO}_3^-$ , or inorganic to organic  $\text{PO}_4$ ). The different dynamics of  $\text{NH}_4^+$  and  $\text{HPO}_4^{2-}$  are also represented by the principal component analysis of NTF of individual throughfall traps, i.e. in their strong positive relation to principal component PC3. However, any estimates presented for canopy exchange and dry deposition of these ions have to be taken cautiously as model outputs were non-significant.

Interestingly dry deposition of the tracer ion,  $\text{Na}^+$ , of the canopy budget model was close to zero, NTF being dominated by canopy exchange processes which would prevent application of the canopy budget model in the study area. Though other tracer ions (e.g.  $\text{Cl}^-$ ,  $\text{Ca}^{2+}$ ) have also rarely been used (Staelens et al. 2008),  $\text{Na}^+$  is the most commonly used tracer ion and we therefore calculated the canopy budget model with  $\text{Na}^+$  to be compared with the multiple regression model.

The canopy budget model has been validated for areas with high wet and dry deposition rates of N and S (Draaijers and Erisman 1995). The filtering approach is based on medium to high dry deposition rates of  $\text{Na}^+$  and base cations and the reference approach particularly applies where deposition of  $\text{H}^+$  and  $\text{NH}_4^+$  is high and therefore is a major driver of ion-exchange processes in the canopy. In the reference approach deposition of  $\text{H}^+$  and  $\text{NH}_4^+$  is neutralized by an equivalent release of base cations. The canopy budget model is therefore considered to be built on several assumptions of mechanisms which are sometimes questionable. When a specific assumption is not valid this propagates into successive calculations by which an accumulation of errors may arise (Staelens et al. 2008). We might expect that in remote and in clean air areas the processes being dominant in high deposition areas are not representative and that therefore the canopy budget model is based on a ‘wrong’ mechanistic basis. This becomes evident from the strong deviations in anticipated solute relationships based on the canopy budget model and those found by principal component analysis of NTF (Table 5). Principal component PC1 was controlled by NTF of base cations (which would fit canopy budget model assumptions) but also by NTF of DOC and DON indicating a similar canopy leaching mechanism. PC2 was strongly dominated by NTF of sea salts i.e.  $\text{Na}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Cl}^-$  and  $\text{SO}_4^{2-}$  but also of  $\text{NO}_3^-$ , indicating a strong dry deposition component that also affected NTF of  $\text{NO}_3^-$ . PC3 was related to NTF of  $\text{NH}_4^+$  and  $\text{HPO}_4^{2-}$ , two elements that most probably have similar biological sink/source relationships in the forest canopy. Only in PC4 we find a typical ion-exchange component as indicated by the negative relation between NTF of  $\text{H}^+$  and  $\text{K}^+$  and predicted by the canopy budget model.

The major weakness of the filtering approach is the assumed relation between wet and dry deposition of particles (Draaijers et al. 1996). The assumption of the filtering approach that  $\text{Mg}^{2+}$ ,  $\text{Ca}^{2+}$ ,  $\text{Cl}^-$  and  $\text{K}^+$  containing particles are deposited with equal efficiency as  $\text{Na}^+$  containing particles will certainly introduce an error as the particle-size distribution of these constituents is not the same. In general mass median diameters of aerosols containing  $\text{Ca}^{2+}$  and to a lesser extent  $\text{Mg}^{2+}$  were found to be larger than those of  $\text{Na}^+$ , while mass median diameters of  $\text{K}^+$

aerosols can be considered smaller (Ruijgrok et al. 1997). As a result dry deposition of  $\text{Ca}^{2+}$  and to a lesser extent of  $\text{Mg}^{2+}$  containing particles will be underestimated by the model and dry deposition of  $\text{K}^+$  containing particles will be overestimated (Draaijers et al. 1997). In this study, however, we found very high estimates for dry deposition of most elements but especially  $\text{Ca}^{2+}$  in the exposed PRi forest site (compared to the multiple regression model). These high dry deposition estimates further translate into much higher rates of canopy uptake of  $\text{NO}_3^-$ ,  $\text{NH}_4^+$  and TDN and especially unrealistically high canopy uptake of  $\text{Ca}^{2+}$  at PRi compared to the multiple regression model estimates. The most plausible explanation of low NTF but high dry deposition and therefore canopy uptake fluxes of  $\text{Ca}^{2+}$  at PRi is the enhanced TF:BP ratio (DDF) for  $\text{Na}^+$  at this site which gives rise to high dry deposition fluxes of all base cations in the filtering approach. In a study by Staelens et al. (2008) it was reported that part of NTF of  $\text{Na}^+$  may actually result from canopy leaching instead of dry deposition and that canopy exchange of  $\text{Na}^+$  is most critical in regions with low marine deposition inputs, which would impair the use of  $\text{Na}^+$  as a tracer in remote areas. In contradiction, previous research suggests that the enrichment of  $\text{Na}^+$  in TF is mainly derived from dry deposition although evidence for the canopy inertness of  $\text{Na}^+$  is scarce (Staelens et al. 2008). Further error is introduced when based on these dry deposition values, canopy leaching of base cations is computed which in turn is used to calculate canopy uptake of  $\text{H}^+$  and  $\text{NH}_4^+$  in the reference approach. Application of the weak acid approach assumes generally larger canopy leaching of base cations, since weak acid leaching may release extra base cations from the plant tissues. Although in this study the application of the weak acid approach resulted in minor changes in  $\text{H}^+$  but not base cation estimates, it has been reported that base cations leached in association with weak acids accounted for 6–30% of canopy leaching of base cations (Zhang et al. 2006). In the latter two approaches (reference and weak acid approaches) we found negative dry deposition for  $\text{NO}_3^-$  and  $\text{H}^+$ . Such negative dry deposition fluxes are actually impossible, but result from calculating dry deposition of  $\text{H}^+$  and  $\text{NH}_4^+$  as NTF minus estimated canopy exchange, where the latter depends on the calculated canopy leaching of base cations. This shows how errors in the estimated

base cation fluxes result in erroneously negative  $\text{H}^+$  and  $\text{NH}_4^+$  flux estimates (Staelens et al. 2008).

Some differences between the multiple regression and canopy budget model reported above might be explained by the fact that the characteristics of wet tropical climates with high relative humidity (>90%), large rainfall volumes and frequent rain events will generally accelerate element cycling and in particular enhance canopy leaching or more generally canopy exchange processes. Moreover, relatively long residence times during drizzle (e.g. in tropical regions) were shown to account for relatively high leaching rates compared to short rain periods with large rainfall intensities (Lovett and Lindberg 1984), and the amount of rainfall is one of the most important factors controlling the leaching of  $\text{K}^+$  and DOC and the exudation of weak acids from plant tissues (Likens et al. 1996; Prescott 2002). Based on the discussion above we used the multiple regression model estimates of canopy exchange and dry deposition, as they are relatively unbiased in terms of assumptions on the underlying canopy ion-exchange and dry deposition processes compared to the canopy budget model. For future applications of the canopy budget model, more studies of dry deposition and canopy exchange fluxes in tropical rainforest canopies should be performed to generate a realistic mechanistic basis of canopy exchange processes applicable to remote and high-precipitation forests.

#### Contribution of canopy exchange and dry deposition to net throughfall

Based on NTF only we could not distinguish whether the enrichment in throughfall of solutes (Fig. 1) was due to dry deposition, canopy leaching, both processes, or dry deposition exceeding canopy uptake. Multiple linear regression analysis, however, demonstrated that on average NTF of  $\text{Na}^+$ ,  $\text{HPO}_4^{2-}$ ,  $\text{SO}_4^{2-}$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{NH}_4^+$ ,  $\text{Ca}^{2+}$ , and DOC (in declining order) was controlled by canopy exchange processes (>50% canopy exchange of NTF). For DOC and  $\text{K}^+$  strong net throughfall enrichment was linked to canopy leaching. Potassium and DOC are considered to be highly soluble substances that are easily washed out from canopy materials (Tobón et al. 2004b), explaining the highest canopy leaching fluxes at all three sites.  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  leaching were shown to depend on the nutrient status of the forest site (Filoso

et al. 1999), as shown here by highest canopy leaching of both ions at PRa where soil solution concentrations were highest.

For total nitrogen dry deposition was dominant, thereby probably masking the uptake of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  from rainfall. Canopy uptake of inorganic N (particularly  $\text{NO}_3^-$ ) was to some extent balanced by canopy leaching of DON (and  $\text{NH}_4^+$ ), resulting in net canopy leaching of TDN. The major source of DON to net throughfall in tropical forests has been considered to be foliar leaching or phyllosphere processes such as  $\text{N}_2$  fixation by free-living diazotrophic organisms (Förnkrantz et al. 2008; Wanek and Pörtl 2005). Moreover, it has been debated whether  $\text{NH}_4^+$  and  $\text{NO}_3^-$  uptake by the forest canopy is counterbalanced by DON release from epiphytes and epiphylls (Gaige et al. 2007; Wanek and Pörtl 2005). The latter pattern might hold to some extent in the study area where negative net throughfall of  $\text{NO}_3^-$  (and  $\text{NH}_4^+$ ) pointed to net uptake of solutes from throughfall during passage through the canopy layer and DON increased in two out of three forest sites. Transformation of DIN to DON and  $\text{N}_2$  fixation would most plausibly be subsumed under the dry deposition flux of DON while foliar leaching adds to the canopy exchange flux. However,  $\text{N}_2$  fixation is highly dependent on sufficient surface moisture, therefore  $\text{N}_2$  fixation products are thought to accumulate mostly during wet periods. In contrast the release of N fixed (DON,  $\text{NH}_4^+$ ) occurs mostly after dry spells, eventually increasing with the length of dry period. A recent paper discusses this issue to some extent, noting that  $\text{N}_2$  fixation did not greatly contribute to net throughfall fluxes of DON (Hinko-Najera Umana and Wanek 2010). Nitrogen is a 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 and 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. 2007) and across a soil nutrient gradient from nutrient-rich alluvial soils to nutrient-depleted upland terraces (Tobón et al. 2004b). Uptake of inorganic N forms in the canopy of our study site evidently was of less importance, as net canopy uptake of inorganic N occurred only at PRi site where the flux comprised

less than 2% of the annual litterfall N flux, and NTF of TDN demonstrated net release of N in the canopy.

Interestingly, we found a trend towards  $\text{HPO}_4^{2-}$  leaching from the forest canopy at all three sites, though lowland rainforests are considered to be P rather than N limited (Tanner et al. 1998). However, relatively low P use efficiencies and high litter P contents (Sigrid Drage, unpublished data) in this forest pointed to higher than average soil P availabilities, as a result of rapid land lift, enhanced erosion and weathering in the Golfo Dulce area (Gardner et al. 1992; Porder et al. 2006). Canopy leaching of  $\text{HPO}_4^{2-}$  can also be enhanced during 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 et al. 1999). The retention of  $\text{H}^+$  (and  $\text{NH}_4^+$ ) is considered to be the result of ion exchange processes with base cations in the forest canopy which decreases the acidity of rain and results in an enrichment of base cations and organic acids (Asman et al. 1998; Lovett et al. 1996). In support of the latter reaction principal component analysis of annual net throughfall based on individual throughfall traps yielded a principal component PC 4 in which the highly exchangeable elements  $\text{H}^+$  and  $\text{K}^+$  were negatively related. These reverse ion-exchange processes did not differ between forest type but followed more general physicochemical processes in the canopy (see also Tobón et al. 2004b).

Compared to canopy exchange dry deposition represented a large forest input of DOC, TDN, DON and  $\text{K}^+$  and less for inputs of  $\text{Cl}^-$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ , and  $\text{SO}_4^{2-}$ . Dry deposition controlled NTF of DON, TDN,  $\text{Cl}^-$  (and  $\text{NO}_3^-$ ) i.e. contributed >50% to NTF. Sodium,  $\text{Cl}^-$ ,  $\text{Mg}^{2+}$  and  $\text{SO}_4^{2-}$  are the major components of sea water, and external inputs are therefore commonly related to dry deposition of marine aerosols. Such a clear marine source of NTF of  $\text{Na}^+$ ,  $\text{Cl}^-$ ,  $\text{Mg}^{2+}$  and  $\text{SO}_4^{2-}$  was reflected in principle component PC 2 (Table 5). In contrast the multiple regression model indicated that dry deposition of  $\text{Na}^+$  was negligible and the PCA results might therefore also be interpreted in terms of similar canopy exchange behaviour of these elements (see also discussion above). Potassium and  $\text{Ca}^{2+}$  are only minor solutes in sea water, and marine concentrations of  $\text{NH}_4^+$  and DOC are negligible. These components are closely linked to biogenic emissions and biomass burning (Artaxo et al. 1998). Generally it is assumed

that dry deposition is of less importance than canopy exchange for base cations since they do not occur in gaseous phases and there is low aeolian transport of soil and dust particles in remote areas of continuous forests. In a Brazilian forest archipelago canopy exchange was therefore the dominant source of base cations to net throughfall, while dry deposition was important only during the dry season (Filoso et al. 1999). Although for  $\text{SO}_4^{2-}$  and  $\text{Cl}^-$  dry deposition was reported to be the main source to NTF in the Amazonian forest (Filoso et al. 1999), in our study this was the case for  $\text{Cl}^-$  but not for  $\text{SO}_4^{2-}$  which was dominated by canopy exchange processes. It has been shown that dry deposition changes seasonally with anthropogenic biomass burning during the dry season since forest burning increases emissions of  $\text{NO}_x$ , organic C and other elements such as  $\text{K}^+$  and P and thus dry deposition of these compounds (Clark et al. 2001b). Biomass burning and natural background sources may therefore explain the dry deposition flux of P but especially that of DOC and DON in this study. Alternatively, dry deposition of DOC may represent migration of organic compounds from the interior of the leaf to the leaf surface to accumulate there during dry periods (Draaijers et al. 1997), while dry deposition of DON may be the same process, or  $\text{N}_2$  fixation in the phyllosphere.

Dry deposition and canopy exchange represent the major mechanisms that control the chemical composition and deposition via NTF as shown above and discussed elsewhere (Filoso et al. 1999; Lovett and Lindberg 1984). It has been suggested that canopy exchange is mainly affected by species assemblage, vegetation structure, soil fertility and concentration of solutes in precipitation, whereas dry deposition is primarily influenced by climate (seasonality) and exposure of the canopy layer to atmospheric deposition (Levia and Frost 2006). Both dry deposition and canopy exchange vary in space and time since they are related to biological characteristics of the forest e.g. stand age, soil fertility, plant nutrient status, presence of insects, leaf area and epiphyte activity (Levia and Frost 2006). These seasonal and biological effects are discussed below.

#### Seasonal effects

In the tropics seasonal climate variations i.e. distinct wet and dry seasons can profoundly affect deposition



of elements resulting from differences in leaf area and litterfall patterns and in precipitation amounts. Season markedly affected throughfall fluxes, being due to higher volume weighted mean concentrations of most solutes (except  $\text{NH}_4^+$ ,  $\text{Ca}^{2+}$ ) during the dry season, and due to higher rainfall volumes in the wet season for  $\text{NH}_4^+$ ,  $\text{Mg}^{2+}$  and  $\text{Ca}^{2+}$ . High dry season concentrations are directly linked to higher aerosol loads in air above the canopy that is washed out during precipitation events. In a Brazilian forest archipelago (Filoso et al. 1999) also a clear pattern of seasonality was found in NTF—in the rainy season the contribution of canopy exchange to NTF was significant for all ions except  $\text{Na}^+$ , whilst dry deposition significantly contributed to  $\text{Cl}^-$  only. During the dry season dry deposition affected NTF of most ions (except  $\text{Cl}^-$ ,  $\text{HPO}_4^{2-}$  and  $\text{H}^+$ ), whereas canopy exchange had an effect on all ions except  $\text{Ca}^{2+}$  and  $\text{NH}_4^+$ . These variations in volume weighted mean concentration and deposition of solutes between wet and dry seasons were also explained on the basis of large seasonal variations in rainfall depth and biogenic emissions (Filoso et al. 1999).

#### Topographic effects

Topography is strongly correlated with (i) altitude and exposure to wind, precipitation and aerosols and (ii) erosion and nutrient transfers from upland to downslope areas. While the first factor affects microclimate and deposition velocity, the second effectively controls soil fertility across topographic gradients. Topography may therefore increase dry deposition by exposure to aerosol laden air masses at ridges and canopy exchange by increasing soil fertility at downslope areas. We found clear evidence for increased dry deposition to the ridge forest (PRi) where NTF of  $\text{Na}^+$  was significantly higher than at the ravine site (PRa). Moreover, principle component PC 2 from PCA analysis of net throughfall which was composed of sea salt ions ( $\text{Na}^+$ ,  $\text{Cl}^-$ ,  $\text{Mg}^{2+}$ ,  $\text{SO}_4^{2-}$ ) and  $\text{NO}_3^-$ , was significantly higher at the PRi site (compared to SRa) which was situated at a ridge at higher elevation and thus was more exposed to deposition of aerosols (see also (Eklund et al. 1997)). The contribution of  $\text{NO}_3^-$  to principle component PC 2 may 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 Tobón et al. (2004b). Higher nutrient availability at the ravine site was supported by 12-fold higher soil water  $\text{NO}_3^-$  and 5-fold higher soil water  $\text{HPO}_4^{2-}$  concentrations at PRa compared to PRi (Table 2). This actually translated into higher NTF of  $\text{NO}_3^-$  and  $\text{HPO}_4^{2-}$  at the PRa site, and showed up in significantly higher factor loadings for principle component PC 3, which was determined by  $\text{HPO}_4^{2-}$  and  $\text{NO}_3^-$ . Greater NTF of  $\text{HPO}_4^{2-}$  can be attributed to higher soil fertility and lower nutrient use efficiency of N and P reflecting less nutrient limitation of the ravine site. This was also confirmed by nutrient inputs deriving from leaf litterfall (fine & coarse litter), where highest litterfall fluxes of C, N,  $\text{Ca}^{2+}$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$  and P occurred at the PRa forest site, the site which turned out to be the most nutrient rich with fastest nutrient cycling rates (Table 3). Topography therefore had a significant effect on NTF in the Esquinas forest. Similarly NTF of  $\text{K}^+$ , P and  $\text{Mg}^{2+}$  were found to vary across other toposequences, with lower throughfall fluxes at upper slopes and higher ones at downslope sites in tropical forest sites in Mexico and Colombia (Campo-Alves 2003; Tobón et al. 2004b). Low NTF of N or P may be associated with a more economic use of these elements by trees and epiphytes at specific topographies. This would be in accordance with the conclusions of Veneklaas (1990) and Clark et al. (1998), suggesting limited availability and efficient use of N and P in tropical forests situated at higher altitudes.

#### Disturbance effects

Disturbance and forest regrowth have a strong impact on tree species composition, vegetation structure, and biomass and nutrient distribution. Tree species composition and vegetation structure were significantly affected by stage of succession (Table 6, Supplementary Table 3) but these parameters did not significantly affect NTF in secondary and primary ravine forests (Supplementary Table 2). However, the large demand for nutrients to allow regrowth and biomass accrual of secondary forests commonly leads to an intermittent decrease in soil nutrient availability (Hughes et al. 1999). Comparing primary ravine forest (PRa) and secondary ravine forest (SRa)

nutrient depletion was evident since  $\text{NO}_3^-$  and  $\text{HPO}_4^{2-}$  concentrations in soil water were 36- and 1.7-fold lower in the secondary forest (Table 2). Decreases in soil fertility at the SRa site also corresponded to significantly lower NTF of  $\text{HPO}_4^{2-}$  and  $\text{NO}_3^-$ . However, identification of sources of nutrients in net throughfall conducted by principal component analysis and further ANOVAs for differences between forest sites revealed that principle component PC 1 accounting for solutes that derived mainly from canopy exchange processes ( $\text{K}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Ca}^{2+}$ , DON and DOC) showed highest values at the SRa site. This result may be attributed to the characteristics of plant species in the secondary ravine forest in a relatively young stage of succession ( $\sim 20$  years after disturbance). Forests in different stages of succession exhibit differences in plant life forms, nutrient allocation and leaf traits of the characteristic species (Reich et al. 1992). Leaves of fast growing early successional species have a shorter leaf life time (Reich et al. 1991), are less sclerotic but are more nutrient rich (Poorter et al. 2004) and the present tree species at SRa are therefore more likely to leach readily soluble elements (Tukey 1970).

#### Canopy characteristics and tree species composition

Microclimate and soil fertility are also key determinants of vegetation composition and canopy characteristics such as the plant area index, which differed between PRa and PRi. Plant area index as a proxy for canopy cover is a major determinant of NTF by 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 poly-cultures with canopy covers ranging between 7 and 100%. In this study plant area indices measured by SunScan system were high and varied between 6.9 and 8.3 (Table 6). Plant area indices from hemispheric photography were markedly lower due to saturation effects with increased overlapping of leaves and leaf clumping. The plant area index was significantly higher at the PRa forest site where highest NTF was found for  $\text{HPO}_4^{2-}$  and a trend towards increased net throughfall of DOC,  $\text{K}^+$ ,  $\text{Mg}^{2+}$  and  $\text{Ca}^{2+}$  compared to the other sites. A greater variability in canopy characteristics at PRa, as suggested by higher

coefficients of variation of plant area indices and tree height, also results in greater canopy roughness. Canopy roughness may further increase NTF by enhancing dry deposition processes and thus nutrient deposition (Hansen et al. 1994; Lovett 1992; Parker 1983). However, on an individual throughfall trap basis, we found no correlation between plant area index and NTF of any solute. At this small scale the variation in NTF is therefore not accounted by simple canopy structure measures as applied above, and more elaborate models of throughfall fluxes have to be adopted (Levia and Frost 2006). The magnitude of water and nutrient fluxes inside the canopy, however, is also affected by non-vascular plants (mosses, liverworts and lichens) which may account for a large part of the vegetation's aboveground biomass, particularly in montane rainforests (Hölscher et al. 2004). In the Esquinas rainforest year-round high humidity resulted in dense epiphyte colonisation of ravine but not of ridge forests (PRa > PRi), while after  $\sim 20$ -years of succession epiphytes in SRa were virtually absent (Roland Albert, data not shown).

ANOSIM and SIMPER analysis revealed significant differences in tree species composition between forest sites due to distinct stages of succession and different topography (Supplementary Table 3). Tree species composition has been shown to significantly affect the hydrology and fluxes of nutrients and thus contribute to spatial variability of throughfall fluxes, especially in species-poor tree-based land use systems (Schroth et al. 1999). In this study, however, Spearman matrix rank correlations did not show that species composition exerted a significant influence on NTF compared between primary and secondary forest stands and between ravine and ridge forests. This is probably the effect of high species diversity in tropical lowland rainforests (160 species on 0.36 ha total surveyed site) what seems to outweigh the impact of certain tree species in terms of nutrient deposition.

#### Internal nutrient cycling via litterfall and canopy exchange

Comparison of nutrient cycling showed that litterfall generally represented a higher quantity of element input to the forest floor compared to throughfall (Fig. 2). Element inputs by litterfall in this study ranged among the highest reported for tropical forest

sites (Wood et al. 2006) (Table 3). Whereas internal cycling of N,  $\text{Ca}^{2+}$  and P mainly is associated with litterfall, other nutrients (e.g.  $\text{K}^+$ ) are more susceptible to leaching of the canopy layer (Cavelier et al. 1997; Johnson 1992; Tobón et al. 2004b; Veneklaas 1991) and thus mainly cycle via throughfall (Levia and Frost 2003; Parker 1983). Chuyong et al. (2004) reported that the percentage of rain-based input (TF + SF) to gross inputs including litterfall was about 77% ( $\text{K}^+$ ), 42% ( $\text{Mg}^{2+}$ ), 35% (P), 27% ( $\text{Ca}^{2+}$ ) but only 4% (N) for two different forest sites in Cameroon.

However, in terms of internal element cycling, litterfall cannot be compared directly to throughfall or net throughfall but rather to canopy exchange. According to our knowledge, we here present the first direct comparison of internal nutrient cycling via litterfall and canopy exchange for tropical forest ecosystems. Our data indicate that the contribution of canopy exchange to aboveground inputs of elements to the forest floor was low to negligible for C, N and  $\text{Ca}^{2+}$ , contributed about 10% to  $\text{Mg}^{2+}$  and P but >50% to  $\text{K}^+$  (Fig. 2). Therefore, canopy exchange contributed to aboveground nutrient cycling where solutes are easily leached from the canopies i.e.  $\text{K}^+$ ,  $\text{HPO}_4^{2-}$  and  $\text{Mg}^{2+}$ , while naturally the contribution of canopy exchange to internal cycling of C was negligible (<1%). DON leaching was partly counterbalanced by  $\text{NH}_4^+$  and  $\text{NO}_3^-$  uptake, and the contribution of canopy exchange of TDN was therefore only 1.5% for total N. However, the contributions were substantial for  $\text{K}^+$ , i.e. 53%, and for  $\text{Mg}^{2+}$  and P, i.e. 12.3% and 8.2%. In comparison, in pine and birch forests as well as regenerating forests stands in Belgium, canopy exchange did not contribute to aboveground cycling of N due to strong net canopy uptake of inorganic N (DON was not assessed) and little to  $\text{Ca}^{2+}$  (0–16%) while it contributed by 44–78% to  $\text{K}^+$  and 17–48% to  $\text{Mg}^{2+}$  (De Schrijver et al. 2009; De Schrijver et al. 2004). This enhanced canopy exchange contribution was most probably due to strong acid and enhanced N deposition triggering base cation leaching and therefore enhanced canopy exchange fluxes for  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  compared to litterfall.

#### Quantification of external nutrient inputs via wet and dry deposition

Contributions of dry deposition to total atmospheric deposition (sum of bulk/wet and dry deposition) were greatest for DON (90%), high for DOC, TDN and  $\text{K}^+$

(43–48%) and  $\text{Cl}^-$  (29%) but <10% for the other elements. Therefore bulk deposition fluxes would have to be corrected by a factor of approximately 1.0 to 1.9 (DON: 10.4) to estimate total atmospheric deposition to forests, depending on the element considered. For solutes such as  $\text{Cl}^-$ ,  $\text{NH}_4^+$ ,  $\text{SO}_4^{2-}$ ,  $\text{HPO}_4^{2-}$ ,  $\text{Ca}^{2+}$ , and  $\text{Mg}^{2+}$  the correction factor ranged from 1.0 to 1.4 while for  $\text{K}^+$ , DOC, TDN and DON it was between 1.8 and 10.4. Only few studies on tropical forests are available that reported estimates of dry deposition and bulk deposition fluxes and therefore allow us to assess total atmospheric deposition. Correction factors calculated from published data by far exceeded ours for specific solutes. For instance in an off-shore mangrove ecosystem dominated by *Rhizophora mangle* (Wanek et al. 2007) the correction factors ranged from 2.2 to 3.4 for base cations ( $\text{K}^+$ ,  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$ ) and was 2.8 for  $\text{SO}_4^{2-}$ . Sea-salt derived solutes i.e.  $\text{Na}^+$  and  $\text{Cl}^-$  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) correction factors were even higher, and ranged between 1.5 and 35 for cations ( $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$ ) and were 1.6 and 6.8 for  $\text{SO}_4^{2-}$  and  $\text{HPO}_4^{2-}$ . Although situated far from the coast values for  $\text{Na}^+$  and  $\text{Cl}^-$  input had to be corrected by 1.6 and 3.2 (Filoso et al. 1999). These results therefore indicate that previous calculations of atmospheric inputs to tropical forest ecosystem have been profoundly underestimated, depending on the ionic form and element.

#### Conclusions

Two models, the multiple regression model and the canopy budget model, were tested for their suitability to partition NTF into canopy exchange and dry deposition contributions. In places with rainfall >5 m per year and an average dry period of <0.5 days between rain events it is very difficult to accurately estimate dry deposition based on the multiple regression model. Sampling and analysis of more rainfall events with greater variability in the length of the antecedent dry period may improve these estimates. Moreover, the high biological dynamic of N and P in the forest canopy resulted in non-significant models for  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and  $\text{HPO}_4^-$ . Biochemical transformations such as mineralization and

assimilation reactions link the pools of inorganic and organic N forms (as well as P forms) and therefore did not allow using multiple regression models to dissect the contribution of dry deposition and canopy exchange to net throughfall of inorganic N and P though this was possible for the sum of inorganic and organic N. Based on the multiple regression model but considering the constraints presented above, we showed that former estimates, which accounted for bulk precipitation only, underestimated atmospheric deposition as external input of elements to tropical rainforests. Further, we demonstrated that factors affecting the amount and ratio of dry deposition and canopy exchange strongly affected NTF. Tree species composition did not explain the differences found in NTF between forest sites, and vegetation characteristics had no (tree height) or little effect (plant area index) on NTF. Compared to a mature forest, a younger forest had lower leaching of N and P but higher canopy exchange of highly leachable solutes. Topography most significantly affected NTF, possibly from enhanced dry deposition to higher elevation sites and higher soil fertility and canopy exchange at down slope sites. The application of approaches to partition NTF therefore will allow further insights into the biotic and geochemical controls of internal nutrient cycling of tropical rainforests, allowing better understanding of climatic versus nutrient controls of net primary production in times of globally changing environments.

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# CONTROLS OF HYDROCHEMICAL FLUXES VIA STEMFLOW IN TROPICAL LOWLAND FORESTS: EFFECTS OF METEOROLOGY AND VEGETATION CHARACTERISTICS







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## Controls of hydrochemical fluxes via stemflow in tropical lowland rainforests: Effects of meteorology and vegetation characteristics

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### SUMMARY

So far stemflow has been underrepresented in studies of ecosystem ecology as it usually contributes less than 10% to hydrological input to the forest floor. However, in terms of nutrient cycling, stemflow may constitute an important pathway for the localized input of highly enriched solutes to the forest floor. We measured stemflow hydrology and biogeochemistry in three different ecosystem types (primary forests on ridge and ravine, as well as secondary forest) in South-West Costa Rica. Stemflow hydrochemistry was mainly controlled by meteorology (precipitation magnitude and duration), ecosystem characteristics (topography and plant area index) and species-specific traits (stem diameter and tree height). Stemflow was enriched 7.5-fold in nutrients compared to bulk precipitation and 2.9-fold compared to throughfall. In net stemflow most solutes (especially DOC and K) were leached, while inorganic nitrogen and phosphorus (i.e.  $\text{NO}_3$  and  $\text{PO}_4$ ) were retained along the stemflow pathway. Computation of multiple regression models allowed dissecting the contributions of canopy exchange and dry deposition processes to net stemflow fluxes. Net stemflow was dominated by canopy exchange processes and to a lesser extent by dry deposition fluxes. Including throughfall and litterfall nutrient flux data we calculated that stemflow comprised 1–10% of dissolved internal recycling of nutrients and up to 1.5% of total aboveground nutrient returns. However, dissolved returns by canopy exchange via throughfall plus stemflow contributed up to 50% of total aboveground nutrient return. This demonstrates that stemflow *per se* represents a small but localized proportion of total above nutrient recycling but that total dissolved returns of (highly available) nutrients and DOC can be important as a part of the internal nutrient cycle of tropical rainforests.

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### 1. Introduction

Only recently the notion that stemflow represents a minor part of the hydrochemical cycle of tropical forests has been challenged (Germer et al., 2010). Although in many tropical forests stemflow represents only a small fraction of hydrological input to the forest floor (1–10% of total precipitation) in others it can contribute >20% (Herwitz, 1986a; Hoelscher et al., 1998; Levina and Frost, 2003). Moreover, stemflow constitutes a highly enriched localized input of nutrients (K, Ca, Mg, DON) near tree stems (Durocher, 1990; Herwitz and Levina, 1997). Stemflow therefore represents an important contributor to the ecosystem flux of water via preferential soil water infiltration and to the internal recycling of nutrients by strongly enhanced nutrient concentrations (Herwitz, 1991; Levina and Herwitz, 2000).

Globally stemflow fluxes have been reported to be controlled by factors like species assemblage (Herwitz, 1991; Levina and Herwitz,

2000), canopy structure (Crockford et al., 1996; Levina and Herwitz, 2002), meteorological conditions (Lindberg et al., 1986) and seasonality (Soulsby et al., 1997). Among these controls meteorological conditions and species-specific traits (stem diameter, branch inclination, bark texture, and epiphyte cover) constitute the key factors controlling stemflow hydrology and chemistry by affecting the residence time of water (Levina and Herwitz, 2000). Compared to temperate and boreal forests much less is known on the controls of stemflow in tropical forests. Especially in tropical forest ecosystems several architectural parameters may strongly affect stemflow as the nutrient and water flux in stemflow depends on stem diameter, tree height and tree species, e.g. stemflow volume is significantly greater for trees reaching the upper canopy than sub-canopy trees (Hoelscher et al., 2003). The greatest amount of stemflow flux at plot scale, however, was attributed to trees below 10 cm in diameter at breast height due to their high abundance (Germer et al., 2010; Manfroi et al., 2004). Therefore the quantity of small but numerous trees may overrule higher stemflow yields of canopy overstory trees. Nevertheless, few studies have investigated the quantities and controls of stemflow fluxes in complex tropical forest ecosystems.

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This study is embedded within a larger project characterizing above ground nutrient cycles (litterfall, throughfall, wet and dry deposition, canopy exchange) in different forest types of the Golfo Dulce region, SW Costa Rica (Hinko-Najera Umana and Wanek, 2010; Hofhansl et al., 2011; Weissenhofer et al., 2008). We report results on water and nutrient fluxes in stemflow and applied statistical and mathematical modelling techniques to (1) investigate the factors controlling the hydrology and biogeochemistry of stemflow (tree-level and plot-level basis), (2) to quantify the contribution of dry deposition and canopy exchange processes to net stemflow fluxes, and (3) relate these data to external and internal above-ground nutrient fluxes in different types of wet tropical lowland rainforest.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in the vicinity of the Tropical Research Station La Gamba (TRSLG; N8°42'03", W83°12'06", 70 m.a.s.l.) situated at the border of the Piedras Blancas National Park, in the province Puntarenas in the Southwest of Costa Rica. The vegetation is characterized by wet tropical lowland rainforest (Holdridge, 1967) covering from sea level up to 580 m altitude. Ultisols and Inceptisols are the major soil types found in the region (Vasquez, 1989). Ultisols are strongly acidic, highly weathered soils, being abundant especially on ridges and upper slopes. On lower slopes and valley bottoms ultisols are replaced by moderately weathered, younger Inceptisols (Pamperl, 2001).

Mean annual temperature (MAT) in a large opening (TRSLG) was 27.4 °C and ranged from 26.5 °C to 28.1 °C on monthly average (Weber et al., 2001). Inside the forest mean annual temperature was 25.2 °C and humidity was high (98%) throughout the year (Weissenhofer, 1996). Average annual bulk precipitation (MAP) was 5910 ± 190 mm (1998–2010) with a moderate dry season from January to March (monthly mean precipitation approx. 180 mm), and a pronounced wet season from September to November (monthly mean precipitation approximately 800 mm).

### 2.2. Study design

Study plots were randomly established in three different forest types: primary ridge forest (PRi; N8°42'16", W83°12'20", 120 m.a.s.l.), primary ravine forest (PRa; N8°42'16", W83°12'15", 80 m.a.s.l.) and secondary ravine forest (SRa; N8°42'01", W83°12'09", 80 m.a.s.l.). Secondary stands were formerly used for tree logging but have remained undisturbed for over 20 years. Plots (0.04 ha) were set up in triplicate either as squares of 20 × 20 m, separated by a distance of >10 m and divided into subplots of 10 × 10 m each, or as rectangles of 10 × 40 m subdivided into subplots of 10 × 10 m and separated by 10–30 m due to spatial restriction at the ridge forest site. Distance between sites was approximately 1.5 km and each forest type was covered by 0.12 ha of survey area. Inside the 10 × 10 m subplots all tree species above 10 cm diameter at breast height (DBH) where tagged and determined to species level. In every fourth 10 × 10 m subplot trees between 2.5 and 10 cm DBH were also tagged 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). The plant (leaf) area index (PAI) was estimated by light absorbance through the canopy using a SunScan probe v1.05 and the Sunshine Sensor BF3 (Delta-T Ltd., UK) at five evenly spaced points per subplot ( $n = 60$  per site).

### 2.3. Sampling design

Sites were equipped with collectors for litterfall (10 per forest type), throughfall (15 per forest type), stemflow (12 per forest type) and soil water (6 per forest type), and two bulk precipitation samplers were located in the opening at TRSLG. After each rainfall event the total amount of water in collectors of bulk precipitation, throughfall and stemflow was determined volumetrically using measuring cylinders. We only provide information on stemflow sampling in this paper as details on other sampling procedures were reported in Hofhansl et al. (2011).

For the collection of stemflow, stems were classified into four categories based on tree diameter at breast height (2.5–10, 10–20, 20–30 and >30 cm DBH) and representative trees in each size class ( $n = 3$  per site) were selected in the field. In total (3 sites, 4 stem classes, 3 replicates) 36 individual trees were monitored. Two types of stemflow collectors were used for trees above and below 10 cm DBH. For trees <10 cm DBH, 0.5 L polyethylene bottles were longitudinally cut on one side and mounted upside down around the stems. Bottles were sealed to the stem by sanitary silicone and connected to collection bottles of 1–5 L volume using silicone tubing. Trees with a diameter >10 cm DBH were equipped with a flexible tubing (garden hose) 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 stemflow losses. Collection vessels (allowing up to 25 L of stemflow sampling from large trees above 30 cm DBH) were connected to the flexible tubes when sampling was performed or disconnected between sampling events.

Sampling for hydrochemistry was performed on an event basis ( $n = 30$ ) from February to April and August to October 2005 after single rainstorms. Precipitation events below 5 mm were discarded in consideration of canopy interception storage. Of the total 30 precipitation events collected (4–133 mm rainfall), seven were studied for solute concentrations in stemflow. We individually analyzed each collector sample to assess the heterogeneity of stemflow fluxes and its controls, and therefore did not combine them to pooled samples for each event, tree size class and plot.

### 2.4. Chemical analyses

Directly after sample collection the pH was measured in all water samples at TRSLG using a Sentron ArgusX pH meter (Sentron, Roden, Netherlands). However, due to technical problems pH data are only available for four rainfall events. From each collector two sample aliquots (15 mL) were then transferred into 20 mL HDPE vials and stabilized against microbial transformation by addition of HgCl<sub>2</sub> (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. The following chemical analyses were conducted at the Department of Terrestrial Ecosystem Research, University of Vienna, Austria.

Inorganic anions (Cl<sup>–</sup>, NO<sub>3</sub><sup>–</sup>, SO<sub>4</sub><sup>2–</sup>, HPO<sub>4</sub><sup>2–</sup>) and cations (Na<sup>+</sup>, NH<sub>4</sub><sup>+</sup>, K<sup>+</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup>) were analyzed by HPLC (high pressure liquid chromatography, DX 500, Dionex, Vienna, Austria) and conductivity detection. Anions were separated on an anion exchange column (AS11, 4 × 250 mm, Dionex) using a linear KOH gradient (2–30 mM in 6 min, total run time 10 min). Cations were separated on a cation exchange column (CS16, 5 × 250 mm, Dionex) by an isocratic method with methanesulfonic acid as eluent (30 mM methanesulfonic acid for 26 min and 40 °C). Data analysis was performed using Chromeleon Version 6.70 Build 1820.

Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) were measured using high temperature Platinum-catalyzed



combustion with a Shimadzu TOC-V<sub>CPH/CPN</sub>/TNM-1 analyzer (Shimadzu, Japan). DOC is measured as non-purgeable organic carbon after acidifying and purging the sample to free it from DIC. Carbon is quantified using oxidative high-temperature combustion-infrared analysis of CO<sub>2</sub> and nitrogen using oxidative high-temperature combustion-chemiluminescence analysis of NO. Dissolved organic nitrogen (DON) was calculated by subtracting dissolved nitrate and ammonium (DIN) from measured TDN. Details of analytical performance (e.g. linearity, limit of quantification, precision) are presented in Hofhansl et al. (2011).

### 2.5. Calculations

Stemflow (SF, Eq. (1)) is the fraction of open bulk precipitation (BP) that runs down tree stems and thus is altered in hydrochemistry due to canopy exchange (CE) and dry deposition (DD) processes:

$$SF = BP + CE + DD \quad (1)$$

Volume-weighted mean concentrations (VWM, Eq. (2)) of each stemflow and bulk deposition collector were used to express solute concentration during the study period where  $C_i$  represents the concentration of a specific solute and  $V_i$  being the stemflow volume during this event, and were calculated as follows:

$$VWM = \frac{\sum_{i=1}^n (C_i * V_i)}{\sum_{i=1}^n V_i} \quad (2)$$

Annual stemflow fluxes per tree (Eq. (3)) were calculated by multiplication of volume-weighted mean values of each stem (VWM<sub>SF</sub>) with the ratio of stemflow volume: bulk precipitation volume of the respective tree during the rain events sampled ( $\sum SF_{vol} / \sum BP_{vol}$ ) times annual precipitation volume (BP<sub>annual</sub>).

$$SF_{flux} = VWM_{SF} * (\sum SF_{vol} / \sum BP_{vol}) * BP_{annual} \quad (3)$$

Net stemflow flux (Eq. (4)) can be defined as the difference between the solute flux in stemflow and in bulk precipitation:

$$NSF = SF - BP = CE + DD \quad (4)$$

Net stemflow fluxes were calculated by two approaches: (1) annual net stemflow fluxes for comparison to internal (litterfall and canopy exchange) and external (bulk and dry deposition) inputs, and (2) event based net stemflow for the calculation of a multiple regression model investigating the contribution of canopy exchange and dry deposition processes to net stemflow.

Annual net stemflow (Eq. (4a)) was calculated as described for annual stemflow flux per tree (Eq. (3)). To correct for variation between individuals of a size class at a site, the mean values of annual SF for each stem class (2.5–10 cm, 10–20 cm, 20–30 cm, >30 cm DBH) were multiplied with the number of tree stems per square meter in the respective size class in a plot. Then annual solute fluxes in bulk precipitation were multiplied with the quotient of basal area to plot area of the respective tree size class and these values were subtracted from the SF values. At last net stemflow fluxes were summed over stem classes to calculate annual net stemflow fluxes of the respective PRi, PRa and SRa forest plots.

$$NSF = [\text{mean } SF_{flux} * (\text{stems}/m^2)] - [BP_{flux} * (\text{basal area}/\text{plot area})] \quad (4a)$$

Event based net stemflow (Eq. (4b)) was calculated for each tree and precipitation event by multiplication of solute concentrations (SF<sub>conc</sub>, BP<sub>conc</sub>) times volumes (SF<sub>vol</sub>, BP<sub>vol</sub>) of the respective stemflow and bulk precipitation traps. Bulk precipitation fluxes were multiplied with the quotient of basal area to plot area for individual tree stems to correct for the fraction of BP obtained in SF, and subtracted from the respective stemflow fluxes. Again net stem-

flow fluxes were summed over stem classes to calculate event net stemflow fluxes of the respective PRi, PRa and SRa forest plots which then were used as input for the multiple regression model.

$$NSF = (SF_{vol} * SF_{conc}) - [(BP_{vol} * BP_{conc}) * (\text{basal area of tree}/\text{plot area})] \quad (4b)$$

Based on these calculations of event net stemflow we computed a multiple regression model that was originally proposed by Lovett and Lindberg (1984) for the separation of canopy exchange and dry deposition components of net throughfall based on event sampling (Eq. (5)):

$$NSF_x = a + b1 * A + b2 * P \quad (5)$$

With this model it is possible to investigate whether a certain element rather derives from dry deposition or canopy exchange processes and therefore originates from external or internal sources in terms of nutrient cycling (Hofhansl et al., 2011). A similar model has recently been applied to net stemflow in temperate oak-beech stands (Andre et al., 2008). In the regression equation applied here factor  $b1$  (dry period constant) and factor  $b2$  (bulk precipitation constant) represent coefficients of the calculated linear model for  $A$  (antecedent dry period; in days) and  $P$  (magnitude of precipitation; in mm) and  $a$  is the intercept term. A negative canopy exchange coefficient ( $b2$ ) indicates uptake of the solute, while a positive coefficient points to canopy leaching of the solute. For a given precipitation event DD is the product of the dry deposition coefficient ( $b1$ ) and the antecedent dry period ( $A$ ), while CE is the product of the canopy exchange coefficient ( $b2$ ) times the amount of precipitation ( $P$ ). Multiple regression model calculations were performed with the summed net stemflow fluxes of the four stem classes on the respective forest site per event. By multiplying the values for  $b1$  by annual number of dry days (80 days during the study year) and  $b2$  by the annual amount of precipitation (5840 mm during the study year) we estimated the annual fluxes of dry deposition and canopy exchange in stemflow.

As trees naturally differ in structural parameters (i.e. DBH and height) we computed linear regression models as presented in Manfro et al. (2004) to calculate the value of stemflow commencement ( $b0$ ; i.e. the magnitude of precipitation needed to produce stemflow by the respective tree stem) (Eq. (6)):

$$SF_x = b0 + b1 * BP \quad (6)$$

To investigate the controls of stemflow hydrology and hydrochemistry we computed linear models of stemflow yield or net stemflow fluxes including the variables bulk precipitation (BP), antecedent dry period (ADP), bark area (BA) and plant area index (PAI) (Eq. (7)):

$$NSF_x = a + b1 * BP + b2 * ADP + b3 * BA + b4 * PAI \quad (7)$$

To estimate bark surface area (BA) we employed allometric equations that relate tree dbh to stem bark surface area (SBA, Eq. (8)) and branch bark surface area (BBA, Eq. (9)) (Whittaker and Woodwell, 1967) and summed these estimates for each tree. These equations were also used recently to examine the effect of bark area on stemflow hydrology and hydrochemistry (Levia and Herwitz, 2005). Though these equations have been developed for temperate tree species, based on an exhaustive destructive sampling campaign, the use of these equations provides a much better measure of bark surface area than calculating bark surface area from tree dbh and height alone. By using the combined allometric equations for all the species sampled inherent differences among the species are assumed to be balanced.

$$\log_{10} SBA \text{ (cm}^2\text{)} = 2.6716 + 1.5881 * \log_{10} dbh \text{ (cm)} \quad (8)$$

$$\log_{10} \text{BBA}(\text{cm}^2) = 2.9319 + 2.0346 \times \log_{10} \text{dbh}(\text{cm}) \quad (9)$$

## 2.6. Statistical analyses

Statistical analyses such as one-way analysis of variance, linear and multiple regression models were performed in R Development Core Team (2008). The multiple regression approach critically depends on several assumptions that have to be met (Osborne and Waters, 2002). (1) *Variables are normally distributed.* Non-normally distributed variables such as highly skewed variables, or variables with substantial outliers can distort relationships and significance tests. Kolmogorow–Smirnov test and Shapiro–Wilk test were run to check for normality and in case of non-normality data were Box–Cox-transformed (see below). (2) *Assumption of a linear relationship between the independent and dependent variables.* Multiple regression can only accurately estimate the relationship between dependent and independent variables if the relationships are linear in nature. In case of non-linearity, the results of the regression analysis will under-estimate the true relationship. Curvilinearity was tested by using plots of the standardized residuals as a function of standardized predicted values, showing no departure from linear relationships of Box–Cox transformed variables. (3) *Variables are measured without error (reliably).* In multiple regressions effect sizes of other variables can be over-estimated if the covariate is not reliably measured, as the full effect of the covariate would not be removed. In this study the precision and accuracy of measurements of stemflow chemistry and stemflow volumes was typically better than 5%. (4) *Assumption of homoscedasticity.* Homoscedasticity means that the variance of errors is the same across all levels of the independent variable. Slight heteroscedasticity has little effect on significance tests; however, when heteroscedasticity is marked it can lead to serious distortion of findings and seriously weaken the analysis. This assumption was tested by visual examination of a plot of the standardized residuals (the errors) by the regression standardized predicted value, and by Bartlett test. Data transformation can help to minimize heteroscedasticity. In our case we did not find heteroscedasticity in net stemflow fluxes after Box–Cox transformation. (5) Other assumptions such as *normal distribution of errors* have been reported to be robust to violation, and others are fulfilled in the proper design of a study, e.g., *independence of observations*, as given in this study. We here applied Box–Cox transformations of net stemflow data for the multiple regression approach, to comply to the assumptions of multiple regression analysis. The Box–Cox transformation represents a family of power transformations that provide a potential best practice where normalizing data or equalizing variance is desired (Box and Cox, 1964).

Differences in fluxes between study sites were investigated by one-way ANOVA after testing whether the assumptions underlying ANOVA were met by Bartlett test (homogeneity of variance) and Shapiro–Wilk test (normality test). Kruskal–Wallis ANOVA was calculated for data which did not meet homogeneity of variances and normality after log-transformation. Tukey HSD multiple range tests at the 95% level were calculated to test for differences between forest sites.

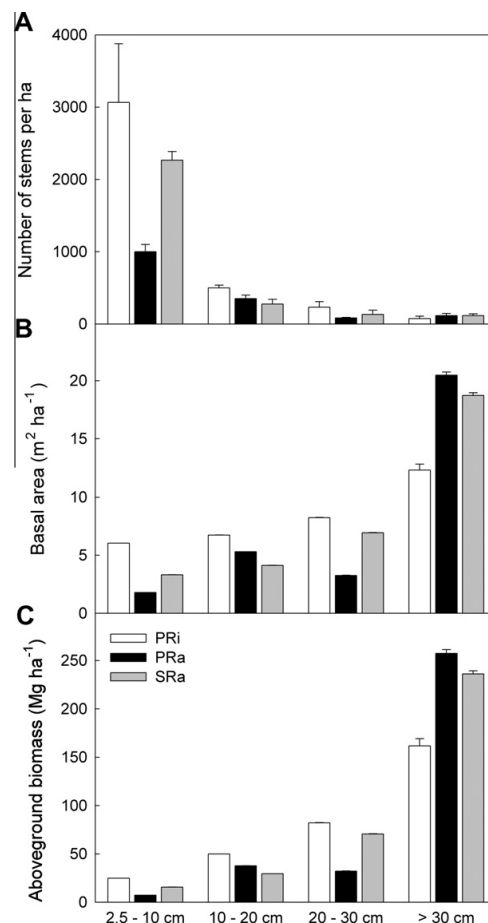
Statistical analysis investigating tree species assemblages were computed with PRIMER 6.0 (Clarke and Gorley, 2006). After Bray Curtis distances (Legendre and Anderson, 1999) of square rooted data were calculated for nutrient fluxes, plant area index and tree species composition of each plot, the matrices were related using the Spearman Rank Correlation Method testing two resemblance matrices for relationships between NSF and tree species assemblages, soil nutrient availability or PAI on the respective forest site. This rank correlation method performs a test of the hypothesis that there is no relationship between multivariate patterns from two

sets of samples and compares this with results from randomly permuted samples.

## 3. Results

### 3.1. Vegetation characteristics

Number of stems >10 cm per hectare did not differ significantly between forest sites (PRI (1148 ± 541), PRa (388 ± 113) and SRa (681 ± 267) but between stem classes, decreasing on a logarithmic scale with increasing stem diameter, from trees <10 cm DBH (2300 ± 567) to trees 10–20 cm (383 ± 69.2), 20–30 cm (150 ± 45.8) and >30 cm (122 ± 16.9) DBH. Standing stocks in terms of aboveground biomass, however, revealed the inverse trend increasing with diameter at breast height. Aboveground biomass (Mg ha<sup>-1</sup>) increased from trees <10 cm DBH (15.95 ± 5.08) to trees 10–20 cm (39.05 ± 5.93), 20–30 cm (61.66 ± 15.11) and >30 cm (218.46 ± 29.01) DBH (Fig. 1). Plant area index (PAI) was



**Fig. 1.** Distribution of vegetation characteristics for (A) number of tree stems per hectare, (B) basal area (m<sup>2</sup> ha<sup>-1</sup>) and (C) aboveground biomass (Mg ha<sup>-1</sup>) presented for the respective stem classes (<10 cm, 10–20 cm, 20–30 cm and >30 cm DBH) and forest sites: PRI (white bars), PRa (black bars) and SRa (gray bars) (Piedras Blancas National Park, SW Costa Rica). PRI – Primary ridge forest, PRa – primary ravine forest, SRa – secondary ravine forest.

significantly higher at PRa ( $8.87 \pm 0.24$ ) compared to PRI ( $7.78 \pm 0.1$ ) and SRa ( $6.82 \pm 0.13$ ) forest ( $F_{(2,33)} = 31.14$ ,  $p < 0.001$ ). Tree height (m) was not significantly different between PRI ( $19.08 \pm 2.58$ ), PRa ( $19.33 \pm 2.96$ ) and SRa ( $18.25 \pm 2.63$ ) forest ( $F_{(2,33)} = 0.14$ ,  $p = 0.87$ ) but differed significantly between stem classes  $<10$  cm ( $6.78 \pm 0.62$ ) and  $10$ – $20$  cm ( $17.44 \pm 2.06$ ) but not between  $20$ – $30$  cm ( $24.89 \pm 2.25$ ) and  $>30$  cm ( $26.44 \pm 1.08$ ) DBH. Therefore correlations of DBH and tree height showed a strong positive relationship with minor differences between stem classes (Full Model:  $R^2 = 0.77$ ,  $p < 0.001$ ).

### 3.2. Hydrology

In this study the hydrological flux via stemflow represented  $0.7$ – $1\%$  of incident precipitation compared to  $96\%$  via throughfall and  $3\%$  canopy interception (latter data from Hofhansl et al. (2011)). Rainfall event size ( $n = 7$ , ranging from  $4$  to  $133$  mm) was positively related to stemflow volume (ranging from  $0.15$  to  $10.7$  L) per tree and event (Fig. 1).

Computation of a generalized linear model ( $R^2 = 0.40$ ,  $p < 0.001$ ) investigating stemflow yield in relation to bulk precipitation, antecedent dry period, bark area and PAI revealed significant influences of precipitation amount ( $p < 0.001$ ) and bark area ( $p < 0.001$ ) but not of the number of antecedent dry days ( $p = 0.20$ ) and PAI ( $p = 0.07$ ) on stemflow yield (Table 1).

Based on the assumption that differences of tree height and bark area of individual trees (tree species) will lead to differences in stemflow yield, single regressions of stemflow catch (volume) and precipitation magnitude were calculated for each tree as discussed in Manfroi et al. (2004). The calculated value of *stemflow commencement* is a proxy for several vegetation characteristics, i.e. tree height, DBH, bark texture and thus tree species. The minimal precipitation magnitude required for stemflow production, investigated by two-way ANOVA, did not differ significantly ( $F_{(2,24)} = 0.48$ ;  $p = 0.62$ ) between forest sites PRI ( $19.1 \pm 3.2$  mm), SRa ( $17.7 \pm 2.7$  mm) and PRa ( $15.5 \pm 3.3$  mm) but between stem classes ( $F_{(3,24)} = 5.22$ ;  $p < 0.01$ ). Thus stems  $<10$  cm DBH needed significantly higher precipitation magnitudes ( $26.9 \pm 4.8$  mm) to produce stemflow than stems  $20$ – $30$  cm DBH ( $17.8 \pm 2.9$  mm),

stems  $>30$  cm ( $13.0 \pm 1.0$  mm) and stems  $10$ – $20$  cm ( $12.0 \pm 1.7$  mm) (Table A1).

Trees  $>30$  cm DBH collected most stemflow volume per event and tree ( $R^2 = 0.93$ ,  $p < 0.001$ ) followed by stems  $<20$  cm DBH ( $R^2 = 0.55$ ,  $p < 0.001$ ) (Fig. 1). Interestingly trees  $20$ – $30$  cm yielded less stemflow ( $R^2 = 0.92$ ,  $p < 0.001$ ) and least stemflow was accumulated by the smallest stem class  $<10$  cm DBH ( $R^2 = 0.40$ ,  $p = 0.002$ ). However, on a plot basis trees  $<10$  cm DBH showed highest abundance of stems per hectare (Fig. 2) and therefore collected most overall stemflow volume on a plot basis. Two-way ANOVA of area-based stemflow volume showed non-significant effects of site ( $F_{(2,24)} = 0.38$ ,  $p = 0.68$ ) and of the interaction of site & stem class ( $F_{(6,24)} = 0.78$ ,  $p = 0.59$ ) but significant effects of the factor stem class ( $F_{(3,24)} = 5.87$ ,  $p = 0.004$ ). Stemflow yield differed significantly between stem classes. On a plot scale stems  $<10$  cm DBH exhibited highest precipitation inputs followed by trees  $10$ – $20$  cm,  $>30$  cm and  $20$ – $30$  cm DBH (data not shown).

### 3.3. Hydrochemistry

Two-way ANOVA of volume-weighted solute concentrations in stemflow revealed significant effects of the factors site and stem class (Table 2). Analyzing forest sites for differences in volume-weighted stemflow concentrations revealed that Mg ( $F_{(2,24)} = 6.17$ ;  $p < 0.01$ ), Cl ( $F_{(2,24)} = 5.95$ ;  $p < 0.01$ ),  $SO_4$  ( $F_{(2,24)} = 5.91$ ;  $p < 0.01$ ), DOC ( $F_{(2,24)} = 4.37$ ;  $p < 0.05$ ) and DON ( $F_{(2,24)} = 4.84$ ;  $p < 0.05$ ) showed significant differences between forest sites, with generally highest concentrations at the PRI forest site. Investigating stem classes for differences in stemflow solute concentrations revealed differences for DOC ( $F_{(3,24)} = 6.87$ ;  $p < 0.01$ ) and DON ( $F_{(3,24)} = 3.11$ ;  $p < 0.05$ ).

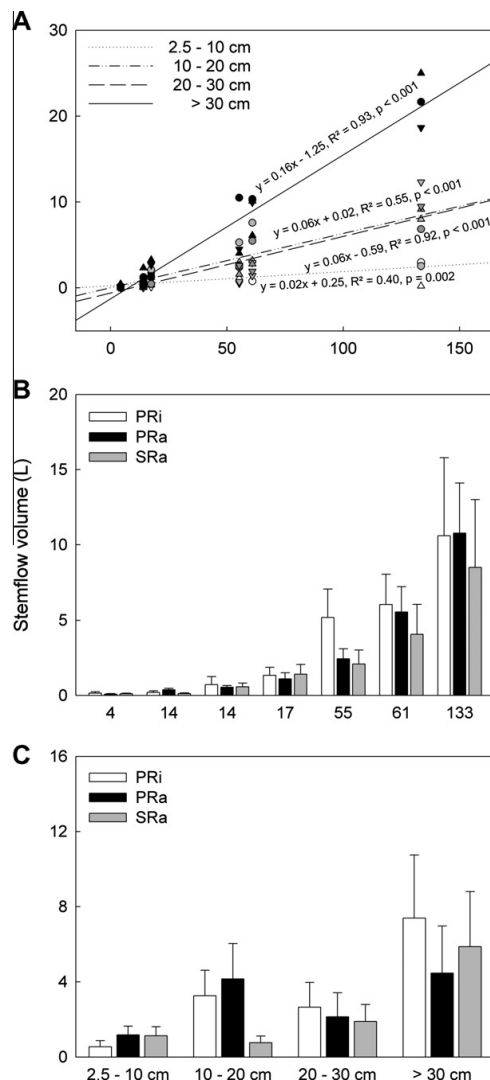
The enrichment ratios used here are based on concentrations compared to flux-based enrichment ratios reported by e.g. Germer et al. (2012). Compared to bulk precipitation and throughfall, volume-weighted solute concentrations in stemflow were enriched by a factor of  $1$ – $10$  (Fig. 3). Average enrichment ratios for stemflow to bulk precipitation were  $7.5 \pm 1.5$ , ranging from  $5.5$  (SRa) to  $10$  (PRI). For throughfall to bulk precipitation the average enrichment ratio was  $2.9 \pm 0.5$ , ranging from  $2.4$  (PRI) to  $3.5$  (PRa). For stemflow to throughfall the average enrichment ratio was  $2.3 \pm 0.3$ ,

**Table 1**

Results of multiple regression models investigating tree stemflow yield and hydrochemistry according to the predictor variables bulk precipitation (BP, mm), antecedent dry period (ADP, days), bark area ( $m^2$ ), and PAI ( $m^2/m^2$ ).

Coefficients	SF yield	Na	NH <sub>4</sub>	K	Mg	Ca	Cl	NO <sub>3</sub>	SO <sub>4</sub>	PO <sub>4</sub>	DOC	DON	TDN
Intercept	−1.19	11.30	−12.22	15.52	18.41	10.87	40.78	38.34	−1.73	1990.31	2058.45	−16.11	−7.21
SE	0.45	6.76	4.17	34.03	7.81	11.37	17.48	17.65	1.64	406.83	400.55	15.73	20.33
p-Value	<b>0.01</b>	0.10	<b>0.00</b>	0.65	<b>0.02</b>	0.34	<b>0.02</b>	<b>0.03</b>	0.29	<b>0.00</b>	<b>0.00</b>	0.31	0.72
BP (mm)	0.02	0.23	0.11	1.51	0.30	0.42	0.06	0.06	0.01	5.81	5.80	0.20	0.32
SE	0.00	0.04	0.02	0.20	0.05	0.07	0.05	0.05	0.01	1.25	1.23	0.05	0.06
p-Value	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	0.28	0.28	<b>0.02</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
ADP (d)	0.04	0.67	0.26	10.26	1.22	1.19	3.79	3.34	0.47	52.66	66.20	2.48	2.71
SE	0.03	0.38	0.26	2.09	0.48	0.70	1.14	1.13	0.11	26.98	26.90	0.97	1.37
p-Value	0.20	0.08	0.32	<b>0.00</b>	<b>0.01</b>	0.09	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	0.05	<b>0.01</b>	<b>0.01</b>	<b>0.05</b>
Bark area ( $m^2$ )	0.01	0.07	0.02	0.31	0.11	0.11	0.29	0.30	0.02	6.25	6.10	0.18	0.26
SE	0.00	0.01	0.01	0.07	0.02	0.02	0.04	0.04	0.00	0.86	0.85	0.03	0.04
p-Value	<b>0.00</b>	<b>0.00</b>	<b>0.02</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
PAI ( $m^2/m^2$ )	0.10	0.73	1.69	13.81	−1.69	0.40	3.18	3.45	0.32	−10.87	−18.44	6.20	9.11
SE	0.06	0.85	0.52	4.28	0.98	1.44	2.23	2.25	0.21	51.52	50.71	1.99	2.57
p-Value	0.07	0.40	<b>0.00</b>	<b>0.00</b>	0.09	0.78	0.15	0.13	0.13	0.83	0.72	<b>0.00</b>	<b>0.00</b>
R <sup>2</sup>	<b>0.45</b>	<b>0.23</b>	<b>0.15</b>	<b>0.33</b>	<b>0.30</b>	<b>0.23</b>	<b>0.25</b>	<b>0.25</b>	<b>0.22</b>	<b>0.23</b>	<b>0.23</b>	<b>0.24</b>	<b>0.25</b>
F-statistic	49.43	13.70	10.00	25.09	22.14	15.56	20.96	20.60	17.97	18.81	19.06	16.59	20.80
p-Value	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>

Data represent predictor coefficients  $\pm$  standard error, coefficients of determination ( $R^2$ ) and p-values from linear models, combined for primary ridge (PRI), primary ravine (PRa) and secondary ravine (SRa) forests (Piedras Blancas National Park, SW Costa Rica). Bold values indicate statistically significant relationships between net stemflow and respective predictor variables ( $p < 0.05$ ).



**Fig. 2.** Stemflow yield (L) against (A) magnitude of bulk precipitation (mm) given for stem classes <10 cm (open symbols), 10–20 cm (light gray symbols), 20–30 cm (dark gray symbols), >30 cm DBH (black symbols) and for the respective forest sites PRi (▲), PRa (▼) and SRa (●); (B) for different bulk precipitation event sizes ( $n = 7$ ; ranging from 4.2 to 133 mm) and (C) stem classes (<10 cm, 10–20 cm, 20–30 cm and >30 cm DBH) for respective PRi (white bars), PRa (black bars) and SRa (gray bars) forest sites (Piedras Blancas National Park, SW Costa Rica). PRi – Primary ridge forest, PRa – primary ravine forest, SRa – secondary ravine forest.

ranging from 1.7 (PRa) to 3.3 (PRi). Stemflow was especially enriched in K, Cl, DOC and DON compared to bulk precipitation and throughfall, stemflow showing higher enrichment ratios than throughfall to bulk precipitation. Enrichment ratios for stemflow to bulk precipitation were tested by two-way ANOVA for differences between sites and stem classes. For forest sites significant differences could be found for Mg ( $F_{(2,22)} = 5.94$ ;  $p < 0.01$ ), Cl ( $F_{(2,22)} = 6.72$ ;  $p < 0.01$ ),  $SO_4$  ( $F_{(2,22)} = 4.92$ ;  $p < 0.05$ ) and DON ( $F_{(2,22)} = 4.84$ ;  $p < 0.05$ ) showing highest values at the PRi forest

site. Stem class affected stemflow enrichment for Mg ( $F_{(3,22)} = 3.56$ ;  $p < 0.05$ ) and DOC ( $F_{(3,22)} = 5.71$ ;  $p < 0.01$ ) (Fig. 3).

Statistical comparisons of resemblance matrices were performed applying Spearman rank correlations testing the relation of soil fertility and net stemflow fluxes to species composition and plant area index. Correlation for net stemflow showed that nutrient fluxes of Cl ( $R = 0.33$ ;  $p = 0.047$ ) and DON ( $R = 0.46$ ;  $p = 0.008$ ) were affected by species composition and fluxes of  $NO_3$  ( $R = 0.40$ ;  $p = 0.017$ ) by plant area index. Further Spearman Rank Correlations of soil fertility (i.e. soil water nutrient composition; data from Hofhansl et al. (2011)) and species composition showed significant correlations for  $NH_4$  ( $R = 0.53$ ;  $p = 0.001$ ), K ( $R = -0.34$ ;  $p = 0.043$ ),  $PO_4$  ( $R = -0.46$ ;  $p = 0.004$ ) and DOC ( $R = -0.43$ ;  $p = 0.008$ ), whereas soil water concentrations of Ca ( $R = 0.39$ ;  $p = 0.019$ ) and in particular nitrogen compounds like  $NO_3$  ( $R = 0.75$ ;  $p < 0.001$ ), DON ( $R = 0.48$ ;  $p = 0.005$ ) and TDN ( $R = 0.67$ ;  $p < 0.001$ ) were significantly correlated with PAI.

#### 3.4. Net stemflow nutrient fluxes

Positive net fluxes of stemflow indicated the release of most solutes with pronounced net stemflow of K ( $1.26 \pm 0.15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) and DOC ( $2.75 \pm 0.73 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) and in decreasing order of Cl ( $0.57 \pm 0.33$ ), Ca ( $0.33 \pm 0.06$ ), Mg ( $0.16 \pm 0.06$ ) and TDN ( $0.16 \pm 0.03$ ). In contrast negative net fluxes pointed to the retention of  $NO_3$  along the stemflow path in all forest types (Fig. 4). Two-way ANOVA of net stemflow fluxes with the factors site and stem class revealed similar patterns as the results from volume-weighted solute concentrations except an additional significant effect of site on Na ( $F_{(2,24)} = 5.24$ ;  $p < 0.05$ ) with highest concentrations at the PRi forest site. No significant differences were evident for the factor stem class (Table 2).

The effect of meteorology and vegetation characteristics on stemflow hydrochemistry was investigated by computing multiple regression models of net stemflow fluxes for each solute including the variables bulk precipitation, antecedent dry period, bark area and PAI. Rainfall volume had a significant effect on most stemflow fluxes (i.e. Na,  $NH_4$ , K, Mg, Ca,  $SO_4$ ,  $PO_4$ , DOC, DON, TDN) while antecedent dry period showed less significant effects (K, Mg, Cl,  $NO_3$ ,  $SO_4$ , DOC, DON, TDN). Bark area was an important factor influencing stemflow hydrochemistry for all solutes while PAI only affected N compounds (TDN, DON,  $NH_4$ ) and K (Table 1). All significant correlations showed positive coefficients pointing to an enrichment of the respective solute with the amount of bulk precipitation, antecedent dry period, plant area index or bark area, the latter three resulting in increased retention times of rain water and thus enrichment in stemflow solutes.

#### 3.5. Contribution of canopy exchange and dry deposition to net stemflow

The multiple regression models of NSF versus rainfall volume and antecedent dry period were highly significant throughout all solutes for “all sites” combined ( $p < 0.001$  and  $R^2 = 0.49\text{--}0.84$ ) and also significant for the different sites, i.e. PRi, PRa, and SRa (Table A2). Based on the coefficients for canopy exchange and dry deposition annual fluxes were calculated (Table A3). No significant differences in canopy exchange or dry deposition were evident between forest types (Table A3), as indicated by the overlapping confidence intervals of estimates for the three forest sites (CI is calculated as the product of standard error times 1.96). Therefore, for comparative analysis of canopy exchange versus dry deposition in net stemflow, results of the multiple regression model combined for all three sites were used. Canopy exchange fluxes were positive for all solutes, indicating strong leaching from the forest canopy for DOC, K, Cl, Ca, Mg, Na, DON

**Table 2**

Volume weighted means of stemflow hydrochemistry (VWM,  $\mu\text{mol L}^{-1}$ ) in primary ridge (PRi), primary ravine (PRa) and secondary ravine (SRa) forests (Piedras Blancas National Park, SW Costa Rica).

Site	Stem class	H	Na	NH <sub>4</sub>	K	Mg	Ca	Cl	NO <sub>3</sub>	SO <sub>4</sub>	PO <sub>4</sub>	DOC	DON	TDN
PRi	2.5–10 cm	16.4	7.87	16.3	72.1	9.23	26.4	40.0	0.53	7.65	0.66	308	7.34	24.1
PRi	10–20 cm	11.7	8.07	6.49	88.9	12	19.9	42.5	0.11	2.45	0.72	1606	44.1	50.7
PRi	20–30 cm	10.6	14.5	11.7	284	41.8	74.4	161	2.23	45.0	0.56	920	18.4	38.5
PRi	>30 cm	117	31.5	7.7	96.4	40.1	27.6	178	0.38	10.5	0.14	533	17.8	25.9
PRa	2.5–10 cm	2.91	10.0	8.34	55.0	7.59	20.5	12.8	0.65	2.64	0.30	150	6.56	15.6
PRa	11–20 cm	5.62	9.53	8.49	116	7.5	23.3	41.7	0.34	2.16	1.17	205	15.4	18.5
PRa	21–30 cm	7.54	8.69	16.2	77.7	7.92	20.1	19.9	4.84	0.98	0.86	331	12.3	33.4
PRa	>30 cm	4.39	6.84	9.86	79.3	10.6	24.7	14.7	0.34	1.81	0.51	673	36.9	47.1
SRa	2.5–10 cm	5.33	6.77	17.2	88.9	8.55	14.6	16.3	0.11	1.85	0.28	234	3.61	18.7
SRa	12–20 cm	5.23	14.7	10.1	107	16.3	35.1	26.8	0.21	1.97	0.26	791	25.8	26.6
SRa	22–30 cm	12.54	6.48	29.2	22.5	16.4	18.6	22.3	0.06	1.19	0.14	673	3.24	18.8
SRa	>30 cm	8.09	5.72	14.0	13.4	28.2	16.5	11.7	0.13	0.9	0.74	442	8.61	22.7
Site	PRi	156	61.9	42.2	541	103a	148	421a	3.26	65.7a	2.08	3367a	87.5a	139
	PRa	20.5	35.1	42.9	328	33.6b	88.6	89.0b	6.17	7.60b	2.83	1359b	71.2ab	114
	SRa	31.2	33.7	70.4	232	69.4a	84.8	77.1b	0.51	5.90b	1.41	2140a	41.3b	86.8
Stem class	2.5–10 cm	8.21	8.21	13.92	71.98	8.46	20.5	23.1	0.43	4.05	0.41	231b	5.84b	19.5
	10–20 cm	7.52	10.8	8.36	104	11.9	26.1	37.0	0.22	2.19	0.72	867a	28.4a	31.9
	20–30 cm	10.2	9.88	19.0	128	22.0	37.7	67.6	2.38	15.7	0.52	641a	11.3ab	30.2
	>30 cm	43.2	14.7	10.5	63.1	26.3	22.9	68.1	0.28	4.41	0.46	550a	21.1ab	31.9

Data represent means. Tukey HSD post hoc test (b < a) indicates significant differences ( $p < 0.05$ ) between sites or stem classes as analyzed by two-way ANOVA.

and TDN, ranging from 0.1 to 1.9 kg ha<sup>-1</sup> yr<sup>-1</sup>. Canopy exchange fluxes of NH<sub>4</sub>, NO<sub>3</sub>, SO<sub>4</sub> and PO<sub>4</sub> were lowest (0.003–0.054 kg ha<sup>-1</sup> yr<sup>-1</sup>). Dry deposition estimates were relatively higher for DOC, K and Cl but generally small compared to canopy exchange estimates and ranged from <0.001 to 0.25 kg ha<sup>-1</sup> yr<sup>-1</sup> (Table A3, Fig. 5).

#### 4. Discussion

Generally stemflow was reported to range from 1% to 23% in tropical forests (Hoelscher et al., 1998; Schroth et al., 2001; Tobon et al., 2004) (see data compilation in Table 3). We here report low values of 0.7–1% stemflow in three forest ecosystems of different topography and successional state, which are situated slightly below the median value of 2% for mature lowland tropical rainforests (Table 3). However, aside of the hydrological role of stemflow much less is known on its biogeochemical role and the controls of net stemflow fluxes in tropical rainforests.

##### 4.1. Controls of stemflow hydrology

We found that stemflow yield was related to several factors such as meteorology (i.e. the magnitude of a precipitation event and antecedent dry period) as well as vegetation characteristics (stem diameter, tree height, bark texture and PAI). While the amount of precipitation significantly increased the production of stemflow, the length of the antecedent dry period did not significantly affect stemflow hydrology. Coefficients of the multiple regression model showed that precipitation volume was positively related to stemflow volume, whereas length of antecedent dry period was negatively though not significantly related to stemflow catch (Table 1). Bark area was positively related to stemflow catch as emergent trees yielded most stemflow. PAI showed only a trend ( $p = 0.07$ ) in enhancing stemflow catches by channelling rainwater to the trunk.

Interestingly precipitation events between 5 and 25 mm did not result in significant enhancement of stemflow production, while event sizes above 25 mm significantly increased stemflow volume (Fig. 2). Therefore a certain amount of rainwater, wetting the surface area of individual trees, is needed to produce minimal stemflow catch (offset or stemflow commencement value). This value

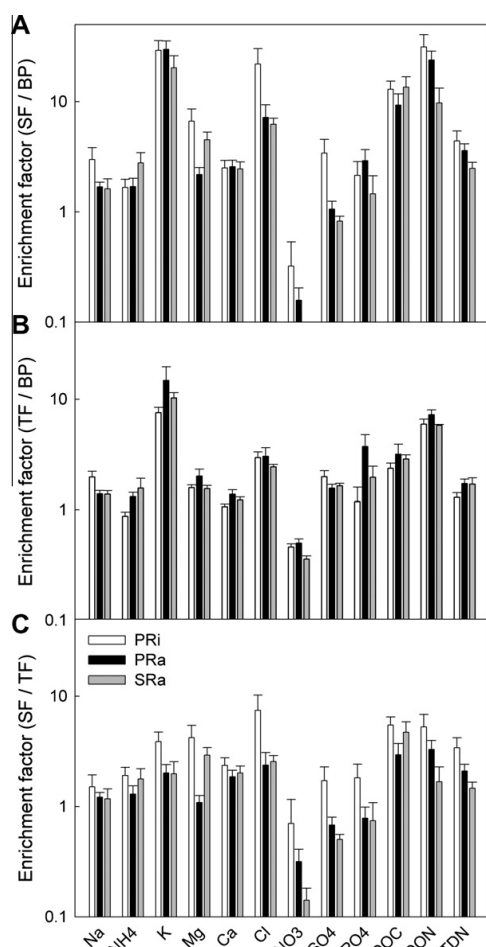
was calculated for each individual tree according to Manfro et al. (2004) but can be stated for stem class or forest site as well. In this study offset values for stemflow commencement did not differ between forest sites but between stem classes (Table A1). This is mirrored by the fact that stems with higher circumferences are usually taller ( $R^2 = 0.77$ ,  $p < 0.001$ ) reaching higher canopy strata compared to small sub-canopy trees and therefore produce stemflow first (Hoelscher et al., 2003). Conversely bigger trees are generally older and therefore have greater epiphyte cover resulting in the retention and deceleration of stemflow (Levia and Herwitz, 2000). Thus stems of the smallest stem class needed significantly higher precipitation magnitudes ( $26.9 \pm 4.8$  mm) to produce stemflow than stems of bigger stem classes (12–17 mm) (Table A1).

While trees of the biggest stem class (DBH > 30 cm) collected most rainwater and produced maximum amounts of stemflow per mm precipitation, on a plot scale we found a negative correlation between stemflow volume and stem diameter (but also with plant area index). On all three forest sites trees of the smallest size class (<10 cm) were the most abundant (1000–3000 stems/ha) and collected 65–81% of overall stemflow at the PRa and PRi site respectively. Therefore, on a plot scale, increasing tree height or DBH did not result in higher stemflow production as the high number of trees <10 cm DBH overruled stemflow catches of the relatively low number of trees >30 cm DBH (Fig. 2). This is also in accordance to a study of Jordan (1978) where stems <10 cm in DBH accounted for 80% of stemflow volumes. The differences in distribution of stems per hectare is also mirrored in a tendency of about 0.2% higher stemflow inputs at the PRi site, which can be attributed to generally higher number of tree stems <30 cm in DBH (Fig. 2). The higher number of tree stems <30 cm at the PRi and SRa forest site can be attributed to higher turnover and disturbance at the secondary and ridge forest sites (e.g. development of forest gaps due to drought or storms).

##### 4.2. Controls of stemflow biogeochemistry

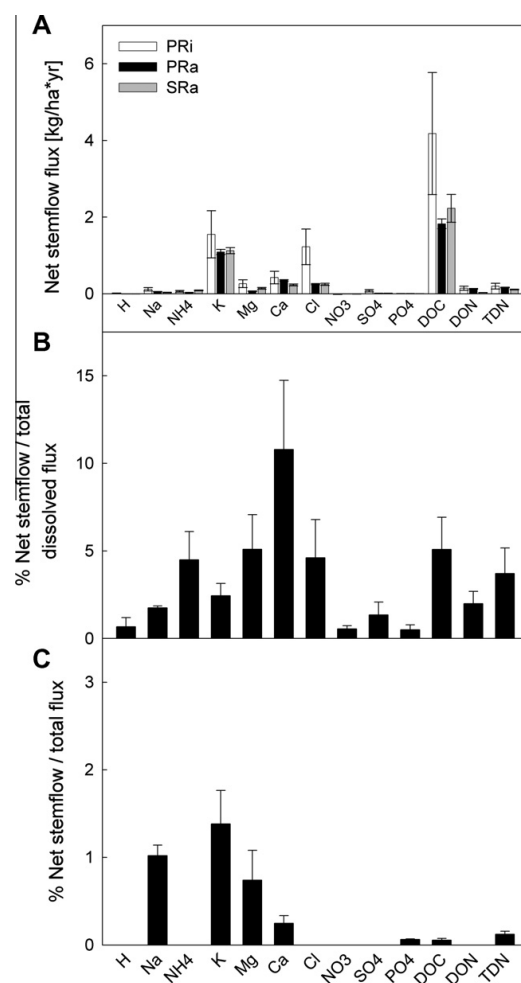
The comparison of stemflow between forest sites revealed no significant differences in hydrological fluxes but distinct differences in biogeochemistry. While the amount of stemflow channelled to tree trunks comprised only approximately 1% of bulk precipitation, nutrients in stemflow were enriched up to 10-fold in comparison to throughfall and bulk precipitation. Average





**Fig. 3.** Concentration-based enrichment factors for (A) throughfall to bulk precipitation, (B) stemflow to bulk precipitation and (C) stemflow to throughfall of the respective forest sites: PRI (white bars), PRa (black bars) and SRa (gray bars) (Piedras Blancas National Park, SW Costa Rica). PRI – Primary ridge forest, PRa – primary ravine forest, SRa – secondary ravine forest.

enrichment ratios were  $7.5 \pm 1.5$  for stemflow to bulk precipitation and  $2.3 \pm 0.3$  for stemflow to throughfall (Fig. 3). Generally we found enrichment of the solutes Mg, Cl,  $\text{SO}_4$ , DOC and DON with increased elevation (PRI) and tree height (or DBH or bark area) pointing to higher deposition rates at the ridge forest and increased leaching rates with higher bark area due to higher residence time of rainwater. To elaborate the influence of meteorology and vegetation characteristics on net stemflow nutrient fluxes we computed generalized linear regression models (Table 1). While precipitation magnitude had a significant effect on net stemflow fluxes of all solutes but Cl and  $\text{NO}_3$ , the length of antecedent dry period resulted in increased K, Mg, Cl,  $\text{NO}_3$ ,  $\text{SO}_4$ , DOC, DON and TDN inputs via net stemflow. Bark area significantly affected all solute fluxes, whereas PAI was found only significant for fluxes of  $\text{NH}_4$ , K, DON and TDN. The models were all highest significant ( $p < 0.001$ ) and explained a variable part of the variability in net stemflow solute fluxes, ranging from  $R^2 = 0.15$  ( $\text{NH}_4$ ) to  $R^2 = 0.32$  (K) (Table 1).

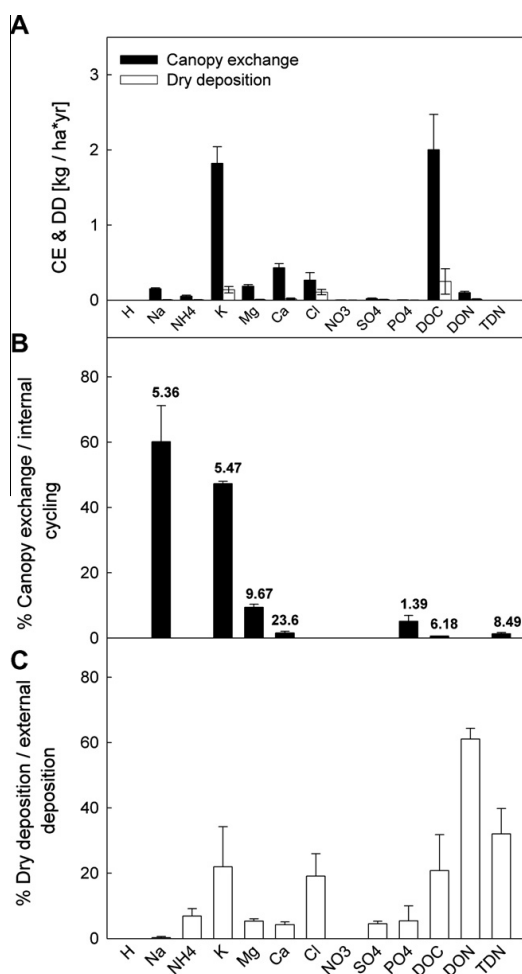


**Fig. 4.** Net stemflow fluxes indicating solute leaching (positive values) and solute retention (negative values) on the respective forest sites: PRI (white bars), PRa (black bars) and SRa (gray bars) (A), as well as net stemflow as a percentage of total dissolved aboveground solute flux (B) and as a percentage of total aboveground solute inputs (C). Data are given as means  $\pm 1$  standard error ( $\text{kg ha}^{-1} \text{a}^{-1}$ ) for primary ridge (PRI), primary ravine (PRa) and secondary ravine (SRa) forests (Piedras Blancas National Park, SW Costa Rica). NSF – Net stemflow, NTF – net throughfall, LF – litterfall.

The characteristics of leaching versus uptake processes of these nutrients along the stemflow path was also visible in the sign of net stemflow fluxes, where all nutrients except  $\text{NO}_3$  and  $\text{PO}_4$  contributed to net inputs to the forest floor (positive NSF) while the latter were retained or taken up by plant tissues (negative NSF, Fig. 4). Similar results were obtained in earlier studies on the same forest sites for throughfall (Hofhansl et al., 2011), showing net retention of dissolved inorganic N and  $\text{PO}_4$ , and an experiment with epiphyte-laden branches, demonstrating rapid gross rates of N uptake and exchange by the branch mesocosms and epiphytic N retention (Hinko-Najera Umana and Wanek, 2010).

Net stemflow solute fluxes of different stem classes showed that DOC and DON were significantly higher for trees  $< 20$  cm DBH. This phenomenon may be explained by two facts: (1) small





**Fig. 5.** Contribution of canopy exchange and dry deposition to net stemflow fluxes (A), canopy exchange as a percentage of internal aboveground solute cycling (B), and dry deposition as a percentage of total atmospheric deposition (C). Data are given as means  $\pm$  1 standard error ( $\text{kg ha}^{-1} \text{a}^{-1}$ ) for primary ridge (PRi), primary ravine (PRa) and secondary ravine (SRa) forests (Piedras Blancas National Park, SW Costa Rica). Numbers above bars in (B) indicate the contribution of canopy exchange by stemflow to total canopy exchange via stemflow plus throughfall.

trees (<10 cm) made up approximately 80% of total stems per hectare (Fig. 1) and (2) stemflow solute fluxes collected by understory trees where reported to originate from throughfall drip points of the upper canopy (which is enriched compared to rainfall) resulting in higher stemflow fluxes of understory trees with low stem diameters. In contrast old trees with high circumferences are assumed to exhibit lower net stemflow fluxes of essential nutrients such as inorganic N and P because of rough bark texture and higher epiphyte cover (Levia and Frost, 2003).

An influence of topography on net stemflow nutrient fluxes could be confirmed for Na, Mg, Cl, SO<sub>4</sub> and DOC that yielded highest fluxes at the exposed ridge (PRi) forest site (Table 2). Elements like Na, Cl, Mg and SO<sub>4</sub> usually derive from atmospheric deposition of sea salt aerosols especially when measured at sites located near to the seashore as was the case in this study (Filoso et al., 1999;

Hofhansl et al., 2011; Wanek et al., 2007). Topography may also affect stemflow by effects on soil development and soil nutrient availability as well as on tree species composition. Differences in PAI, DBH and tree height indicate possible growth limitation of the PRi forest where trees were smaller in height and DBH and the canopy was more open (Table A1). Similar results were observed for litterfall at the study sites, being depleted in N and P at the ridge forest compared to valley bottom forest (Hofhansl et al., 2011). This trend is also supported by a study of Homeier et al. (2010) where aboveground biomass productivity was lower on tropical ridge forest sites. On the contrary values of plant area index (PAI) were highest at the PRa site and therefore attributed to the more fertile ravine forest site that showed higher concentrations of soil nutrients (Hofhansl et al., 2011), a trend also found by others (Homeier et al., 2010). This is also in accordance with higher soil water nutrient concentrations on the PRa forest site (Hofhansl et al., 2011) and the fact that soil solution nitrogen and calcium were positively related to PAI, major nutrients for the build-up of plant biomass including leaf cell walls.

Tree species composition was shown to significantly affect the hydrology and biogeochemistry and thus contribute to the spatial variability of throughfall fluxes (Schroth et al., 1999, 2001). Previous analyses of throughfall chemistry on the same study plots could not confirm any effect of species diversity on throughfall chemistry, due to high species diversity and multiple canopy strata contributing to nutrient enrichment of throughfall (Hofhansl et al., 2011). To our knowledge to date no studies investigated the effect of tree species composition on stemflow nutrient fluxes in tropical rainforests. For stemflow, we found a significant effect of tree species composition on net stemflow fluxes, though only those of Cl and DON were influenced. In turn soil fertility was argued to influence species composition (Gentry and Dodson, 1987; Gentry and Emmons, 1987; Homeier et al., 2010) and thereby bark and foliar nutrient concentrations which may subsequently affect nutrient concentrations in net stemflow and net throughfall (Filoso et al., 1999; Tobon et al., 2004). In this study soil fertility as indicated by soil solution chemistry was also related to tree species composition and thus potentially to tree specific traits such as bark texture and plant nutrient concentrations that may affect net stemflow fluxes.

#### 4.3. Aboveground nutrient fluxes

The notion that stemflow is insignificant in the hydrological and nutrient cycle of tropical forest ecosystems has recently been challenged (Germer et al., 2010). Given that at our study sites only 1% of rainfall reached the forest floor via stemflow it is not surprising that the inputs of the macro-elements such as C, N, K, Ca, Mg and P by net stemflow were low compared to throughfall and litterfall, net stemflow ranging from 0.01 (NO<sub>3</sub>) to 4.1 (DOC)  $\text{kg ha}^{-1} \text{yr}^{-1}$  (Fig. 4A). In comparison to other tropical studies on stemflow nutrient fluxes (Table 3) our results were in the range of other tropical forest ecosystems except being at the lower range for DOC, NO<sub>3</sub>, P, Na and SO<sub>4</sub> suggesting low anthropogenic impact and low air pollution of the study area. The measured net stemflow fluxes amount to a maximum contribution to aboveground nutrient recycling (sum of litterfall, throughfall and stemflow) of about 1.3% for K and less for other elements such as Na, Mg and Ca (Fig. 4C). In contrast we found higher contributions of net stemflow to the hydrological (dissolved) return of nutrients to the forest floor, i.e. net stemflow contributed between 1–2% (Na, K, NO<sub>3</sub>, SO<sub>4</sub>, PO<sub>4</sub>, DON), 4–5% (NH<sub>4</sub>, Mg, Cl, DOC, TDN) and 11% (Ca) to total dissolved aboveground element fluxes (Fig. 4B). As outlined in Materials and Methods net stemflow represents the integral of dry deposition and canopy exchange contributions. Therefore to better understand the sources of elements in stemflow, being

**Table 3**  
Element fluxes ( $\text{kg ha}^{-1} \text{a}^{-1}$ ) in litterfall, bulk precipitation, throughfall and stemflow in tropical rainforests.

Site	Forest/soil type	Rainfall ( $\text{mm a}^{-1}$ )	Altitude (m.a.s.l.)	TF/SF (%BP)	Cl <sup>-</sup> ( $\text{kg ha}^{-1} \text{a}^{-1}$ )	Nt	NO <sub>3</sub> <sup>-</sup>	NH <sub>4</sub> <sup>+</sup>	DON	Pi	Pt	H <sup>+</sup>	Na <sup>+</sup>	Mg <sup>2+</sup>	K <sup>+</sup>	Ca <sup>2+</sup>	Cl <sup>-</sup>	S	Reference
<b>Litterfall</b>																			
Esquinas, Costa Rica	Inceptisol, Primary	5850	80		6040	180					9.9		2.4	28	47	165			1
Esquinas, Costa Rica	Inceptisol, Secondary	5850	80		4990	120					6.0		2.2	18	39	150			1
Esquinas, Costa Rica	Ultisol, Primary	5850	80		4470	100					4.4		1.9	15	30	94			1
Mangrove, Belize	Mangrove	930	0		2340	30					0.8			62	47	107			2
La Selva, Costa Rica	Inceptisol	4300	<150		2970	125					5.9		3.3	13	22	53		12	3
La Selva, Costa Rica	Ultisol plateau	4300	<150		3240	115					5.0		4.3	17	14	60		12	3
La Selva, Costa Rica	Ultisol slope	4300	<150		2925	111					4.6		3.9	13	16	46		11	3
Costa Rica	Montane	2812	2900																4
Amazonia, Colombia	Lowland	3400	200		3110	79					1.1		0.3	5.8	13	7.2			5
Amazonia, Brazil	Lowland	2500	<100																6
Amazonia, Brazil	Lowland	2672	<100																7
Amazonia, Brazil	Primary forest		<50		4260	144													8
Amazonia, Brazil	Secondary forest		<50		4040	103													8
Premontane, Venezuela	Tall forest	2215	1300			46					0.6			10	11	34			9
Premontane, Venezuela	Medium forest	2215	1300			45					0.5			12	9	20			9
Premontane, Venezuela	Low forest	2215	1300			30					0.4			11	17	38			9
Central Africa	LEM	5370	50			150					6.1			20	40	111			10
Central Africa	HEM	5370	50			136					5.9			20	35	96			10
<b>Bulk precipitation</b>																			
Esquinas, Costa Rica	Lowland	5850	80		36	10	2.5	5.6	1.9	0.4		1.4	10	4.5	9.3	17	9	5	1
Mangrove, Belize	Mangrove	930	0		66	13	1.7	0.9	9.9	0.3			101	12	6.1	13	208	12	2
Costa Rica	Montane	2812	2900				1.7	1.7				0.1	4.5	1.1	6.7	4.5			4
Amazonia, Colombia	Lowland	3400	200		134	3	3.1	5.5		0.3		0.5	16	2.3	12	9.3	31	40	5
Amazonia, Brazil	Lowland	2500	<100			5	1.4	1.6	2.4	0.0		0.2	26	3.8	3.2	5.7	55	6	6
Amazonia, Brazil	Lowland	2672	<100											0.3	2.7	0.8			7
Amazon, Venezuela	Laterite	2861	120																11
Amazon, Venezuela	Podsol	3087	120																11
Premontane, Venezuela	Open savanna	2215	1300			1								1.3	2.2	0.8			9
Central Africa	Lowland	5370	50			2				0.1	1.1		1.7	0.9	0.7	9.0	12		10
Congo, Africa	Savanna	1500	160		11		0.7	0.4			2.4		218	16	20	30		2	12
Subtropical, Japan	Maritime	3325	260		139	22													13
Australia	Dry	1450	720											0.1	0.5				14
Australia	Wet	6570	1000											0.0	0.2				14
<b>Throughfall</b>																			
Esquinas, Costa Rica	Inceptisol, Primary	5850	80	88	54	8	0.7	3.8	3.9	1.1		0.3	5.1	7	50	19	12	4	1
Esquinas, Costa Rica	Inceptisol, Secondary	5850	80	86	50	8	0.4	4.1	3.0	0.5		0.5	4.8	5	36	17	9	3	1
Esquinas, Costa Rica	Ultisol, Primary	5850	80	90	43	6	0.6	2.6	2.7	0.3		0.6	8.0	5	26	14	13	4	1
Mangrove, Belize	Mangrove	930	0	85	78	44	1.7	0.3	42	0.1			291	36	17	22	808	38	2
Costa Rica	Montane	2812	2900	73	163		9.0	0.8				0.0	5.5	9	118	20			4
Amazonia, Colombia	Lowland	3400	200	87			9.8	11		0.9		0.4	16	6	38	10	24	56	5
Amazonia, Brazil	Lowland	2622	<100	85		13				0.2				2	18	2			6
Amazonia, Brazil	Lowland	2500	<100	65		6				0.8		0.0	21	4	21	10	46	7	7
Premontane, Venezuela	Tall forest	2215	1300	71		1					0.2			5	36	6			9
Premontane, Venezuela	Medium forest	2215	1300	77		1					0.2			5	38	4			9
Premontane, Venezuela	Low forest	2215	1300	77		0								4	32	7			9
Central Africa	LEM	5370	50	97		7					3.0			12	122	36			10
Central Africa	HEM	5370	50	92		3					3.3			16	119	37			10
Congo, Africa	Eucalypt	1500	160	86	16		0.5	0.3		0.2			3.2	2	1	8	12	2	12
Congo, Africa	Savanna	1500	160	88	16		0.1	0.3		0.4			0.9	2	2	3	3	1	12
Subtropical, Japan	Maritime	3325	260	54	204	22					1.6		157	17	41	27			13
Australia	Dry	1450	720											0.3	3.0				14
Australia	Wet	6570	1000											0.1	0.4				14

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jhydrol.2012.05.057>.

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## SENSITIVITY OF TROPICAL FOREST ABOVEGROUND PRODUCTIVITY TO CLIMATE ANOMALIES





1    **1. Title Page**

2    Title:

3    **Sensitivity of tropical forest aboveground productivity to climate anomalies**

4

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22    **Author Guidelines: < 12 Pages**

23    Abstract: (< 250 words): **247**, Introduction: **929**, Methods: **1916**, Results: **907**, Discussion:

24    **2566**, Acknowledgements: **111**

25    **Total Main Text: 6318 words**

26 **2. Key Points (3 points, < 80 characters each)**

- 27     • We study the climate sensitivity of tropical forest aboveground productivity
- 28     • Local site characteristics determine the response to climate anomalies
- 29     • Climate sensitivity differs between tropical lowland forest types

30

31 **3. Abstract (< 250 words)**

32         The productivity of tropical forests is driven by climate (precipitation, temperature,  
 33 light) and soil fertility (geology, topography). While large-scale drivers of tropical  
 34 productivity are well established, knowledge on the sensitivity of tropical lowland net primary  
 35 production to climate anomalies remains scarce. We here investigate seven consecutive years  
 36 of monthly-recorded data (2006-2013) to study the response of tropical aboveground net  
 37 primary production (ANPP) to a recent El Niño Southern Oscillation (ENSO) anomaly at  
 38 forest sites located in southwestern Costa Rica.

39         In general, the ENSO transition period (2009-2011) resulted in increased temperature  
 40 and decreased precipitation during the El Niño dry-period, causing a decrease in ANPP.  
 41 However, the subsequent La Niña wet-period led to disproportionate strong increases in  
 42 ANPP such that drought-induced reductions were overcompensated. Most strikingly, the  
 43 climate sensitivity of ANPP components differed between canopy production (CP) and wood  
 44 production (WP). Whereas CP showed strong seasonal variation, WP decreased significantly  
 45 in response to a 3°C increase in mean annual maximum temperatures during the El Niño  
 46 drought period. Moreover the climate sensitivity of tropical ANPP components was affected  
 47 by local topography and disturbance history of tropical lowland forest sites.

48         Our results suggest that projected climate change could impact tropical carbon  
 49 sequestration by shifting the partitioning of ANPP components (CP vs. WP) in response to  
 50 climate extremes. We conclude that the impact of climate anomalies on tropical forest

51 productivity is strongly related to local site characteristics and thus will likely prevent  
 52 uniform responses of tropical lowland forests to projected global changes.

53

#### 54 **4. Index Terms and Keywords**

55 Aboveground net primary production, canopy production, El-Niño Southern Oscillation,  
 56 lowland rainforest, wood production

57

#### 58 **5. Text**

##### 59 **5.1 Introduction**

60 Tropical forests are key components of global water and carbon cycles and therefore  
 61 highly relevant for earth climate processes [*Field, 1998, DelGrosso et al., 2008*]. In turn,  
 62 climate and associated atmospheric conditions represent key factors driving primary  
 63 productivity of tropical rainforests [*Clark et al., 2001, Mulkey et al., 1997*]. Hence, climate  
 64 anomalies, such as those projected by global climate change scenarios will likely affect the  
 65 productivity of tropical ecosystems [*IPCC, 2007*].

66 For instance it was reported that during El Niño periods decreased precipitation, soil  
 67 moisture deficit and increasing temperatures negatively affect the productivity of tropical  
 68 rainforest ecosystems [*Clark et al., 2003; Phillips et al., 2009; Wagner et al., 2012*]. In  
 69 accordance, studies on tree-ring chronologies [*Christie et al., 2009*] and tree increments  
 70 [*Clark & Clark, 1994; Clark et al., 2003*] indicated that increased temperatures and drought  
 71 negatively affected aboveground net primary production (ANPP) in tropical forests. However,  
 72 most studies investigating the climate sensitivity of tropical forests are based on single ANPP  
 73 components, particularly on wood production (WP) and thus much less information is  
 74 available on the climate sensitivity of canopy production (CP). Just recently, a unique long-  
 75 term study evaluating 12 years of annual ANPP and its relation to climatic factors reported  
 76 that increasing minimum temperatures and greater dry-season water stress negatively affected

77 WP but not CP [Clark *et al.*, 2013]. This indicates that climate controls on tropical ANPP  
 78 cannot be deduced reliably from a single component of ANPP. Both components (CP and  
 79 WP) together comprise ~90% of ANPP in tropical forests [Aragão *et al.*, 2009], with average  
 80 contributions of  $53 \pm 14\%$  for wood and  $47 \pm 8\%$  for canopy production [Malhi *et al.*, 2011].  
 81 These contributions vary between sites [Malhi *et al.*, 2011], but the environmental  
 82 determinants of this variability are largely unknown.

83 Despite the fact that relationships between canopy and wood production proved weak  
 84 [Dybzinski *et al.*, 2011] and variable between continents [Shoo & VanDerWal, 2008; Malhi *et al.*, 2011] such relationships have often been used to extrapolate single data sets of wood  
 85 production (or of canopy production) to total ANPP, in order to investigate controls on ANPP  
 86 at regional or global scales [e.g. Cleveland *et al.*, 2011]. Based on such extrapolations, ANPP  
 87 of tropical forests has been shown to be globally driven by mean annual temperature (MAT),  
 88 mean annual precipitation (MAP) and soil phosphorous [Schoor, 2003; Raich *et al.*, 2006;  
 90 Cleveland *et al.*, 2011]. However, a major weakness of simple climate metrics like MAT and  
 91 MAP is that they are insufficient to capture the effects of seasonal and interannual climate  
 92 variation on tropical forest productivity which are expected to be strongly affected by future  
 93 climate change [Cleveland *et al.*, 2011]. Therefore a major challenge in exploring the  
 94 causality of climate-productivity relationships in tropical forests to date is the paucity of high  
 95 resolution and long-term records on climate and primary production measured at the same site  
 96 and over the same period of time [Clark, Brown, & Kicklighter, 2001a; Clark *et al.*, 2013]. So  
 97 far, respective climate controls could only be assessed at large scales, comparing tropical  
 98 forests across wide climate and soil gradients but rarely over seasonal and interannual time  
 99 scales.

100 Only recently, a few studies have addressed this issue by investigating which factors  
 101 control seasonal and interannual changes in tropical tree growth [Rowland *et al.*, 2014,  
 102 Gliniars *et al.*, 2013, Mendivelso *et al.*, 2014]. In general, they found that precipitation and



103 solar radiation were the main seasonal drivers of tropical tree growth [Wagner *et al.*, 2014],  
 104 while maximum temperatures [Gliniars *et al.*, 2013] and increasing drought periods reduced  
 105 tree growth [Mendivelso *et al.*, 2014]. Furthermore, Rowland *et al.* [2014] demonstrated  
 106 significant differences between tree functional properties and the degree of seasonality of tree  
 107 growth, consistent with a hypothesized trade-off between maximum potential growth rate and  
 108 hydraulic safety of tropical trees. Therefore fast-growing, low wood density, tall and broad-  
 109 stemmed trees experienced greater reductions in dry season increment than slower-growing,  
 110 higher wood density trees, indicating that the functional composition of tropical forests is an  
 111 important determinant of annual patterns of biomass accumulation [Rowland *et al.*, 2014]. On  
 112 the one hand, this suggests that long-term changes in climate variables might trigger shifts in  
 113 species composition in favor of slow-growing, drought-tolerant species, which was reported  
 114 in conjunction with an increase in forest biomass [Fauset *et al.*, 2012]. On the other hand,  
 115 more frequent short-term disturbances such as those linked to ENSO events typically increase  
 116 the mortality of large trees [Phillips *et al.*, 2010], which may trigger a decrease in stand-level  
 117 biomass. Hence, projected short-term climate anomalies could possibly counteract the long-  
 118 term effects of increasing biomass due to shifts in species composition, and thus negatively  
 119 affect the carbon sequestration potential of tropical lowland rainforests.

120         In this study we investigated the sensitivity of tropical lowland ANPP to climate  
 121 anomalies of a recent ENSO transition period (2009-2011) by analyzing seven consecutive  
 122 years of monthly estimates of aboveground biomass increment (as a surrogate for WP) as well  
 123 as total fine litterfall and leaf area index (as a surrogate for CP) at forest sites differing in  
 124 topography and disturbance history in southwestern Costa Rica. We present data on the  
 125 seasonal and interannual variation of CP and WP to elaborate significant relationships with  
 126 interannual climate anomalies (multivariate ENSO index; MEI), and climatic drivers of bulk  
 127 precipitation (BP), number of dry days (DD) as well as monthly maximum ( $T_{\max}$ ) and  
 128 minimum temperatures ( $T_{\min}$ ). We furthermore consider local site characteristics associated to

topography and disturbance history that might determine the sensitivity of tropical WP and thus might affect the C sequestration potential of tropical lowland rainforests in response to projected climate anomalies.

132

## 133 **5.2 Material and Methods**

### 134 *Study Area*

135 The study area is located at the border of the Piedras Blancas National Park,  
136 encompassing 148 km<sup>2</sup> of wet lowland tropical rainforest in the South-West of Costa Rica  
137 (Weissenhofer et al., 2008). Prevailing soil types are Ultisols and Inceptisols. The dominating,  
138 highly weathered, strongly acidic Ultisols on ridges and upper slopes are replaced by younger,  
139 moderately weathered Inceptisols at ravines and lower slopes [Pamperl, 2001]. To investigate  
140 the climate sensitivity of tropical lowland net primary production we selected three forest  
141 types differing in topography and disturbance history located in the surroundings of the  
142 Tropical Research Station La Gamba (TRSLG; N8°42'03", W83°12'06", 70 m.a.s.l.). The  
143 primary ridge forest (PRi; N8°42'16", W83°12'20", 120 m.a.s.l.) is tall, open and exposed and  
144 exhibits the highest species diversity in the region. The primary ravine forest (PRa;  
145 N8°42'16", W83°12'15", 80 m.a.s.l.) is species-rich and characterized by a high abundance of  
146 palms. The secondary ravine forest (SRa; N8°42'01", W83°12'09", 80 m.a.s.l.) was formerly  
147 used for tree logging and thus is relatively poor in species but has remained undisturbed for  
148 over 25 years. More detailed information on vegetation structure, tree species composition,  
149 soil parameters and nutrient contents can be found in earlier studies conducted at the same set  
150 of sites [see: Wanek et al., 2008; Hofhansl et al., 2011; Hofhansl et al., 2012].

151 Starting in 1997 daily records of climate data (precipitation as well as minimum and  
152 maximum temperature) were taken at the Tropical Research Station La Gamba [Weissenhofer  
153 1996; Weber et al., 2001]. During the study period (2006-2013) mean annual precipitation  
154 was 6100±600 mm, the mean number of dry days 85±13 days per year, the number of months

receiving less than 100 mm of precipitation  $0.7 \pm 0.4$  months, and mean annual temperature was  $28.5 \pm 0.4$  °C. Monthly mean precipitation ranged from 150 mm (Feb) to 870 mm (Oct) and was inversely related to the mean monthly number of dry days ranging from 2 days (Nov) to 16 days (Feb) per month (Figure 2). Mean monthly maximum temperature was  $32.8 \pm 0.7$  °C, ranging between 31.3 °C (Oct) and 34.4 °C (Mar) and mean monthly minimum temperature was  $24.2 \pm 0.2$  °C, ranging between 23.4 °C (Jan) and 24.9 °C (Apr).

#### Study Design

In February 2005, plots ( $400 \text{ m}^2$ ) were set up in triplicate either as squares of 20 x 20 m, separated by a distance of >10 m and divided into subplots of 10 x 10 m each, or as rectangles of 10 x 40 meters subdivided into subplots of 10 x 10 m and separated by 10 - 30 m due to spatial restriction at the ridge forest site. Hence, each forest type was covered by 0.12 hectare of survey area. In each subplot tree species above 10 cm diameter at breast height (DBH) as well as in every fourth subplot trees between 2.5 and 10 cm DBH were tagged 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).

*Aboveground biomass increment* (ABI) was investigated by repeatedly measuring the diameters at breast height (DBH) of all trees approx. 1.30 m aboveground or above buttresses or other irregularities according to standard best-practice techniques [Clark, Brown, & Kicklighter, 2001a; Baker *et al.*, 2004]. In February 2006 trees above 10 cm DBH were equipped with dendrometer bands (D1 permanent tree-girth tape-measures with diameter scale and spring, made of thermally inactive Astralon, UMS, Munich, Germany). Trees below 10 cm DBH were measured (twice shifted by 90 degrees) using sliding calipers. Measurements were performed every month for trees >10 cm DBH and every 3 months for trees <10 cm DBH throughout the study period between 2006 and 2013. Tree height was

181 estimated for all trees of this study (n=349) using inclinometers (Suunto PM-5/360 PC  
 182 clinometer, Valimoti, Finland) and wood density ( $\rho$ ) was measured for 13 out of 61 tree  
 183 species in this study for which data were not available in the literature. For the remaining  
 184 species wood density data were retrieved from the global wood density database [Zanne *et al.*,  
 185 2009]. We used the allometric equation for wet forest stands ( $AGB = \exp [-2.557 + 0.940 \ln (\rho$   
 186  $D^2 H)]$ ) published by Chave *et al.*, [2005] to calculate aboveground biomass increment in  $Mg$   
 187  $ha^{-1} yr^{-1}$  [Keeland & Sharitz, 1993; Clark & Clark, 2000].

188 *Fine litterfall* (LF) was collected in litter traps (50 x 50 cm), fixed 100 cm above  
 189 ground level. Traps were made of PVC tubing, covered by a 1x1 mm nylon mesh, and  
 190 positioned in the center of ten of the twelve subplots in each of the three forest sites. Starting  
 191 in February 2005, fine litter samples were collected in intervals ranging from 2 – 4 weeks and  
 192 divided into leaf litter (consisting of leaves below 50 cm in length) and non-foliar litter  
 193 (consisting of twigs below 2 cm in diameter, reproductive material and fine unidentifiable  
 194 material), oven dried and weighed [Drage, 2007]. The sum of these fractions was used to  
 195 calculate total fine litterfall in  $Mg ha^{-1} yr^{-1}$  [but see: Clark, Brown & Kicklighter, 2001a].

196 In this study we opted to investigate the seasonal variation of ANPP and therefore  
 197 used aboveground biomass increment as indicator of wood production (WP), as well as total  
 198 fine litterfall corrected for changes in leaf area as surrogate for canopy production (CP), at  
 199 monthly time resolution. To that end, we calculated canopy production (CP in  $g m^{-2}$ ) from  
 200 litterfall (LF in  $g m^{-2}$ ) corrected for changes in leaf area index (LAI in  $m^2 m^{-2}$ ) times leaf mass  
 201 area (LMA in  $g m^{-2}$ ) following the equation:  $CP = LF + (LAI_t - LAI_{t-1}) * LMA$  and then  
 202 converted CP to  $Mg ha^{-1}$  for comparison to WP. LAI was estimated from ground-based  
 203 measurements taken between February 2008 and August 2011 using a SunScan probe v1.05  
 204 and Sunshine Sensor BF3 (Delta-T Ltd, U.K.), as well as from remotely sensed MODIS  
 205 products available from the Land Processes distributed active archive center (LPDAAC;  
 206 [https://lpdaac.usgs.gov/products/modis\\_products\\_table/mcd15a2](https://lpdaac.usgs.gov/products/modis_products_table/mcd15a2)). The MCD15A2 product is

207 composited of 8 days data at 1-kilometer resolution on a Sinusoidal grid and includes global  
 208 leaf area index (LAI3d) and the fraction of photosynthetically active radiation (FPAR3g).  
 209 LAI3d and FPAR3g measures are available as world map images for each time point. The  
 210 images have a resolution of 4320x2160 pixels, i.e. each pixel represents an area of 5 minutes  
 211 of longitudinal and latitudinal extent. The pixel value represents the LAI3d/FPAR3g for the  
 212 respective area. Value 250 means that no data are available for this area. The data extraction  
 213 for a time series of LAI of a specific area was created with MATLAB (TM). The images were  
 214 sorted according to the timestamps in their filenames. With the 'imread' function the images  
 215 were loaded iteratively. The pixels of the corresponding desired map coordinates were saved  
 216 in a list and exported as csv-files ('csvwrite') for further evaluation. We subsequently removed  
 217 outliers defined as data beyond three standard deviations, applied a 12-months moving  
 218 average smoother and then adjusted the LAI3d values obtained for each forest site to in-situ  
 219 measurements of LAI, taken between February 2008 and August 2011 [Hofhansl *et al.*, 2012].  
 220 Mean leaf mass area (LMA;  $93.1 \text{ g m}^{-2}$ ) was calculated as average from published literature  
 221 providing LMA values for nearby tropical lowland forest sites in Costa Rica [Cavaleri *et al.*,  
 222 2010] and Panama [Asner *et al.*, 2011].

223

#### 224 *Multivariate ENSO index*

225 Bimonthly values of the Multivariate ENSO Index (MEI) were obtained from the  
 226 National Oceanic and Atmospheric Administration (NOAA -  
 227 <http://www.esrl.noaa.gov/psd/enso/mei/>). MEI is a multivariate measure of the ENSO signal  
 228 that is calculated as the first principal component in an analysis of sea level pressure, surface  
 229 temperature, surface air temperature and cloudiness over the tropical Pacific Ocean [Wolter &  
 230 Timlin, 1993; Wolter & Timlin, 2011]. Negative values represent the cold ENSO phase  
 231 associated with heavy precipitation events (La Niña), while positive values represent the  
 232 warm ENSO phase accompanied by droughts in the study region (El Niño). The ENSO cycle

year typically starts in May (year X) and ends in April (year X+1). We therefore calculated annual sums of climate and productivity variables for the corresponding periods from May 2006 to April 2013.

236

#### 237 *Statistical Analysis*

238       To test for effects of climate on forest productivity we linked daily records of climate  
239 variables i.e. bulk precipitation magnitude (BP), number of dry days (DD), maximum  
240 temperature ( $T_{\max}$ ) and minimum temperature ( $T_{\min}$ ) to collection intervals of litterfall (2-4  
241 weeks) and stem increment (1-3 months) using the aggregate algorithm in R (R Core Team  
242 2012). From the period of May 2006 to April 2013, we calculated monthly sums of canopy  
243 production (CP), wood production (WP), aboveground net primary production (ANPP), bulk  
244 precipitation (BP), and number of dry days (DD), as well as averaged monthly mean ( $T_{\text{med}}$ ),  
245 minimum ( $T_{\min}$ ) and maximum temperatures ( $T_{\max}$ ). Data distributions were analyzed for  
246 normality and non-normal data were log-transformed to attain normality. Prior to further  
247 analysis we removed outliers, defined as data that were beyond three standard deviations of  
248 the mean, from the dataset. Residuals of linear regression analyses were analyzed for  
249 normality and data with leverage and influence inconsistent with the full dataset were  
250 identified and removed. All statistical analyses were performed using R (R Core Team 2012).

251       To further explore the climate sensitivity of tropical lowland net primary production  
252 and to separate patterns of interannual and seasonal variation we calculated annual sums and  
253 monthly means of climate and productivity variables and computed complementary statistical  
254 approaches:

255       We calculated annual sums of climate variables recorded over the period 1997-2013  
256 and computed linear regressions to test for significant relationships of multivariate ENSO  
257 index (MEI) with mean annual precipitation (MAP), annual number of dry days (DD), mean  
258 annual maximum temperature ( $\text{MAT}_{\max}$ ), number of months receiving <100 mm rainfall,



mean annual minimum temperature ( $\text{MAT}_{\min}$ ) as well as the relationship between MAP and  $\text{MAT}_{\max}$ . We moreover calculated monthly means of climate and productivity variables recorded over the period 2006-2013 and computed a canonical correlation analysis (CCA) to visualize the relation of climate variables and productivity parameters with respect to the ENSO transition period (2009-2011). We furthermore computed multiple linear regression models of that dataset to investigate significant effects of multivariate ENSO index (MEI), precipitation magnitude (BP), number of dry days (DD) and maximum temperatures ( $T_{\max}$ ) on canopy production (CP), wood production (WP) and aboveground net primary production (ANPP).

We applied time series analysis and performed seasonal decomposition of time series into seasonal, trend and irregular components to test for patterns in interannual and seasonal variation of climate and productivity variables. Seasonal variation is calculated during the routine as the respective monthly mean of the study period (2006-2013), which then is subtracted from the time series to produce a seasonally de-trended interannual signal. We then computed linear mixed effects models (with interannual trend as fixed factor and seasonal variation as random effect) to test for significant trends in interannual climate and productivity signals during the time series (2006-2013).

We calculated de-trended interannual and seasonal anomalies following *Clark et al.*, [1994] by subtracting monthly means to derive the interannual anomaly and subtracting annual means to derive the seasonal anomaly dataset respectively. We used one-way ANOVA to test for significant differences in the seasonally de-trended interannual data set, as well as in the annually de-trended seasonal data set, respectively. We eventually performed lagged correlation analysis to investigate maximum correlation coefficients between seasonally de-trended climate and productivity variables at different time lags and plotted Spearman's R-values for the correlation between climate and productivity variables to indicate the most significant drivers of tropical lowland net primary production.

285

286 **5.3 Results**

287       During the period of May 1997 to April 2013 the most recent ENSO transition period  
 288 (2009-2011) resulted in decreased mean annual precipitation (MAP) but increased mean  
 289 maximum annual temperature ( $\text{MAT}_{\text{max}}$ ) and number of rain free dry days (DD) as indicated  
 290 by significant relationships with the multivariate ENSO Index (Figure 1). During the study  
 291 period (2006-2013) the ENSO anomaly reduced MAP from an average of 6100 mm to 5360  
 292 mm during the 2009/10 El Niño and subsequently reached the highest value ever recorded of  
 293 7950 mm during the 2010/11 La Niña, whereas  $\text{MAT}_{\text{max}}$  increased by 3 °C during the 2009  
 294 drought period (Figure 1; Figure 2). Moreover, the ENSO transition reduced ANPP by -20%  
 295 in response to increased temperatures (+3° C) and decreased precipitation (-780 mm) during  
 296 the El Niño period (2009/10), whereas subsequently ANPP recovered by +24% following  
 297 disproportionate strong increases in rainfall (+1810 mm) during the La Niña period (2010/11),  
 298 such that drought-induced ANPP reductions were overcompensated (Table S1).

299       We moreover found that ANPP components of canopy production (CP) and wood  
 300 production (WP) exhibited distinct patterns in seasonal and interannual variation (Figure 2;  
 301 Figure 3). Whereas WP showed a strong interannual pattern peaking in 2011 (Figure 2), but  
 302 did not respond significantly to seasonal climate variation (Figure 3; Table S1), CP in  
 303 contrast, followed a strong seasonal pattern peaking in the dry season (Figure 3), but did not  
 304 vary significantly between years (Figure 2; Table S2). Furthermore we found that ENSO  
 305 affected the seasonality of climate variables, such that monthly mean bulk precipitation was  
 306 significantly reduced and monthly mean maximum temperatures significantly increased  
 307 during the El Niño period (Figure 3).

308       A canonical correlation analysis helped to visualize the distinct relations of ANPP  
 309 components to climate variables (Figure 4). Whereas WP was positively related to BP and  
 310  $T_{\text{min}}$  and inversely to DD and  $T_{\text{max}}$ , CP was positively related to DD and  $T_{\text{max}}$  but negatively to

BP and  $T_{\min}$ . Moreover DD and  $T_{\max}$  were associated with the El Niño drought (2009/10), and opposed to BP and  $T_{\min}$  during the La Niña wet period (2010/11). Further investigation of multiple regression models revealed significant climatic controls on ANPP components. While DD showed no significant effect on ANPP and any of its components, BP was negatively related to CP and ANPP but not to WP. In addition,  $T_{\min}$  was negatively related to CP and ANPP, whereas  $T_{\max}$  negatively affected WP at the PRi and SRa but not the PRa forest site (Table 1).

We furthermore applied decomposition of time-series to dissect seasonal and interannual climate variations and investigate seasonally de-trended interannual signals of climate and productivity variables (Figure 5). The analysis confirmed that interannual variations in the amplitude of climatic variables were associated with the ENSO signal. While MEI decreased during the period of 2006-2008 and peaked at the end of 2009, the de-trended interannual signal of BP showed a negative peak in 2009 (inverse but lagged to the de-trended interannual signal of DD) and thus indicated a prolonged period of drought during the El Niño period. Correspondingly the interannual trend of  $T_{\max}$  revealed a dramatic temperature increase of around 3 °C at the end of the dry period in 2009. However, interannual trends of the seasonally de-trended time-series were only significant for climate variables of DD ( $\text{Chi}^2=69.33$ ;  $p<0.001$ ),  $T_{\max}$  ( $\text{Chi}^2=5.91$ ;  $p<0.05$ ) and  $T_{\text{med}}$  ( $\text{Chi}^2=6.22$ ;  $p<0.05$ ; Table S3). Concomitantly, seasonally de-trended interannual time-series of ANPP components showed fluctuations in response to the ENSO signal (Figure 5). Whereas, CP showed no significant response to neither the dry-warm El Niño period (2009/10) nor the wet-cool La Niña period (2010/11), WP in contrast slightly decreased during the dry-warm El Niño period, but subsequently strongly increased due to a lagged response to the wet La Niña period (Figure 5; Table S3). As a result, ANPP decreased in response to the drought period, but subsequently showed a lagged recovery after the ENSO anomaly (Figure 5).

336 We eventually performed lagged cross-correlation analysis of seasonally de-trended  
 337 climate and productivity variables (by subtracting monthly means to derive the interannual  
 338 anomaly) and found that the recent ENSO anomaly (2009-2011) exhibited significant and  
 339 moreover lagged-effects (ranging from 0 to 36 months) on tropical ANPP and its components,  
 340 CP and WP (Table S4). The analysis revealed few significant effects of interannual climate  
 341 fluctuations on CP but strong significant and lagged effects on WP and thereby on ANPP  
 342 (Figure 6). Although MEI significantly decreased WP and ANPP during the first 12 months  
 343 following the El Niño drought period, WP subsequently peaked 27 months after the drought  
 344 anomaly due to a lagged response (12-15 months) to the La Niña wet period (Table S4).  
 345 Whereas DD showed only weak effects on CP, WP and ANPP, BP primarily increased WP  
 346 peaking 18 months after the drought and thus during the onset of the wet period. Interestingly,  
 347  $T_{\min}$  positively affected WP peaking after 9 and after 27 months, whereas  $T_{\max}$  negatively  
 348 affected WP during the first 9 months following the drought but 27 months later showed  
 349 strong positive effects on WP. We furthermore found that the climate sensitivity of WP  
 350 differed between tropical lowland forest sites. Most strikingly,  $T_{\max}$  significantly decreased  
 351 WP at the more exposed ridge (PRi) and secondary (SRa) forest sites, but did not significantly  
 352 affect WP at the down-slope ravine (PRa) forest site (Figure 6). Therefore this analysis  
 353 highlights the differential climate sensitivity of nearby tropical lowland forest sites in terms of  
 354 WP (and thus C sequestration) to ENSO anomalies.

355

#### 356 **5.4 Discussion**

357 Current predictions of increasing climate variability and climate extremes [*Lintner et*  
 358 *al.*, 2012] highlight the need of high resolution and long-term investigations of tropical NPP  
 359 [*Clark et al.*, 2013]. Only then effects of interannual climate variations such as those  
 360 associated with El Niño Southern Oscillation (ENSO) can be distinguished from seasonal  
 361 patterns in order to assess seasonally de-trended interannual climate-productivity couplings

and apply these as a proxy for global change effects on tropical ecosystems processes [Clark *et al.*, 2007]. Hence, we here investigated the sensitivity of tropical lowland aboveground net primary production (ANPP) by evaluating a unique data set including seven years of monthly-recorded data on tropical canopy production (CP) and wood production (WP) from forest sites differing in topography and disturbance history located in south-western Costa Rica.

#### *Seasonal variation and climate-productivity coupling*

What determines the seasonal and interannual variation of tropical ecosystem processes has become a recent subject of studies investigating the productivity of tropical forest ecosystems [Rowland *et al.*, 2013; Malhi *et al.*, 2013; Doughty *et al.*, 2014]. So far, it remains unknown whether direct effects of climate on tropical NPP or rather inherent phenological rhythms in growth allocation dominate the growth response of tropical forests ecosystems to seasonal climatic signals. Nonetheless, more and more studies report on a decoupling between leaf and stem economics in rainforest trees [Baraloto *et al.*, 2010] and thus suggested that changing tree growth rates could reflect shifts in NPP allocation between wood and canopy (or wood and fine root) components rather than changes in overall productivity [Doughty *et al.*, 2014]. Similar to the findings in this study, it was reported that leaf and wood production showed asynchronous seasonal patterns, as leaf production peaked at the beginning of the dry season and wood production during the onset of the rainy season [Wagner *et al.*, 2013]. Therefore, Malhi *et al.* [2014] suggested that phenological rhythms rather than direct climatic controls (such as water stress) drive tropical NPP allocation in Amazonian lowland forests. In accordance, the strong seasonality in NPP of Peruvian montane forests was reported to be driven by changes in photosynthesis and variation in solar radiation, such that trees invested more in biomass production in the cooler season with lower solar radiation and more in maintenance during the warmer high solar radiation period [Girardin *et al.*, 2013]. As a result, temporal or spatial variation in the allocation of NPP

388 between wood, canopy and fine roots could have the potential to be an important feature  
 389 determining the C sink-strength of tropical forest ecosystems [Doughty *et al.*, 2014].  
 390

#### 391 *Sensitivity of lowland ANPP components to climate anomalies*

392 During seven consecutive years of monthly-recorded data on tropical forest ANPP in  
 393 this study, we found that a recent ENSO transition (2009-2011) reduced ANPP by -20% in  
 394 response to increased drought (-780 mm MAP) and maximum temperatures (+3° C MAT<sub>max</sub>)  
 395 during the El Niño drought period. However, subsequently ANPP recovered by +24 % due to  
 396 a lagged growth response after the La Niña wet period, such that drought-induced reductions  
 397 were overcompensated (Figure 6). Interestingly this growth response was largely due to  
 398 variations in woody biomass production rather than leaf production as we found that ANPP  
 399 components of CP and WP followed distinct temporal patterns during the 84 months of the  
 400 study period (Figure 2; Figure 3). Whereas CP showed strong seasonal variation (CV 81%;  
 401 Table S2) but did not differ significantly between years (CV 13%; Table S1), WP showed less  
 402 seasonal variation (CV 43%; Figure 3) but did respond more sensitively to interannual climate  
 403 variation (CV 25%; Figure 2). This could indicate that WP rather than CP accounts for  
 404 drought-induced reductions of tropical ANPP in response to interannual climate anomalies  
 405 and thus would highlight the importance of WP in terms of the C sequestration potential of  
 406 tropical forest ecosystems.

407 Indeed, we here show that the ANPP components CP and WP responded to different  
 408 climatic factors, such that CP increased with the number of dry days and maximum  
 409 temperatures, whereas WP was positively related to bulk precipitation and negatively to  
 410 maximum temperatures (Figure 4). Our findings emphasize recent studies investigating the  
 411 climate sensitivity of tropical forests, reporting that ANPP in tropical forests was positively  
 412 related to precipitation inputs and soil water content but negatively affected by maximum  
 413 temperatures [Clark *et al.*, 2013; Rowland *et al.*, 2013; Gliniars *et al.*, 2014]. Most strikingly,



414 this emerging pattern of climate-induced ANPP variation was found largely due to a response  
 415 in wood production rather than litterfall [*Vasconcelos et al.*, 2012]. Supporting this finding, it  
 416 has been demonstrated that there exists a substantial decoupling between the irradiance driven  
 417 leaf renewal and the water-driven wood production, triggering a temporal asynchronism in  
 418 leaf and wood production in tropical forests [*Wagner et al.*, 2013]. Therefore, in this study CP  
 419 peaked during the dry season associated to high levels of irradiance, whereas WP was  
 420 significantly reduced during the drought period but subsequently recovered significantly in  
 421 response to increased water availability (Figure 6).

422 In the advent of increasing long-term datasets on tropical forest productivity it was  
 423 shown that there is significant interannual variation in total ANPP and each of its components  
 424 in a Caribbean wet lowland rainforest region in northeastern Costa Rica [*Clark et al.*, 2013].  
 425 However, whereas short-lived components (leaf, twig and reproductive litterfall) were not  
 426 significantly related to interannual climate variation, the production of long-lived tissues  
 427 (wood production) was negatively affected by water limitation and higher temperatures  
 428 [*Clark et al.*, 2013]. In accordance, we here found that WP (-24%) was the more responsive  
 429 ANPP component compared to CP (-17%) to the El Niño drought period. Moreover, the  
 430 investigation of lagged correlation coefficients (0-36 months) between ANPP components and  
 431 climatic variables indicated that whereas CP followed a more seasonal pattern, WP more  
 432 strongly responded to interannual variations in precipitation and temperature associated to the  
 433 ENSO signal (Figure 6; Table S4).

434 Adding to this, recent studies suggest that carbon allocation strategies in tropical  
 435 forests trigger a temporal decoupling between NPP components [*Doughty et al.*, 2014].  
 436 During their four-year high temporal resolution dataset from two forest plots in the Bolivian  
 437 Amazon a strong 2010 drought strongly reduced photosynthesis, whereas NPP remained  
 438 constant and even increased in the six-month period following the drought. The authors  
 439 conclude that allocation trade-offs might dominate the response of tropical forest growth to

environmental changes due to carbon allocation priorities and non-structural carbohydrate storage in tropical trees. In detail, they reported that allocation initially increased towards the canopy followed by increased allocation to fine root production in the following year, such that trees grew wood more slowly because they prioritized the build-up of new leaves or roots during the dry period (Doughty 2014). We here similarly found a lagged response of tropical wood production during this study of seven-consecutive years of monthly censuses, such that WP peaked 27 months after the drought period (Figure 6). This might indicate that during drought anomalies initially increased CP is used to replenish carbon stores in tropical trees, followed by greater fine-root production to explore soil water resources, which finally results in increased wood production when water availability is restored after the drought period. In accordance, we found that whereas CP varied more seasonally, WP showed a strong decline during the 12 months after the drought anomaly but a strong increase in the 12-15 months following thereafter (Figure 6).

Nonetheless, both ANPP components respectively increased by +52% (WP) and +18% (CP) after the drought period. Therefore the strong resilience of tropical ANPP components after the ENSO anomaly could indicate that wet tropical forests have the potential to overcome short-term ANPP reductions when water availability is recovered after the drought period. The strong resilience of tropical tree biomass production, as indicated by the marked response of tropical WP compared to CP, further suggests that tropical lowland forests possess the potential to strongly recover carbon stocks (and thus C sequestration) after short-term climate anomalies.

461

#### 462 *Effects of local site characteristics (topography and disturbance history)*

Beyond the results on seasonal and interannual responses of ANPP components to climatic signals we found a pattern indicating the importance of local site characteristics in determining the responses of tropical WP to large-scale climate anomalies (Figure 6).

Therefore reductions in WP were most prominent at the exposed ridge forest site (PRi; -35%) but less intense at the ravine forest site (PRa; -26%) and the downslope secondary re-growth forest site (SRa; -26%). This site-specific climate sensitivity was attributed to topographic differences in soil type and soil depth and thus water availability as was indicated by differences in soil bulk density and soil moisture between the respective study sites [Wanek *et al.*, 2008]. It is therefore plausible that increased  $T_{\max}$  and decreased BP triggered drought stress of trees at the more exposed ridge forest and secondary regrowth forest site but did not significantly affect WP at the moist ravine forest site (Table 1).

In accordance, a recent analysis investigating the response of tropical forest growth to seasonal and interannual drought in the Bolivian Amazon reported site-specific differences associated to topoedaphic characteristics of the respective forest site [Doughty *et al.*, 2014]. The authors found that although soil type and soil texture were relatively similar between the two Amazonian forest plots, the major difference was due to differences in soil depth and thus water availability between shallow and deep soil plots. These topoedaphic differences caused increased water stress at the shallow-soil plot compared to the deep-soil plot and thus led to differences in the composition of tree species. Whereas the deep-soil plot inhabited species typical of humid regions, the shallow-soil plot comprised species more typical of a dry deciduous forest with more seasonal leaf and wood production. As a result, the shallow-soil plot showed a more regular seasonal but also substantial interannual variation in NPP, suggesting a greater drought sensitivity of dry deciduous tree species [Doughty *et al.*, 2014]. Therefore, local topoedaphic characteristics associated with water availability have the potential to determine the composition of tree species, which in turn could have important consequences for the drought-tolerance of tropical lowland forests to climate anomalies.

It has been shown that the drought sensitivity of tropical tree growth differed among Neotropical tree species, such that diverse growth responses among coexisting tree species were related to species-specific responses of wood formation to water availability

492 [Mendivelso *et al.*, 2014]. Therefore, more sensitive species require more water and more  
 493 efficient water transport for growth than less sensitive species and thus drought sensitivity is  
 494 related to different life history strategies of drought-tolerant versus fast growing opportunistic  
 495 species that determine water use and storage [Markesteijn *et al.*, 2011]. Consistently, the  
 496 sensitivity of wood production to climate variations was found to be associated to functional  
 497 trade-offs between early and late-successional species in Amazonian lowland rainforests  
 498 [Rowland *et al.*, 2014]. In general, early successional tree species with low wood density  
 499 rather invest into rapid growth to prevent shading, whereas late-successional climax species  
 500 tend to be shade-tolerant but slow growing to reduce mortality risks [Rowland *et al.*, 2014].  
 501 As a result, short-term drought anomalies could have the potential to kill trees selectively  
 502 since fast-growing, light-wooded trees might be especially vulnerable to drought by cavitation  
 503 or carbon starvation [Condit *et al.*, 1996; McDowell *et al.*, 2008]. In accordance, Phillips *et*  
 504 *al.*, [2009] found that Amazonian tree species dying during the drought period had lower  
 505 wood densities than those dying before. Therefore, species with denser wood were less  
 506 vulnerable to drought and thus may become dominant after longer periods of water deficit  
 507 [Phillips *et al.*, 2010]. Indeed, we here found some evidence for this relationship, as low wood  
 508 density trees showed a trend of increased tree mortality of during the 2009/10 El Niño period  
 509 ( $F=2.33$ ;  $p=0.06$ , data not shown).

510       Moreover, it was reported that long-term drought-induced shifts in the functional  
 511 composition of tropical forest trees in favor of drought-tolerant species were associated with  
 512 an increase in aboveground biomass [Fauset *et al.*, 2012]. Similar findings of increasing  
 513 biomass over recent decades in other African [Lewis *et al.*, 2009] and Amazonian forests  
 514 [Phillips *et al.*, 2009] suggest that despite such long-term droughts these forests are capable to  
 515 maintain their carbon stocks due to compositional shifts of tree species in response to low-  
 516 intensity disturbances [Fauset *et al.*, 2012]. However, during more extreme and short-term  
 517 droughts, in contrast, increased tree mortality dominates the proposed long-term natural

518 selection effects and thus causes substantial decreases in aboveground biomass [*Fauset et al.*,  
519 2012].

520       Therefore our findings of differential responses of tropical ANPP between lowland  
521 forest sites could be based on differences in the composition and thus functional trade-offs  
522 among life-history strategies of tropical tree species. Indeed, earlier studies conducted at the  
523 same set of sites have found pronounced differences (92-99%) in the composition of tree  
524 species [*Hofhansl et al.*, 2011] and reported differences in site-averaged wood density for  
525 primary ridge (PRi; 0.57 g/cm<sup>3</sup>), secondary ravine (SRa; 0.54 g/cm<sup>3</sup>) and primary ravine  
526 (PRa; 0.52 g/cm<sup>3</sup>) forest sites [*Taylor et al.*, unpublished data]. Although the primary ridge  
527 forest site with the highest mean wood density faced the strongest reductions in WP (PRi; -  
528 35%) compared to the lower wood density secondary (SRa; -26%) and ravine forest site (PRa;  
529 -26%), it also most strongly recovered by more than two-fold (PRi; +83%) compared to the  
530 secondary (SRa; +41%) and ravine forest site (PRa; +31%) after the drought anomaly. Our  
531 findings likely relate to inverse effects of topography on edaphic parameters (water  
532 availability) as well as on life-history strategies (drought tolerance) among tropical tree  
533 species that eventually determine the site-specific sensitivity of tropical lowland ANPP to  
534 climate anomalies. It is therefore plausible that the greater climate sensitivity of low-density  
535 trees at the moist ravine forest site (PRa) was buffered via high soil water availability and less  
536 temperature fluctuations, whereas high-density trees at the more exposed ridge forest site  
537 (PRi), though being better adapted to droughts, were more prone to anomalous climate  
538 extremes. This further indicates that on the one hand local topography and water availability  
539 overrides functional adaptations of tropical tree species in terms of drought tolerance, but on  
540 the other hand highlights that drought-adapted communities show a higher degree of  
541 resilience and recovery after such climate excursions.

542       Overall, our results suggest that (1) the proximate short-term tolerance to the strong El  
543 Niño drought period is predetermined by topoedaphic factors such as soil water availability,

544 and (2) the functional adaptation of the respective tree species community could potentially  
 545 compensate short-term disturbances via drought-induced shifts in tree species composition  
 546 that further regulate the long-term sensitivity of tropical lowland rainforests to climate  
 547 anomalies.

548

#### 549 *Conclusions*

550 Predicted changes in tropical climate are stated to result in intermittent precipitation  
 551 events and increasing temperatures, causing prolonged periods of drought and thus water  
 552 deficit [Prentice *et al.*, 2007]. Such climate excursions and long-term climate change might  
 553 shift the carbon balance of tropical rainforest ecosystems towards decreased wood production  
 554 and thus decrease the carbon stocks of high productive lowland forests.

555 While short-term climate extremes generally trigger increased tree mortality, long-  
 556 term responses to periodic climate anomalies are related to species turnover and thus  
 557 compositional shifts of the remaining tree species community. This indicates that tropical  
 558 lowland forests are on the one hand prone to climatic changes, but on the other hand have the  
 559 potential to maintain their carbon stocks by shifting tree species composition in favor of  
 560 drought-tolerant species.

561 Our findings of site-specific differences in drought sensitivity suggest that changes in  
 562 future climate could differentially affect the carbon sequestration potential of tropical lowland  
 563 rainforests, i.e. primary vs. secondary forests as well as uphill vs. downslope forests due to  
 564 differences in local resource availability and tree species composition.

565 Therefore, the spatial diversity of tropical lowland rainforests - associated with soil  
 566 moisture and forest disturbance - will likely prevent uniform responses of tropical lowland net  
 567 primary production to projected global changes and thus highlights the need of further high-  
 568 resolution and long-term studies in tropical forest ecosystems.

569

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## 8. Tables

### Table 1: Effects of climate on tropical aboveground forest productivity<sup>a</sup>

<sup>a</sup>Results of multiple regression models investigating the effects of monthly means of climate variables: multivariate ENSO index (MEI), number of dry days (DD), bulk precipitation (BP), minimum temperature ( $T_{\min}$ ), maximum temperature ( $T_{\max}$ ) on monthly means of tropical aboveground productivity: canopy production (CP), wood production (WP) and aboveground net primary production (ANPP) recorded during the period 2006-2013 at primary ridge forest



(PRi), primary ravine forest (PRa) and secondary ravine forest (SRa) located in south-western Costa Rica.

780

## 781 9. Figures

782 **Figure 1:** Relationship of multivariate ENSO index (MEI) with climate variables: mean  
783 annual precipitation (MAP), annual number of dry days (DD), mean annual maximum  
784 temperature ( $\text{MAT}_{\text{max}}$ ), number of months receiving <100 mm rainfall, mean annual  
785 minimum temperature ( $\text{MAT}_{\text{min}}$ ) as well as the relationship between MAP and  $\text{MAT}_{\text{max}}$   
786 recorded over the period 1997-2013 at the Tropical Research Station La Gamba, Costa Rica.  
787 Significant relationships are indicated by respective  $R^2$  and p-values.

788

789 **Figure 2:** Interannual variation in annual sums of climate and productivity variables: dry days  
790 (DD), multivariate ENSO index (MEI), mean monthly maximum temperature ( $\text{MAT}_{\text{max}}$ ),  
791 mean annual bulk precipitation (MAP), mean annual leaf area index (LAI), mean monthly  
792 minimum temperature ( $\text{MAT}_{\text{min}}$ ) as well as annual sums of litterfall (LF), canopy production  
793 (CP), wood production (WP) and aboveground net primary production (ANPP) recorded  
794 during the period 2006-2013 at primary ridge forest (PRi; red bars), primary ravine forest  
795 (PRa; blue bars), and secondary ravine forest (SRa; green bars) located in south-western  
796 Costa Rica. Levels of significant interannual variation are indicated by asterisks (\*\*\*,  
797  $p < 0.001$ ; \*\*,  $p < 0.01$ ; \*,  $p < 0.05$ ; °,  $p < 0.1$ ; n.s., non-significant) and were calculated from  
798 seasonal de-trended variables using one-way ANOVA (see Table S1). Additionally colored  
799 bars in climate variables (DD, MEI,  $T_{\text{max}}$ , BP,  $T_{\text{min}}$ ) represent respective climate anomalies  
800 during the El Niño dry period (white bars) as well as the subsequent La Niña wet period  
801 (black bars) compared to non-ENSO conditions (grey bars). The ENSO cycle year typically  
802 starts in May (year X) and ends in April (year X+1), we therefore computed annual sums of

climate and productivity variables for the corresponding periods from May 2006 to April 2013.

**Figure 3:** Seasonal variation in monthly means of climate and productivity variables: dry days (DD), multivariate ENSO index (MEI), mean monthly maximum temperature ( $T_{\max}$ ), bulk precipitation (BP), mean annual leaf area index (LAI), mean monthly minimum temperature ( $T_{\min}$ ) as well as monthly means of litterfall (LF), canopy production (CP), wood production (WP) and aboveground net primary production (ANPP) recorded during the period 2006-2013 at primary ridge forest (PRi; red bars), primary ravine forest (PRa; blue bars), and secondary ravine forest (SRa; green bars) located in south-western Costa Rica. Bars represent monthly means and whiskers represent standard errors. Levels of significant seasonal variation are indicated by asterisks (\*\*\*,  $p < 0.001$ ; \*\*,  $p < 0.01$ ; \*,  $p < 0.05$ ; °,  $p < 0.1$ ; n.s., non-significant) and were calculated from interannual de-trended variables using one-way ANOVA (see Table S2). Additional line plots in climate variables (DD, MEI,  $T_{\max}$ , BP,  $T_{\min}$ ) represent respective climate anomalies during the El Niño period (open symbols) as well as the subsequent La Niña period (closed symbols) compared to non-ENSO conditions (grey bars). The ENSO cycle year typically starts in May (year X) and ends in April (year X+1), we therefore computed monthly means of climate and productivity variables for the corresponding periods from May 2006 to April 2013.

**Figure 4:** Canonical correspondence analysis indicating (A) the relation of monthly means of climate variables: multivariate ENSO index (MEI), number of dry days (DD), precipitation magnitude (BP), maximum temperature ( $T_{\max}$ ), minimum temperature ( $T_{\min}$ ) and productivity variables: canopy production (CP; green symbols), wood production (WP; red symbols) and aboveground net primary production (ANPP; blue symbols) recorded during the period 2006-2013 at primary ridge forest (PRi), primary ravine forest (PRa) and secondary ravine forest

(SRa) located in south-western Costa Rica, as well as (B) the relation of climate variables (MEI, DD, BP, T<sub>min</sub>, T<sub>max</sub>) to the 84 monthly records of productivity variables (CP, WP and ANPP) with respect to the ENSO transition period (El Niño dry period 2009/10; La Niña wet period 2010/11).

833

**Figure 5:** Seasonal de-trended time series of climate and productivity variables: dry days (DD), multivariate ENSO index (MEI), mean monthly maximum temperature (T<sub>max</sub>), bulk precipitation (BP), mean annual leaf area index (LAI), mean monthly minimum temperature (T<sub>min</sub>) as well as monthly means of litterfall (LF), canopy production (CP), wood production (WP) and aboveground net primary production (ANPP) recorded during the period 2006-2013 at primary ridge forest (PRi; red bars), primary ravine forest (PRa; blue bars), and secondary ravine forest (SRa; green bars) located in south-western Costa Rica. Levels of significant variation in time series are indicated by asterisks (\*\*\*,  $p < 0.001$ ; \*\*,  $p < 0.01$ ; \*,  $p < 0.05$ ; °,  $p < 0.1$ ; n.s., non-significant) and were calculated from seasonal de-trended variables using linear mixed effects models (see Table S3). Additional grey areas indicate the impact of the 2009 El Niño drought period on climate and productivity variables.

845

**Figure 6:** Spearman's R values of lagged cross-correlations between seasonally de-trended climate variables: multivariate ENSO index (MEI), number of dry days (DD), precipitation magnitude (BP), minimum temperature (T<sub>min</sub>), maximum temperature (T<sub>max</sub>), mean temperature (T<sub>med</sub>) and seasonally de-trended productivity variables: canopy production (CP), wood production (WP) and aboveground net primary production (ANPP) recorded during the period 2006-2013 at primary ridge forest (PRi), primary ravine forest (PRa) and secondary ravine forest (SRa) located in south-western Costa Rica. Significant correlation coefficients are indicated by dashed lines ( $p < 0.05$ ) and were calculated from seasonal de-trended variables using lagged correlation analysis (see Table S4).

855

856 **10. Copyrighted Material**

857 The authors declare no competing interests.

858

859 **11. Supporting Material**860 **Table S1:** Results of one-way analysis of variance (ANOVA) on seasonal de-trended

861 interannual variations in climate variables: multivariate ENSO index (MEI), number of dry

862 days (DD), precipitation magnitude (BP), minimum temperature ( $T_{\min}$ ), maximum863 temperature ( $T_{\max}$ ), and mean temperature ( $T_{\text{med}}$ ); as well as productivity variables: leaf area

864 index (LAI), litter fall (LF), canopy production (CP), wood production (WP) and

865 aboveground net primary production (ANPP) recorded during the period 2006-2013 at

866 primary ridge forest (PRi), primary ravine forest (PRa) and secondary ravine forest (SRa)

867 located in south-western Costa Rica.

868

869 **Table S2:** Results of one-way analysis of variance (ANOVA) on interannual de-trended

870 seasonal variations in climate variables: multivariate ENSO index (MEI), number of dry days

871 (DD), precipitation magnitude (BP), minimum temperature ( $T_{\min}$ ), maximum temperature872 ( $T_{\max}$ ), and mean temperature ( $T_{\text{med}}$ ); as well as productivity variables: leaf area index (LAI),

873 litter fall (LF), canopy production (CP), wood production (WP) and aboveground net primary

874 production (ANPP) recorded during the period 2006-2013 at primary ridge forest (PRi),

875 primary ravine forest (PRa) and secondary ravine forest (SRa) located in south-western Costa

876 Rica.

877

878 **Table S3:** Results of linear mixed effects models on seasonally de-trended time series

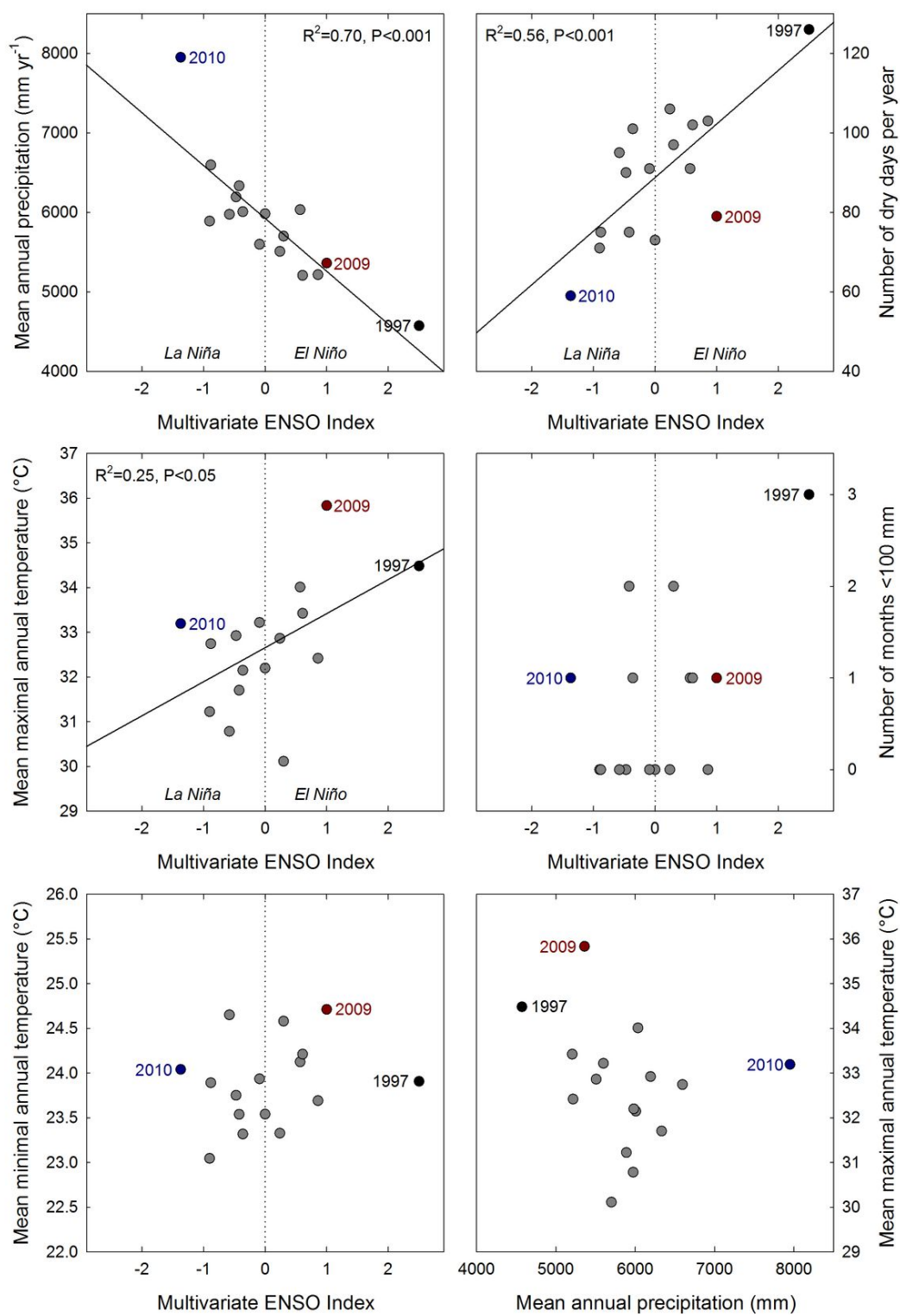
879 investigating significant trends in climate variables: multivariate ENSO index (MEI), number

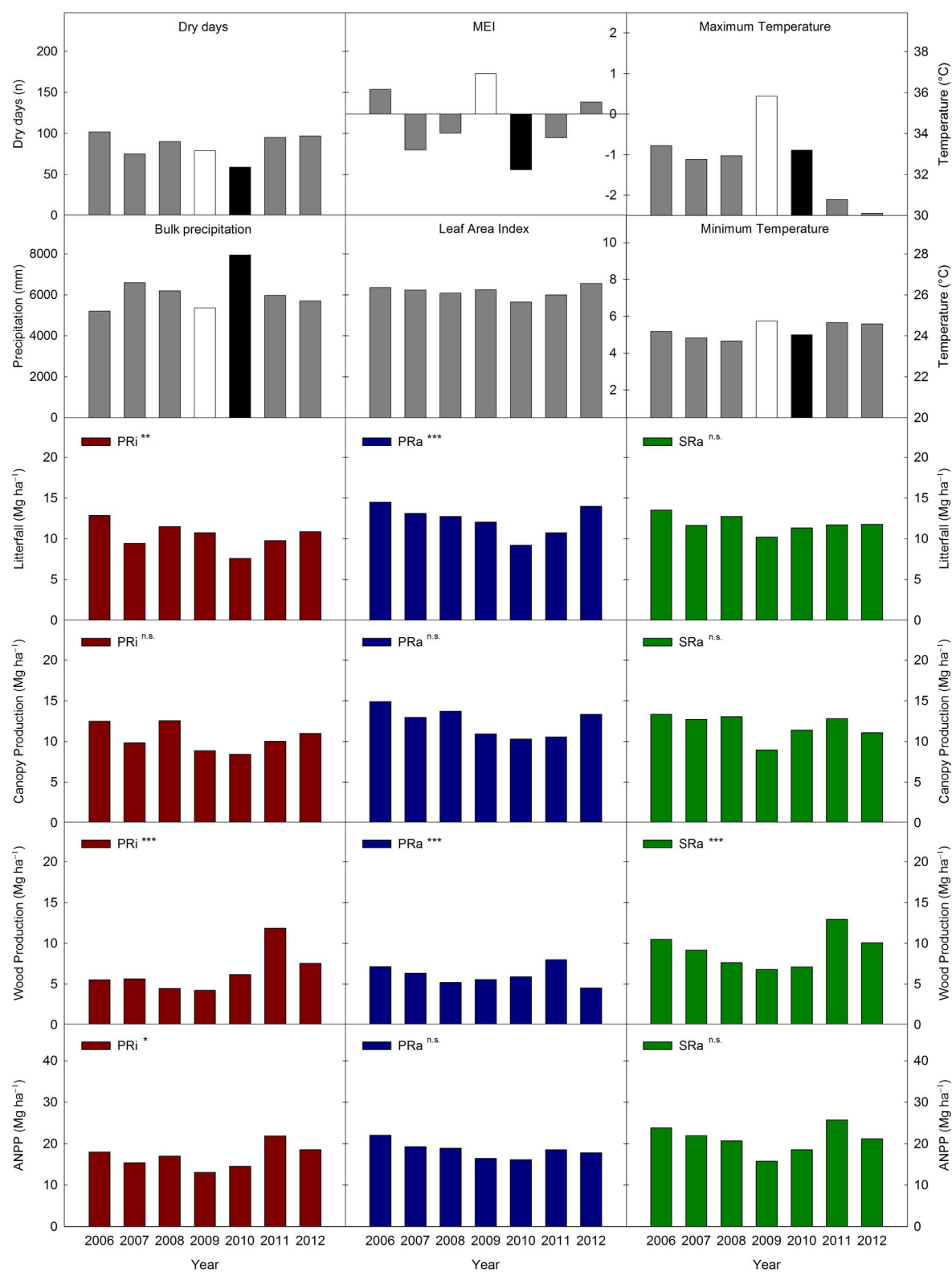
880 of dry days (DD), precipitation magnitude (BP), minimum temperature ( $T_{\min}$ ), maximum

881 temperature ( $T_{\max}$ ), and mean temperature ( $T_{\text{med}}$ ); as well as productivity variables: leaf area  
 882 index (LAI), litter fall (LF), canopy production (CP), wood production (WP) and  
 883 aboveground net primary production (ANPP) recorded during the period 2006-2013 at  
 884 primary ridge forest (PRi), primary ravine forest (PRa) and secondary ravine forest (SRa)  
 885 located in south-western Costa Rica.

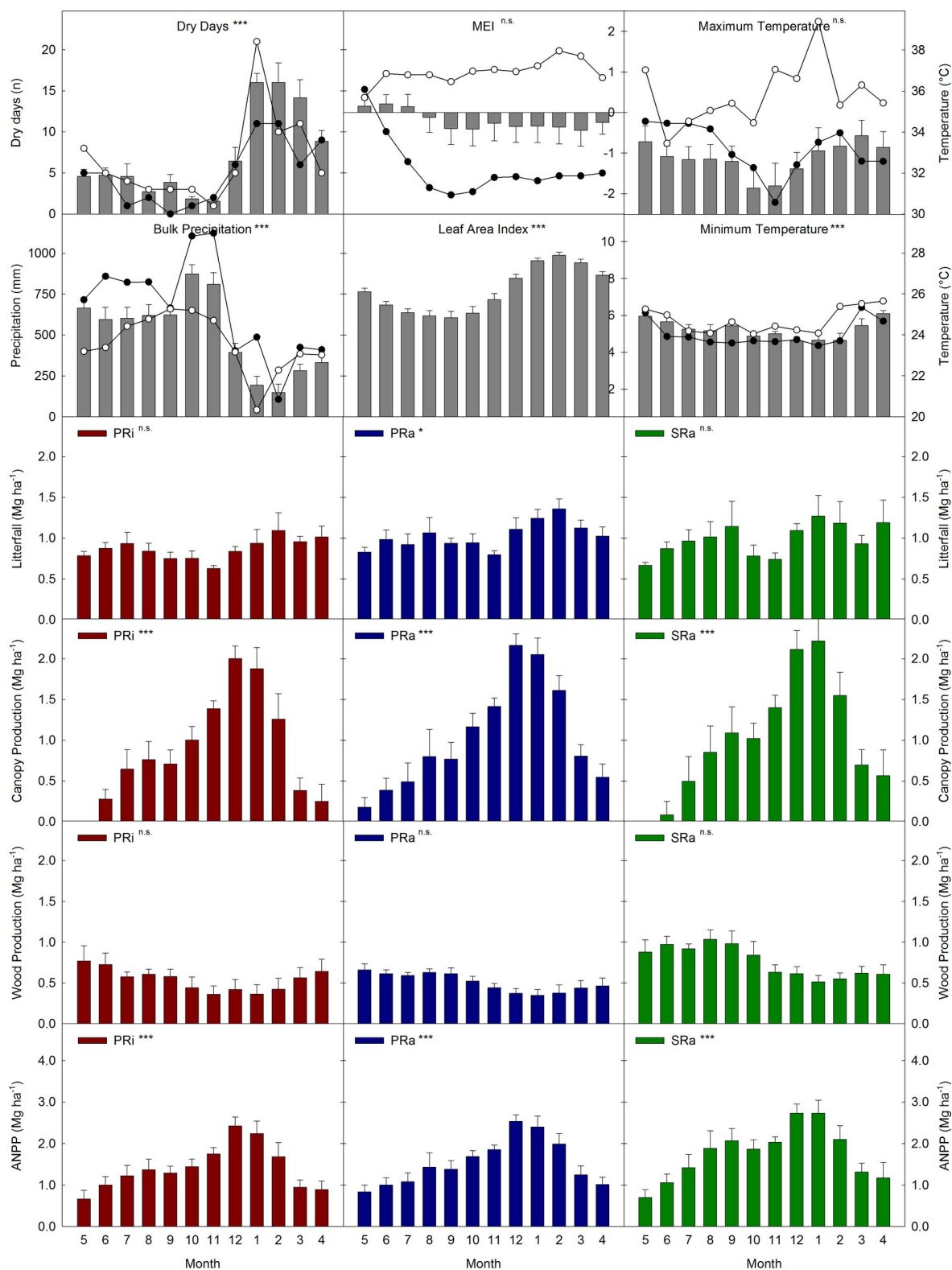
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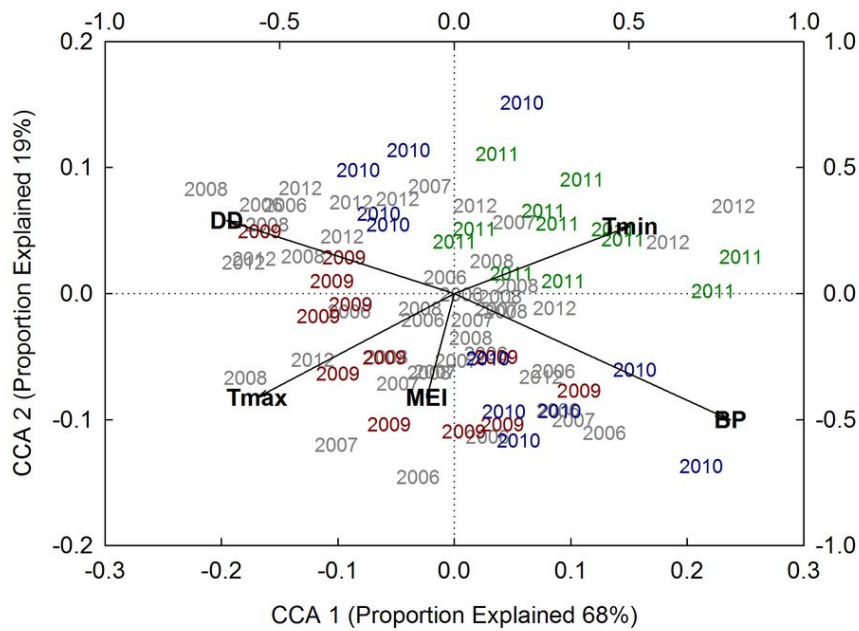
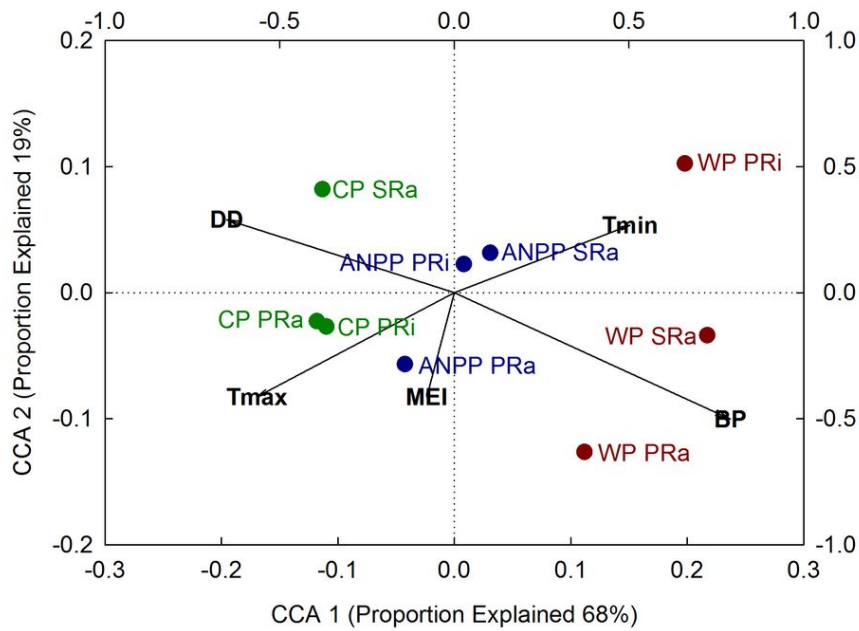
887 **Table S4:** Results of lagged cross-correlations between seasonal de-trended climate and  
 888 productivity variables indicating maximum correlation coefficients at different time lags (0-36  
 889 month) for correlations between climate variables: multivariate ENSO index (MEI), number  
 890 of dry days (DD), precipitation magnitude (BP), minimum temperature ( $T_{\min}$ ) and maximum  
 891 temperature ( $T_{\max}$ ); as well as productivity variables: litter fall (LF), canopy production (CP),  
 892 wood production (WP) and aboveground net primary production (ANPP) recorded during the  
 893 period 2006-2013 at primary ridge forest (PRi), primary ravine forest (PRa) and secondary  
 894 ravine forest (SRa) located in south-western Costa Rica.

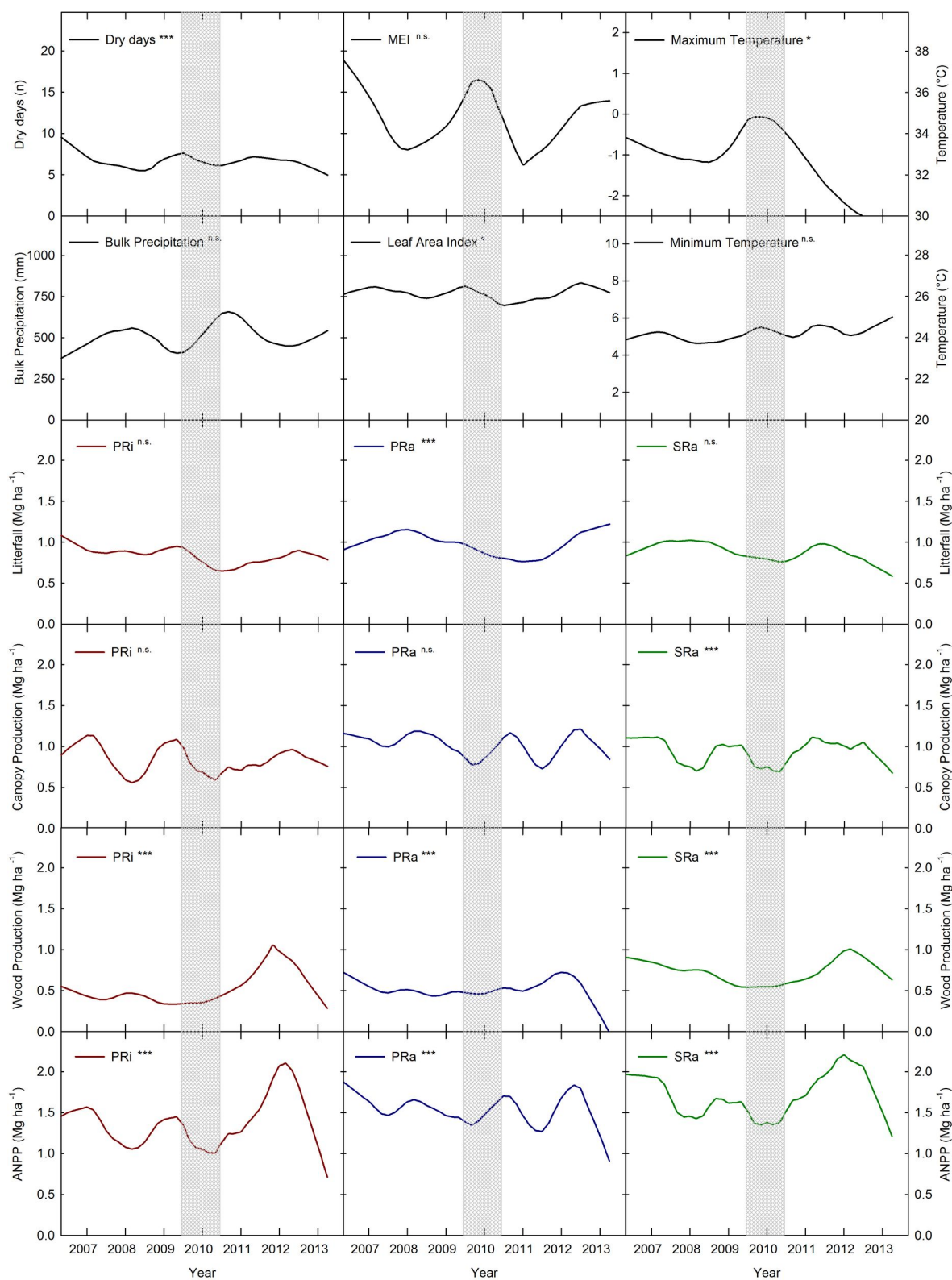


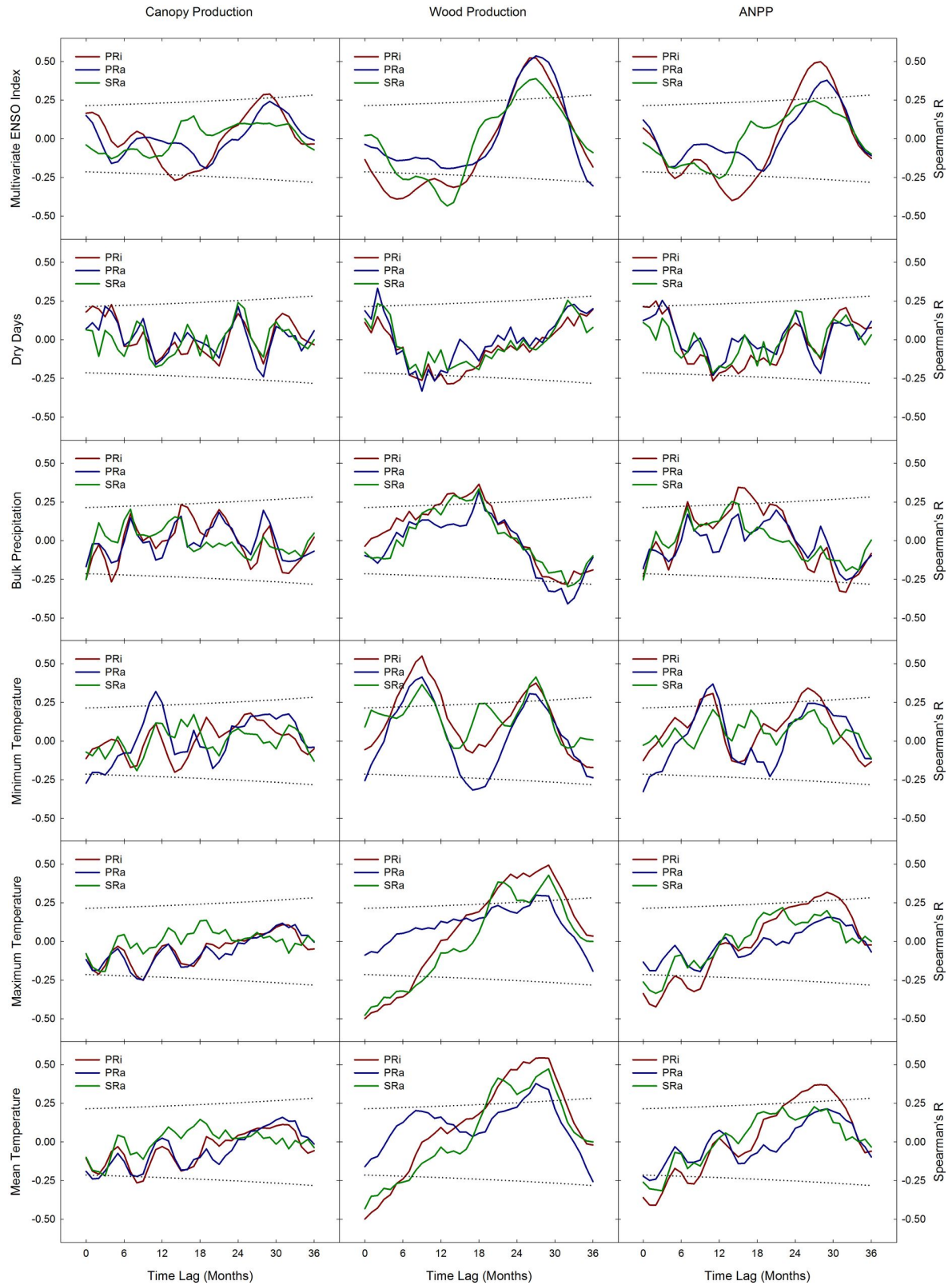












**Table 1:** Effects of climate on tropical aboveground forest productivity<sup>a</sup>

Parameter	CP.Pri			CP.PRa			CP.SRa			WP.Pri			WP.PRa			WP.SRa			ANPP.Pri			ANPP.PRa			ANPP.SRa		
	Est.	P	Sign.	Est.	P	Sign.	Est.	P	Sign.	Est.	P	Sign.	Est.	P	Sign.	Est.	P	Sign.	Est.	P	Sign.	Est.	P	Sign.	Est.	P	Sign.
CONSTANT	19216.00	0.00	***	20253.20	0.00	***	17945.60	0.00	***	293.89	0.84		802.64	0.39		1482.61	0.27		19509.90	0.00	***	21055.90	0.00	***	19428.20	0.00	***
MEI	182.22	0.04	*	157.85	0.05		-30.98	0.77		-9.86	0.82		25.79	0.35		65.48	0.10		172.36	0.04	*	183.64	0.02	*	34.50	0.75	
DD	-24.84	0.25		-21.56	0.27		-42.52	0.11		1.57	0.88		-1.01	0.88		-4.81	0.62		-22.27	0.25		-22.57	0.23		-47.33	0.08	
BP	-1.26	0.01	*	-1.39	0.00	**	-2.15	0.00	***	-0.05	0.84		0.17	0.26		0.14	0.53		-1.31	0.01	**	-1.21	0.01	**	-2.00	0.00	**
T <sub>min</sub>	-587.58	0.00	***	-630.36	0.00	***	-520.10	0.00	***	90.12	0.08		-11.17	0.74		56.57	0.24		-497.46	0.00	***	-641.53	0.00	***	-463.54	0.00	***
T <sub>max</sub>	-98.75	0.01	**	-92.73	0.01	**	-89.92	0.04	*	-58.97	0.00	***	-3.14	0.78		-64.72	0.00	***	-157.72	0.00	***	-95.87	0.00	**	-154.64	0.00	***
R-squared	0.37			0.46			0.33			0.17			0.07			0.26			0.42			0.47			0.31		
P-Value	0.00			0.00			0.00			0.01			0.31			0.00			0.00			0.00			0.00		

<sup>a</sup>Results of multiple regression models investigating the effects of monthly means of climate variables: multivariate ENSO index (MEI), number of dry days (DD), bulk precipitation (BP), minimum temperature (T<sub>min</sub>), maximum temperature (T<sub>max</sub>) on monthly means of tropical aboveground productivity: canopy production (CP), wood production (WP) and aboveground net primary production (ANPP) recorded during the period 2006-2013 at primary ridge forest (PRI), primary ravine forest (PRa) and secondary ravine forest (SRa) located in south-western Costa Rica.







## SYNTHESIS

Tropical forests will likely experience major changes in environmental conditions during this century. Understanding the responses of tropical ecosystem functions to such changes is crucial to accurately predict future alterations of global carbon cycling (Zuidema et al., 2013). How tropical forests respond and feedback to climate and land-use change is however still largely unknown at the ecosystem and landscape level (Zhou et al., 2013). Although several complementary approaches have been evaluated the results are conflicting due to confounding effects of multiple factors (Zhou et al., 2013). For instance mean annual temperature (MAT) was often found the main driver of tropical net primary production (e.g. Raich et al., 2006), however, Cleveland et al., (2011) showed that this was only caused by temperature differences between warm lowland and cool montane forest sites. Instead, when the differences in temperature were accounted for, soil P was the next important predictor of lowland forest productivity, indicating the impact of local edaphic parameters (i.e. soil texture and fertility) on tropical aboveground productivity (Cleveland et al., 2011). Moreover, it was proposed that NPP of tropical forests peaks at mean annual precipitation (MAP) inputs of about 2500 mm (Schoor, 2003) due to reductions of mineralization rates and decomposition processes in water-saturated soils.

Nonetheless, we here report among the highest wood increments and litterfall rates published to date for tropical lowland forests thriving at high MAT (28° C) and MAP (6000 mm). These high rates of production were explained by high litterfall and decomposition rates, fast cycling of nutrients and continued supply of cations and phosphorus through high rates of weathering, tectonic uplift and erosion in the study region located in southwestern Costa Rica (Wanek et al., 2008). During the seven years of this study we observed distinct responses of the three in-

vestigated forest sites to climate fluctuations, which were related to the effects of local topography, soil fertility and disturbance history of the respective study sites (Hofhansl et al., 2011; Hofhansl et al., 2012; Hofhansl et al., 2014). Whereas ravine forests were characterized by high water and nutrient availability and thus fast turnover, element cycling and high rates of primary production, ridge forests exhibited relatively lower aboveground productivity, and in secondary forests nutrient demand exceeded nutrient supply after disturbance as was indicated by high nutrient use efficiencies (Wanek et al., 2008). As a result, respective site characteristics eventually determined the sensitivity of tropical ecosystem processes to a recent climate anomaly. In the following, we discuss and compare the patterns and mechanisms found in this study to present findings reported in the available literature in order to evaluate future potential responses of tropical ecosystem functions to projected global changes.

In chapter one of this thesis we investigated the mechanisms driving carbon allocation in tropical rainforests using structural equation modeling to disentangle multiple drivers of tropical NPP and evaluate interrelated pathways among environmental controls on tropical wood production in a literature synthesis of more than 100 pantropical forest sites. We identified a global pattern of increased wood production along tropical gradients in forest productivity, suggesting greater C sequestration in wood biomass in high productive lowland compared to low productive montane forests. Most strikingly we found that, whereas along the pantropical productivity gradient temperature and soil nutrient content indirectly enhanced wood production through increasing aboveground forest productivity, dry season length and the amount of precipitation both directly increased wood production via trade-offs along the plant

economics spectrum according to the life-history strategy of tropical tree species (Fig. 8). Our results further imply that predicted increases in temperature and dry season length could potentially increase wood production in montane tropical forests, but decrease wood production in tropical lowland forests that already thrive close to their thermal optimum. Concomitant decreases in annual precipitation (or increases in heavy precipitation with prolonged intermittent dry periods) could therefore decrease wood production in the most productive rainforests, thus causing C sequestration to decrease.

Our results emphasize recent findings that indicated the importance of plant functional traits in association to life-history strategies of tropical tree species that determine the C sequestration potential of tropical forests.

Along the world-wide ‘fast-slow’ plant economics spectrum (Reich, 2014) early successional, opportunistic tree species were found to rather invest into height growth to rapidly reach the canopy in the “race for light” (Wolf et al., 2011). In contrast, late successional climax species tend to be shade-tolerant but slow-growing to increase hydraulic safety and reduce mortality risks during drought periods (Markesteijn et al., 2011; Poorter et al., 2009). As a result, periodic short-term drought disturbances, such as those associated with El Niño Southern Oscillation (ENSO) phenomena, could have the potential to kill trees selectively since fast-growing, light-wooded trees might be especially vulnerable to drought by cavitation or carbon starvation (Condit et al., 1996; McDowell et al., 2008; Rowland et al., 2014). On the one hand, such short-term droughts were reported to increase the mortality of fast-growing opportu-

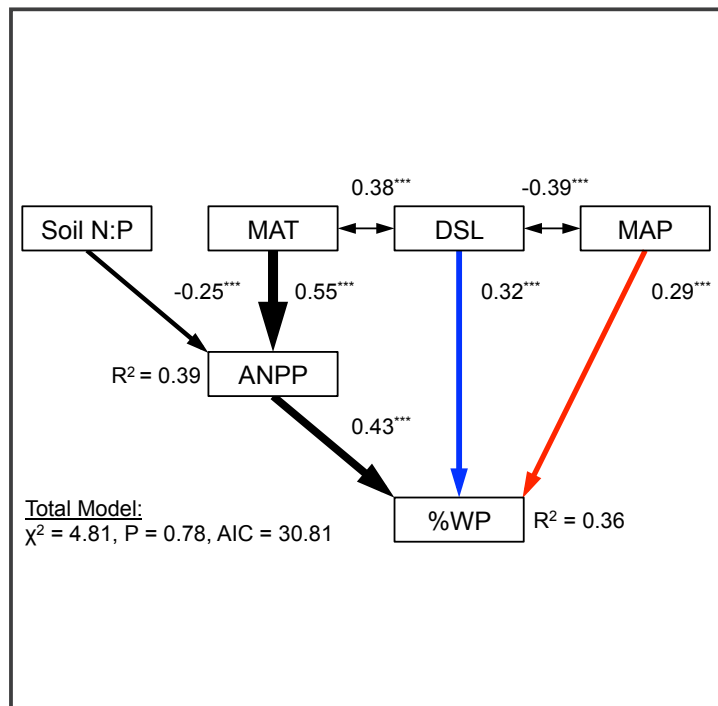


FIGURE 8: MECHANISMS DRIVING CARBON ALLOCATION TO WOOD PRODUCTION IN TROPICAL FORESTS. (SOURCE: HOFHANSL ET AL., 2014).

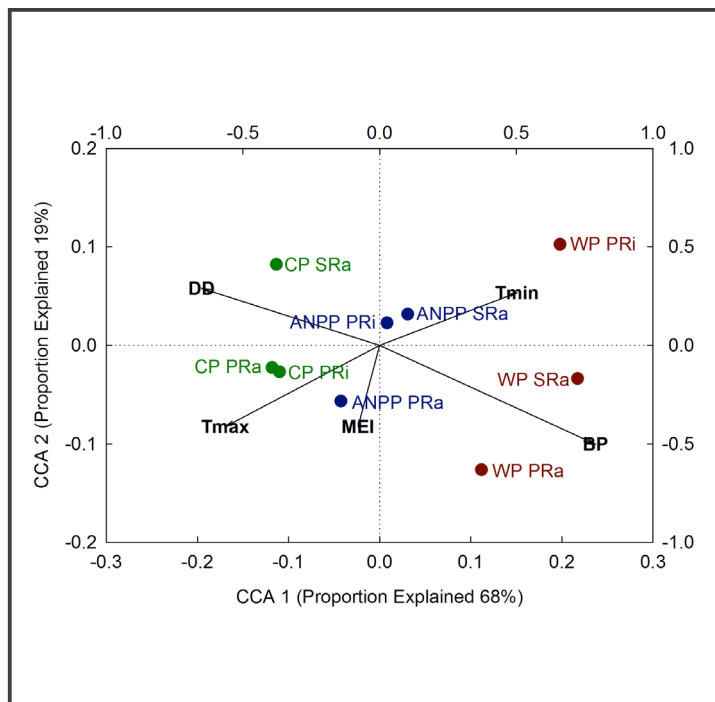
nistic tree species (Phillips 2009), in association with a net carbon release (Clark, 2004; Clark et al., 2013). On the other hand, over the long-term less vulnerable drought-tolerant species could become dominant after long periods of water deficit (Phillips et al., 2010), in association with increasing aboveground biomass, thus suggesting increased C sequestration (Fauset et al., 2012). As a result, short-term reductions in C sequestration caused by increased temperatures and drought could be partially alleviated by drought-induced shifts in the functional composition of tropical rainforest trees, favoring drought-tolerant species over less competitive species (Phillips et al., 2009) in the long run.

In chapter four of this thesis we investigated the climate sensitivity of tropical forest aboveground productivity in response to a recent ENSO transition by evaluating a unique long-term dataset comprising seven years of monthly censuses on tropical aboveground biomass increment and litterfall during the study period from 2006–2013 at Costa Rican lowland forest sites differing in topography and disturbance history. Whereas during the El Niño drought period a 3°C tem-

perature increase significantly decreased wood production, concomitant increasing dry season length promoted canopy production (Fig. 9). Hence both processes were inversely related to bulk precipitation and peaked during different seasons. Beyond the seasonal and interannual responses of aboveground forest productivity to climatic signals a common pattern emerged indicating the importance of local site characteristics in determining the response of tropical wood production to large-scale drought anomalies. We found that drought-induced reductions in wood production were most prominent at the more exposed ridge forest site, followed by the secondary re-growth forest site, but less intense at the downslope ravine forest site. This site-specific climate sensitivity was related to topographic differences in soil type and soil depth and thus water availability, as was indicated by differences in soil bulk density and soil moisture between the respective study sites [Wanek et al., 2008]. Hence, we suggested that due to differences in soil depth and thus water availability between the forest sites, increased temperatures and decreased water availability during the El

Niño drought period triggered water stress of trees at the more exposed ridge and secondary re-growth forest site, but did not significantly affect wood production at the moist ravine forest site. However, during the subsequent La Niña wet period wood production recovered by more than two-fold at the ridge forest site, indicating a higher degree of resilience and recovery of aboveground C stocks by the resident tree species community compared to the ravine forest site. We suggested that our findings relate to differences in tree species composition among the forest sites, due to functional adaptations and different life-history strategies of tropical tree species (Markesteijn et al., 2011). In accordance, we found pronounced differences (92-99%) in the species composition of the 379 tree individuals between the three lowland forest sites investigated (Hofhansl 2011). Additionally, we found differences in site-averaged wood density for primary ridge (0.57 g cm<sup>-3</sup>), primary ravine (0.52 g cm<sup>-3</sup>) and secondary forest sites (0.54 g cm<sup>-3</sup>). We conclude that inverse effects of topography on edaphic parameters (water availability), as well as on life-history strategies (drought tolerance) among tropical tree species, eventually determined the site-specific sensitivity of tropical lowland aboveground forest productivity to climate anomalies. Hence, the greater climate sensitivity of low-density trees at the moist ravine forest site was buffered via high soil water availability and less temperature fluctuations, whereas high-density trees at the more exposed ridge forest site, though being better adapted to droughts, were more prone to anomalous climate extremes. Therefore our results indicate that, although the proximate short-term tolerance to the strong El Niño drought period

FIGURE 9:  
CLIMATIC  
CONTROLS  
ON CANOPY  
PRODUCTION  
AND WOOD  
PRODUCTION  
IN TROPICAL  
FORESTS.  
(SOURCE:  
HOFHANSL ET  
AL., 2014).



triggered water stress of trees at the more exposed ridge and secondary re-growth forest site, but did not significantly affect wood production at the moist ravine forest site. However, during the subsequent La Niña wet period wood production recovered by more than two-fold at the ridge forest site, indicating a higher degree of resilience and recovery of aboveground C stocks by the resident tree species community compared to the ravine forest site. We suggested that our findings relate to differences in tree species composition among the forest sites, due to functional adaptations and different life-history strategies of tropical tree species (Markesteijn et al., 2011). In accordance, we found pronounced differences (92-99%) in the species composition of the 379 tree individuals between the three lowland forest sites investigated (Hofhansl 2011). Additionally, we found differences in site-averaged wood density for primary ridge (0.57 g cm<sup>-3</sup>), primary ravine (0.52 g cm<sup>-3</sup>) and secondary forest sites (0.54 g cm<sup>-3</sup>). We conclude that inverse effects of topography on edaphic parameters (water availability), as well as on life-history strategies (drought tolerance) among tropical tree species, eventually determined the site-specific sensitivity of tropical lowland aboveground forest productivity to climate anomalies. Hence, the greater climate sensitivity of low-density trees at the moist ravine forest site was buffered via high soil water availability and less temperature fluctuations, whereas high-density trees at the more exposed ridge forest site, though being better adapted to droughts, were more prone to anomalous climate extremes. Therefore our results indicate that, although the proximate short-term tolerance to the strong El Niño drought period

is predetermined by local topo-edaphic factors such as soil water availability, the functional adaptation of the respective tree species community could potentially compensate short-term disturbances via drought-induced shifts in tree species composition that further regulate the long-term C storage of tropical lowland forests.

Community-wide differences in plant functional traits influence the decomposability of senesced tissue and thus potentially alter rates of biogeochemical cycling, depending on the phylogenetic structure of the species pool (Pietsch et al., 2014). It has been suggested that the legacy of plant functional traits results in plant-soil feedbacks, such that rapidly decomposing nutrient-rich litter maintains high soil fertility, whereas slowly decomposing nutrient-poor litter reduces the fertility of soils (Chapin, 2003). In accordance, recent studies conducted at the same set of Costa Rican lowland forest sites indicated strong differences in litter decomposition and turnover, as well as mineralization and nitrification rates between adjacent tropical lowland forests (Drage, 2007). Whereas turnover rates of fine litter were significantly higher at the high productive downslope ravine site ( $3.7 \text{ yr}^{-1}$ ) compared to the exposed ridge forest and secondary re-growth forest site (both;  $2.3 \text{ yr}^{-1}$ ), nutrient use efficiencies for N, P and  $\text{Ca}^{2+}$  were highest at the ridge forest site (Wanek et al., 2008), indicating a relatively stronger limitation of these nutrients at hilltop versus downslope sites. In turn, high nutrient cycling rates could be clearly related to high nutrient content, low C/N ratios and low nutrient use efficiencies of litter and soils at topographic depressions (Drage et al., unpublished data). This suggests that at the ridge forest site plant productivity was limited by relatively lower soil water and nutrient availability, whereas at the primary ravine forest site increased soil water and nutrient supply enhanced nutrient cycling rates (Hofhansl

et al., 2011), thus triggering increased above-ground biomass (Hofhansl et al., 2012) and forest productivity (Hofhansl et al., 2014). Nonetheless, wood increment was still largest at the secondary re-growth forest site, demonstrating persistent biomass accumulation more than 20 years after disturbance (Wanek et al., 2008).

Besides effects on tropical forest productivity, projected climatic changes are expected to accelerate processes that operate within the hydrological cycle as increasing temperatures enhance the capacity of the air to carry moisture (Wohl et al., 2012). The current understanding of key interactions between climatic changes and hydrologic processes in tropical forests is limited geographically and relies heavily on modeling from remotely sensed rather than empirical data. Satellite-based monitoring of dynamic hydrologic variables such as evapotranspiration and rooting-zone water content however still poses a challenge, because optical and thermal sensors cannot penetrate clouds, and radar sensors have difficulty breaking through thick canopies in the humid tropics (Wohl et al., 2012). Therefore, precipitation products based on satellite observations typically present regional and seasonal biases, but they can be considerably improved by using gauge measurements of precipitation.

In chapter two and three of this thesis we investigated ground-based measurements of element fluxes via bulk precipitation, throughfall and stemflow (plus litterfall; Drage et al., unpublished data) to examine the effects of local topography and disturbance on tropical hydrochemistry and compare external (atmospheric dry and wet deposition) and internal nutrient cycling processes (litterfall and canopy exchange) in different types of Costa Rican lowland rainforests. We found that besides litterfall constituting the major pathway of internal nutrient recycling, dissolved nutrient inputs via hydrological pathways of throughfall and stem-

flow derived from dry deposition and canopy exchange processes contribute up to 50% of total aboveground nutrient returns (Hofhansl et al., 2012). Moreover, topography most significantly affected nutrient inputs via increased dry deposition at sites of higher elevation and via soil fertility increasing canopy exchange at downslope sites (Hofhansl 2011). Most interestingly, dry deposition contributed 60% of DON, 30% of TDN and 20% of DOC (and  $K^+$ ) to total atmospheric deposition (bulk precipitation, dry deposition), while canopy exchange contributed 10% of P (and  $Mg^{2+}$ ) but more than 50% of  $K^+$  to internal nutrient returns (litterfall, canopy exchange). This indicates the importance of dry deposition and canopy exchange processes for the overall budget of available nutrients in tropical forests stocking on rather nutrient depleted tropical soils. Moreover, the high rates of nitrogen inputs via dry deposition highlight the potential of increasing anthropogenic nitrogen deposition of reactive N that might affect nutrient cycles in terrestrial ecosystems.

In general, developing ecosystems are N limited when symbiotic N fixation is constrained and P weathering inputs are high relative to atmospheric N deposition and plant N:P demand. However, as ecosystems develop over long timescales N accumulates and weathering depletion favours P limitation on older soils when continual P inputs are low, so nutrient limitation at the terminal equilibrium depends on the balance of these input and loss effects (Menge et al., 2012). In this regard, a recent study investigating long-term changes in the nitrogen cycle of tropical forests found that leaf N and the ratio of  $^{15}N/^{14}N$  isotopes in leaves as well as in tree rings increased substantially during recent decades (Hietz et al., 2011). These findings indicate widespread increases in N availability in tropical forests due to increased anthropogenic N emissions. On the one hand, increases in foli-

ar N could enhance photosynthetic carbon gain and thus increase forest productivity (Wright et al., 2004). On the other hand, increased N deposition could result in a further up-regulation of the tropical N cycle (Hedin et al., 2009) thus triggering increased N and cation losses and increasing soil acidification and aluminum toxicity, with a potentially negative effect on other nutrients limiting plant growth (Matson et al., 1999). As nitrogen deposition over tropical land is projected to further increase due to anthropogenic N emissions (Galloway et al., 2004) the competitive ability of trees that are in symbioses with nitrogen-fixing microorganisms is likely to decrease, potentially altering tree species composition (Hietz et al., 2011). However, across environmental gradients in Panamanian forests dry-season intensity and plant-available phosphorus rather than nitrogen availability were the main drivers of tree distributions, such that both rainfall patterns and soil phosphorus availability partition the community into species that preferentially grow at sites with high versus low phosphorus soils (Condit et al., 2013). While deciduous species may require high phosphorus due to frequent turnover of leaves (Givinish et al., 2002), low phosphorus specialists were found to acquire organic or recalcitrant inorganic forms by associating with mycorrhizal symbionts efficient at phosphorus acquisition (Turner, 2008).

Terrestrial plants acquire most essential mineral nutrients from soil by direct absorption via roots and indirectly via symbiotic mycorrhizal fungi (Lambers et al., 2010). Although the vast majority of tropical trees are capable of taking up phosphorous via both pathways, they are considered to depend primarily on symbiosis with mycorrhizal fungi to acquire phosphorous (Smith & Read, 2008). Moreover, plants limited by phosphorus show concomitantly low leaf nitrogen concentrations, reflecting the down-re-



gulation of their N uptake rate and assimilation (Lambers et al., 2010). In support of the “growth rate hypothesis” plants require a high activity of rRNA (and thus P availability) to sustain rapid rates of protein (N) synthesis (Lambers et al., 2008). In turn, extracellular phosphate enzyme activities are highly responsive to changes in N and P supply, such that increasing N availability tends to increase P cycling rates (Marklein et al., 2012), indicating the tight coupling of N and P cycling in plants. Therefore, globally increasing N deposition may induce terrestrial P limitation (Vitousek et al., 2010), although the up-regulation of phosphatase activity may delay the onset of P limitation by years to decades (Marklein et al., 2012). In the light of the finding that between 86% and 90% of plants are mycorrhizal on a global scale (Brundrett, 2009) and that plants adjust the rate of N and P cycling (Lambers et al., 2010) in compliance to the complicated nature of coupled resource limitation (Marklein et al., 2012), it is plausible that alterations affecting nitrogen availability, such as increasing N deposition, will also affect the cycling of other growth-limiting nutrients in tropical forest ecosystems, where P availability was reported to limit productivity (e.g. Cleveland et al., 2011). Overall, these findings indicate that global environmental changes of increasing CO<sub>2</sub> and N deposition could have a fertilization effect on terrestrial net primary productivity, however, the extent of that effect depends largely on nutrient availability of N and P in terrestrial ecosystems (Reich et al., 2006).

Although species traits that might govern the observed ranges of responses to soil phosphorus and drought are poorly understood in tropical trees (Condit et al., 2013), it is common

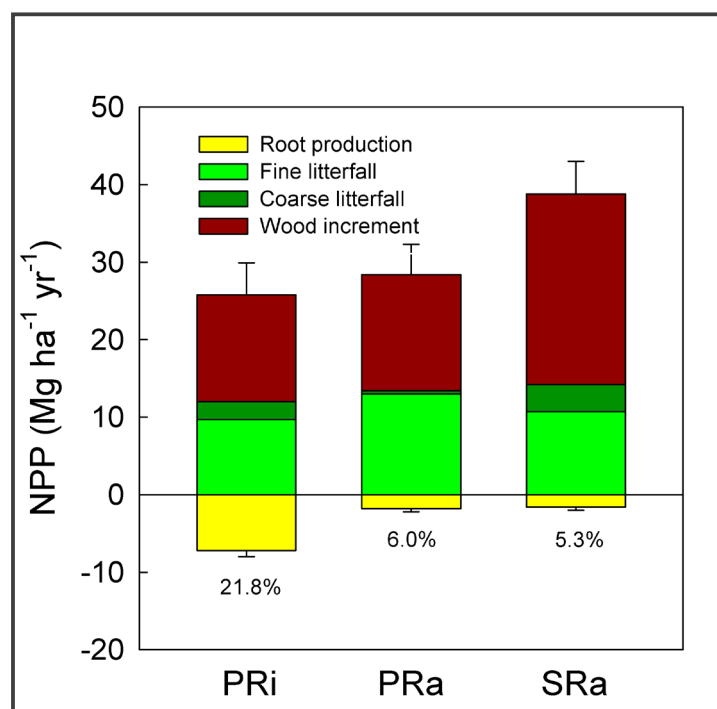


FIGURE 10: PARTITIONING OF NET PRIMARY PRODUCTION AT FOREST SITES DIFFERING IN TOPOGRAPHY AND DISTURBANCE HISTORY LOCATED IN SOUTHWESTERN COSTA RICA. (SOURCE: WANKE ET AL., 2008).

knowledge that plants growing in nutrient-poor habitats are characterized by functional traits that increase leaf lifespan and defense against herbivores (Poorter et al., 2009; Wright et al., 2002). For instance, specific leaf mass per area was found to increase along gradients of nutrient limitation in order to reduce nutrient losses caused by herbivory (Wright & Canon, 2001). While increased leaf longevity potentially increases the plant's fitness, it concomitantly diminishes its growth potential (Lambers et al., 2008). On the other hand, fast-growing opportunistic species rather invest in low-cost tissues to maintain high growth rates, at the risk of greater mortality (Kitajima, 1994). These investment strategies refer to the commonly accepted classification of fast-growing short-lived r-species that occur in frequently disturbed environments, opposed to longer-lived slow-growing K-species predominating under more stable conditions (Lambers et al., 2008).

In concordance, we found that at sites of secondary forest re-growth wood increment was largest and nutrient use efficiencies for N and P were higher compared to undisturbed primary

forest, indicating that nutrient demand for biomass production exceeded nutrient supply due to the rapid growth of the secondary succession (Fig. 10). Such a large demand for nutrients to allow re-growth and biomass accrual of secondary forests commonly leads to an intermittent decrease in soil nutrient availability (Hughes et al., 1999), as was also indicated by lower soil water concentrations of  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  in the secondary forest site (Hofhansl et al., 2011). In contrast, concentrations of solutes that derived from canopy exchange processes ( $\text{K}^+$ , DON, DOC) were most enriched in secondary forests due to less sclerotic but nutrient rich leaves of fast-growing early successional species (Poorter et al., 2004). This forest site was also characterized by high litter stocks and low turnover rates of fine and coarse litter, indicating reduced decomposition caused by alterations of litter quality and quantity during secondary forest re-growth (Drage, 2007). In addition, total carbon stocks and aboveground biomass were lowest at the secondary forest site (Wanek et al., 2008) most probably due to the high number of tree stems below 30 cm in diameter above breast-height (Hofhansl et al., 2012), and higher turnover rates of fast-growing tree species in response to increased disturbance.

Global changes that lead to more frequent disturbances could therefore likely affect decomposition and turnover rates, triggering alterations in nutrient limitation that further determine the quality of leaf litter and canopy leaching rates by shifting the composition of tropical tree species and associated plant functional traits. As a result, projected alterations in climate and further anthropogenic N deposition could affect biomass turnover and decomposition rates via alterations in litterfall, litter quality and canopy exchange processes that overall foster fast-growing tree species and thus reduce C stocks in tropical forest ecosystems. Nonetheless, the high spatial and temporal variability of tropical ecosystem processes further highlights the need of high resolution and long-term studies, as well as manipulative long-term experiments to reveal and disentangle interrelated environmental controls affecting tropical forest productivity. Knowledge of the underlying mechanisms - as indicated in this thesis - will be key to identify the responses of tropical ecosystem processes and to accurately predict the C sequestration potential of tropical forests in future scenarios of global climatic and anthropogenic changes.



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## SCIENTIFIC PROJECTS

- CostaRica– “Carbon and element cycling in a tropical lowland forest, Costa Rica: Interannual variability and climate coupling” – Project Funding: Commission for Interdisciplinary Ecological Studies, Austrian Academy of Sciences (KIÖS - ÖAW). URL [http://www.oeaw.ac.at/kioes/prob/costarica\\_e.htm](http://www.oeaw.ac.at/kioes/prob/costarica_e.htm)
- EcoCatch – “Understanding the effects of global change on ecosystem processes and services at catchment scale” – Project Funding: Government of Lower Austria and Clean Air Commission, Austrian Academy of Sciences (KRL - ÖAW). URL [http://www.oeaw.ac.at/krl/projekte/aktuell/EcoCatch/EcoCatch\\_en.htm](http://www.oeaw.ac.at/krl/projekte/aktuell/EcoCatch/EcoCatch_en.htm)
- MICDIF – “Linking microbial diversity and functions across scales and ecosystems” – Project Funding: Austrian Science Fund (FWF). URL <http://www.micdif.net>
- BDEF – “Biodiversity and Ecosystem Functions - Landscape and climate controls of biodiversity and ecosystem processes in tropical rainforests of SW Costa Rica” – Project Funding: Austrian Federal Ministry of Science and Research (BMWF). URL <http://www.univie.ac.at/bdef>

## FURTHER QUALIFICATIONS

- Languages: German (native), English (fluent), Spanish (conversant), French (basic).
- Driving License: Category A & B (1998).
- Diving License: CMAS (1993).
- Flight License: Gyrocopter Ultra-Light (2007).



## PEER-REVIEWED

- Hofhansl F**, Wanek W, Kobler J, Schnecker J, Singer G, Drage S, Pölz EM, Richter A (2014) Sensitivity of tropical forest aboveground productivity to climate anomalies. *Global Biogeochemical Cycles* – submitted.
- Hofhansl F**, Wanek W (2014) New insights into mechanisms driving carbon allocation in tropical rainforests. *New Phytologist* – accepted.
- Mooshammer M, Wanek W, Hämmerle I, Fuchslueger L, **Hofhansl F**, Knoltsch A, Schnecker J, Takriti M, Watzka M, Wild B, et al. (2014) Adjustment of microbial nitrogen use efficiency to carbon:nitrogen imbalances regulates soil nitrogen cycling. *Nature Communications* 5: 1–7.
- Prommer J, Wanek W, **Hofhansl F**, Trojan D, Offre P, et al. (2014) Biochar Decelerates Soil Organic Nitrogen Cycling but Stimulates Soil Nitrification in a Temperate Arable Field Trial *PLoS ONE* 9(1): e86388.
- Schnecker J, Wild B, **Hofhansl F**, et al. (2014) Effects of soil organic matter properties and microbial community composition on enzyme activities in cryoturbated arctic soils: *PLoS ONE* 9(4): e94076. doi: 10.1371/journal.pone.0094076
- Wild B, Schnecker J, Barta Jiri, Capek P, Guggenberger G, **Hofhansl F**, Kaiser C, Lashchinsky N, Mikutta R, Mooshammer M, Santruckova H, Shibistova O, Urich T, Zimov SA, Richter A (2013) Nitrogen dynamics in topsoil, subsoil and cryoturbated horizons of tundra soils from Siberia and Greenland. *Soil Biology & Biochemistry* 67: 85-93.
- Adlassnig W, Sassmann S, Lendl T, Wernitznig S, **Hofhansl F**, Lang I, Lichtscheidl IK (2013) Metal contamination and retention of the former mining site Schwarzwand (Salzburg, Austria). *Applied Geochemistry* 35: 196-206.
- Hofhansl F**, Wanek W, Drage S, Huber W, Weissenhofer A, Richter A (2012) Controls of hydrochemical fluxes via stemflow in tropical lowland rainforests: Effects of meteorology and vegetation characteristics. *Journal of Hydrology* 452: 247-258.
- Mooshammer M, Wanek W, Schnecker J, Wild B, Leitner S, **Hofhansl F**, Blöchl A, Hämmerle I, Frank A, Fuchslueger L, Keiblinger K, Zechmeister-Boltenstern S, Richter A (2012) Stoichiometric controls of nitrogen and phosphorus cycling in decomposing beech leaf litter. *Ecology* 93: 770–782.
- Hofhansl F**, Wanek W, Drage S, Huber W, Weissenhofer A, Richter A (2011) Topography strongly affects atmospheric deposition and canopy exchange processes in different types of wet lowland rainforest, Southwest Costa Rica. *Biogeochemistry* 106: 371-396.

## BOOK SECTIONS

- Schulze C, Freudmann A, Friesenbichler K, Gallmetzer N, Binz H, **Hofhansl F**, Mollik P, Reyes Páez A F, Riedl I G, Schneeweih S & Seaman B (2013) Biodiversität von Landschaftselementen im biologischen Korridor und den Randbereichen des Regenwaldes In: 20 Jahre Tropenstation La Gamba, Costa Rica. Verein zur Förderung der Tropenstation La Gamba, Costa Rica.
- Popp M (ed.), Wanek W, Richter A, Battin T, Dörninger M, **Hofhansl F** & Watzka M (2010) *EcoCatch LUNZ – „Auswirkungen des Globalen Wandels auf ökosystemare Prozesse und Leistungen: Immissionen, Retention und Austräge von Schadstoffen und Nährstoffen“* Project Report for the Austrian Academy of Sciences.

- Hofhansl** F, Schneeweih S (2010) Dragonflies. In Stream ecosystems of Costa Rica 55-62 pp. Publisher: Verein Freunde zur Förderung der Tropenstation La Gamba, Wien.
- Schneeweih S, **Hofhansl** F (2009) Dragonflies of the Golfo Dulce Region, Costa Rica 56 pp. Publisher: Stapfia.
- Wanek W, Drage S, Hinko N, **Hofhansl** F, Pölz EM, Ratzer A, Richter A (2008) Primary production and nutrient cycling in lowland rainforests of the GolfoDulce region – Producción primaria y ciclo de nutrientes en bosques lluviosos de tierras bajas de la región de Golfo Dulce- Case study, 155-177. In Natural and Cultural History of the Golfo Dulce Region, Costa Rica 768 pp. Stapfia - ISBN: 978-3-85474-195-4.
- Hofhansl** F, Schneeweih S (2008) Banderillas: Effects of deforestation on dragonflies (Insecta , Odonata ) in the Pacific lowland of Costa Rica - Banderillas: Efectos de la deforestación sobre libélulas (Insecta , Odonata) en la tierra baja Pacífica en Costa Rica - Case study, 237-247. In Natural and Cultural History of the Golfo Dulce Region, Costa Rica 768 pp. Stapfia - ISBN: 978-3-85474-195-4.

## CONFERENCE TALKS

- Hofhansl** F, Kobler H, Drage S, Pölz EM, Wanek W (2014) Sensitivity of tropical lowland net primary production to climate anomalies - Geophysical Research Abstracts Vol. 16, EGU2014-10585, 2014 EGU General Assembly, Vienna, Austria.
- Hofhansl** F, Schnecker J, Singer G, Wanek W (2014) Mechanisms driving carbon allocation in tropical rainforests - Geophysical Research Abstracts Vol. 16, EGU2014-10223, 2014 EGU General Assembly, Vienna, Austria.
- Schnecker J, Wild B, **Hofhansl** F, et al. (2014) Microbial community composition and enzyme activities in cryoturbated arctic soils are controlled by environmental parameters rather than by soil organic matter properties - Geophysical Research Abstracts Vol. 16, EGU2014-5430, 2014 EGU General Assembly, Vienna, Austria.
- Adlassnig W, Sassmann S, Lendl T, Wernitznig S, **Hofhansl** F, Lang I, Lichtscheidl IK (2013) Bioremediation by Phormidium biofilms: A case study from a historic mine site - Eurobiotech, Kraków, Poland.
- Hofhansl** F, Wanek W (2013) Controls on aboveground net primary production of tropical rainforests – 50th Anniversary Meeting of the Association for Tropical Biology and Conservation (ATBC) and the Organization for Tropical Studies (OTS) (ATBC/OTS 2013) San José, Costa Rica.
- Hofhansl** F, Seaman B, Binz H, Riedl I, Schneeweih S, Schulze CH (2013) The importance of small gallery forest strips as biological corridors for forest species in a human-dominated landscape in southern Costa Rica – 50th Anniversary Meeting of the Association for Tropical Biology and Conservation (ATBC) and the Organization for Tropical Studies (OTS) (ATBC/OTS 2013) San José, Costa Rica.
- Hofhansl** F, Drage S, Pölz EM, Wanek W (2013) Climatic controls on primary productivity and the partitioning between canopy and wood production in tropical rainforests – Annual Conference of the Society for Tropical Ecology (GTOE 2013) Vienna, Austria.
- Mooshammer M, Wanek W, Wild B, **Hofhansl** F, Richter A (2012) Do We Need to Account for Variable Microbial Nitrogen-Use Efficiency in Biogeochemical Models? – American Geoscience Union

(AGU Fall Meeting 2012) San Francisco, USA.

- Hofhansl F**, Drage S, Pölz EM, Richter A, Wanek W (2012) Climatic controls of seasonal and interannual variations in aboveground net primary productivity of tropical lowland rainforests, Southwest Costa Rica – Science Day of the Faculty of Life Sciences (Science Day 2012) Vienna, Austria.
- Mooshammer M, Wanek W, Frank AH, **Hofhansl F**, Keiblinger KM, Zechmeister-Boltenstern S, Richter A (2011) Organic nitrogen cycling during organic matter decomposition. 21th Annual V.M. Goldschmidt Conference 2011. Prague, Czech Republic, August 14-19. *Mineralogical Magazine*, 75:1495.
- Hofhansl F**, Wanek W, Drage S, Huber W, Weissenhofer A, Richter A (2010) Topography strongly affects atmospheric deposition and canopy exchange processes in different types of wet lowland rainforest, Southwest Costa Rica – 18th Conference of the Austrian Society of Plant Biology (ATSPB 2010) Illmitz, Austria.
- Wanek W, Drage S, Hinko N, **Hofhansl F**, Pölz EM, Ratzer A, Richter A (2009) Impact of climate change on the performance of tropical lowland forests in SW Costa Rica – Association for Tropical Biology and Conservation Conference (ATBC/GTOE 2009) Marburg, Germany.
- Seaman B, Schneeweih S, **Hofhansl F**, Schulze C (2009) The importance of small gallery forest strips for maintaining biodiversity – case studies from a human-dominated landscape in southern Costa Rica – Association for Tropical Biology and Conservation Conference (ATBC/GTOE 2009) Marburg, Germany.

## POSTER PRESENTATIONS

- Hofhansl F**, Kobler H, Drage S, Pölz EM, Wanek W (2014) Sensitivity of tropical lowland net primary production to climate anomalies - Geophysical Research Abstracts Vol. 16, EGU2014-10585, 2014 EGU General Assembly, Vienna, Austria.
- Hofhansl F**, Schneckner J, Singer G, Wanek W (2014) Mechanisms driving carbon allocation in tropical rainforests - Geophysical Research Abstracts Vol. 16, EGU2014-10223, 2014 EGU General Assembly, Vienna, Austria.
- Hofhansl F**, Drage S, Pölz EM, Richter A, Wanek W (2012) Climatic controls on aboveground net primary productivity and the partitioning between canopy and wood production in tropical lowland rainforests – American Geoscience Union (AGU Fall Meeting 2012) San Francisco, USA.
- Koller MW, Ramírez-Santa Cruz C, Leder K, Bauer H, Dorninger M, **Hofhansl F**, Wanek W, Kasper-Giebl A (2010) Fog collection and deposition modelling – EcoCatch Lunz” – 5th International Conference on Fog, Fog Collection and Dew (FOGDEW 2010) Münster, Germany.
- Hofhansl F**, Watzka M, Wanek W (2009) The use of isotope measurements for the separation of discharge components during hydrological events in a riparian forest ecosystem, Lunz/See, Austria.” – 9th Austrian Stable Isotope User Group Meeting (SINA 2009) Innsbruck, Austria.



#### TO MY ELDER TRISTAM FLATTERY

*The Age of the Mages is over, and all the secrets of their magical arts are thought to be lost to the world. There are even those who suspect that the last of the great Mages spent their final years scrupulously eradicating all traces of their craft from the pages of history – insuring that their art will never be practiced again. It is the dawn of a new era: an age of reason, science, and exploration, and Tristam Flattery, is one of its most promising young naturalists.*

*But when Tristam is summoned to the royal court of Farrland to try to revitalize a failing species of plant which seems to have mysterious, almost magical, medicinal properties – a plant without which, he is told, the aging king will surely die – he soon realizes that he has been drawn into the heart of a political struggle which spans generations, a conflict which threatens the very foundations of his civilization. And before long, Tristam is caught in the grip of a destiny which will lead him to the ends of the known world – on a voyage of discovery that has more to do with magic than with science...*

SEAN RUSSEL - WORLD WITHOUT END