Productivity of a tropical montane forest in Panama

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1. General introduction

1.1 Productivity in tropical forests

Productivity, the rate at which biomass is synthesized, is an important ecological parameter. Ecosystem productivity is an index, which integrates the cumulative effects of the many processes, and interactions, which are proceeding simultaneously within the ecosystem. If productivity in a natural ecosystem changes little over a long period of time, it suggests that either the environment in unchanging, or that organisms or populations are compensating for changes which are occurring. If productivity changes dramatically, it could mean that an important environmental change is occurring, or that there has been an important change in the interactions of organisms within the ecosystem (Jordan 1985). Factors which are important in controlling productivity, and which have patterns caused by global and regional trends are energy, water, and nutrients.

Tropical rain forests have often been thought to have high rates of ecosystem processes such as productivity, decomposition and nutrient cycling compared to temperate forests. This impression remained until in the beginning of the 1980s, when this generalization was more and more questioned. Jordan (1989) discusses factors governing these processes and states that there are a number of physical factors involved. One is light energy, which consists of several parameters as total solar radiation, net solar radiation, photosynthetic active radiation and temperature. The second factor that has a strong effect on ecosystem process rates is moisture. This factor is primarily determined by rainfall, which can be correlated with global or regional patterns of ecosystem processes. Humidity parameters are always coupled and interrelated to temperature. The third, for the tropics especially important factor, is soil fertility. There are a number of other factors that can have an impact on plant productivity, as O_2 and CO_2 concentration in the air and soil, soil texture and biotic influences as herbivory or diseases. These processes are always determined by the three above mentioned and will therefore not be discussed in detail at this point.

Processes such as plant photosynthesis and leaf decomposition generally increase until saturation with an increase in light, humidity and nutrients. Saturation levels for each factor differ for each plant species and ecosystem. If one of the mentioned factors exceeds the saturation level, a decline in productivity may occur. In contrast, there may be also a minimum factor limiting plant productivity. This factor certainly also differs markedly between plant species, depending on successional status, growth form and physiological and anatomical adaptation.

Tropical moist lowland forests productivity is in the literature intrinsically described to be nutrient limited (Vitousek 1984, Medina and Cuevas 1990, Veneklaas 1991, Grubb 1995, Austin and Vitousek 1998, Cuevas 2001). Sometimes understory plants in such forests are demonstrated to be light limited (Wright and van Schaik 1994). Seasonal tropical lowland forests plants may become more and more limited by drought and some species, therefore, become deciduous to avoid negative productivity in dry periods (Wright and Cornejo 1990, Wright 1996). Williams-Linera (1997) showed that in tropical montane forests, temperature is linked to an increase on leaf production of deciduous tree species. These processes determining plant productivity in ecosystems are only approachable with at least three-dimensional models (Jordan 1989), despite their general validity is still controversial. Nevertheless, such models allow estimations of productivity and moreover a characterization of which parameters are most decisive for plant growth also in tropical ecosystems.

The generalization that process rates are higher in the tropics compared to temperate ecosystems seems justified, as long as the sites examined on the tropical-temperate gradient have comparable humidity regimes and soil fertility (Jordan 1989). Although total net primary productivity is often higher in tropical forests (1000-3500 g m^{-2} a^{-1}) than in temperate (600-2500) or boreal forests (400-2000) (Whittaker and Likens 1975), these higher rates seem to be due almost entirely to greater leaf production. Wood production does not differ significantly along a gradient from high latitudes to the tropics in mesic lowland or lower montane late successional or mature hardwood forests (Jordan 1985). It appears that in the tropics relatively more of the photosynthetic products in trees is allocated to leaves, whereas at higher latitudes, relatively more is allocated to stems.

It is even postulated that despite striking differences in climate, soils, and evolutionary history among diverse biomes ranging from tropical and temperate forests to alpine tundra and desert, similar interspecific relationships among leaf structure and function and plant growth in all biomes occurred (Reich et al. 1997). This is explained with convergent evolution and global generality in plant functioning, despite the enormous diversity of plant species and biomes. Potential carbon gain (photosynthesis) and carbon loss (respiration) increase in similar proportion with decreasing leaf life span, increasing leaf nitrogen concentration, and increasing leaf surface area-to-mass ratio (Reich et al. 1997). Productivity of individual plants and of leaves in vegetation canopies also changes in constant proportion to leaf life span and surface area-to-mass ratio. These global plant functional relationships have significant implications for global scale modeling of vegetation-atmosphere CO_2 exchange.

1.1.1 Carbon cycle in tropical forests

Tropical forests form the largest component of the natural terrestrial carbon cycle. Tropical forests store 102 gigatons (102,000,000,000 metric tons) of carbon in living biomass and recycle 9.5 gigatons of carbon each year, through photosynthesis and net primary production (Brown and Lugo 1984, Melillo et al. 1993). In contrast, the use of fossil fuels added 5.7 gigatons of carbon to the atmosphere in the form of carbon dioxide each year during the 1980s (Schimel et al. 1996).

A predictive understanding of the carbon uptake capacity of tropical forests is crucial because tropical forests are themselves in flux. Humans have removed more than 40% of all tropical forests worldwide and remove approximately another 76,000 km^2 each year. This extensive landscape changes alter regional climates, reducing rainfall and intensifying seasonality in the remaining forests (Shukla et al. 1990). Global climate change will further reduce rainfall and intensify seasonality in the tropics (Melillo et al. 1993). Increasing atmospheric concentrations of carbon dioxide also affect plant metabolism directly through photosynthesis, and this has altered the dynamics of tropical forests (Phillips and Gentry 1994). The factors limiting carbon sequestration capacity must be understood to predict the changing role of tropical forests in the global carbon cycle.

1.1.2 Nutrient limitation of productivity

For decades, ecologists have investigated how plant species cope with different levels of nutrient availability in their natural habitat (summarized in Aerts and Chapin 2000). In the literature there exists no consistent definition, but also no contrasting concepts to nutrient limitation of plants. Vitousek et al. (1993) define the occurrence of nutrient limitation wherever the addition of a nutrient causes increased plant growth, but also point out some difficulties to assess it in practice. It has to be considered, that “plant growth” includes several physiological responses in development of plants, like for example: primary production, biomass increment, increase of plant height, trunk increment, root mass growth etc. Grubb (1995) demonstrated that plants adapted to infertile sites may hardly show any response to nutrient additions, or plants may respond differently in the long- and short-term to added nutrients, and/or other processes in the soil may compete with the plants for the added nutrients (Chapin et al. 1986). Tanner et al. (1998) summarized that limitation by a nutrient is shown if the rate of an ecosystem process is increased by addition of that nutrient, and that, strictly speaking, this can only be determined experimentally. Latest findings postulate that fertilization of herbaceous plant communities with N does increase primary productivity, but on the other hand it decreases species richness masking fertilization effects that may lead to different results for single species (Gough et al. 2000). Nutrient limitation can be evaluated for individual species or at ecosystem level. It is important to distinguish between these levels, because in communities several plant species may coexist that are differentially limited by e.g. N and P (Koerselman and Meuleman 1996, Aerts and Chapin 2000), although the causes of differential nutrient limitation are not well understood.

However, understanding and assessing nutrient limitation is crucial in the characterization of primary production of ecosystems especially in the tropics. Evidence for nutrient limitation can be provided by fertilization experiments applying different strategies to quantify plant response:

1. <u>Nutrient concentration in leaves and litterfall of control and fertilized plants determine retranslocation efficiency</u>. A correlation of leaf nutrient rates and leaf litter mass/leaf nutrient ratios was described. With decreasing leaf nutrient the litter mass/litter nutrient ratios increased indicating a better retranslocation efficiency (nutrient use efficiency) at lower leaf nutrient contents (Vitousek 1982, 1984). However, it was described that this ratio is not a valid measurement to examine nutrient use efficiency in relationship to ecosystem fertility because there is a strong autocorrelation between litterfall dry mass per unit of nutrient and the amount of nutrients (Knops et al. 1997) and there was no indication that nutrient use efficiency is greater in nutrient-poor ecosystems. In contrast, decreasing nutrient response and nutrient use efficiency with lower nutrient availability was shown for peatlands in North Carolina, forests in

Wisconsin and nutrient-poor tropical forests (Pastor and Bridgham 1999). The general trends of a decrease of litterfall mass from tropical lowland to montane sites was confirmed (Veneklaas 1991). Retranslocation of nutrients tended to be higher at montane sites and suggested that these elements are in lower concentrations at higher elevation and is considered as possible causes for low productivity at two montane forests in Colombia (Veneklaas 1991), but a better insight requires studies of photosynthesis and availability of essential nutrients in the soil. N limitation results in the reduction of plant carbon gain, with long leaf lifespans and high leaf mass per area. P limitation results in high P-use efficiency and disproportional large increases in P uptake after fertilization (Harrington et al. 2001). Comparing trunk growth in circumference and litterfall in fertilized and non fertilized plots showed, that trunk growth responded more to fertilization than litterfall (Tanner et al. 1992), but it was also hypothesized, that nutrients were not fully available to plants due to following reasons: the uptake systems were not sufficiently flexible to take advantage of the increased nutrients, or the nutrients remained in the soil in immobilized forms (Tanner et al. 1992).

2. Root ingrowth experiments as a measure for nutrient availability. The response of fine roots to added nutrients was not always consistent with other plant growth parameters. Despite N limitation to aboveground growth, N fertilization had small effects on root parameters on a geologically “young” site (Ostertag 2001). In contrast, fertilization with P at an old site in Hawaii increased P concentrations, belowground net primary productivity was greater and root turnover rates increased. These results suggest that root dynamics differ dramatically between ecosystems low in N or low in P, despite each system being considered as “infertile” (Ostertag 2001). Cuevas and Medina (1988), in contrast, described that fine root growth at a N limited site in Amazonian forest was increased by addition of N, and P stimulated root growth in a Ca/Mg limited and a N limited site (Cuevas and Medina 1988).
3. Nutrient ratios and the interplay of nutrients in plant growth. Apparently different vascular plant species require a similar balance of nutrient supply for optimal growth and exhibit the same nutrient ratios in tissues, unless some element is limiting growth (Chapin and Van Cleve 1989). However, nutrient ratios of single plants can also reflect temporary storage of one nutrient in excess (Chapin and Van Cleve 1989). For example, the N:P ratio is a meaningful and easy first approach to determine nutrient limitation in plants species and communities (Koerselman and Meuleman 1996), but does imply, that the analyzed system is either N or/and P limited (Aerts and Chapin 2000). Moreover, it is necessary to differentiate between nutrient limitation at community and at species level (Aerts and Chapin 2000), because within communities, the nutrient ratios of individual species can be so different from that of the community as a whole that it must be concluded that the growth of these species is controlled by an element that does not control community biomass production (Aerts and Chapin 2000).

4. The plant/ecosystem $\delta^{15}N$ values may reflect N sources, mineralization rates or N input and output of the system. N is reported to constitute an excess nutrient in tropical soils (with exceptions on white sand soils and montane tropical forests), which have a more open nitrogen cycle with higher N losses through leaching of nitrification/denitrification processes and more input and output of N relative to internal cycling (Martinelli et al. 1999). In such systems ^{15}N accumulates and ^{15}N concentrations in plants increase, thus it is possible to compare ecosystems regarding N cycling, general N availability and general substrate age (relative turnover rates) (see further in the text: biogeochemical theory). These losses of ^{15}N depleted N are only significant when there is abundant N within the system (Martinelli et al. 1999).

Several studies have provided information on the annual uptake and loss of carbon and nutrients by plants allowing predictions on the cycling of these elements (Vitousek and Sanford 1986, Proctor 1987). Often, from such studies, element ratios (C:N, N:P) in leaves and litter can easily be calculated, again indicating which nutrients may be potentially limiting plant growth (Vitousek 1982, 1984, Aerts and Chapin 2000).

Such studies provide useful hypotheses, but are not sufficient to conclusively demonstrate N or P or other nutrient limitation situations solely from nutrient relations (Vitousek et al. 1993).

Comparisons of nutrient availability in tropical forests from different altitudes indicate that N is abundant in lowland forests and P and Ca are lacking compared to e.g. temperate forests, and tropical montane forests are often insufficiently supplied with N and P relative to lowland forests (Grubb 1977, Cuevas and Medina 1986, Vitousek and Sanford 1986, Vitousek et al. 1988, Veneklaas 1991, Grubb 1995, Vitousek and Farrington 1997, Tanner et al. 1998).

Fertilization experiments monitoring the direct response of plant growth allow immediate conclusions, but, as mentioned above, additional parameters are likely to influence the results especially in the tropics. Nevertheless, the basic knowledge about nutrient limitation of plants in the tropics was provided by fertilization studies. It was shown that the supply of N and P significantly increased trunk growth and annual litterfall in a Venezuelan montane forest (Tanner et al. 1992), with N being the more important limiting nutrient at this site and a complete fertilizer (N-P-K, plus micronutrients) stimulated tree growth in two Hawaiian montane forests (Gerrish et al. 1988). In an Amazonian forest on an oxisol, tree root growth was increased after additions of P and Ca, while those on a forest on a spodosol responded to added N (Cuevas and Medina 1988).

Fertilization experiments may indicate which specific nutrients limit growth at certain tropical forest sites, but they do not provide sufficient information to determine the patterns of nutrient limitation or its controls across a range of tropical forest sites (Vitousek et al. 1993).

A general theory about the development and nutrient limiting processes during the ontogeny of soils was presented by Walker and Syers (1976). They pointed out that most soils at the very beginning of succession have the highest concentrations of P and Ca, Mg, K etc., due to fast weathering especially under tropical conditions, rapidly transforming these elements into forms available for plants providing them with sufficient nutrients. In contrast, young soils usually contain little to no nitrogen. This element has to be accumulated from the atmosphere and primary production in early successional systems should therefore be N limited (Vitousek et al. 1989b). With the development of the soil, P and other rock-derived elements are lost or immobilized for plants and N continues entering the system by biological N_2 fixation (Walker and Syers 1976) at a greater degree than all other elements are added by precipitation and dry deposition. With ongoing soil development and age the nutrient limitation gradually switches from N to the rock derived elements (Vitousek and Sanford 1986, Vitousek et al. 1989a).

Tanner et al. (1998) state that, to find out about limitation of sites or individual trees it is not necessary to perform large scale fertilization experiments, instead the nutrient status can be accessed by measurements of foliar and litter concentrations. In general, nutrient limitation of growth is correlated with low concentrations of the limiting nutrient in leaves and litter (Tanner et al. 1998). Several studies report of strong relationships between A_{max} and N (or other nutrients) as a result of a specific nutrient limitation of photosynthetical processes (Field and Mooney 1986, Reich and Schoettle 1988, Reich et al. 1991, Reich et al. 1992, Reich and Walters 1994, Reich et al. 1994, Raaimakers et al. 1995, Reich et al. 1995a, Ellsworth and Reich 1996, Reich et al. 1998). Again, with such methods some more complex problems arise hindering a linear interpretation (see discussion about SLA in chapter 2.5). In the above-mentioned studies, limitation of photosynthetic capacity by nutrients is consistently quantified as the significance of the linear correlation between A_{max} and leaf nutrient content. The high investment in photosynthetic structures and enzymes needed to achieve a high A_{max}-N slope will be advantageous only when leaf N is sufficiently high enough to result in a high A/leaf N and when other resources, such as light, are also sufficiently available that high photosynthetic rates per unit leaf N can occur (Reich et al. 1994).

To date, not many studies provide data and discuss colimitation of two or more nutrients affecting plant growth (Cuevas and Medina 1988, Reich and Schoettle 1988, Raich et al. 1996, Vitousek and Farrington 1997). Probably a real colimitation of two or more nutrients is rather an exception, representing the case of the exact balance of the minimum amount of nutrients needed for a certain plant to exhibit maximum growth rates. In most of the cases one nutrient or other parameters as light or water availability etc., will become growth limiting for plants. Growth of plants is not for an undefined period of time, exclusively determined by solely one parameter. As an ecosystem or the ecological situation for single plants is steadily changing, e.g. during succession or due to seasonal fluctuations, along with that plant growth conditions change also.

It is hypothesized, that light is not always a limiting parameter for plant growth, due to adaptation of plants to their usual photosynthetic photon flux density environment. At for example montane forests, where cloud cover is increased compared to lowland forests, plants show photosynthetic saturation at already much lower light levels occurring there and than at surrounding lowlands.

Fertilization studies to define nutrient limitation of tropical lowland forests are still rare and Tanner et al. (1998) conclude, that to date there is insufficient information to say whether in general, montane forests differ from lowland forests in the extent of nutrient limitation or even which nutrients generally limit growth, despite indirect evidence that they might differ in both respects.

Additionally, studies where the experimental nutrient limitation (e. g. fertilizer studies) is combined with the related restrictions of photosynthetic capacities are also lacking, so that a direct response of soil nutrient limitation to photosynthetic performance of plants could rarely be demonstrated.

1.2 Tropical montane cloud forests

Tropical montane cloud forests are in a special situation worldwide. They occur where mountains are frequently covered by tradewind-derived orographic clouds and mist in combination with convective rainfall (Foster 2001). Many features of these forests are directly or indirectly related to cloud formation, from vegetation morphology to nutrient budgets to solar insolation (Bruijnzeel and Proctor 1995). One of the most direct impacts of frequent cloud cover is the deposition of cloud droplets through contact with soil and vegetation surfaces (horizontal precipitation) (Stadtmüller 1987). Total horizontal precipitation is greater than that from vertical rainfall events in some systems during the dry season, when these forests may experience water shortage (Bruijnzeel and Proctor 1995). Because the combination of horizontal precipitation and lowered evapotranspiration due to frequent cloud contact significantly increases precipitation minus evaporation in these forests, they function as important local and regional watersheds. Also, due to the sponge-like effect of epiphytes and epiphylles, these forests act as capacitators in regulating the seasonal release of precipitation, thereby providing flood and erosion control in the rainy season and water storage in the dry season (Foster 2001).

In addition to their hydrological importance, these ecosystems typically harbour an impressive array of plants and animals. Although the biodiversity of tropical montane cloud forests is not as high as that of lowland moist tropical forests (Hamilton et al. 1995), the level of endemism found is exceptional. For example, 32% of Peruvian endemic vertebrates are localized in cloud forests (Leo 1995) and 12% of the endemic plants of Panama are found in the Cerro Jefe region within an area of 53 km^2 and of this 31.5% are local endemics (Carrasquilla 1997). The conservation status of these unique ecosystems is unsteady as they are among the most endangered of all tropical forest types. A high annual deforestation rate in tropical mountain forests caused by harvesting fuel wood, resource logging and agricultural conversion is increasingly threatening cloud forests worldwide (Hamilton et al. 1995).

To date ecophysiology of tropical montane forests has been rarely investigated. A very important question is whether montane cloud forests, especially in Central America, are evolutionary hot-spots and a possible puffer zone for plants and associated animals during climatic fluctuations. Again it is very important to understand the physiology and ecology of such ecosystems to find out about their tolerances and flexibility for climatic and nutritional changes, having in mind that this forest types are refuge areas for organisms from surrounding ecosystems in transition. Tropical montane forests seem to provide a genetical backup for plants downslope migration during glacial times (Colinvaux et al. 1996).

Climatically, these forests are characterized by lower air and soil temperatures, an increased cloud cover resulting in less photosynthetic photon flux density and increased precipitation, more frequent and increased winds. Soils are often acidic, nutrient poor and especially on ridges and slopes humus layers are low due to erosion and sometimes lower soil layers are water logged.

1.2.1 Climatic situation in Panama

The movements of the intertropical convergence zone (ITCZ) influence seasonality over large parts of the tropics (Hastenrath 1985). The ITCZ develops when air warmed by the zenithal sun rises and cools adiabatically to form clouds and rain. Outside the ITCZ, the surface tradewinds rush to replace air rising within the ITCZ, and cloud cover and rainfall are reduced. The ITCZ moves latitudinally some two months after the zenithal sun, and its movements bring wet and dry seasons to large parts of the tropics. Rainfall, cloud cover, irradiance, atmospheric saturation deficits, windspeed, and potential evapotranspiration all covary seasonally. In addition to direct effects on plant growth, these seasonal patterns may affect populations of animals and microbes that interact with plants. As a consequence, most tropical forest plants experience simultaneous seasonal change in several environmental factors.

Differences between lowlands and montane sites have to be considered. In the case of the forests on the top of the continental divide in east Panama, the metereological situation is determined by frequent fog as a result of the climatic conditions that characterize this region. Winds from the north and north-east loaded with moisture from the Caribbean Sea prevail, resulting in an annual average rainfall of approximately 4000 mm (Valdespino 1988). The temperature on 1000 m.a.s.l. during the year is described to range between 17^{o}C and 26^{o}C.

1.2.2 Cerro Jefe area in detail

1.2.2.1 Geography

The Cerro Jefe region is in the Province of Panama 52 km north-east of the capital (Panama City). The region is located in the Cordillera de San Blas; the Cerro Jefe peak reaches 1007 m. The topography is uneven, with ravines of varying depth.

The Cerro Jefe uplift is on the continental divide and the source of rivers flowing to both oceans – on the Pacific slope, including the Pacora, Tocumen and Juan Díaz rivers; on the Caribbean slope, including several rivers of the Chagres watershed which supplies major reservoirs. Gatún Lake (423 km^2) was formed by damming the Chagres River in 1910 during construction of the Panama Canal and is an integral part of the watercourse for the transit of ships; Alajuela (Madden) Lake (57 km^2) was formed in 1936.

Geologically, Cerro Jefe is possibly part of the Cerro Azul pluton. Comparison of magmatic rocks shows similarities between the plutons of Cerros Azuero and Azul and the Pito (Darién) River (Destro de 1986). This supports Recchi's hypothesis on the geological evolution of Panama, that the Azuero Peninsula and the area spreading out from Cerro Azul to the Pito River were aligned in pre-Tertiary and Paleocene eras, and the pluton outcropped there, having arisen from a common magma. Later tectonic plate action moved the plutonic block northward that has become Cerro Jefe and adjacent areas. In nearby regions, there are various geologic faults due to past volcanic and tectonic activity. One of these faults is along the course of the Chagres River, interrupted upstream by the volcanic crater in Alajuela Lake.

According to the geologic map of Panama (IGN 1988), the bedrock of Cerro Azul is igneous-extrusive, including basalt, andesite, tuff and ignimbrite, whereas the bedrock of Cerro Jefe and its boundary areas is igneous-intrusive, including granodiorite, quartz-monzonite and diorites.

The soils are moderately to very stony latosols, and acid to very acid; they are non-arable (class VII), suitable only for forests and reserves. On the Cerro Jefe summit the considerably different concentrations of elements found in the soils have been sampled – especially iron, potassium and manganese (Valdespino 1988).

1.2.2.2 Vegetation

This region includes three life zones in the Holdridge system: tropical premontane wet forest, tropical wet forest and tropical premontane rain forest (Tosi 1971).

In the tropical premontane wet-forest zone at 300-500 m, as a result of many years of human activities, generally the more or less fallow vegetation is mostly herbaceous. *Saccharum spontaneum*, an aggressive introduced grass to 3 m tall, has extended widely and partially displaced fodder pastures of the African grasses *Hyparrhenia rufa* and *Panicum maximum*, as well as native plants.

Shrubs of the families of Dilleniaceae, Melastomataceae and Compositae, and high light trees such as *Apeiba tibourbou*, *Xylopia aromatica*, *X. frutescens*, *Anarcardium occidentale*, *Cecropia* sp., *Vismia* sp. and *Cordia alliodora* occur, if *Saccharum spontaneum* is absent.

In disturbed older secondary vegetation occur trees such as *Enterolobium schomburgkii*, *Didymopanax morototonii*, *Spondias mombin*, *Pseudobombax septenatum* and *Calycophyllum candidissimum*. On degraded soils predominate *Roupala montana* and some *Clusia* and Melastomataceae.

At 600-800 m climax forest is found, interrupted by areas converted by the poultry-breeding industry, settlement and coffee cultivation. In this forest there are several arboreal strata and emergents 30 m or more tall, including *Callophyllum longifolium*, *Pouteria* sp., *Podocarpus* cf. *oleifolius* and the palms *Welfia georgii*, *Socratea durissima*, *Euterpe precatoria* and *Wettinia augusta*.

The diversity of epiphytes is high, including for example bryophytes, lichens, ferns, Bromeliaceae, Orchidaceae, Araceae, Cyclanthaceae and Ericaceae.

Toward the Caribbean slope mature forest is relatively better preserved, both tropical wet forest and tropical premontane rain forest, due partly to the rough topography and the abundant precipitation. Nonetheless, there is an area near Cerro Jefe known as Cerro Pelón where the vegetation consists of almost non woody species, with *Rhynchospora cephalote* predominating, accompanied by species such as *Trachypogon plumosus*, *Andropogon bicornis*, *A. leucostachys* and *Scleria* sp. Occasionally the palm *Colpothrinax aphanopetala* is found.

The forest on the summit of Cerro Jefe is influenced by frequent strong winds, having a vegetation of shrubby trees, generally 8-15 m tall with medium-sized to small leathery leaves; it shows a tendency towards sclerophylly (Gentry 1982). In this of forest flourish *Ardisia* sp., *Alchornea* sp., *Mysine* sp., *Clusia* spp. and some Sapotaceae, and endemics such as *Psychotria olgae*, *Licania jefensis* and *Vismia jefensis*. Epiphytic plants are abundant, dominated by Orchidaceae and Bromeliaceae (Torres 1989). At the tank-forming *Vriesea* sp., *Guzmania* sp. and other bromeliads that retain water it is easy to find *Utricularia jamesoniana*, a carnivorous plant that feeds on organisms in the accumulated solutions.

Colpothrinax aphanopetala is prominent because of its dense populations; it is distributed up to 900 m. In primary forest with emergents it is infrequent or absent, and instead occur *Socratea durissima* (*S. exorrhiza*), *Wettinia augusta* and *Euterpe precatoria* – which tend to be shorter and stouter on hillsides and on the summit of Cerro Jefe. *Olyra standleyi* is sometimes concentrated in pure populations in open and disturbed areas.

1.2.2.3 Flora

Of the 1230 species endemic to Panama, 143 have been found on Cerro Jefe – including 45 local endemics. The angiosperm families with the highest number of endemic species are Rubiaceae (25), Araceae (13), Gesneriaceae (12), Ericaceae (8), Myrsinaceae (8), Compositae (7), Solanaceae (7) and Orchidaceae (5). Among the characteristic genera are *Psychotria* (16), *Anthurium* (13), *Columnea* (7) and *Ardisia* (4) (Carrasquilla 1987).

Lewis (1971) concluded that the Cerro Azul-Cerro Jefe region, like other relatively high regions in Panama, has been a site of refuge and evolution for many taxa that were geologically isolated from the North American range of mountains which reaches western Panama. The flora of western Panama is more allied with flora to its north-west, because of the continental connection by the Middle Miocene that united Central America and North America. At that time the flora of present eastern Panama was still on groups of low volcanic islands, which included Cerro Jefe, and which were populated by long-distance dispersal from nearby South America, as well as continental Panama. The Panamanian land-bridge between North America and South America became established approximately 3.5-2.4 million years ago during the Late Pliocene (Graham 1972, Gentry 1982, Rich and Rich 1983, Gentry 1985, Graham 1985, 1993).

Study of the flora of Cerro Azul-Cerro Jefe was initiated by P.H. Allen in the mid 1940s (Dwyer 1967); especially from 1965 onward, other foreign and Panamanian specialists have contributed much to the knowledge of the regional flora (Martínez 1977-1978, Dwyer 1985, Hampshire 1989, Aranda 1991, Pierce and Aranda 2000, Pierce 2001, Pierce and Grant 2002). Altogether, approximately 840 species of flowering plants are recorded for Cerro Azul-Cerro Jefe. According to Carrasquilla (1987), on Cerro Jefe approximately 486 species have been collected, 119 of which are epiphytes (Torres 1989).

The pteridophytes on Cerro Azul-Cerro Jefe are frequent and quite diverse – 98 species have been identified. On Cerro Jefe most of the species are in Polypodiaceae (14), Hymenophyllaceae (10), Dyopteridaceae (6), Gleicheniaceae (5) and Cyantheaceae (4), and in the genera *Grammitis*, *Trichomantes* and *Elaphoglossum*. Tree ferns are distinctive components of the Cerro Jefe forest – *Trichipteris williamsii* is most abundant, then *Cyanthea* sp. (Valdespino 1988).

Among the disjunct species on Cerro Azul-Cerro Jefe, *Hymenophyllum apiculatum* is also known from Venezuela (e.g. Guayana Highlands) and Colombia (Meta and Valle), so the population in Panama probably resulted from long distance dispersal. *Licania affinis* also has been recorded in the Guayana area. A number of species seem to be disjunct from the Guayana region and especially the Guayana Highlands, probably representing pre-Andean survivors of the flora of the pre-isthmian uplifted islands (Gentry 1985). This isolated situation in the past may also be indicated by several species shared with the Cerro Tacarcuna (1900 m) bordering

Colombia: *Eleagnia nitidifolia*, *Conomorpha gentryi*, *Columnea mira* and *Vochysia jefensis*. *Colpothrinax aphanopetala* has recently been collected in a remote area of the Talamanca mountains in Costa Rica, occurs as well in certain areas in the SE Nicaragua and on both the Caribbean and Pacific slopes in Costa Rica and Panama, 350-1000 (-1400) m, typically in premontane, sometimes lowland, wet forests (Evans 2001).

Of the c. 486 flowering plant species documented on Cerro Jefe, 101 extend in distribution only to Costa Rica and Colombia. Slightly more of the species extend from Mexico to South America (Carrasquilla 1987). As an example of the greater southern affiliation, five species of *Miconia* are shared between Panama and South America, but only one species is shared with Central America.

The floristic affinities on Cerro Jefe partly reflect the relative likelihood of the phytogeographic opportunities from the neighboring regions. South America is much larger and more diverse than Central America, and the pre-isthmian islands were more or less to the west of South America – receiving the westward-prevailing air currents of the Intertropical Convergence Zone and oceanic current. Thus the greater dispersal of plant propagules was from east to west.

1.7 Aims and scopes of the project

This Ph.D. thesis was part of the project “The carbon dynamics of tropical forest canopies” initiated by Klaus Winter, Joseph Wright and Steven Mulkey and funded by the Richard Lounsbery Foundation through the Smithsonian Tropical Research Institute in Panama.

Therefore the thesis was structure that way that chapters 2, 3 and 4 can be easily be turned into manuscripts. However, they are strongly interrelated and complementary and were deliberately introduced together.

The main task of this study was to check if those prediction methods reported by Zotz and Winter (1993, 1994c) for a lowland rainforest are also applicable to montane species. On the one hand it was shown for 8 lowland rainforest species of different life forms (Zotz and Winter 1993) that diel life carbon gain can be derived from short-term photosynthetic capacity measurements. On the other hand the annual carbon balance correlated with leaf nitrogen in four species of different life forms (Zotz and Winter 1994c).

The lower productivity reported so far for montane rain forests could be partly due to nutrient limitation. To clarify this issue photosynthetic capacity and leaf nutrient concentrations were compared between species of the montane and the two lowland forest sites. To eliminate possible nutrient limitation of plants, an adjacent plot was fertilized.

In addition to photosynthetic capacity, carbon gain, leaf nutrient concentrations, leaf phenology was monitored to proof which external factors (light, temperature, rainfall, nutrients) are most influential besides the endogenous control of leaf production patterns.

This basic research is essential as a background for further ecophysiological studies on plant productivity, conservation or reforestation activities at tropical montane forests and possibly as an additional information about ongoing global evolution of plants and, linked to that, of organisms in general.

2. Photosynthetic capacity, leaf nutrient contents and nutrient limitation of a tropical montane ecosystem in comparison with two tropical lowland forests.

2.1 Abstract

- Photosynthetic capacity (A_{max}), leaf mineral contents and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios were determined for the foliage of plants from a tropical montane and two lowland forests. Understanding nutrient availability and its effect on photosynthesis and growth is an important predictor of plant community response to nutrient status.
- Light response curves were conducted on plants in the field, leaf nutrient contents were determined thereafter.
- The highest A_{max}, N and P values (26.8 µmol m^{-2} s^{-1}, 29.1 and 1.69 mg g^{-1}, respectively) were measured in the secondary lowland forest with the lowest values (5.7 µmol m^{-2} s^{-1}, 6.8 and 0.2 mg g^{-1}, respectively) for the montane forest site. N:P ratios correlated significantly with A_{max} at the montane site.
- Correlations of nutrient ratios (e.g. N:P) with A_{max} and with the single nutrients, offers a faster means of assessing nutrient limitation in different ecosystems. Results indicate a N-limitation of photosynthesis at the montane site and a possible K-limitation at the primary lowland forest site.

2.2 Introduction

The physiological ecology of tropical montane cloud forest (TMCF) ecosystems is to date little understood. These forests are characterized by a low stature and a high abundance of water demanding plant life forms such as epiphytic angiosperms, mosses, ferns and fungi. Abiotic factors affecting the growth of plants include the low air and soil temperatures, high air humidity, high precipitation rates, low light intensities resulting from cloud cover (Still *et al.*, 1999), mist and constant trade winds (Grubb & Whitmore, 1966, 1967; Baynton, 1968; Cavelier & Mejia, 1990; Cavelier & Goldstein, 1989). Small, thick and tough leaves, sometimes windblown trunks and commonly low productivity characterize plants living under these conditions.

To describe these structural and functional features of TMCFs, Bruijnzeel & Veneklaas (1998) proposed a variety of possible explanations: **a)** periodic or seasonal water shortage, especially in the case of shallow and stony soils, **b)** water logged soils resulting in inhibition of root respiration, **c)** reduced leaf temperatures and photosynthesis associated with low solar radiation inputs, **d)** limited nutrient uptake due to climate dependent low transpiration, **e)** soil acidity and/or low nutrient availability, often coupled with reduced decomposition and mineralization rates, **f)** exposure to strong winds and, **g)** toxicity of phenolic compounds in the rhizosphere. Additionally the low stature of vegetation has been considered as a response to higher intensities of UV-B light enhanced by up to 70 % by reflection from cloud cover (Flenley, 1995).

Various approaches where used to assess nutrient limitation of plant primary production at different elevations and successional stages in the tropics. Examples are experiments were nutrient retranslocation was determined comparing nutrient contents of non-senescent leaves with leaf litter and studies where fertilized plants were compared with non-fertilized ones concerning increase in trunk-diameter, litterfall and N and P content in leaves (summarized in Tanner *et al.*, 1998).

Carbon dioxide (CO_2) fixation of leaves is a useful physiological parameter with which carbon assimilation rates and plant primary production at montane sites can be compared with existing data from lowland sites (Kitajima *et al.*, 1997a,b: Zotz & Winter, 1996). Photosynthesis-nutrient relationships showed that photosynthetic capacity (A_{max}) is dependent on leaf nitrogen (N) content in many ecologically diverse species, allowing comparison even among different ecosystems (Reich *et al.*, 1991 & 1992). Peterson *et al.* (1999) reviewed the physiological background of this correlation: **a)** the majority of leaf N is partitioned to proteins (mainly Rubisco) of the reductive pentose phosphate cycle (Evans, 1989), **b)** leaf N can be used to estimate the maximum rate of carboxylation (Vc_{max}) and the light-saturated rate of electron transport (J_{max}) (Farquhar *et al.*, 1980) as Vc_{max} is proportional to Rubisco content and J_{max} proportional to thylakoid protein content (Field, 1983; Evans 1989; Harley *et al.*, 1992), **c)** the relationship between A_{max} and leaf N has been used to predict photosynthesis over scales ranging from leaf to the globe (e.g. Aber & Federer, 1992; Harley *et al.*, 1992; Kirschbaum *et al.*, 1994; Woodward & Smith, 1994a,b; Aber *et al.*, 1996), **d)** the correlation between A_{max} and leaf N has been implicated as evidence for global-scale convergent evolution of photosynthetic constraints (Reich *et al.*, 1997 & 1998).

Reich *et al.* (1991, 1992, 1994 & 1995) considered N- and P-use efficiencies respect to other ecophysiological factors and drew the following conclusions: Slow growing primary vegetation has low leaf nutrient contents, low specific leaf area (SLA) and, therefore, also low photosynthetic activities. Such plant species occur in resource-poor undisturbed sites with low turnover rates, and light saturated photosynthesis is low, but relatively stable over leaf lifetime. Investment in carbon-based leaf structural defenses (sclerophylly) is high and leaf lifespans are also higher. Hence, the nutrient-use efficiency of plants in such ecosystems is generally low.

Secondary vegetation is usually fast growing, has short-lived foliage and occupies relatively resource- and light-rich environments (Uhl, 1987). In order to establish, plants must gain height as quickly as possible, thereby rapidly acquiring nutrients from the soil. Maximum photosynthetically active leaf area is produced with a minimum of investment (i.e. high SLA) and light saturated photosynthetic rates are high, but decrease rapidly with leaf aging mainly due to N reallocation from senescent to younger leaves (Kitayima *et al.*, 1997a). Leaf longevity is reported to be low and soil nutrient turnover rates are high at such sites. Nutrient-use efficiency in this plastic environment is also high.

In a comparative approach assessing photosynthetic and nutritional characteristics of a montane cloud forest and two different lowland rain forests, the present study addressed the following hypotheses: **a)** photosynthesis is limited by leaf nutrient content to a greater extent in the montane forest (c.f. lowland plants) with concomitant leaf structural differences, **b)** growth in tropical montane forests is predominantly N-limited (Grubb, 1995), whereas P-limitation predominates at the lowland sites (Cuevas & Medina, 1986), **c)** co-limitation through other macro- and micro-nutrients occur at all three sites, **d)** these differences in productivity and nutrient constraints will also be reflected in the stable isotope composition of leaf material ($\delta^{13}C$ and $\delta^{15}N$).

2.3 Materials and Methods

2.3.1 Location of study sites and plant material

The main study site, an elfin cloud forest, is located in the Province of Panama approximately 52 km northeast of the capital of the Republic of Panama (Panama City) on the peak of Cerro Jefe (1007 m.a.s.l., 09°13.794' N, 079°22.995' W). Soils are moderately stony latosols, ranging from acid to very acid (pH in water: 6-4). Frequent strong winds and a near constant cloud cover with mist mainly during the night and sunny periods during the day characterize the site. Mean daily temperatures are approximately 20°C (18°C minimum) during the rainy season (April to December) and 18°C (16.5°C minimum) during the dry season (Carrasquilla, 1997). The vegetation at Cerro Jefe is open and composed of shrubby trees approximately 3-15 m tall with mostly sclerophyllous medium-sized to small leathery leaves (Gentry, 1982). The emergent recently for south Nicaragua, Costa Rica and Panama described Palm *Colpothrinax aphanopetala* (Evans, 2001) is abundant and probably plays an important role as a windbreak and in collecting mist. The open vegetation of shrubby trees, palms and a widespread grass, gives pioneers a chance to establish in between climax species. For a more complete characterization of the flora see Carrasquilla (1997). Approximately 20 abundant early to late successional species of different life forms were chosen at random for analysis (Table 1).

Comparisons were made with lowland forests at Fort Sherman and the Parque Nacional Metropolitano (PNM), Panama; a detailed site characterization is given by Kitajima *et al.* (1997) and Zotz *et al.* (1995). Fort Sherman is a primary lowland tropical forest located approximately 5 kilometers southwest of Gatun locks on the Panama Canal mouth at the Atlantic coast and PNM is a secondary lowland tropical forest on the Pacific coast with less annual rainfall and a more pronounced dry season. Construction cranes at the lowland forest sites provided access to canopy sun leaves where measurements and leaf sampling were carried out on a selected range of tree species (Table 1).

2.3.2 Light response curves

Gas-exchange measurements were performed at all three study sites, with a portable open flow infrared gas analysis (IRGA) system (Li- 6400; Li-Cor Inc., Lincoln, Nebraska, U.S.A). The reference air supply was connected to a 23-liter buffer volume. Measurements were made from 8.00-12.00 hours local time at constant water vapor pressure and ambient temperature.

Light response curves were produced by IRGA in conjunction with a red LED lightsource (Li-Cor Inc.), and data analysed using Photosynthesis Assistant Version 1.1.2 (Dundee Scientific, Dundee, U.K.) sofware. Photosynthetic photon flux densities (PPFD) used ranged between 0 and 2000 μmol m^{-2} s^{-1}. The cuvette was shaded to avoid overheating by sunlight.

Taking into account that leaf longevity varies among populations, species and leaves of different ages (Reich *et al.*,1991; Oleksyn *et al.*, 2000), photosynthetic capacities, nutrient concentrations and SLA were determined for leaves of similar physiological state. Fully expanded, non-senescent sun leaves were used; at this developmental stage leaf physiological characteristics are relatively constant (Reich *et al*., 1991).

2.3.3 Leaf nutrient content

Foliage was harvested following gas-exchange measurements, and leaf area measured using a Li-3100 (Li-Cor Inc.) leaf area meter. Subsequently, samples were dried, weighed, ground and analysed with an EA 1100 elemental analyser (CE Instruments, Milan, Italy), linked to an isotope ratio masspectrometer (Delta^{Plus}, Finnigan MAT, Bremen, Germany) in continuous-flow mode. Values for $\delta^{13}C$, $\delta^{15}N$ and weight percentage of N and C were obtained. Samples were also analysed for other macro- and micronutrients using a CHN-O Elemental analyser (Heraeus, Hanau, Germany) and a ICP JY 70 Plus spectrometer (ISA, München, Germany).

Instantaneous photosynthetic N- and P-use efficiencies (PNUE and PPUE, respectively) and N:P and C:N were calculated.

2.3.4 Regression analysis

Correlations were calculated between A_{max} and foliar N, P, N:P; between SLA, N:P and foliar N, P and N:P; between P and N; and between $\delta^{15}N$ and N, C/N, respectively and are given in table 2.

Graphs and regression statistics were obtained with Sigma Plot 4.01 (SPSS Inc., Chicago, Illinois, U.S.A.) graphing software and Statgraphics Plus 4.0 (Statistical Graphics Corp., U.S.A.) statistical software.

2.4 Results

The highest significant correlations of A_{max} with leaf N and P were apparent on a dry weight basis (Fig.1a,2a). Correlations on an area basis were always weaker or there was no significant relationship (Fig.1b,2b). Trends indicate that photosynthetic capacity of the species at Cerro Jefe increased relatively little with increasing leaf N content (on a dry mass basis) when compared to the two lowland sites (Fig. 1a). Cerro Jefe vegetation showed the greatest positive response of A_{max} to P for all three sites, although this was statistically not significant, but it had the lowest absolute leaf P concentrations (Fig. 2a). Nitrogen content increased most with increasing SLA for Cerro Jefe plants; Fort Sherman and Parque Metropolitano plants showed no significant increase of N with SLA (Fig. 3).

Photosynthetic capacities from Cerro Jefe plants ranged between 5.7 and 15.0 μmol m^{-2} s^{-1}, at Fort Sherman the values ranged between 8.8 and 20.5 μmol m^{-2} s^{-1}, however highest A_{max} rates were measured at Parque Metropolitano site, where values of between 12.2 and 26.8 μmol m^{-2} s^{-1} were obtained (Table 3).

Leaf N contents at Cerro Jefe ranged between 6.5 and 25.2 mg g^{-1} (Table 4). Fort Sherman plants had values of between 12.2 and 23.5 mg g^{-1} and in the Parque Metropolitano values between 19.1 and 29.1 mg g^{-1} were measured.

Leaf P content at Cerro Jefe varied between 0.2 and 0.7 mg g^{-1}, at Fort Sherman between 0.6 and 1.1 mg g^{-1} and at the Parque Metropolitano site between 1.0 and 1.7 mg g^{-1} (Table 4).

PNUE was lowest in plants from Cerro Jefe and there was a positive trend to Fort Sherman and Parque Metropolitano plants (Table 3). PPUE was highest in plants from Cerro Jefe (i.e. those with the lowest P content) and lower for lowland forest plants (Table 3).

C:N and N:P ratios decreased from the montane through the wet lowland to the drier lowland site (Table 3), but this was only significant between Cerro Jefe and Parque Metropolitano site. Photosynthetic capacity increased with increasing N:P at Cerro Jefe, but was independent of N:P at the Fort Sherman and Parque Metropolitano sites (Fig.4a). N:P ratios increased significantly with increasing leaf N content at Cerro Jefe site, but showed no statistical relation at the two lowland sites (Fig.5a). Leaf P showed negative slopes with increasing N:P at both lowland sites, but was completely independent of N:P at Cerro Jefe (Fig.5b) and correlations for all three sites were not significant (Table 2). All sites showed an increase in leaf P content concomitant with increasing foliar N content, but with decreasing altitude this relationship was less apparent, and N and P levels generally tended to be lower at the montane site (Fig.4b). Furthermore, the values for N at the montane site showed a broader range compared with the other sites and P content.

Values of δ^{13}C were not significantly different for the three sites, but there was a positive trend in δ^{15}N from Cerro Jefe to Parque Metropolitano plants (Table 3).

Trends show that δ^{15}N signatures were more positive with increasing N content and altitude, particularly at low N contents (Fig.6a). The relationship was only significant for the montane plants. Furthermore, δ^{15}N became more negative with increasing C:N (Fig.6b), but again this was only significant for the montane site.

Other nutrient contents did not show significant differences between study sites, but some trends were apparent: S, Na^+ and Mn^{2+} contents decreased from Cerro Jefe through Fort Sherman to Parque Metropolitano whereas Ca^{2+}, Mg^{2+} and Zn^{2+} contents increased with altitude. Leaves of the Fort Sherman plants had in average the lowest values of potassium (6.9 ±2.9 mg g^{-1}). All Melastomataceae (*Clidemia* spp. and *Miconia* spp.) and *Eugenia* sp. showed at least a ten-fold higher aluminium content than other taxa (Table 4). However, no correlations of A_{max} and nutrient contents other than N, P and K were found.

Table 1 Plant species, growth form and position within the rainforest succession for the 3 study sites. Nomenclature follows Index Kewensis (Plant Name Project, http://www.ipni.org {accessed 26 June 2000}).

Species	**Family**	**Growth-form**	**Succession/ occurrence**
Elfin cloud forest Cerro Jefe			
Guatteria jefensis K. Barringer	Annonaceae	small tree	late / endemic[1]
Philodendron cf. *panamensis*	Araceae	hemiepiphyte	late
Stenospermation robustum Engl.	Araceae	epiphyte	late
Schefflera panamensis M.J. & J.F.M. Cannon	Araliaceae	tree	intermediate - late
Colpothrinax aphanopetala R.J. Evans	Arecaceae	tree	late
Hedyosmum bomplandianum H. B. & K.	Chloranthaceae	tree	intermediate - late
Calophyllum nubicola W.G. D'Arcy & R.C. Keating	Clusiaceae	tree	late / endemic[2]
Clusia salvinii Donn. Sm.	Clusiaceae	tree	late
Clusia coclensis Standley	Clusiaceae	tree	late
(species 1) not identified	Ericaceae	tree	(late)
Vaccinium jefense J.L. Luteyn & R.L. Wilbur	Ericaceae	tree	late / endemic[1]
Lisianthius jefensis A. Robyns & T. S. Elias	Gentianaceae	small tree	intermediate / endemic[1]
Vismia jefensis N.K.B. Robson	Hypericaceae	small tree	early / endemic[1]
Clidemia af. *neglecta* D. Don	Melastomataceae	small tree	early
Miconia dodecandra Cogn.	Melastomataceae	small tree	early
Miconia reducens Triana	Melastomataceae	small tree	early
Miconia pileata D.C.	Melastomataceae	small tree	early
Ardisia tysonii Lundell	Myrsinaceae	tree	late / endemic[2]
Eugenia cf. *octopleura* Krug & Urb. ex Urb.	Myrtaceae	tree	late
Olyra standleyi Hitchcock	Poaceae	herb	early
Cosmibuena valerii (Standley) C.M. Taylor	Rubiaceae	small tree or hemiepiphyte	intermediate - late
Primary lowland forest Fort Sherman/Atlantic			
Tapirira guianensis Aubl.	Anarcadiaceae	tree	late
Dendropanax arboreus (L.) Decne. & Planch.	Araliaceae	tree	intermediate
Cordia bicolor A. DC. ex DC.	Boraginaceae	tree	intermediate
Clusia cf. *rotundata* Standley	Clusiaceae	hemiepiphyte	intermediate
Ocotea ira Mez & Pittier ex Mez	Lauraceae	tree	late
Carapa guianensis Aubl.	Meliaceae	tree	late
Brosimum utile Fittier	Moraceae	tree	late
Poulsenia armata (Miq.) Standley	Moraceae	tree	intermediate
Virola elongata Warb.	Myristicaceae	tree	late
Manilkara bidentata (A. DC.) A. Cheval.	Sapotaceae	tree	late
Marila laxiflora Rusby.	Ternstroemiaceae	tree	intermediate
Apeiba membranaceae Spruce ex Benth.	Tiliaceae	tree	late
Secondary lowland forest Parque Nacional Metropolitano/Pacific			
Annona spraguei Saff.	Annonaceae	tree	intermediate / endemic[2]
Schefflera morototoni (Aubl.) B. Maguire, J.A. Steyermark & D.G. Frodin	Araliaceae	tree	intermediate
Pseudobombax septenatum (Jacq.) Dugand	Bombacaceae	tree	intermediate
Ficus insipida Willd.	Moraceae	tree	early
Cecropia obtusifolia Bertol.	Moraceae	tree	early
Cecropia longipes Pittier	Moraceae	tree	early
Castilla elastica Sessé in Cerv.	Moraceae	tree	early
Antirhea trichantha (Griseb) Hemsl.	Rubiaceae	tree	intermediate / endemic[2]
Luehea seemannii Planch. & Triana	Tiliaceae	tree	intermediate

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[1] local endemic to Cerro Jefe.

[2] endemic to Panama.

Table 2 Regression equations, r^2 and *P* values of data in the figures as indicated.

figure	*grouping*	*Dependent variable* (y)	*Independent variable* (x)	*Equation*	r^2	*P*
1a)	Cerro Jefe	Amax/mass	N/mass	$y=-11.43+6.87x$	0.83	<0.001
1a)	F. Sherman	Amax/mass	N/mass	$y=-75.86+10.80x$	0.75	<0.001
1a)	P. Metrop.	Amax/mass	N/mass	$y=-67.48+11.44x$	0.53	0.03
1b)	Cerro Jefe	Amax/area	N/area	$y=3.36+4.00x$	0.36	<0.01
1b)	F. Sherman	Amax/area	N/area	$y=5.05+3.72x$	0.15	0.22
1b)	P. Metrop.	Amax/area	N/area	$y=5.41+5.88x$	0.42	0.06
2a)	Cerro Jefe	Amax/mass	P/mass	$y=-1.28+205.07x$	0.43	<0.01
2a)	F. Sherman	Amax/mass	P/mass	$y=-22.24+171.24x$	0.53	<0.01
2a)	P. Metrop.	Amax/mass	P/mass	$y=-0.76+155.03x$	0.32	0.11
2b)	Cerro Jefe	Amax/area	P/area	$y=8.86+32.85x$	0.04	0.37
2b)	F. Sherman	Amax/area	P/area	$y=7.55+54.75x$	0.17	0.19
2b)	P. Metrop.	Amax/area	P/area	$y=8.34+81.91x$	0.38	0.08
3a)	Cerro Jefe	N/mass	SLA	$y=1.47+0.16x$	0.78	<0.001
3a)	F. Sherman	N/mass	SLA	$y=7.80+0.16x$	0.61	<0.01
3a)	P. Metrop.	N/mass	SLA	$y=18.80+0.04x$	0.06	0.53
4a)	Cerro Jefe	Amax/mass	N:P	$y=-50.28+3.87x$	0.44	0.001
4a)	F. Sherman	Amax/mass	N:P	$y=107.86+0.14x$	0.00	0.97
4a)	P. Metrop.	Amax/mass	N:P	$y=5.49+10.53x$	0.08	0.46
4b)	Cerro Jefe	P/mass	N/mass	$y=0.13+0.02x$	0.68	<0.001
4b)	F. Sherman	P/mass	N/mass	$y=0.07+0.04x$	0.61	<0.01
4b)	P. Metrop.	P/mass	N/mass	$y=0.16+0.05x$	0.71	<0.01
5a)	Cerro Jefe	N/mass	N:P	$y=-1.42+0.44x$	0.32	<0.01
5a)	F. Sherman	N/mass	N:P	$y=13.78+0.16x$	0.02	0.64
5a)	P. Metrop.	N/mass	N:P	$y=13.90+0.51x$	0.05	0.57
5b)	Cerro Jefe	P/mass	N:P	$y=0.39+0.00x$	0.00	0.95
5b)	F. Sherman	P/mass	N:P	$y=1.38-0.03x$	0.24	0.11
5b)	P. Metrop.	P/mass	N:P	$y=2.60-0.04x$	0.11	0.39
6a)	Cerro Jefe	$\delta^{15}N$	N/mass	$y=-7.43+0.47x$	0.57	<0.001
6a)	F. Sherman	$\delta^{15}N$	N/mass	$y=-1.57+0.14x$	0.20	0.15
6a)	P. Metrop.	$\delta^{15}N$	N/mass	$y=-2.14+0.16x$	0.23	0.2
6b)	Cerro Jefe	$\delta^{15}N$	C/N	$y=5.49-0.16x$	0.59	<0.001
6b)	F. Sherman	$\delta^{15}N$	C/N	$y=2.78-0.07x$	0.20	0.14
6b)	P. Metrop.	$\delta^{15}N$	C/N	$y=4.92-0.17x$	0.26	0.16
7a)	Cerro Jefe	Amax/mass	K/mass	$y=76.03+0.56$	0.00	0.78
7a)	F. Sherman	Amax/mass	K/mass	$y=30.86+11.61$	0.67	<0.01
7a)	P. Metrop.	Amax/mass	K/mass	$y=97.77+8.90$	0.10	0.41
7b)	Cerro Jefe	N/mass	K/mass	$y=11.74+0.20$	0.03	0.44
7b)	F. Sherman	N/mass	K/mass	$y=9.86+1.08$	0.89	<0.001
7b)	P. Metrop.	N/mass	K/mass	$y=21.75+0.12$	0.00	0.86

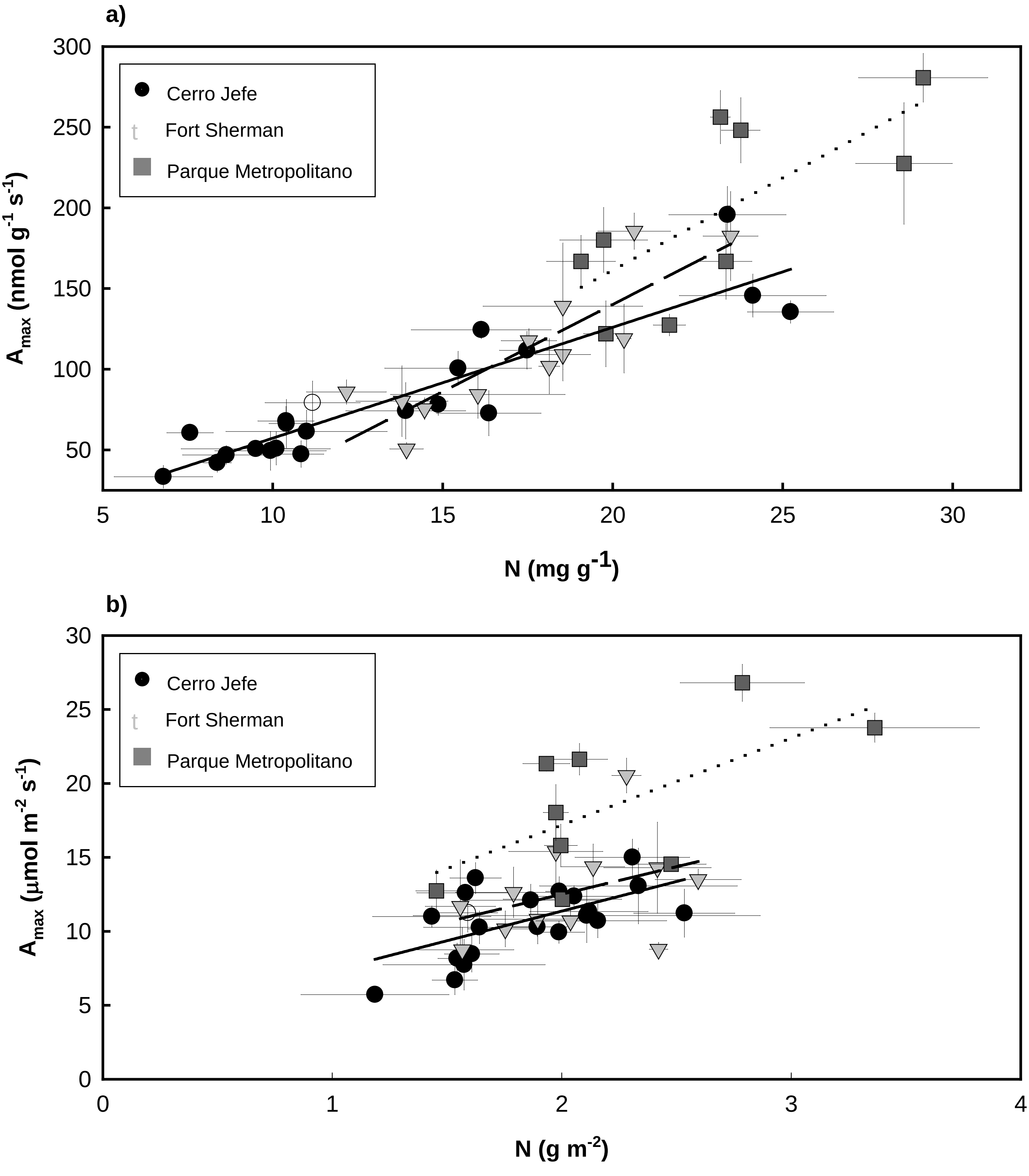

Fig. 1 Photosynthetic capacity (A_{max}) in relation to leaf N content of plant species for each site on a **a)** leaf dry mass basis, and **b)** leaf area basis. Values represent the mean of three replicates ± one SD. Black circles (●) represent Cerro Jefe montane cloud forest, light-gray triangles ( ) Fort Sherman primary lowland forest and dark gray squares (■) Parque Metropolitano secondary lowland forest, Panama. Solid regression lines represent the montane, the short-dashed the primary lowland and the dotted line the secondary lowland forest. Results from correlation analyses are given in Table 2.

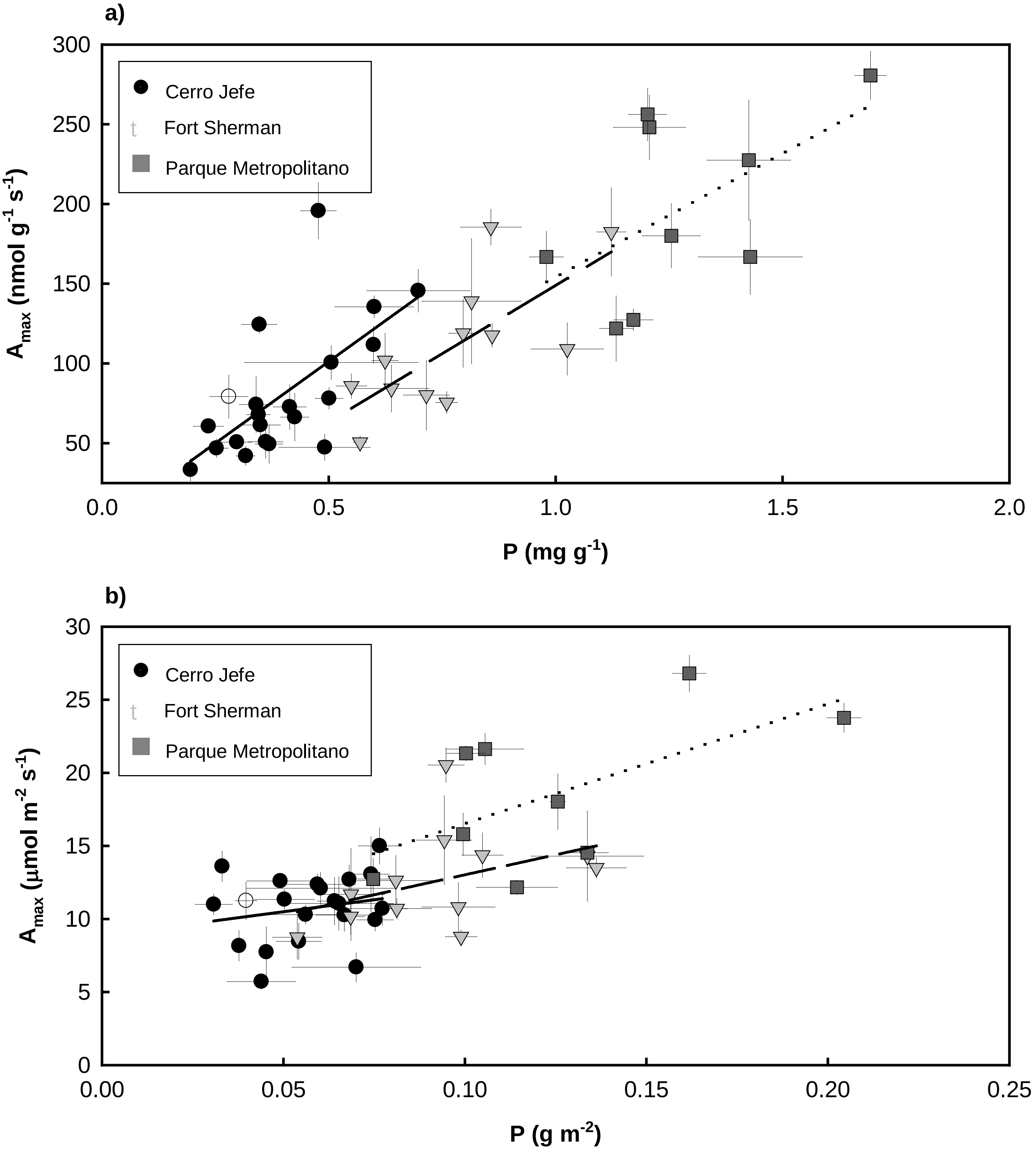

Fig. 2 Photosynthetic capacity (A_{max}) in relation to leaf P content of plant species for each site on a **a)** leaf dry mass basis, and **b)** leaf area basis. Values represent the mean of three replicates ± one SD. Black circles (●) represent Cerro Jefe montane cloud forest, light gray triangles ( ) Fort Sherman primary lowland forest and dark gray squares (■) Parque Metropolitano secondary lowland forest, Panama. Solid regression lines represent the montane, the short dashed the primary lowland and the dotted line the secondary lowland forest. Results from correlation analyses are given in Table 2.

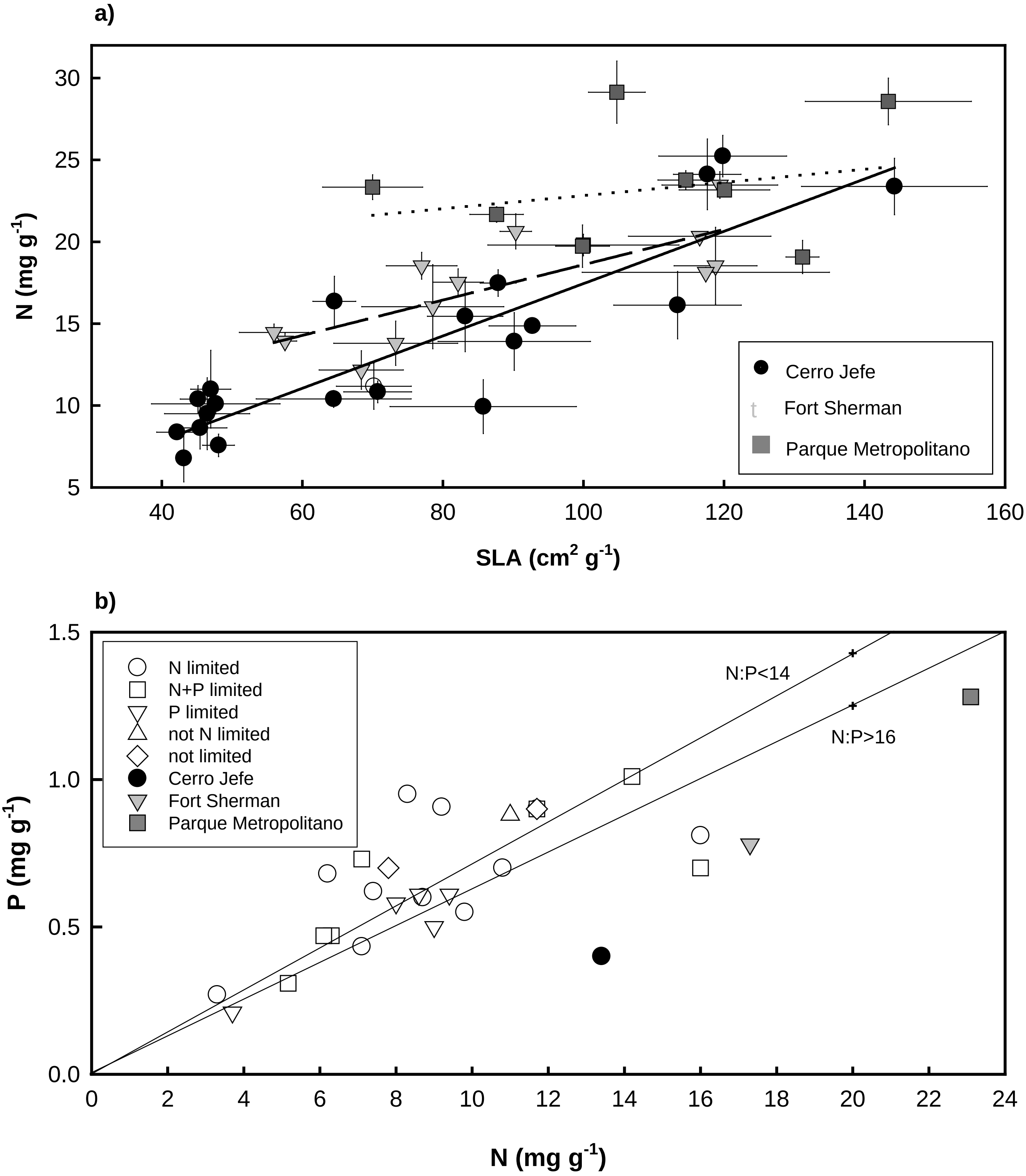

Fig. 3 a) Leaf N content on a leaf dry mass basis in relation to specific leaf area (SLA) for each tropical rainforest site. Values represent the mean of three replicates ± one SD. Black circles (●) represent Cerro Jefe montane cloud forest, light gray triangles ( ) Fort Sherman primary lowland forest and dark gray squares (■) Parque Metropolitano secondary lowland forest, Panama. Solid regression lines represent the montane, the short dashed the primary lowland and the dotted line the secondary lowland forest. Results from correlation analyses are given in Table 2. **b)** leaf N content in relation to leaf P content of sites from this study compared to other tropical sites from different altitudes and nutrient limitations (data extracted from fertilization studies: Cuevas & Medina 1988; Gerrish *et al*. 1988; Vitousek *et al*. 1993; Raich *et al*. 1997; Vitousek & Farrington 1997; Tanner *et al*. 1998; Vitousek 1998; Hobbie & Vitousek 2000; Cordell *et al*. 2001; Ostertag 2001). Lines depict range of N:P ratios between 14 and 16 (adapted from Koerselman & Meuleman 1996) and shows the transition of N limitation (<14) to P limitation (>16) for fertilization experiments in 40 European wetland ecosystems.

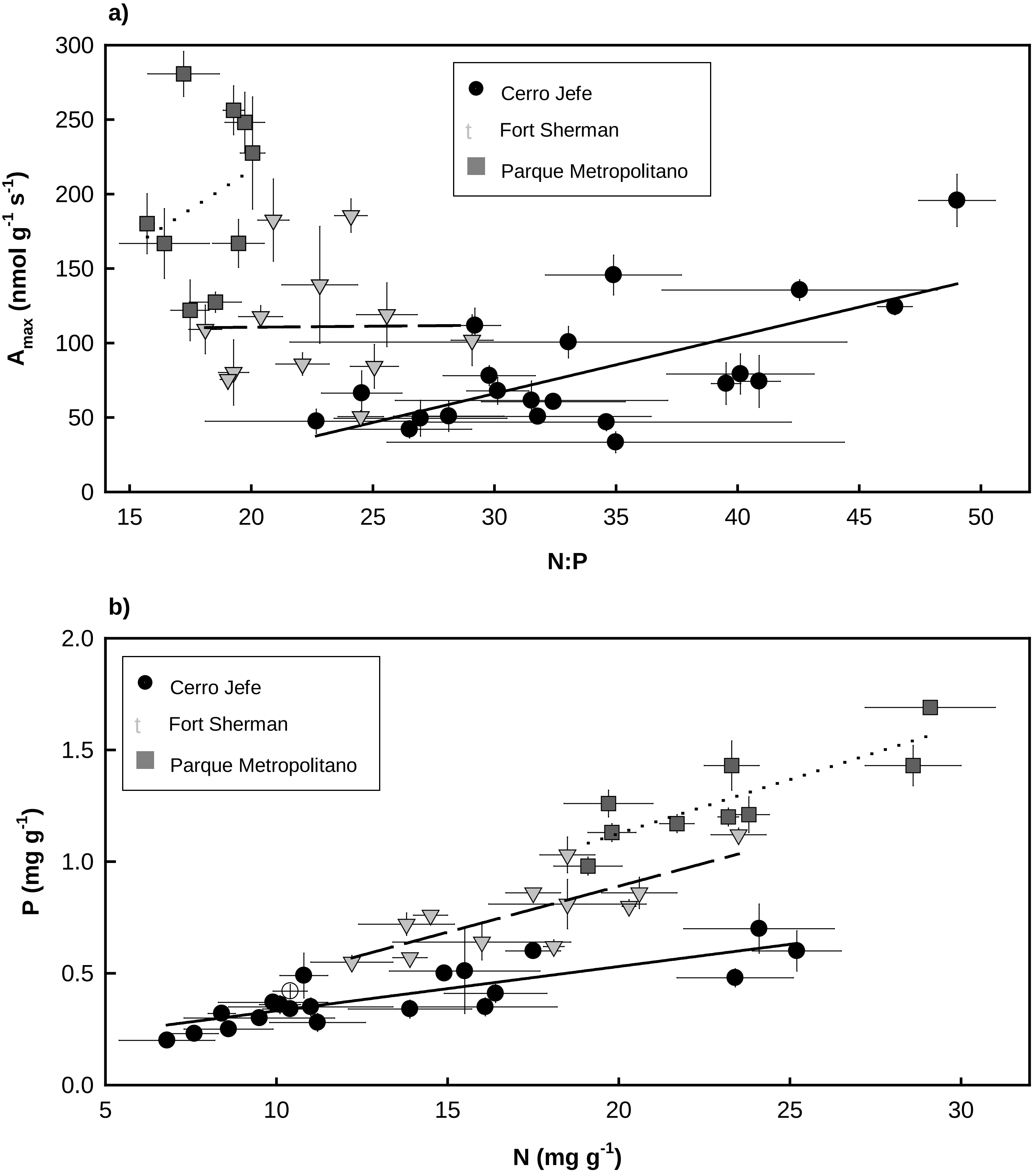

Fig. 4 a) Photosynthetic capacity (A_{max}) on a leaf dry mass basis in relation to leaf N:P ratio, and **b)** leaf P content in relation to leaf N content on a leaf dry mass basis of plant species for each site. Values represent the mean of three replicates ± SD. Black circles (●) represent Cerro Jefe montane cloud forest, light gray triangles ( ) Fort Sherman primary lowland forest and dark gray squares (■) Parque Metropolitano secondary lowland forest, Panama. Solid regression lines represent the montane, the short dashed the primary lowland and the dotted line the secondary lowland forest, Panama. Results from correlation analyses are given in Table 2.

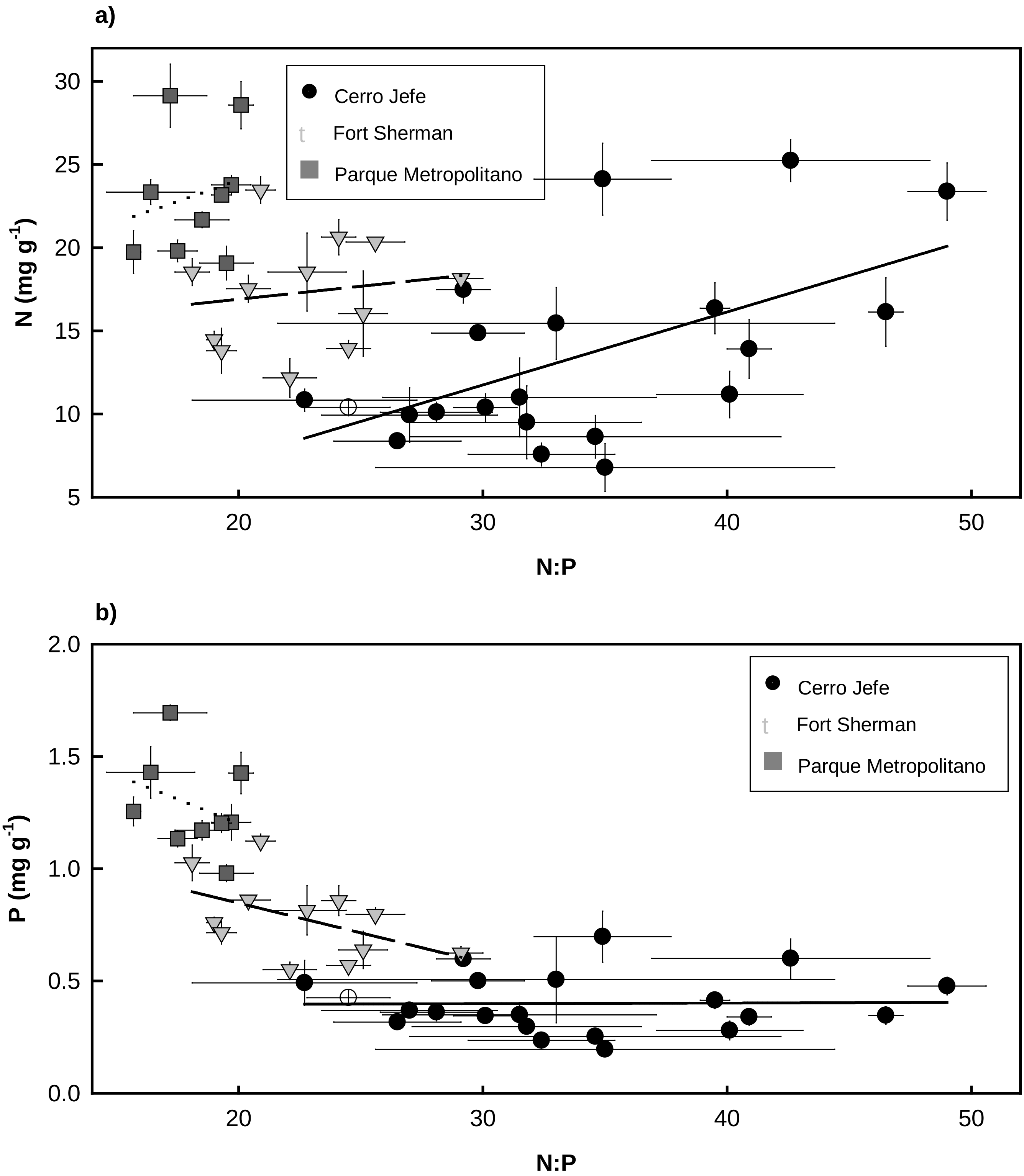

Fig. 5 a) Leaf N of plant species for each site N on a dry mass basis, and **(b)** leaf P contents on a dry mass basis in relation to leaf N:P ratio, respectively. Values represent the mean of three replicates ± one SD. Black circles (●) represent Cerro Jefe montane cloud forest, light gray triangles ( ) Fort Sherman primary lowland forest and dark gray squares (■) Parque Metropolitano secondary lowland forest, Panama. Solid regression lines represent the montane, and the short dashed the lowland forest. Results from correlation analyses are given in Table 2.

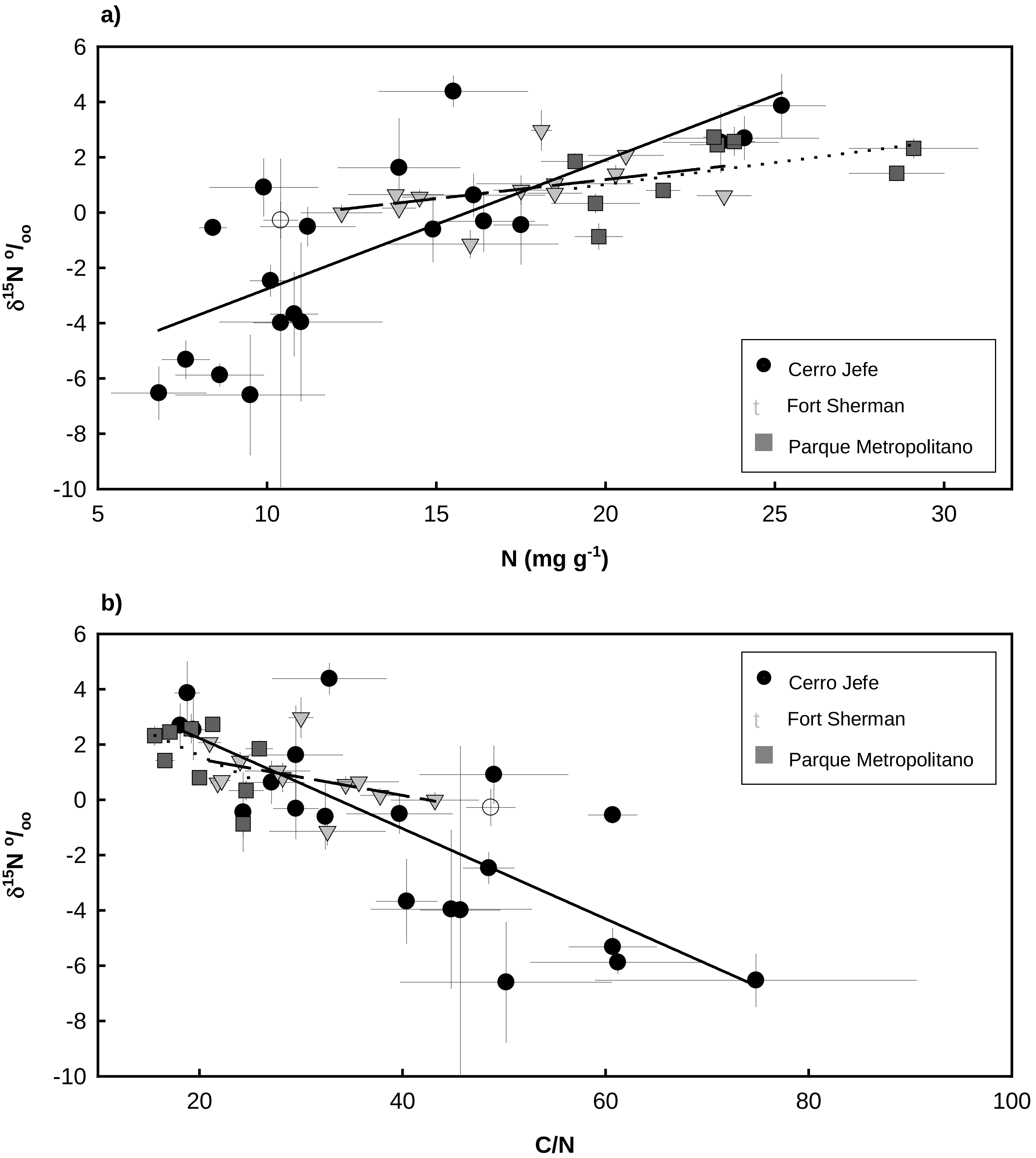

Fig. 6 Leaf $\delta^{15}N$ signature in relation to **a)** leaf N content on a dry mass basis, and **b)** the leaf C/N ratio, of plant species for each site. Values represent the mean of three replicates ± one SD. Black circles (●) represent Cerro Jefe montane cloud forest, light gray triangles ( ) Fort Sherman primary lowland forest and dark gray squares (■) Parque Metropolitano secondary lowland forest, Panama. Solid regression lines represent the montane, and the short dashed the lowland forest. Results from correlation analyses are given in Table 2.

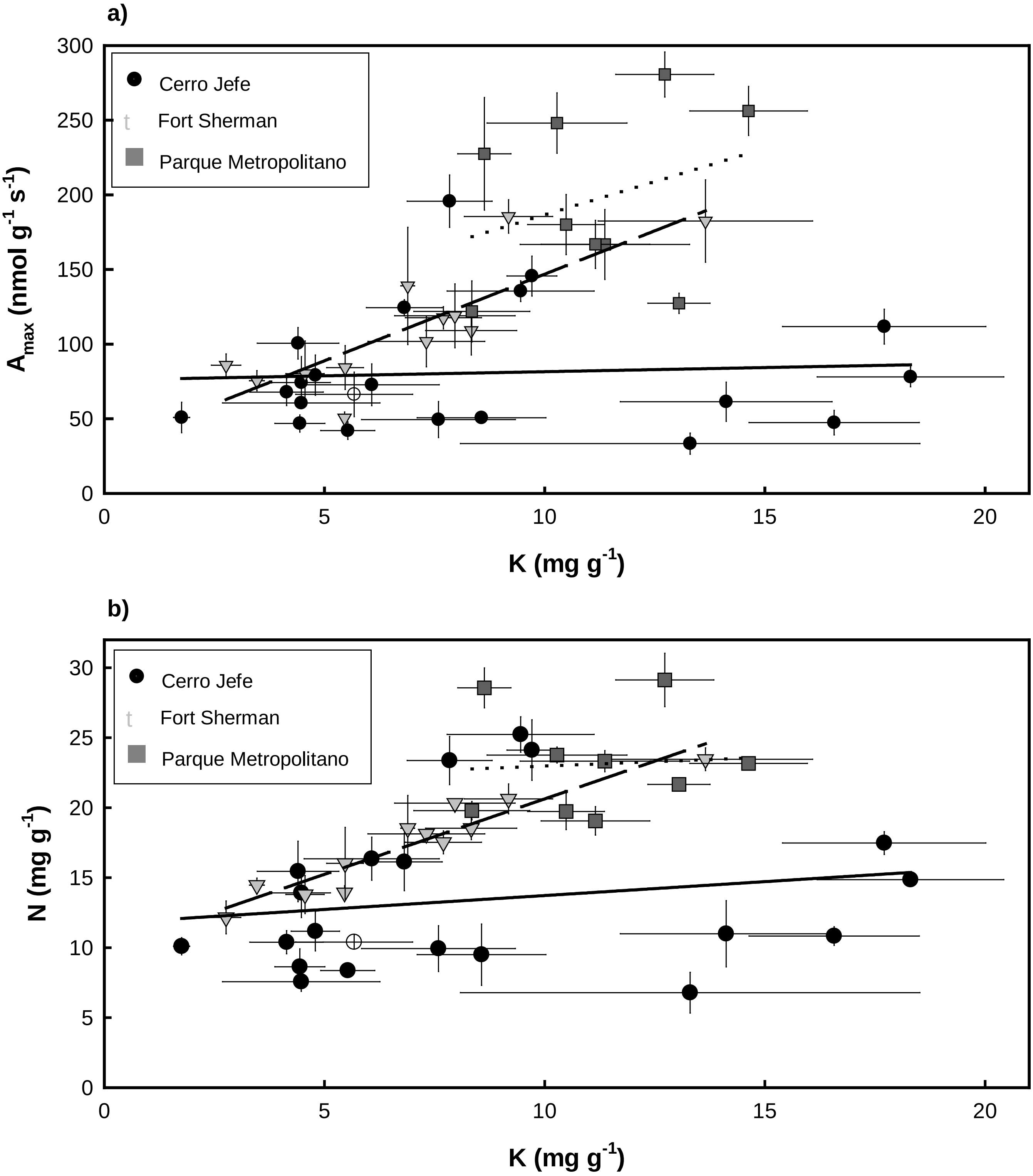

Fig. 7 a) Photosynthetic capacity (A_{max}) on a leaf dry mass basis in relation to leaf K content on a dry mass basis, and **b)** leaf N content in relation to leaf K content on a leaf dry mass basis of plant species for each site. Values represent the mean of three replicates ± SD. Black circles (●) represent Cerro Jefe montane cloud forest, light gray triangles ( ) Fort Sherman primary lowland forest and dark gray squares (■) Parque Metropolitano secondary lowland forest, Panama. Solid regression lines represent the montane, the short dashed the primary lowland and the dotted line the secondary lowland forest, Panama. Results from correlation analyses are given in Table 2.

Table 3 Photosynthetic capacity (A_{max}, in μmol CO_2 m^{-2} s^{-1}), instantaneous photosynthetic nitrogen-use efficiency (PNUE, in μmol CO_2 mol^{-1} N s^{-1}), instantaneous photosynthetic phosphorus-use efficiency (PPUE, in mmol CO_2 mol^{-1} P s^{-1}), specific leaf area (SLA, in m^2 kg^{-1}), $\delta^{13}C$ and $\delta^{15}N$ (in $^{o}/_{oo}$), C/N and N:P are ratios of plant leaves from 3 tropical rainforest sites, Panama. Values are means of three replicates (n=3) ± one standard deviation (SD).

Species	A_{max}	PNUE	PPUE	SLA	$\delta^{13}C$	$\delta^{15}N$	C/N	N:P
Cerro Jefe elfin cloud forest								
Ardisia tysonii	10.3±1.1	89.3±19.7	4.8±0.7	6.4±1.1	-28.5±1.6	-0.28±0.7	48.7±2.4	24.5±1.7
Calophyllum nubicola	9.9±0.7	70.4±8.9	4.1±0.4	4.2±0.3	-28.5±0.8	-0.55±0.3	60.7±2.4	26.5±2.6
Clidemia af. neglecta	13.6±1.0	117.2±1.9	12.7±0.5	14.4±1.3	-28.6±0.5	2.54±1.1	19.4±1.2	49.0±1.6
Clusia coclensis	15.0±1.2	91.8±12.2	6.1±0.6	4.5±0.3	-28.1±1.7	-3.99±5.9	45.7±3.9	30.1±1.3
Clusia salvinii	11.1±1.8	76.9±14.5	5.3±0.5	4.6±0.6	-28.1±0.8	-6.60±2.2	50.2±10.4	31.8±4.7
Colpoth. aphanopetala	5.7±0.5	72.1±25.6	4.2±1.4	8.6±1.3	-26.4±0.7	0.91±1.0	49.0±7.3	27.0±3.6
Cosmibuena valerii	12.6±0.5	113.1±16.5	8.1±1.5	4.8±0.2	-28.5±0.5	-5.32±0.7	60.7±4.3	32.4±3.0
Ericacea species 1	7.7±1.7	68.9±0.2	5.3±1.4	4.3±0.0	-30.8±1.2	-6.53±0.9	74.8±15.8	35.0±9.4
Eugenia cf. octopleura	10.7±1.1	70.3±11.6	4.4±1.1	4.8±0.9	-30.2±0.1	-2.47±0.6	48.5±2.5	28.1±2.3
Guatteria jefensis	11.2±1.6	62.2±9.8	5.4±0.8	6.5±0.3	-30.1±1.3	-0.32±1.1	29.5±2.2	39.5±0.6
Hed. bomplandianum	12.7±1.0	89.4±5.7	5.8±0.5	8.8±0.3	-28.2±0.2	-0.45±1.4	24.3±0.0	29.2±1.1
Lisianthius jefensis	11.3±0.7	75.5±7.5	7.1±1.2	12.0±0.9	-26.9±0.6	3.86±1.1	18.8±1.2	42.6±5.7
Miconia dodecandra	11.0±0.7	109.0±12.8	11.2±1.2	11.3±0.9	-28.0±0.5	0.63±0.8	27.1±3.2	46.5±0.7
Miconia pileata	8.2±1.0	74.1±9.2	6.7±0.9	9.0±1.1	-27.5±0.4	1.62±1.8	29.5±4.6	40.9±0.9
Miconia reduscens	11.3±1.3	98.9±4.7	8.8±0.7	7.0±0.5	-28.3±0.6	-0.51±0.7	39.7±5.2	40.1±3.0
Olyra valerii	12.4±0.7	84.9±8.8	6.6±1.0	11.8±0.5	-26.5±0.4	2.69±0.8	18.1±1.8	34.9±2.8
Phil. cf. panamensis	8.5±1.2	73.5±5.3	4.8±0.4	9.3±0.6	-28.8±0.7	-0.61±1.2	32.4±0.8	29.8±1.9
Schefflera panamensis	13.1±2.6	81.7±27.3	5.5±1.0	4.7±0.3	-28.0±0.3	-3.96±2.9	44.8±7.9	31.5±5.6
Stenosp. robustum	6.7±1.0	61.0±6.6	3.0±0.6	7.1±0.5	-26.3±1.0	-3.67±1.5	40.4±3.0	22.7±4.6
Vaccinium jefense	10.3±0.6	76.2±3.3	5.8±1.1	4.5±0.4	-30.2±0.4	-5.88±0.4	61.2±8.6	34.6±7.6
Vismia jefensis	12.1±1.1	93.3±23.3	6.8±2.4	8.3±0.5	-31.7±0.8	4.38±0.6	32.8±5.6	33.0±11.4
	10.7±2.3[3]	**83.3±16.0**	**6.3±2.3**	**7.5±3.0**	**-28.5±1.4**	**-1.17±3.3**	**40.8±15.8**	**33.8±7.1**
Fort Sherman humid primary lowland forest								
Apeiba membranaceae	15.4±3.0	108.9±16.0	5.0±0.9	11.9±0.8	-28.3±0.5	0.61±0.1	21.8±0.7	20.9±0.6
Brosimum utile	14.4±1.5	94.1±5.9	4.2±0.2	8.2±0.4	-29.6±0.5	0.81±0.5	28.2±1.2	20.4±0.9
Carapa guianensis	13.5±0.7	73.2±6.8	3.1±0.2	5.6±0.5	-29.5±0.4	0.56±0.3	34.4±1.2	19.0±0.3
Clusia rotundata	12.6±1.7	98.9±0.8	4.8±0.2	6.8±0.6	-30.1±0.3	-0.01±0.3	43.2±4.3	22.1±1.1
Cordia bicolor	20.5±1.2	126.0±6.8	6.7±0.5	9.0±0.2	-31.9±0.2	2.07±0.0	21.0±1.1	24.1±0.7
Dendropanax arboreus	10.2±1.2	82.1±15.3	4.6±0.7	11.7±1.0	-31.4±0.2	1.40±0.3	24.0±0.5	25.6±1.2
Manilkara bidentata	8.8±0.5	50.8±3.1	2.8±.3	5.8±0.2	-27.9±0.1	0.16±0.2	37.8±1.9	24.5±0.9
Marila laxiflora	11.7±3.1	103.9±19.6	5.2±0.8	11.9±0.6	-28.9±0.1	1.04±0.2	27.7±3.2	22.8±1.6
Ocotea ira	10.7±0.7	74.0±9.3	4.1±0.4	7.9±1.0	-31.9±0.5	-1.14±0.5	32.6±5.7	25.1±1.0
Poulsenia armata	14.3±3.1	82.3±9.5	3.3±0.3	7.7±0.5	-27.5±0.6	0.70±0.1	22.2±0.8	18.1±0.7
Tapirira guianensis	10.8±1.7	81.1±17.6	3.5±0.8	7.3±0.9	-29.9±0.2	0.65±0.1	35.7±3.9	19.3±0.6
Virola elongata	8.8±1.5	78.7±13.4	5.1±0.9	11.7±1.8	-32.5±0.3	2.97±0.7	30.0±1.2	29.1±0.9
	12.6±3.3	**87.8±19.8**	**4.4±1.1**	**8.8±2.4**	**-29.9±1.7**	**0.82±1.0**	**29.9±7.1**	**23.4±3.2**
Parque Metropolitano seasonally dry secondary lowland forest								
Annona spraguei	15.8±1.4	111.2±13.9	4.9±0.5	14.3±1.2	-28.2±0.2	1.42±0.2	16.6±0.9	20.1±0.5
Castilla elastica	14.5±0.3	82.4±5.6	3.4±0.2	8.8±0.4	-28.7±0.3	0.80±0.2	20.0±0.4	18.5±1.1
Cecropia longipes	26.8±1.3	135.6±16.2	5.1±0.2	10.5±0.4	-27.8±0.2	2.32±0.3	15.6±0.7	17.2±1.5
Cecropia obtusifolia	21.6±1.1	146.4±14.8	6.4±0.9	11.5±0.4	-28.4±0.6	2.57±0.5	19.2±0.9	19.7±0.8
Ficus insipida	23.8±1.0	100.5±16.9	3.6±0.2	7.0±0.7	-27.5±0.6	2.45±0.0	17.1±0.5	16.4±1.8
Luehea seemannii	12.2±0.5	86.3±14.3	3.3±0.4	10.0±1.4	-29.1±0.9	-0.87±0.5	24.3±0.6	17.5±0.8
Antirhea trichanta	12.7±1.4	122.4±6.4	5.3±0.4	13.1±0.2	-30.5±0.4	1.85±0.3	25.9±1.3	19.5±1.1
Pseudob. septenatum	18.0±1.9	128.0±14.0	4.5±0.5	10.0±0.4	-28.3±0.3	0.33±0.3	24.6±1.7	15.7±0.3
Schefflera morototoni	21.3±0.5	154.9±9.1	6.6±0.3	12.0±0.6	-28.7±0.2	2.73±0.1	21.3±0.4	19.3±0.4
	18.5±5.1	**118.6±25.6**	**4.8±1.2**	**10.8±2.2**	**-28.6±0.9**	**1.51±1.2**	**20.5±3.8**	**18.2±1.6**

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[3] Values in bold are means ± SD for each habitat, respectively.

Table 4 Mineral content of plant leaves from three distinct tropical forest habitats, Panama. Values are given in mg g^{-1} leaf dry mass and represent means of three replicates (n=3) ± one standard deviation (SD).

Species	Mineral content (mg g^{-1})											
	N	P	S	K	Na	Ca	B	Zn	Mn	Fe	Mg	Al
Cerro Jefe elfin cloud forest												
Ard. tysonii	10.4±0.5	0.42±0.0	2.3±0.2	5.7±1.3	5.49±2.1	4.6±1.3	0.01±0.0	0.01±0.0	0.05±0.0	0.14±0.0	2.22±0.1	0.19±0.1
Cal. nubicola	8.4±0.4	0.32±0.0	1.2±0.1	3.5±3.0	1.67±0.5	3.7±1.4	0.01±0.0	0.01±0.0	0.02±0.0	0.06±0.0	1.06±0.1	0.08±0.0
Cli. af. *neglecta*	23.4±1.7	0.48±0.0	1.7±0.1	7.8±1.0	0.54±0.2	5.9±0.8	0.02±0.0	0.02±0.0	2.55±0.5	0.35±0.1	0.82±0.3	8.06±0.5
Clu. coclensis	10.4±0.8	0.34±0.0	1.4±0.5	4.1±0.8	1.60±0.6	13.0±2.1	0.03±0.0	0.01±0.0	1.42±0.3	0.08±0.0	1.32±0.3	0.08±0.0
Clu. salvinii	9.5±2.2	0.30±0.0	2.1±0.3	8.6±1.5	0.37±0.3	14.3±2.7	0.02±0.0	0.03±0.0	1.73±0.6	0.13±0.0	1.40±0.4	0.10±0.0
Col. aphanopetala	9.9±1.6	0.37±0.0	1.2±0.1	7.6±1.7	0.28±0.0	0.4±0.1	0.01±0.0	0.01±0.0	0.13±0.0	0.23±0.2	0.52±0.1	0.21±0.2
Cos. valerii	7.6±0.7	0.23±0.0	1.6±0.8	4.5±1.8	3.93±1.2	15.7±5.0	0.02±0.0	0.01±0.0	0.07±0.1	0.06±0.0	7.03±1.6	0.09±0.0
Ericacea sp. 1	6.8±1.4	0.20±0.0	1.6±1.0	13.3±5.2	0.23±0.1	6.8±4.4	0.03±0.0	0.02±0.0	0.82±0.6	0.04±0.0	2.85±1.5	0.10±0.0
Eug. cf. *octopleura*	10.1±0.6	0.36±0.0	1.2±0.1	1.8±0.2	3.42±3.4	3.6±0.7	0.01±0.0	0.01±0.0	0.07±0.0	0.16±0.2	3.18±0.8	1.33±0.1
Gua. jefensis	16.4±1.5	0.41±0.0	2.5±0.2	6.1±1.5	0.81±0.3	5.4±0.6	0.04±0.0	0.01±0.0	0.10±0.0	0.09±0.0	1.64±0.4	0.11±0.0
Hed. bompland.	17.5±0.8	0.60±0.0	8.3±1.4	17.7±2.3	1.50±0.9	13.1±2.0	0.02±0.0	0.02±0.0	0.85±0.5	0.30±0.3	3.98±0.4	0.20±0.1
Lis. jefensis	25.2±1.3	0.60±0.1	2.2±0.2	9.5±1.7	4.84±1.4	1.6±0.3	0.02±0.0	0.04±0.0	0.86±0.2	0.15±0.0	2.80±0.3	0.15±0.0
Mic. dodecandra	16.1±2.1	0.35±0.0	5.3±0.8	6.8±0.9	1.30±0.3	16.0±1.3	0.02±0.0	0.01±0.0	0.23±0.0	0.17±0.0	0.82±0.1	7.08±2.5
Mic. pileata	13.9±1.8	0.34±0.0	7.4±1.8	4.5±0.7	1.32±0.3	18.5±5.6	0.03±0.0	0.04±0.0	0.04±0.0	0.14±0.0	2.25±0.3	11.83±2.6
Mic. reduscens	11.2±1.4	0.28±0.0	2.7±0.2	4.8±0.5	2.02±0.9	6.5±1.1	0.04±0.0	0.01±0.0	0.04±0.0	0.10±0.0	1.85±0.3	1.38±1.2
Oly. valerii	24.1±2.2	0.70±0.1	3.1±0.4	9.7±0.6	0.11±0.1	0.7±0.1	0.00±0.0	0.03±0.0	0.72±0.2	0.21±0.0	1.08±0.1	0.15±0.0
Phi. cf. panam.	14.9±0.2	0.50±0.0	3.8±0.6	18.3±2.1	0.07±0.0	10.0±1.7	0.03±0.0	0.05±0.0	0.47±0.0	0.09±0.0	1.34±0.5	0.11±0.1
Sch. panamensis	11.0±2.4	0.35±0.0	1.5±0.4	14.1±2.4	0.19±0.1	5.9±2.2	0.02±0.0	0.02±0.0	0.49±0.1	0.06±0.0	2.56±0.5	0.07±0.0
Ste. robustum	11.0±0.7	0.49±0.1	2.2±0.7	16.6±1.9	0.55±0.6	22.4±2.7	0.01±0.0	0.06±0.0	0.21±0.1	0.09±0.0	3.03±0.7	0.10±0.1
Vac. jefense	8.6±1.3	0.25±0.0	1.2±0.0	4.4±0.6	0.61±0.2	8.4±1.7	0.03±0.0	0.02±0.0	0.30±0.1	0.13±0.0	2.48±0.5	0.24±0.0
Vis. jefensis	15.5±2.2	0.51±0.2	1.3±0.3	4.4±0.9	0.82±0.3	5.6±1.3	0.02±0.0	0.02±0.0	0.75±0.2	0.11±0.0	0.62±0.3	0.13±0.0
	13.4±5.4[1]	**0.40±0.1**	**2.7±2.0**	**8.3±4.9**	**1.51±1.6**	**8.7±6.1**	**0.02±0.0**	**0.02±0.0**	**0.57±0.7**	**0.14±0.1**	**2.14±1.5**	**1.51±3.2**
Fort Sherman humid primary lowland forest												
Ape. membran.	23.5±0.8	1.12±0.0	2.6±0.1	13.7±2.4	0.79±0.1	13.4±2.2	0.05±0.0	0.04±0.0	0.02±0.0	0.09±0.0	3.23±0.1	0.08±0.0
Bro. utile	17.5±0.8	0.86±0.0	1.0±0.0	7.7±0.9	1.68±0.4	4.4±0.0	0.04±0.0	0.03±0.0	0.02±0.0	0.05±0.0	1.84±0.2	0.04±0.0
Car. guianensis	14.5±0.5	0.76±0.0	3.3±0.2	3.5±0.2	0.16±0.1	10.0±0.9	0.04±0.0	0.10±0.0	0.03±0.0	0.07±0.0	1.67±0.2	0.07±0.0
Clu. rotundata	12.2±1.2	0.55±0.0	1.3±0.2	2.8±0.3	2.40±2.1	5.7±0.5	0.03±0.0	0.07±0.0	0.39±0.0	0.04±0.0	1.05±0.1	0.03±0.0
Cor. bicolor	20.6±1.1	0.86±0.1	1.8±0.2	9.2±1.0	0.29±0.0	9.2±1.6	0.06±0.0	0.07±0.0	0.14±0.0	0.11±0.0	3.63±0.4	0.14±0.0
Den. arboreus	20.3±0.2	0.80±0.0	4.1±0.3	8.0±1.4	3.83±0.2	13.3±0.4	0.08±0.0	0.17±0.0	0.44±0.0	0.11±0.0	3.37±0.6	0.15±0.0
Man. bidentata	13.9±0.5	0.57±0.0	2.9±0.1	5.5±0.0	1.14±0.1	6.0±0.9	0.06±0.0	0.05±0.0	0.01±0.0	0.09±0.0	1.90±0.3	0.07±0.0
Mar. laxiflora	18.5±2.3	0.81±0.1	3.5±0.7	6.9±0.2	0.11±0.0	5.2±0.0	0.06±0.0	0.05±0.0	0.26±0.0	0.09±0.0	0.93±0.2	0.07±0.0
Oco. ira	16.0±2.6	0.64±0.1	1.3±0.1	5.5±0.4	0.51±0.0	7.5±1.0	0.02±0.0	0.14±0.0	0.05±0.0	0.06±0.0	1.00±0.2	0.16±0.0
Pou. armata	18.5±0.8	1.03±0.1	2.0±0.4	8.3±1.0	0.40±0.1	18.3±1.1	0.09±0.0	0.04±0.0	0.03±0.0	0.08±0.0	2.49±0.6	0.09±0.1
Tap. guianensis	13.8±1.4	0.72±0.0	2.0±0.3	4.6±0.4	0.22±0.1	12.7±2.1	0.05±0.0	0.01±0.0	0.03±0.0	0.04±0.0	1.83±0.5	0.02±0.0
Vir. elongata	18.1±0.3	0.62±0.0	4.7±0.8	7.3±1.3	0.80±0.3	6.0±0.6	0.04±0.0	0.08±0.0	0.31±0.0	0.11±0.0	3.01±0.6	0.10±0.0
	17.3±3.3	**0.78±0.2**	**2.5±1.2**	**6.9±2.9**	**1.03±1.1**	**9.3±4.3**	**0.05±0.0**	**0.07±0.0**	**0.15±0.2**	**0.08±0.0**	**2.16±1.0**	**0.08±0.0**
Parque Metropolitano sesonal dry secondary lowland forest												
Ann. spraguei	28.6±1.4	1.43±0.1	2.6±0.3	8.6±0.6	0.05±0.0	13.8±0.5	0.05±0.0	0.02±0.0	0.05±0.0	0.25±0.2	0.51±0.9	0.06±0.0
Cas. elastica	21.7±0.5	1.17±0.0	2.1±0.2	13.1±0.7	0.11±0.0	15.6±1.8	0.07±0.0	0.35±0.2	0.03±0.0	0.11±0.0	3.48±0.8	0.07±0.0
Cec. longipes	29.1±1.9	1.69±0.0	2.0±0.0	12.7±1.1	0.06±0.0	23.1±3.1	0.04±0.0	0.15±0.1	0.02±0.0	0.07±0.0	4.28±0.5	0.03±0.0
Cec. obtusifolia	23.8±0.6	1.21±0.1	1.7±0.1	10.3±1.6	0.14±0.0	11.3±1.8	0.02±0.0	0.34±0.5	0.03±0.0	0.10±0.0	3.24±0.5	0.08±0.1
Fic. insipida	23.3±0.8	1.43±0.1	1.5±0.1	11.4±1.9	0.17±0.1	23.0±6.4	0.04±0.0	0.02±0.0	0.06±0.0	0.06±0.0	4.37±0.5	0.09±0.0
Lue. seemannii	19.8±0.7	1.13±0.0	1.3±0.0	8.3±1.3	0.14±0.0	13.3±1.2	0.05±0.0	0.03±0.0	0.14±0.0	0.09±0.0	2.99±0.2	0.05±0.0
Ant. trichanta	19.1±1.0	0.98±0.0	2.1±0.3	11.2±1.2	0.22±0.1	8.4±2.5	0.10±0.0	0.02±0.0	0.02±0.0	0.29±0.0	3.81±1.1	0.11±0.0
Pse. septenatum	19.7±1.3	1.26±0.1	1.8±0.0	10.5±0.9	0.08±0.0	11.3±1.3	0.04±0.0	0.07±0.1	0.02±0.0	0.14±0.0	1.88±0.4	0.04±0.0
Sch. morototoni	23.2±0.3	1.20±0.0	3.2±0.4	14.6±1.3	0.05±0.0	6.0±1.2	0.04±0.0	0.12±0.0	0.05±0.0	0.07±0.0	2.60±0.2	0.06±0.0
	23.1±3.7	**1.28±0.2**	**2.0±0.6**	**11.2±2.1**	**0.12±0.1**	**14.0±5.9**	**0.05±0.0**	**0.12±0.1**	**0.05±0.0**	**0.13±0.1**	**3.02±1.2**	**0.06±0.0**

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[1] Values in bold are means ± SD for each habitat, respectively.

2.5 Discussion

As demonstrated for other tropical ecosystems (Reich & Schoettle, 1988; Reich *et al.*, 1991, 1992, 1994; Reich & Walters, 1994; Reich *et al.*, 1995; Ellsworth & Reich, 1996; Reich *et al.*, 1998) photosynthetic capacity correlates best with N and SLA on a mass basis (A_{mass}), especially when N is limiting (Reich *et al.*, 1994). Reich & Walters (1994) concluded, that A_{mass} is a direct and metabolic function of N on a mass basis and the correlation can be used for comparisons of photosynthetic capacity and nutrient relationships (Reich *et al.*, 1998). Species with higher SLA had a higher photosynthetic capacity per unit leaf N and also varied more in photosynthetic capacities per unit variation in N than those with lower SLA (Uhl, 1987; Medina & Cuevas, 1990; Reich *et al.*, 1998). A joint consideration of SLA and N enables better modelling of photosynthetic capacities, and the relationship with N would be identical on mass and area bases if there was no variation in SLA associated with variation in leaf N (Fig.3). However, SLA tends to increase with increasing N on a mass basis (Reich & Walters, 1994; Reich *et al.*, 1998). Similar correlations have been also described for A_{max} vs. P and implications about limitation of photosynthetic capacity through N and/or P have been derived from strength of such correlations (Reich & Schoettle, 1988; Reich *et al.*, 1994). However, A_{max}-N relationships appear dependent on leaf structure and/or other species-level traits, that may be partially independent of nutrient availability or leaf nutrient concentration (Reich *et al.*, 1994). The nexus of A_{max}-N relationships and genetically determined species specific nutrient-use efficiency have been drawn before.

Field & Mooney (1986) proposed the PNUE as an index of potential performance under defined conditions that allows more simply and direct comparison among species and communities, than A_{max}-N relationships. When plant communities are compared, trends show that Cerro Jefe plants were able to photosynthesize at lower leaf N concentrations (Fig.1a), with the trade-off of being less N-use efficient (Table 3) and, thus, having lower growth rates. Plants from the secondary lowland site had less ability to use N at low foliar concentrations, but exhibited higher potential photosynthetic N-use efficiencies (Reich *et al.*, 1994), whereas the primary lowland plants showed a better efficiency for photosynthesis at lower N concentrations compared to the secondary forest plants (Fig.1a). Field & Mooney (1986) showed that the potential photosynthetic nutrient-use efficiency increases with photosynthetic capacity and leaf N content. PNUE was highest for disturbed secondary forest plants and lowest for primary montane vegetation (Table 3) (see also Ellsworth & Reich, 1996). This may allow greater competitive ability in response to light in secondary forest sites. On the other hand, the Cerro Jefe plants had a lower photosynthetic N-use efficiency and probably little competition for light at this site, because of the relatively open vegetation. Furthermore, N availability was low, as suggested by low extractable mineral N content of soil (data not shown), probably due to low N turnover rates. However, in the long term increased leaf longevity will result in a higher integrated N-use efficiency over the whole leaf lifetime (Reich *et al*., 1995). Concomitantly, more carbon based structures are used to reinforce leaves, diminishing herbivory or other threats (e.g. low C/N and SLA, Table 3), as discussed by Reich *et al.* (1991). In contrast, despite low leaf P contents, photosynthetic P-use efficiency (PPUE) was highest at the Cerro Jefe site (Table 3), and there was little increase of leaf P with higher N content (Fig.4b), suggesting that P content in leaves is available in sufficient amounts for photosynthesis. Hence, photosynthetic nutrient-use efficiencies seem to be inconsistent parameters in ecosystematical nutrient limitation discussions.

To date, the occurrence of N or P limitation or N-P colimitation can conclusively be demonstrated only by long-term and large scale fertilization experiments (Tanner *et al*., 1998). By such studies it was shown that a correlation between the content of a specific nutrient and plant performance (e.g. growth rate) may not indicate growth limitation by this nutrients (e.g. Treseder & Vitousek, 2001). Often concentrations of different nutrients are correlated with each other (e.g. N and P, Fig.4b) hampering the conclusion that those plants are limited by the one or the other mineral. In contrast, N:P ratios were demonstrated to more closely reflect N or P limitation of plant growth, as described for 40 studies conducted in European wetland ecosystems (Koerselman & Meuleman, 1996). Leaf P was plotted against the leaf N contents and nutrient limitation on plant community levels was determined by fertilization experiments. The authors of the above mentioned study convincingly demonstrated that the N:P ratio rather than the absolute nutrient concentration controlled plant growth (see also Aerts & Chapin, 2000). N:P ratios of European wetlands plants with either N limitation were <14 and with P limitation were >16 (Aerts & Chapin, 2000), but apparently this N:P cut-off around 14 to 16 can not be applied to tropical forest sites (Fig.3b). N:P data from montane sites in Puerto Rico, Hawaii and Jamaica (15-25, 15-18 and 18-21, respectively) were in a higher range with extreme values reaching 40 at a site in New Guinea (calculated from data in Tanner *et al.*, 1998). These values would indicate P limitation, which is rather a rare improbable situation for montane rainforests (Grubb, 1995; Tanner *et al.*, 1998). Montane forests occur, as a rule, on younger substrates and such sites are, according to the biogeochemical theory, generally N limited (Vitousek & Farrington, 1997). Furthermore, no general relationship of nutrient limitation within the above mentioned N:P ratio range or another range for data from several fertilization studies of tropical sites all over the world could be found (Fig.3b). Additionally, we plotted N:P ratios against altitude from several tropical sites again obtaining no significant correlation (r^2=0.03 and *P*=0.141). Some studies stated, that foliar N and P content decreased with altitude (summarized in Tanner *et al*., 1998), apparently at similar proportions. When compared with the two lowland sites, the montane site at Cerro Jefe had higher N:P ratios (see Table 3) implying that leaf P content was proportionally lower than leaf N content. Furthermore, N:P ratios would propose a pronounced P limitation of the montane site and a more N limited situation for the lowland sites, what again would be the contrary of what is so far suggested in the literature.

Here we reconsider the suitability of relationships between photosynthetic capacity with nutrient contents and nutrient ratios to give evidence for nutrient limitation of plant growth. Photosynthetic capacity at the montane site was significantly positively correlated with N:P ratios, and foliar N contents increased with increasing N:P ratios (Fig. 4a, 5a). Phosphorus was not correlated with N:P and did not change with increasing N:P ratios (Fig.5b), thus, we suggest N as the major limiting nutrient restricting photosynthesis at Cerro Jefe. Despite significant relations of A_{max} with N and P content, N:P ratios did not significantly correlate with photosynthetic capacity at the lowland sites, implying that other parameters than the N:P balance control photosynthesis at these two sites. There was an indication of photosynthetic capacity at the Parque Metropolitano site being influenced by foliar N and P contents (Fig.1a,2a), but the insignificant correlation with N:P ratios does not allow a firm conclusion on the N or/and P limiting situation at this site. The N:P ratios had no effect on the photosynthetic capacity of the Fort Sherman plants (Fig.4a), which may be the result of a reciprocal effect of N and P (Fig.4b;5a,b) or/and other parameters could be limiting photosynthetic capacity more strongly (Reich *et al*., 1994).

Leaf K was solely significant positively correlated with photosynthetic capacity (Fig.7a) and N content (Fig.7b) at the Fort Sherman site. The measured leaf K contents were in a range of for various crop plants deficient concentrations (deficient <4-14, adequate 7-35 mg g^{-1}, in Chapin & Van Cleve, 1989), thus, suggesting to be co-limiting photosynthetic capacity at this primary lowland site (Table 4).

All other leaf nutrients measured did not show significant correlations with the parameters analysed (data not shown), therefore these macro- and micronutrients probably do not have a limiting effect on photosynthesis and primary production at the three study sites (see also Reich & Schoettle, 1988).

Generally, nutrient supply and limitation may be potentially reflected in leaf carbon and N isotope discrimination. Nitrogen limitation and subsequently, lower photosynthesis and growth rates (e.g. montane plants) lead to a higher discrimination of $^{13}CO_2$ through Rubisco, due to lower CO_2 turnover rates and therefore higher p_i/p_a (intercellular/ambient partial pressure of CO_2) (Sparks & Ehleringer, 1997). Contradictory, plants from higher altitude show a decrease in the p_i/p_a, due to decreasing atmospheric CO_2 concentrations, which results in more positive $\delta^{13}C$ values of leaves (Körner *et al*., 1988, 1991; Cavelier, 1996). These opposing effects could be a possible explanation for the not significant differences in $\delta^{13}C$ values of the three forest stands

(Table 3). Additionally, other effects such as differences in leaf intrinsic water-use efficiency (Guehl *et al*., 1998) could be masking the elevation effect.

Trends in leaf $\delta^{15}N$ values between montane and lowland sites (Table 3) may be explained by the greater age of lowland forests ecosystems (Kitayama & Iwamoto, 2001), resulting in an increased cumulative loss of ^{15}N depleted N through gaseous emissions from high nitrification and denitrification activities, nitrate leaching and ammonia volatilization (e.g. Handley *et al*., 1999; Martinelli *et al*., 1999). A similar phenomenon was observed for forest sites of different substrate age in Hawai (Vitousek *et al*., 1989). Furthermore, nitrogen isotopic differences between montane and lowland forests will be enhanced as N enriched sites and sites with higher N availability are characterized by a faster and more open N cycling (e.g. secondary lowland forest), while N poorer sites exibit tight N cycling (e.g. N limited montane sites) (Handley *et al*., 1999; Martinelli *et al*., 1999; Kitayama & Iwamoto, 2001). Slightly higher $\delta^{15}N$ values from the drier secondary lowland site compared to the primary forest could be a consequence of disturbance and thus, the resulting acceleration of N cycling, transformation and soil organic matter turnover (Austin & Vitousek, 1998; Handley *et al*., 1999). This is further corroborated by data from Kitayama & Iwamoto (2001) showing an enrichment of ^{15}N with increasing organic-matter decomposition, and a decrease of $\delta^{15}N$ with increasing C/N ratio in soil and litter. The here presented data do not differ significantly between sites but trends suggest that organic matter decomposition is lower for the Cerro Jefe site compared to the two lowland forests investigated (Fig.6b). As reported for the Mount Kinabalu, Borneo (Kitayama & Iwamoto, 2001), the N poor site of Cerro Jefe showed a significant positive correlation of foliar $\delta^{15}N$ and leaf N. The large range of N contents in leaves at the montane site (Fig.6a) may be a result of the ability of plants from different life-forms and mycorrhizal types in accessing different soil N pools, which may be isotopically different (Kitayama & Iwamoto, 2001). Such isotopic and concentration differences between plant species seem to be more evident under N poor than N rich conditions. Hence, N limitation in ecosystems is evidently reflected in more negative plant $\delta^{15}N$ values (Martinelli *et al*., 1999) further supporting our conclusion from N:P-A_{max} considerations.

In conclusion, N is the major limiting nutrient for photosynthesis in the upper montane site; K seems to play a limiting role for photosynthetic capacity at the primary lowland forest site, thus this relations have to be considered carefully. Limitation of photosynthetic capacity in plants should be discussed on plant nutrient ratios and not only on correlation of photosynthesis with single leaf nutrient contents. Altitudinal differences in plant nutrition and production were also reflected by the stable isotope ratio of N, but not of carbon, in leaf tissue.

3. The carbon and nitrogen dynamics of three tropical montane tree species during leaf ontogeny

3.1 Introduction

Despite existent approaches to avoid time consuming gas exchange measurements in order to obtain carbon gain of plants (Zotz and Winter 1993, 1994c), it is necessary to consider the effect of leaf age on photosynthetic capacity in order to better estimate the long term carbon budget of a leaf and of the whole canopy (Zotz and Winter 1994a, Kitajima et al. 1997a).

Photosynthetic rates generally exhibit a decline with progressing leaf age (Kitajima et al. 1997a). This is due to retranslocation of resources from older to younger leaves thereby optimizing photosynthetic capacity (Field and Mooney 1983). In tropical plants it has been observed that leaf nitrogen concentrations decline linearly along with photosynthetic capacity and leaf age (Zotz and Winter 1994a, Ackerly and Bazzaz 1995, Kitajima et al. 1997a). Hiremath (2000) reported that potential photosynthetic N-use efficiency (maximum potential photosynthesis/leaf N content) decreased with increasing leaf life span, whereas cumulative photosynthetic N-use efficiency (carbon assimilated over a leaf's life span/total N invested in a leaf) increased with increasing leaf life span. In seasonal tropical forests climatic factors also play an important role in carbon balance of plants. A reduction of photosynthetic capacity due to drought was shown (Mulkey and Wright 1996), but also an increase of photosynthetic rates due to less clouds and thus higher light levels during dry periods was reported (Zotz and Winter 1994b, Kitajima et al. 1997b).

Annual and leaf lifetime carbon balances can only be fully understood when seasonal and ontogenetic changes in morphological and physiological characteristics are observed on a long-term basis, assessing photosynthetic and mineral-nutrient relationships. Thus, this approach requires extensive study periods and often challenges man and machine. Moreover, attempts were undertaken to predict annual carbon balance from more easily obtainable parameters. A close relationship between maximum rates of net CO_2 uptake and diel carbon gain was found for eight lowland rain forest species on Barro Colorado Island, Panama. This dependency has to be tested on more species of different habitats and could be used in the future to avoid time-consuming determinations of complete diel cycles of net CO_2 exchange (Zotz and Winter 1993). There is also limited evidence, that annual leaf-carbon budgets can be estimated by analysing leaf nitrogen at regular intervals, as it was done for 4 different tropical plant species of different lifeforms (Zotz and Winter 1994c). Again this linear correlation has to be tested on additional species to determine if the practical implications of this relationship may prove to be of value for scaling carbon gain from individual leaves to plants and whole ecosystems.

Tropical montane forest ecosystems are known to be of smaller stature and lower productivity than comparable surrounding lowland forests. This was shown by different studies on demographic, dendrologic and ecosystem level (Weaver et al. 1986, Weaver and Murphy 1990, Weaver 1995). Other studies investigated the effect of soil nutrient availability on trunk increment and litterfall (Tanner et al. 1992, Tanner et al. 1998). These have demonstrated that montane forests can be limited by different nutrients depending on substrate age and characteristics. Growth in montane tropical forests can also be limited by low soil nutrients resulting from decreased mineralization rates and nitrogen is reported to be a possible limiting nutrient at montane cloud forest sites (Grubb 1995, Tanner et al. 1998, Gottsberger et al. in preparation).

The present study reports on the carbon balance, photosynthetic capacity and leaf nitrogen content of three tropical montane tree species on a leaf ontogenetic basis. Here, we hypothesize that photosynthetic capacity under natural light conditions, carbon assimilation and leaf nitrogen content are lower than of tropical lowland species, due to lower PPFD and nutrient availability, and that these photosynthetic parameters decrease linearly with leaf age for all examined species and treatments, similarly to tree species studied in a lowland tropical forest (Kitajima et al. 1997a). Additionally, we expect a dependency of carbon gain and photosynthetic capacity on seasonal fluctuations of the photosynthesis-related climatic parameters, during the study period. We also relieved possible nutrient limitation by fertilizing adjacent plots and suggest, that leaf nitrogen content, photosynthetic capacity and carbon balance of fertilized plants will be higher than of control plants. We will test the potential to predict diel leaf carbon gain from short-term measurements of light-saturated photosynthesis (Zotz and Winter 1993). Furthermore, the results will be compared with annual carbon gain and leaf N concentrations of species on Barro Colorado Island (Panama) and fitted in the model of predicting annual carbon balance from leaf nitrogen (Zotz and Winter 1994c).

3.2 Material and Methods

3.2.1 Habitat and Plant Material

The study site represents a montane cloud forest at the peak of Cerro Jefe (1007 m.a.s.l., 09°13.794' N, 079°22.995' W), in the Province of Panama, Republic of Panama. This seasonal montane forest is characterized by a short dry season (February to April) and an extensive rainy season (May to January). For a more detailed description of the vegetation, climate and ecology see Carrasquilla (1997) and Gottsberger et al. (in preparation).

Measurements of CO_2 gas exchange, photosynthetic photon flux density (PPFD) and leaf sampling of the abundant tropical montane tree species, *Clusia salvinii* (Donn. Sm.) Clusiaceae, *Ardisia tysonii* (Lundell) Myrsinaceae and *Hedyosmum bomplandianum* (H. B. & K.) Chloranthaceae were performed from April 1999 to March 2001. Plants were studied every month and single freshly sprouted leaves (four replicates) were marked and studied over the whole leaf life span until senescence and abscission.

3.2.2 Nutrient application

On an adjacent plot, Osmocote Plus controlled release fertilizer (N-P-K 18-6-12 fertilizer and Mg, Fe, Mn, Cu, Mo, and B; Scotts-Sierra Horticultural Products Company, Marysville, Ohio, USA) was applied to plants of the three species. Around every plant four holes with 4.5 cm in diameter and about 10 cm depth were prepared in the soil and filled with the slow release fertilizer. Additional fertilizer was distributed on the soil surface around the plants. The total amount of applied fertilizer was approximately 1 kg per m^2 soil, the upper range of quantity recommended for crop plants (the applied quantity of fertilizer was higher than those typically used in agriculture, to ensure growth of plants without any nutrient limitation) (Winter et al. 2001). Plants were started to be monitored 6 months after fertilization. Six months after commencing the gas exchange monitoring, additional fertilizer (about 300 g per plant) was applied on the soil surface around the plants of the fertilized plot.

3.2.3 Gas exchange and photosynthetic capacity measurements

Every month diel gas exchange measurements of the three examined species and the two treatments were done over the whole leaf life time. These measurements were performed with a portable open-flow infrared gas analysis (IRGA) system (Li- 6400; Li-Cor Inc., Lincoln, Nebraska, U.S.A). The reference air supply was connected to a 23-liter buffer volume. Data were collected every hour, from one hour before dawn until one hour after dusk. Nighttime respiration was constant, so that carbon loss could be integrated from predawn and postdusk measurements.

The diel curves of photosynthetic photon flux density (PPFD) reaching the leaf and photosynthetic rate in leaves were integrated using Canvas 3.5 graphing software (Deneba Systems Inc., Miami, Florida, USA). Night time respiration rates were subtracted from day time

CO_2 assimilation rates. Estimates of annual and leaf lifetime carbon gains are based on calculated diurnal CO_2 assimilation. Light response saturation curves under natural light conditions could not precizely be fitted to the diel photosynthetic data, due to a lack of natural light intensities from approximately 500 to 1500 µmol m^{-2} s^{-1}. Therefore, photosynthetic capacity (A_{max}) was derived from the daily measured maximum photosynthetic rate.

3.3.4 Carbon and nitrogen concentration of leaves

Foliage from comparable replicates plants of the gas exchange measurements with the same physiological age were harvested following the monthly diel gas-exchange measurements and leaf area was measured using a Li-3100 leaf area meter (Li-Cor). Subsequently, samples were dried, weighed, ground and analyzed with an EA 1100 elemental analyser (CE Instruments, Milan, Italy), that was linked to an isotope ratio mass spectrometer (Delta ^{Plus}, Finnigan MAT, Bremen, Germany) in continuous-flow mode. Values for $\delta^{13}C$, $\delta^{15}N$ and atomic percentage of N and C were obtained.

3.3.5 Annual and life-time carbon balance

Annual and life-time carbon balances could only be calculated for *A. tysonii* and *H. bomplandianum*. Leaf life-time of *Hedyosmum* plants was shorter than one year and annual carbon was estimated summing up the average monthly carbon uptake. The leaf lifetime of *C. salvinii* exceeded the study period and carbon gain could be calculated on an annual basis only.

For direct comparison with literature data of tropical lowland plants, the long-term nitrogen-use efficiency (NUE) was estimated as annual CO_2 gain per mean monthly leaf nitrogen concentrations (after Zotz and Winter 1994a).

3.3.6 Statistical analysis

Regression analyses (performed with a linear correlation model), analyses of variance, ANOVA and r-squared were calculated with Statgraphic Plus for Windows 4.0 (Statistical Graphics Corp., U.S.A.) statistical software

3.4 Results

3.4.1 CO_2 exchange pattern of Clusia salvinii

Several *Clusia* species were described to perform crassulacean acid metabolism (CAM), showing net CO_2 uptake during night periods (Franco et al. 1990, 1992, Franco et al. 1994, Grams et al. 1998). On the species analysed here, 24h measurements where done during the rainy and the dry season but no net CO_2 uptake during the night could be observed (data not shown). Additionally, gas exchange measurements on drought stressed seedlings were performed under laboratory conditions and no CAM patterns of CO_2 exchange could be recorded (data not shown). Leaf samples harvested throughout the study period at dusk and dawn did not show any significant increase in total acid accumulation during night time (Fig.8), therefore we suggest *Clusia salvinii* being an obligatory C_3 *Clusia* species as defined by Grams et al. (1998), without showing CAM cycling.

3.4.2 Leaf carbon balance, leaf photosynthetic capacity and nitrogen content during ontogeny

3.4.2.1 Control plants

In *Clusia* plants PPFD was significant positively correlated with A_{max} and A_{24h} (r^2=0.42, P<0.01 and r^2=0.26, P=0.03, respectively). There was also a strong correlation between leaf N and A_{max} and A_{24h} (r^2=0.60, P<0.01 and r^2=0.45, P<0.01 respectively). Leaf N, A_{max} and A_{24h} increased slowly along with PPFD at the beginning of leaf ontogeny, but A_{max} and A_{24h} leveled off after approximately 8-10 months (Fig.10).

Ardisia leaves did not show any significant dependency of PPFD on A_{max} and A_{24h} (P>0.1). In contrast, A_{max} was positively correlated with precipitation (r^2=0.26, P=0.01) (Fig.9 and 11). Again, neither A_{max} nor A_{24h} were correlated with leaf N (P>0.3), when values over the whole monitoring period were compared. In *Ardisia* leaves A_{max}, A_{24h} and N increased to maximum levels at 3-4 months of age and showed fluctuations during the year with peaks at the middle to the end of the rainy season (june-december) (Fig.11).

Hedyosmum leaves showed a significant positive correlation of PPFD and A_{24h} (r^2=0.30, P=0.03), a weak correlation of N and PPFD (r^2=0.19, P=0.1), and no relationship of A_{max} and PPFD (P>0.28). Neither A_{max} nor A_{24h} correlated significantly with leaf N (P>0.25). A_{max} and A_{24h} in very young *Hedyosmum* leaves increased rapidly to maximum levels, decreased during the end of the rainy season and recovered slightly following the increase of PPFD towards the end of the dry season (Fig.12). N increased slowly but steadily during ontogeny and decreased during the approximately three months longing senescence period along with A_{max} and A_{24h} (Fig.12).

For all three studied montane tree species, A_{max} correlated highly significant with A_{24h} (Clusia: r^2=0.78, P<0.01, Ardisia: r^2=0.70, P<0.01 and Hedyosmum: r^2=0.57, P<0.01, respectively).

3.4.2.2 Fertilized plants

Fertilized *Clusia* plants did not show a significant dependency of PPFD with A_{24h} or A_{max}. Only the diel carbon balance decreased significantly with increasing SLA (r^2=0.35, P=0.02). Nitrogen concentrations in leaves of fertilized *Clusia* plants was slightly increased compared to control plants (Fig.10), but did not show any significant relation with A_{24h} or A_{max} (P>0.1). Both, photosynthetic capacity and carbon balance increased in young leaves of fertilized *Clusia* faster than they did in control plants, but fertilized plants showed a stronger decline in A_{max} and A_{24h} at the end of the measurement period (Fig.10).

Fertilized *Ardisia* plants did not show a correlation of PPFD with A_{max} and A_{24h}, nor was N significantly related to A_{24h} or A_{max} (P>0.9). Towards the end of leaf lifetime a similarly strong decrease of A_{max}, A_{24h} and leaf N as seen with control *Ardisia* plants was not evident (Fig.11). Remarkable is, that PPFD levels on the leaf surface of fertilized *Ardisia* plants were diminished from the middle of leaf lifetime until senescence (Fig.11).

Fertilized *Hedyosmum* plants showed significant correlations between PPFD and A_{max} and A_{24h} (r^2=0.52, P=0.02 and r^2=0.53, P=0.02, respectively). Leaf N did not correlate with any of the measured parameters (P>0.4). A nearly linear decline of A_{max} and A_{24h} from young leaves until abscission was obtained (Fig.12). PPFD levels on leaves of fertilized *Hedyosmum* plants decreased from the middle towards the end of lifetime period (Fig.12). Leaf N concentrations increased in young leaves and fluctuated during the rest of leaf lifetime, but were not related to any other measured parameter (Fig.12).

3.4.3 Annual-, lifetime-CO_2 balance and long-term nitrogen use efficiency

The annual CO_2 balance of leaves was lower for fertilized than control plants on an area basis and lower for control than for fertilized *Clusia* and *Ardisia* on a mass basis (Tab.5). Fertilized *Hedyosmum* plants showed a higher annual CO_2 balance of leaves on a mass but not on an area basis. Leaf lifetime CO_2 balance was higher for control than fertilized *Ardisia* on a mass and on an area basis and for control *Hedyosmum* only on an area basis. Higher values of CO_2 balance over lifetime was obtained for fertilized *Hedyosmum* plants on a mass basis. There are no values for lifetime CO_2 balance for *Clusia*, because leaf longevity exceeded the projects scheduled time.

The long-term nitrogen-use efficiency was on average one third higher for control plants than for the fertilized ones, but did not differ markedly between species (Tab.5).

Control and fertilized *Ardisia* leaves had leaf longevities of 22 and 16 months, respectively. Leaves of control and fertilized *Hedyosmum* plants only lived 15 and 11 months, respectively (Tab.5).

3.4.4 Predicting annual carbon gain

Annual carbon gain was correlated with yearly mean foliar nitrogen concentrations (Zotz and Winter 1994c), and data from Zotz and Winter (1994c) and the data of this study (Fig.13b) showed a highly significant correlation ($P<0.01$, $r^2=0.93$ with the equation A_{24h} = 1.32 (mean leaf nitrogen) – 345). Fertilized plants did not fit into the correlation and showed a flatter slope of regression line (Fig.13b) (A_{24h} = 0.78 (mean leaf nitrogen) – 142).

For all species and treatments A_{max} was positively related with A_{24h} as shown in (Zotz and Winter 1993), when data of average values from 4 replicate leaves were plotted (Fig.13a). The significance for the control plants was ($r^2=0.71$; $P<0.001$) with the equation: $A_{24h} = 20.5\ A_{max} - 22.5$, and for the fertilized plants ($r^2=0.83$; $P<0.001$) with the equation: $A_{24h} = 17.5\ A_{max} – 24.5$.

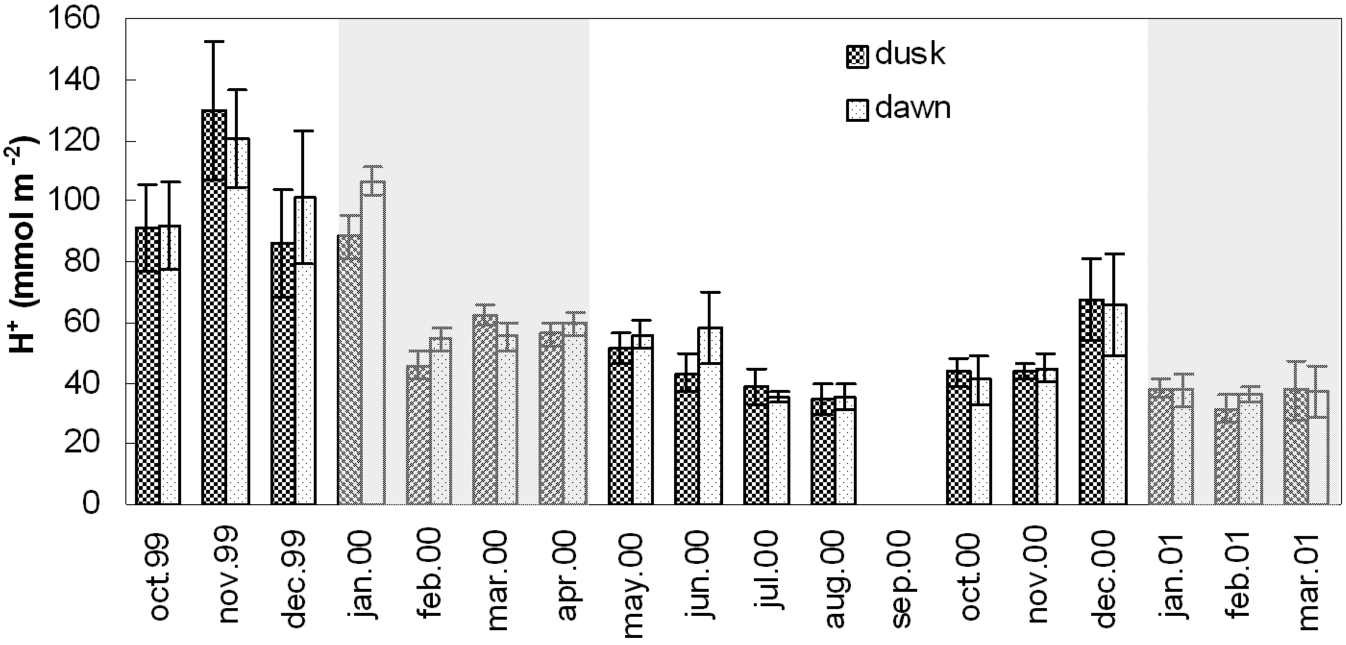

Fig.8 Titratable acidity, H^+(mmol m^{-2}), of *Clusia salvinii* leaves sampled at dawn and dusk during ontogeny. Semitransparent gray areas show the dry season period. Error bars represent standard errors, n=4.

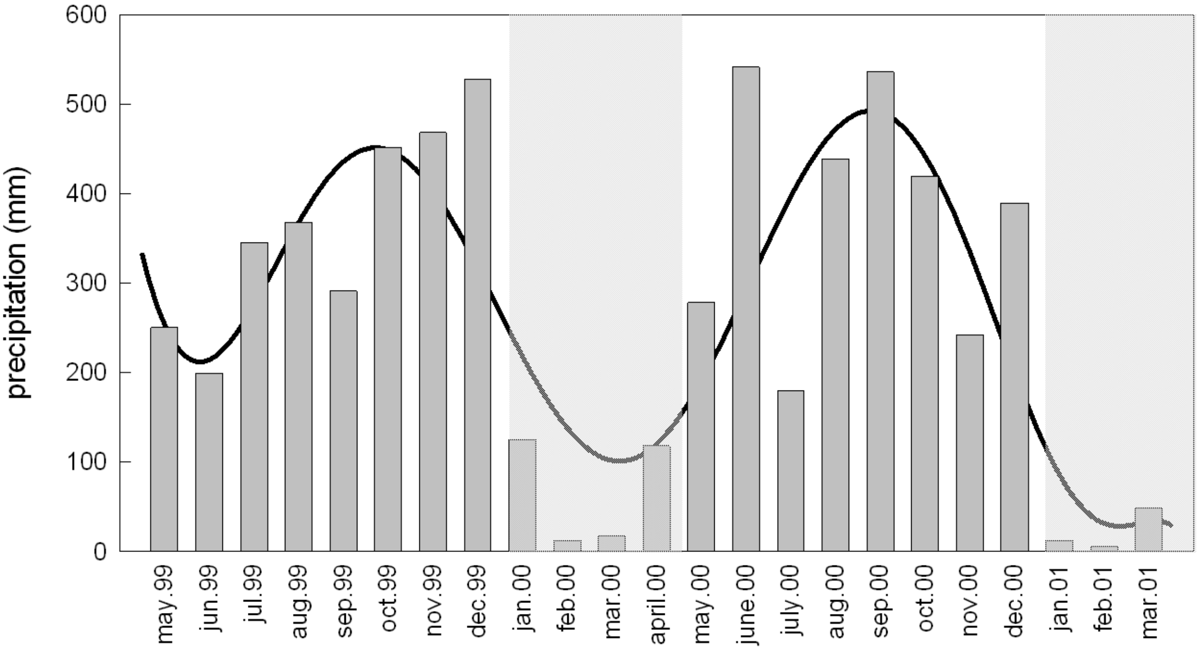

Fig.9 Integrated monthly precipitation for the entire study period in mm. Trendline is polynomial 8. order. Semitransparent gray areas show the dry season period.

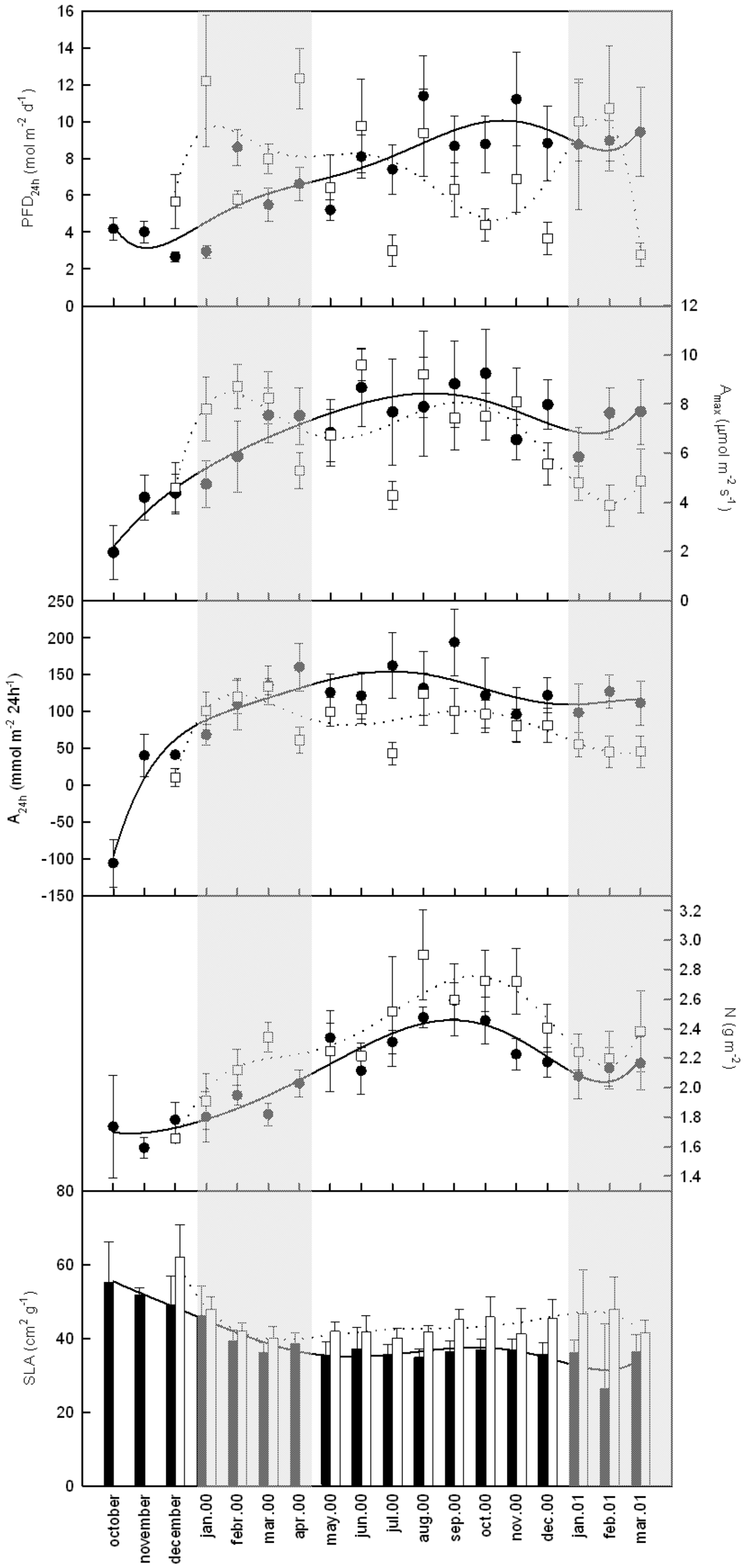

Fig.10 Photosynthetic photon flux density (PPFD, mol m^{-2} d^{-1}), photosynthetic capacity (µmol m^{-2} s^{-1}), carbon gain (mmol m^{-2} 24h^{-1}), leaf nitrogen content (Wt % in dw) and the specific leaf area (SLA, cm^{2} g^{-1}) of controls and fertilized freshly sprouted *Clusia* plants during the study time. Trendlines represent polynomial regressions of 6. order. Semitransparent gray areas are the dry season periods. Error bars represent standard errors, n=4.

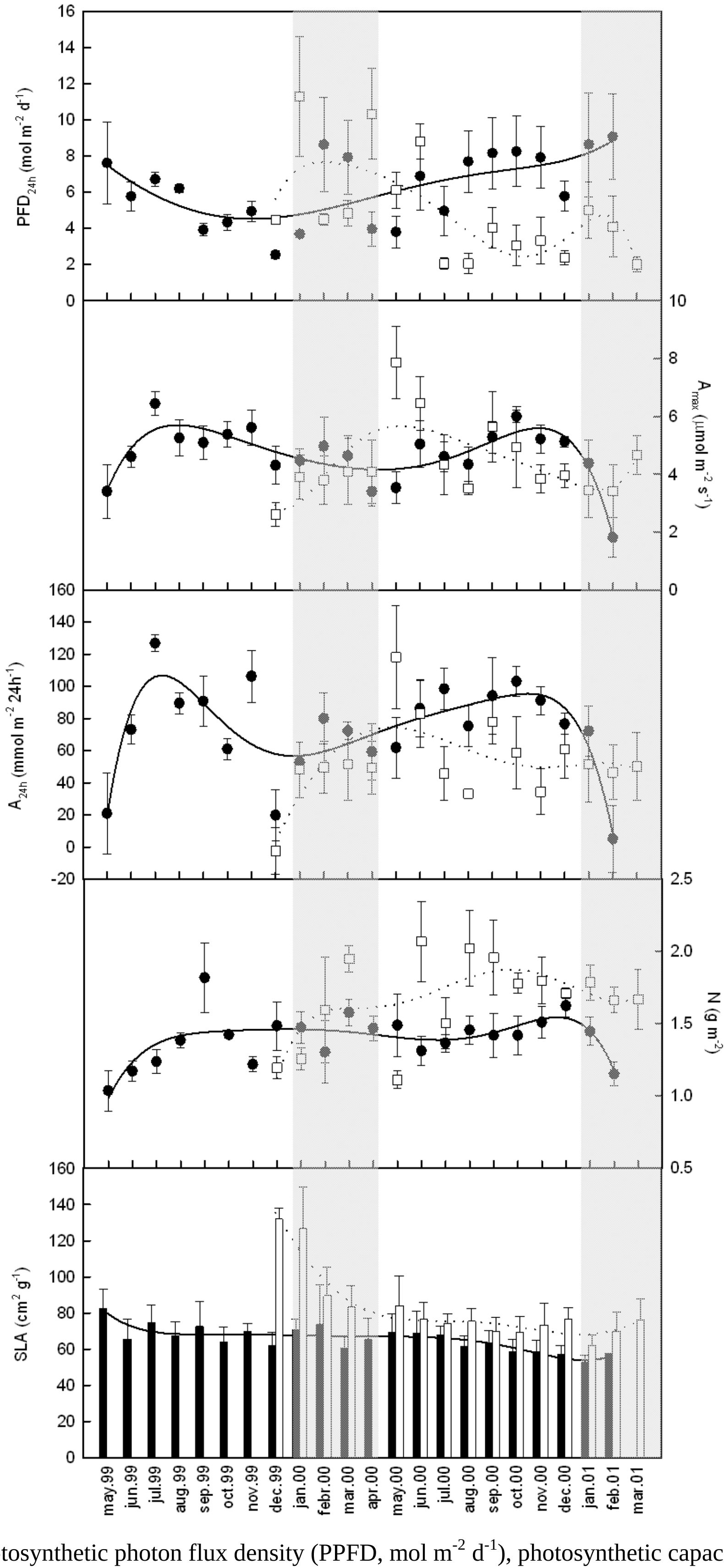

Fig.11 Photosynthetic photon flux density (PPFD, mol m^{-2} d^{-1}), photosynthetic capacity (µmol m^{-2} s^{-1}), carbon gain (mmol m^{-2} $24h^{-1}$), leaf nitrogen content (Wt % in dw) and the specific leaf area (SLA, cm^2 g^{-1}) of controls and fertilized freshly sprouted *Ardisia* over leaf lifetime. Trendlines represent polynomial regressions of 6. order. Semitransparent gray areas are the dry season periods. Error bars represent standard errors, n=4.

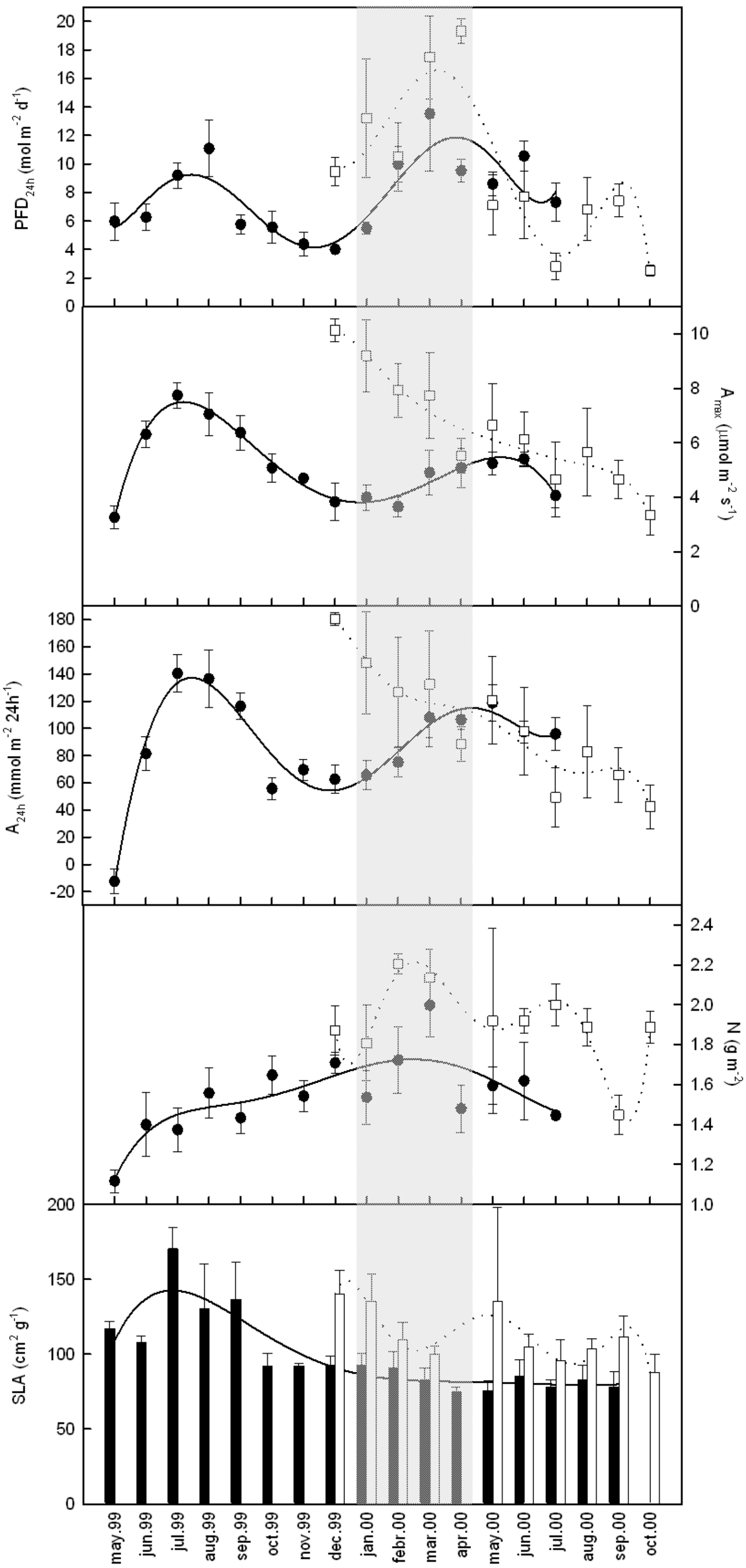

Fig.12 Photosynthetic photon flux density (PPFD, mol m^{-2} d^{-1}), photosynthetic capacity (µmol m^{-2} s^{-1}), carbon gain (mmol m^{-2} 24h^{-1}), leaf nitrogen content (Wt % in dw) and the specific leaf area (SLA, cm^{2} g^{-1}) of controls and fertilized freshly sprouted *Hedyosmum* over leaf lifetime. Trendlines represent polynomial regressions of 6. order. Semitransparent gray areas are the dry season periods. Error bars represent standard errors, n=4.

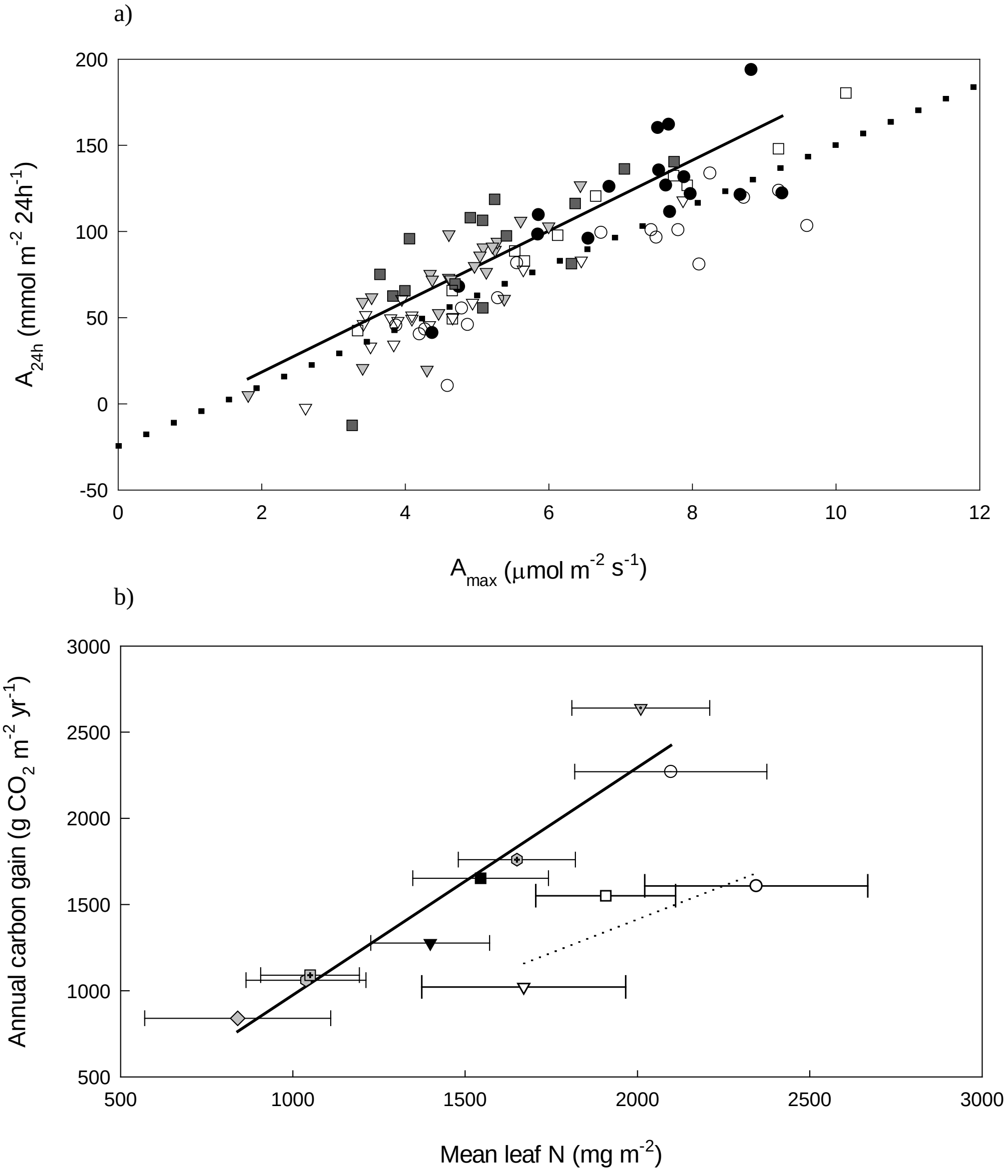

Fig.13a Integrated net carbon gain A_{24h} (control plants, closed symbols) and (fertilized plants, open symbols) versus the maximum rate of net CO_2 assimilation A_{max}. Data were obtained from monthly diel courses of CO_2 exchange in three cloud forest species on Cerro Jefe during 1999 to 2001. *Clusia salvinii* (circles), *Ardisia tysonii* (inverse triangles), *Hedyosmum bomplandianum* (squares). The regression for the control plants (full line) is $A_{24h} = 20.5\ A_{max} - 22.5$ ($r^2 = 0.71$; $P < 0.001$), and for the fertilized plants (dotted line) $A_{24h} = 17.5\ A_{max} – 24.5$ ($r^2 = 0.83$; $P < 0.001$) **b** Correlation of annual carbon gain and mean leaf N content. Black symbols represent control plants from this study and gray symbols are data from Zotz and Winter (1994c). White symbols represent fertilized species of this study. Circles represent *Clusia*, triangles down *Ardisia* and squares show *Hedyosmum*. Error bars describe standard deviations. The full line represent the control plants and the regression is: Annual carbon gain = 1.32 (mean leaf nitrogen) - 345; $r^2 = 0.93$, $P < 0.001$ and the dotted line represent the fertilized plants and the regression is: Annual carbon gain = 0.78 (mean leaf nitrogen) - 142; $r^2 = 0.68$, $P < 0.1$. Error bars represent standard deviations, n=4.

Table 5 Annual CO_2 balance and lifetime CO_2 balance on leaf dry weight and area basis, annual nitrogen use efficiency and leaf longevity of the 3 tree species under natural condition and on fertilized plots.

Parameter		*Clusia salvinii*		*Ardisia tysonii*		*Hedyosmum bomplandianum*	
		natural condition	fertilized	natural condition	fertilized	natural condition	fertilized
Annual CO_2 balance	(g CO_2 g^{-1} d. wt yr^{-1})	8.1	6.9	8.6	8.2	15.5	16.3*
	(g CO_2 m^{-2} yr^{-1})	2270.4	1607.3	1275.9	1021.5	1652.2	1550.4*
Lifetime CO_2 balance	(g CO_2 g^{-1} d. wt $long.^{-1}$)	___	___	14.2	9.1	16.3	17.8
	(g CO_2 m^{-2} $long.^{-1}$)	___	___	2165.2	1143.7	1765.8	1520.8
Annual N-use efficiency	(g CO_2 mg^{-1} N yr^{-1})	1.02	0.66	0.90	0.63	1.06	0.78*
Longevity	months	>18**	>16**	22	16	15	11

* annual CO_2 balance and annual N-use efficiency is projected for fertilized *Hedyosmum* plants

**leaf longevity exceeded the study time and therefore lifetime CO_2 balance for *Clusia* could not be calculated

3.5 Discussion

3.5.1 Developmental and microclimatical variation in diel leaf carbon balance, photosynthetic capacity and nitrogen content

As hypothesized, we demonstrated a relationship between photosynthetic capacity (A_{max}), carbon gain (A_{24h}) and photosynthetic photon flux density (PPFD) over lifetime, but only for *Clusia* plants. With *Hedyosmum* plants only A_{24h} correlated significantly with PPFD, again suggesting light as an important factor controlling carbon gain over the studied developmental period. Apparently, *Clusia* was the only analysed species where all measured photosynthesis-related parameters were determined by the amount of radiation the leaves received over leaf lifetime. Photosynthesis of *Clusia* was additionally controlled by leaf N concentration. On the other hand, photosynthesis of *Ardisia* plants was controlled by possibly intrinsic not climate-related parameters others than the here presented ones. Statistically, only precipitation had a weak negative influence on carbon gain, suggesting drought induced stomatal limitation or biochemical limitation due to photoinhibition in periods of water stress (Mulkey and Wright 1996). However, this hypothesis needs further corroboration by additional experiments. In very young and in senescing leaves of *Ardisia* an influence of leaf N on the two measured photosynthetic parameters was detected. The common pattern of A_{max} and A_{24h} increase with N accumulation in young leaves and decrease with a retranslocation at the end of leaf lifetime (Fig.4), was also observed for five intermediate lowland tropical canopy tree species (Kitajima et al. 1997a). A similar picture concerning N content over lifetime with retranslocation before leaf abscission is given in upper canopy leaves of *Dryobalanops aromatica* in Malaysia (Ishida et al. 1999).

Considering the observed patterns of CO_2 assimilation during leaf lifetime in *Clusia*, PPFD and as a result of that, A_{max}, A_{24h} and leaf N were possibly influenced by the fact that young opposite *Clusia* leaves sprout in vertical position and it takes approximately 4 to 5 months until the leaves unfold into a more or less horizontal position (pers. obs.). This could be one reason for the lower PPFD, A_{max} and A_{24h} levels at the beginning of leaf ontogeny (Fig.10), but also a strategy to avoid early shading of still fully functional older leaves (Ackerly 1999). Unfortunately we could not follow leaf ontogenesis until leaf abscission at this species, and at the end of the experiment, photosynthesis of *Clusia* leaves were in a steady state, no decline of A_{max} or A_{24h} was apparent.

Hedyosmum showed a fast increase of A_{max} and A_{24h} in very young leaves but then a non-systematic fluctuation of these two parameters during leaf ontogeny. Leaf N gradually increased and declined during the last four months of leaf lifetime (Fig.12). *Hedyosmum,* that continuously produces new leaves over the whole year was the species which exhibited the shortest leaf lifetime, and the highest annual carbon balance, leaf nitrogen concentrations and annual nitrogen-use efficiency (Tab.5). Furthermore, it showed an early decline in nitrogen content with increasing leaf age for both treatments, fertilization and controls. This higher rate of pre-senescing nutrient retranslocation was also described for crops, earliest colonizers and early successional species in an oligotrophic Amazonian forest (Reich et al. 1995a). Similar effects concerning the decrease of leaf nitrogen levels over lifetime were reported for five intermediate lowland tropical canopy tree species (Kitajima et al. 1997a).

Comparing values of annual leaf CO_2 balance with literature data shows that the here studied montane tree species had higher values on a dry weight basis (Tab.5) compared to an epiphytic CAM *Clusia* species and an epiphytic fern at a lowland site in Panama (6.1 and 7.4 g CO_2 g^{-1} d.wt yr^{-1}, respectively) (Zotz and Winter 1994a). An epiphytic lowland orchid (*Catasetum viridiflavum*) exhibited higher values of annual carbon balance on a dry weight basis in the same study (26.3 g CO_2 g^{-1} d.wt yr^{-1}), but the three montane tree species had up to two times higher values when compared on an area basis (Tab.5). This could be partly due to lower SLA of the montane plant species. As discussed in (Zotz and Winter 1994a), CO_2 uptake especially in C_3 lowland epiphytes could be restricted due to lower water availability in the tree canopies during periods of potentially high photosynthesis (dry season). Water availability for trees at the montane site is apparently sufficient throughout the year not influencing CO_2 uptake of the studied plants.

The only hypothesized effect evident in leaves of the all three fertilized plant species was that leaf N concentrations were significantly elevated in comparison with control plants. A_{max} and A_{24h} levels were lower in fertilized *Clusia* and *Ardisia* but not in *Hedyosmum* plants (Figs.10,11,12). Why did the former two plant species not show higher rates of photosynthetic capacity and carbon gain in spite of the fertilized N being accumulated in the leaves? There is evidence that also leaf production as a proportion of maximum number of leaves at *Clusia* and *Ardisia* did not respond to fertilization (Gottsberger et al. in preparation) along with the results that photosynthetic capacity and carbon gain at these two species were unaffected and leaf longevity decreased (Tab.5). Different possible explanations are: (i) a genetically determined capability to use a specific amount of N in photosynthesis resulting in unaltered or slightly lower net rates of CO_2 fixation at fertilized *Clusia* and *Ardisia* plants. *Hedyosmum* showed more the patterns of a pioneer species and net CO_2 assimilation rate was increased for young leaves and there was a higher proportion of born compared to died leaves at this life period (Gottsberger et al., in preparation) probably increasing the leaf area ratio (LAR), as it was demonstrated especially for a lowland tropical pioneer tree (*Ficus insipida*) in Panama (Winter et al. 2001). However, leaf lifetime of fertilized plants of this species was significantly decreased (Tab.5), relativizing the net lifetime growth. (ii) SLA of all three tree species was increased after fertilization (Winter et al. 2000, Winter et al. 2001) resulting in a probable further increase of LAR. This could be linked to enhanced nutrient and carbon allocation from root and/or shoot to photosynthetizing leaves. Leaf size and photosynthetic active leaf area is increased again providing more carbon structures for whole plant growth without increasing photosynthetic capacity and carbon gain per leaf area. Possible translocation processes from the leaves to other parts of the studied plants, influencing for example root/shoot ratios, could be a translocation pathway for carbon structures, but this sink source relations were not measured.

Two phenomena may nevertheless indicate N influence on *Clusia* and *Hedyosmum* plants. Fertilized *Clusia* plants photosynthetic parameters were unaffected by leaf N in contrast to control plants. Fertilized *Hedyosmum* plants still showed a significant correlation of A_{max} and PPFD, supporting the hypothesis, that any weak influence of leaf N on photosynthetic parameters was excluded at the fertilized plants. Light became a more important factor determining photosynthesis in this species. This was further supported by the higher significance of the correlation of A_{24h} and PPFD for fertilized plants in contrast to control plants of *Hedyosmum*. Therefore, a small dependency of the analysed species on leaf N suggest N as one possible determining factor for photosynthetical parameters. This nicely fits to the results, that potential photosynthetic capacity obtained through light response curves was correlated with leaf N concentrations of 21 plant species (the species of this study included) at the same site (Gottsberger et al., in preparation).

3.5.2 Prediction of annual carbon gain from leaf nitrogen and short term photosynthesis measurements

The approach to predict annual leaf carbon balance from leaf nitrogen was applied to the here studied montane plants (Fig.13b). Basis for this prediction model are the similar long-term N-use efficiencies of montane tree species (Tab.5) and plants from a drier lowland site (Zotz and Winter 1994a). Apparently, foliar nitrogen determines leaf C gain and primary production of plants also at Cerro Jefe, and other factors that could override this relationship are of minor importance (Zotz and Winter 1994c). Fertilized plants were sufficient supplied with N and the correlation was apparently influenced by other factors (Fig.13b). The theory behind this relation is that the biochemical capacity for CO_2 fixation requires soluble and membrane-bound proteins which represent the majority of leaf N (Zotz and Winter 1994c). However, in fertilized plants, luxurious uptake and accumulation of leaf N without response of photosynthesis altered this relation compared to natural plants (Fig.13b).

The second hypothesis tested was that short-term photosynthesis measurements predict diel leaf carbon balance. This was shown for 8 canopy rain forest species on Barro Colorado Island, Panama (Zotz and Winter 1993). With the montane tree species we obtained a very similar relation, even when data of fertilized plants were included (Fig.13a). Values of A_{max} under natural light conditions and A_{max} obtained through light response curves up to 2000 μmol m^{-2} s^{-1} at the same site with the same species (Gottsberger et al., in preparation) were very similar. The possible reason that this general relationship is applicable to plants of our study are the low light compensation points of photosynthesis of the studied montane plants. Photosynthesis saturated at low light levels (*Clusia* sp. 154±5, *Ardisia* sp. 158±6, *Hedyosmum* sp. 215±13 μmol m^{-2} s^{-1}) for these tropical montane tree species. Even on partly overcast days plants reach their maximum photosynthetic rates at the montane site.

For the lowland species the argument for predominantly light saturated photosynthesis was the exposition of canopy leaves, also reaching saturating levels on overcast days (Zotz and Winter 1993).

We did not analyze the carbon balance on a whole plant basis to quantify the carbon gain on a greater scale than on leaf basis. Observations on leaf longevity, leaf-production and -fall suggest that fertilization could have an effect on the biomass turnover of species with enough flexibility of responding to fertilization with increased leaf production and growth, but in contrast with negative influence on leaf longevity and no influence on photosynthetic parameters on leaf level. Nitrogen could have a masked influence on photosynthetic parameters at least for parts of leaf lifetime, unfortunately the influence could not be shown on whole leaf longevity scale for each species, however we found a strong dependency of leaf N on annual carbon gain for the analysed species when data were pooled (Fig.13b). Although the studied plants belong to taxonomic widely different groups the relationship between A_{max} and A_{24h} and between average yearly foliar N concentration and yearly carbon gain was strong, even when compared to plants of differing lifeforms from proceeding studies (Zotz and Winter 1994a, c).

There is a clear need to make direct measurements of the net CO_2 flux of the main species, particularly in forests, to obtain a net CO_2 balance over at least a full year. Such measurements provide the only information on how an active stand of vegetation is functioning on a time scale short enough to allow processes to be evaluated and reasonably mechanistic models to be made for interpolation, extrapolation, and prediction (Jarvis and Dewar 1993). This study links CO_2 balances with leaf nitrogen concentrations and photosynthetic capacity, demonstrating new powerful tools for scaling carbon and nitrogen relations from leaf to ecosystem level and time scaling from minutes to years (Ehleringer and Field 1993). However, to confirm the general application of the here tested prediction methods, further studies concerning these relationships will be necessary on different ecosystems to allow scaling up from leaf level to canopy C gain on ecosystem level and in the future provide additional input for global scale models (Ehleringer and Field 1993).

4. Adaptations of leaf phenology to seasonality in a tropical montane cloud forest, Panama.

4.1 Introduction

Seasonality apparently plays a lesser role in plant phenology in the tropics compared with temperate regions. However, seasonality becomes more pronounced with increasing distance from the equator. Data from several different tropical forests in the Paleo- and Neotropics show, that all ecosystems exhibit a seasonality, that is related to the proportion of dry to wet periods (Schaik et al. 1993). Adaptations to dry periods in leaf, fruit or flower production are described for several tropical plants (Reich et al. 1991, Schaik et al. 1993, Wright and van Schaik 1994, Kikuzawa 1995, Reich et al. 1995a, Wright 1996). Drought avoidance strategies such as foliage loss to reduce transpiration were documented (Wright 1996). Similar strategies to maximize carbon gain such as production of new leaves during periods of maximum irradiance were described (Wright and van Schaik 1994). This is to counteract a decline in photosynthetic capacity with increasing leaf age (Kitajima et al. 1997a, b). At the onset of the dry season some species shed their old inefficient leaves and produce new leaves, that are adapted to the climatic conditions of the dry season. In *Ceiba pentandra* (Zotz and Winter 1994b), a new flush of leaves is already established shortly after leaf fall at the beginning of the dry period. Different leaf life-spans and leaf production characteristics have been described for different plant species. They are related to the successional status of the single species (Reich et al. 1992, Kitajima et al. 1997a, b). In lowland Pacific sites of Panama most of the tree species are semi-deciduous. They loose most of their leaves at the beginning of the dry season and produce new leaves with the start of the rainy season. These species have developed a variety of strategies to establish a new canopy. Some flush their leaves all at once, others show two flushes per season and some species produce leaves continuously (Wright, S.J. unpublished data). Barone (1998) demonstrated, that under well-watered conditions leaf production of some understory plant species is linked to peaks in irradiance in a deciduous forest on Barro Colorado Island (Panama). This situation occurs when the deciduous species shed their leaves and light levels reaching lower forest strata are increased. Wright and van Schaik (1994) summarizing data of 8 different tropical forests, showed that leaf production is linked to seasonal peaks of irradiance. Leaves produced at different periods of the year differ with respect to photosynthetic traits, water use efficiency, and leaf mass per unit area, and are hence described to develop different phenotypes (Kitajima et al. 1997a, b). Other authors hypothesized that plants showing seasonal leaf phenotypes are regulated by internal factors like endogenous rhythms governing phenology (Mulkey et al. 1992, Reich et al. 1995a).

Eamus and Prior (2001) compiled data of several seasonally dry tropical ecosystems worldwide and classified different categories of deciduous woody species. They argued, that leaf phenology is mainly dependent on plant water status. The degree of deciduousness is also related to the access of roots to soil water. Evergreen species, postulated as developing deeper root systems compared to deciduous species, have access to deeper reserves of soil water in the dry season. They are therefore able to maintain an almost complete canopy in the dry season and hence avoid drought (Eamus and Prior 2001). This suggests a further endogenous related control mechanism for leaf fall and flush.

Leaf phenology is also affected by numerous biotic factors, such as herbivory (Schaik et al. 1993, Williams-Linera 1997). Their role, however, in timing of leaf production is not fully understood. Most commonly they are assumed to be of minor importance in the evolution of leaf traits and phenological patterns. Biotic factors, as herbivoral pressure may either alternate or cluster phenological activities of individual plant species and are described only to optimize timing of leaf production in relation to herbivore development (Schaik et al. 1993). In this study we therefore concentrated on the effect of abiotic influences that are linked to endogenous factors such as adaptive traits and phylogenetic relationships (Wright and Calderon 1995).

Very little is known on leaf phenology processes in montane cloud forests. In a tropical montane cloud forest in central Veracruz (Mexico), minimum temperatures acted as proximate triggers for leaf fall of deciduous trees (Williams-Linera 1999). Maximum temperatures, on the other hand, triggered leaf flushing in both deciduous and evergreen tree species.

The aim of this study was to analyse patterns of leaf production and leaf longevity of typical tropical montane forest tree species. The influence of seasonality, macroclimate and soil conditions on leaf phenology was examined. Leaf longevity was determined or, in species where leaf production exceeded the study period, it was extrapolated from leaf production and mortality rates. The aim was also to provide further data for the general discussion of what may control leaf phenology in tropical plants. The tropical montane cloud forest chosen for our study seems to be a suitable site with only evergreen species and an apparently not very pronounced seasonality. It therefore provides nearly standardized conditions, without much influence of abiotic factors, and allows an easier detection of endogenous mechanisms controlling leaf phenology in plants.

4.2 Material and Methods

4.2.1 Location of the study site

The study site, a montane cloud forest, is located in the Province of Panama approximately 52 km northeast of the capital of the Republic of Panama (Panama City) on the peak of Cerro Jefe (1007 m.a.s.l., 09°13.794' N, 079°22.995' W).

Soils are moderately stony latosols, the pH ranging from acidic to very acidic. There is hardly any humus layer or litter present. Deeper soil horizons are not very distinguishable within the clayish main soil body. This could indicate to a fast turnover of dead plant material probably combined with the presence of mycorrhizae, other fungi or microorganisms symbiotically interacting with the plant roots. However, after heavy rain, superficial humus and nutrients are leached out due to lateral run-off on the steep soil surface. In contrast, deeper layers, consisting of always water-logged very fine-grained soil, are in a steady state and soil solution is more or less not exchanged. Frequent strong winds and a near constant cloud cover with mist mainly during the night characterize the site (Carrasquilla 1997). The vegetation at Cerro Jefe is open and composed of shrubby trees approximately 3-15 m tall with mostly sclerophyllous medium-sized to small leathery leaves. The emergent endemic Palm *Colpothrinax aphanopetala* (Evans) is abundant and probably plays an important role as a windbreak and in collecting mist.

The vegetation structure at this montane site is very distinct and influenced by natural disturbances such as windfall. Windfall is the result of strong winds in combination with shallow rooting of plants and soil erosion. These processes lead to a relatively open vegetation that allows establishment of shrubby trees, palms, a widespread grass, and other pioneers between the climax species. All tree species are evergreen and epiphytic members of the Bromeliaceae, Orchidaceae, Araceae and Ericaceae grow abundandly on the tree trunks or, depending on the light regime, also directly on the ground. A more detailed characterization of the flora is presented by Carrasquilla (1997)

4.2.2 Nutrient application

Osmocote 18-6-12 (Scotts-Sierra Horticultural Products Company, Marysville, Ohio, USA) fertilizer was applied around *Clusia*, *Ardisia* and *Hedyosmum* plants. On an adjacent plot at the same site, four holes 4.5 cm in diameter and about 10 cm deep were made around every plant and filled with the slow release fertilizer. Additionally, fertilizer was spread on the soil surface around the plants. The total amount of applied fertilizer was approximately 1 kg per m^2 soil, which is at the upper end of the amount recommended for crop production. The aim was to diminish any possible nutrient limitation. Monitoring was started 6 months after fertilization.

Another six months after the start of the project, additional fertilizer (about 300 g per plant) was applied on the soil surface around the plants of the fertilized plot. The fertilizer was chosen because of its slow release characteristics, which avoids element toxicities and ensures a constant supply of nutrients over the complete experimental period.

4.2.3 Leaf phenology

To obtain data on leaf longevity, production and fall over the year, leaves of different representative tree species were labeled, and the leaf blade length of every new fully expanded leaf was measured. The following typical tropical montane tree species were selected for this study: *Ardisia tysonii* Lundell, *Calophyllum nubicola* W.G. D'Arcy & R.C. Keating, *Clusia salvinii* Donn. Sm., *Eugenia cf. octopleura* Krug & Urb. ex Urb., *Hedyosmum bomplandianum* H. B. & K., and *Lisianthius jefensis* A. Robyns & T. S. Elias. For each species and treatment, 10 individuals were selected and leaves marked and monitored monthly from sprouting until abscission. Additionally, further individuals of *C. salvinii*, *A. tysonii and H. bomplandianum* were monitored at the fertilized plot. Based on these data the number of leaves as a proportion of the total, the newly produced (leaf appearance) and abscissed leaves (leaf fall) and leaf longevity (in days) were calculated.

4.2.4 Climate monitoring

A LiCor weather station was used to monitor the macroclimatic conditions at the study site. The photosynthetic photon flux density (PPFD) was measured with a LiCor light sensor every minute. The light curve was integrated for the day and furthermore, light maxima and minima were registered. Daily rainfall, relative humidity and air temperature (integrated, minima and maxima) were measured in approximately 2 m height. Soil temperature was monitored in 15 cm depth. Monthly evaporation was obtained with 3 ETgage Model A evaporimeters (ETgage Company) equipped with a Gore-Tex cover. An important aspect of water status of tropical montane forests, the horizontal precipitation (HP) or condensing mist, was not quantified, due to a lack of an accepted standardized method (Cavelier and Goldstein 1989). However, the relative time of nearly water saturated air (about 100% relative humidity), mainly represented by periods of HP, are indirectly included in the monthly rate of evapotranspiration. Nonetheless, the amount of quantitative HP adding to the rainfall could not be determined with this approach.

4.2.5 Daylength calculation

The theoretical daylength was calculated for the geographical position using Photosynthesis Assistant version 1.1.2 (Dundee Scientific, Dundee, U.K.) software. The following equation is used to describe solar elevation:

$$\sin \text{ß} = \cos \text{Ø} = \sin \text{¥} \sin \text{§} + \cos \text{¥} \cos \text{§} \cos h$$

Where ß is the solar elevation, Ø is the solar zenith angle, ¥ is the latitude, § the solar declination, and h is the hour angle of the sun (Jones 1992). The longitude was included to permit the determination of local sunrise and sunset and this is based on Greenwich Mean Time. The equation of time varies slightly each year, although in this application values from Sestak et al. (1971) were interpolated and the estimated times of sunrise and sunset are normally within a few minutes of the actual times.

4.2.6 Soil humidity analyses

Soil water content was measured gravimetrically during the rainy and at the end of the dry season. Eight soil samples were taken with a cylindrical soil auger on two parallel slope gradients. Soil from 0-5 and from about 20cm depth was weighed, then dried in an oven at 110^{o}C to constant weight. Water content of the soil was expressed in percent water per dry weight of the soil (for a more detailed description, Yavitt 2000).

4.3 Results

4.3.1 Meteorological relations

A dry season pattern could be detected in all measured meteorological parameters. Integrated soil temperature was significant positively related to monthly rainfall and integrated air temperature (r^2=0.27 and P=0.01, r^2=0.51 and P<0.01, respectively). It was negatively related to minimum humidity and evapotranspiration (r^2=0.13 and P=0.07, r^2=0.38 and P<0.01, respectively). Rainfall was negatively correlated with integrated PPFD and evapotranspiration (r^2=0.64 and P<0.01, r^2=0.71 and P<0.01, respectively). It was positively correlated with integrated air temperature (r^2=0.24 and P<0.02). PPFD was negatively correlated to minimum humidity and positively to evapotranspiration (r^2=0.39 and P<0.01, r^2=0.71 and P<0.01, respectively). Evapotranspiration was negatively related to both, air temperature and minimum humidity (r^2=0.39 and P<0.01, r^2=0.15 and P=0.08, respectively). Soil and air temperature increased with increasing daylength (r^2=0.42 and P<0.01, r^2=0.32 and P<0.01, respectively).

Relationships of some parameters were however not statistically significant on a 90% or higher confidence level. Integrated soil and air temperatures were not correlated with integrated PPFD levels, and minimum humidity was neither related to rainfall nor to integrated air temperature. Daylength did not correlate with any other climatic parameter.

4.3.3 Leaf phenological characteristics

Trees included in this study were all evergreen species, but nontheless showed different leaf phenology patterns. *Hedyosmum*, *Eugenia* and *Lysianthus* produced new leaves continuously throughout the year (Fig.19,20,21). *Clusia* trees also sprouted new leaves nearly year-round, with lower rates at the beginning of the wet season, increased leaf appearance at the end of the wet season (Fig.18). *Ardisia* plants started to produce new leaves at the beginning of the dry season and stopped with setting in of the rainy season (Fig.16). In contrast, *Calophyllum* showed a very short leaf production period at the beginning the rainy season and a more or less constant leaf fall throughout the year (Fig.17).

Leaf longevities of three species were significantly related to meteorological parameters. Longevity of *Ardisia* leaves born in months of higher rainfall and lower evapotranspiration was decreased (Tab.6). *Calophyllum* leaves produced in periods of increased soil temperature showed extended longevities. Longevity of *Lysianthus* leaves produced in months of increased PPFD levels and lower minimum humidity was reduced.

Blade length of young *Ardisia* leaves was significantly decreased in months of high rainfall and elevated air temperature. The opposite effect could be detected in young *Lysianthus* leaves. Blade length was significantly increased with higher rainfall and air temperature, and in contrast, leaf blade length was decreased with higher PPFD and evapotranspiration levels. Young *Hedyosmum* leaves grew longer blades at increased PPFD levels (Tab.6).

Leaf phenology parameters of *Ardisia*, *Calophyllum* and *Eugenia* were dependent on water (rainfall, minimum humidity, evapotranspiration) and on temperature (soil temperature, air temperature) related parameters (Tab.6). *Lysianthus* additionally showed significant negative relations of leaf phenological parameters with light (PPFD) and negative correlations of air temperature (Tab.6) and daylength with leaf fall. Leaf appearance of *Calophyllum* was reduced with extended daylength ($r^2=0.21$ and $P=0.08$) and number of leaves of *Ardisia* plants was diminished with extended daylength ($r^2=0.31$ and $P<0.01$). Fall of *Clusia* leaves was positively correlated with evapotranspiration, and PPFD levels had a significant positive influence on the leaf count (proportion of maximum leaves) at this species. The only effects of meteorological parameters on *Hedyosmum* leaf phenology was the already mentioned significant positive correlation of PPFD and leaf length and a higher rate of leaf production with increasing daylength ($r^2=0.21$ and $P=0.08$).

4.3.4 Leaf phenology of fertilized plants

The influence of climatic parameters on leaf phenology of all three fertilized species changed compared to the control plants. Fertilized *Ardisia* plants showed a higher rate of leaf appearance and a lower rate of leaf fall, increasing the number of leaves as a proportion of maximum (Fig.16). Blade length of fertilized *Ardisia* leaves was increased, but leaf longevity did not change. Contrary to control plants, evapotranspiration and soil temperature significantly decreased longevity and the number of leaves (proportion of maximum) of fertilized individuals, respectively. Leaf fall increased with higher minimum humidity and lower evapotranspiration (Tab.6) in fertilized plants of *Ardisia*.

Fertilized *Clusia* plants had a decreased rate of leaf appearance, and an even stronger decrease of leaf fall, resulting in an enhanced number of leaves (proportion of maximum) compared to control plants (Fig.18). Leaf longevity and blade length did not change significantly. The number of leaves of fertilized *Clusia* still significantly increased with PPFD, but additionally with increased evapotranspiration and was negatively correlated with soil temperature and rainfall. Leaf blade length increased significantly with rainfall and elevated minimum humidity.

In fertilized *Hedyosmum* plants leaf fall levels remained more or less the same, however leaf appearance was increased, resulting in an increase of the number of leaves (proportion of maximum). Leaf longevity was significantly decreased in fertilized compared to control plants, but blade length remained unchanged (Fig.20). After fertilization leaf phenology of *Hedyosmum* plants became more dependent on temperature and water related meteorological parameters. Leaf fall was significantly increased in months with elevated air temperature (Tab.6) and extended daylength ($r^2=0.32$ and $P<0.05$). Number of leaves was significant positively correlated with evapotranspiration and negatively with soil temperature (Tab.6).

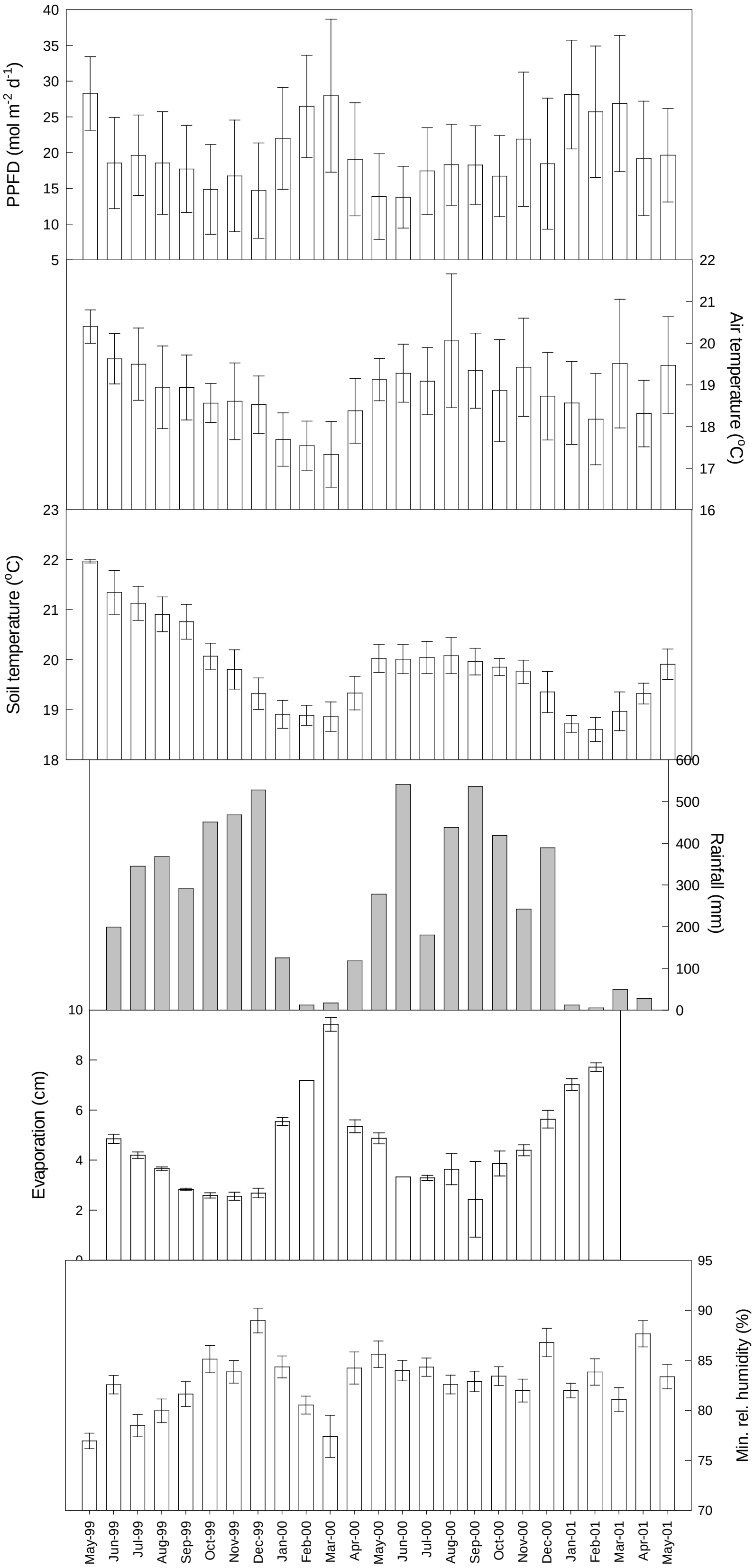

Fig.14 Monthly average values of integrated PPFD,mean air temperature, soil temperature, minimum relative humidity, monthly rainfall and evapotranspiration. Error bars represent standard deviations.

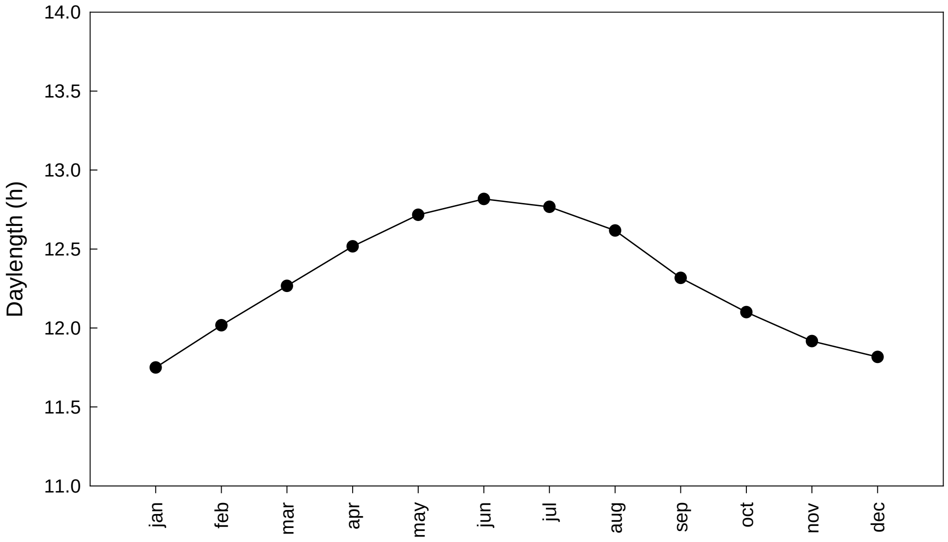

Fig.15 Theoretical monthly daylength in hours for the geographical location (09°13.794' N, 079°22.995' W) of the study site (Cerro Jefe). Data were calculated with Photosynthesis Assistant (Dundee Scientific, Dundee, U.K.) software for analysis of photosynthetic data. Values are means for each month.

Table 6 Correlations between climatic data of the corresponding month and leaf phenological parameters.

	dependent variable	independent variable	regression polarity	r^2	significance	*P*-value
Ardisia	rain	longevity	–	**0.62**	*	0.06
	evaporation	longevity	+	**0.52**	*	0.10
	soil temp.	appearance	–	0.50	**	0.05
	rain	appearance	–	**0.81**	***	<0.01
	air temp.	appearance	–	**0.53**	**	0.04
	evaporation	appearance	+	**0.64**	**	0.03
	soil temp.	leaf number	+	**0.61**	***	<0.01
	air temp.	leaf number	+	0.30	***	<0.01
	humidity	leaf number	–	0.20	**	0.04
	rain	blade length	–	0.50	*	0.07
	air temp.	blade length	–	0.45	*	0.07
	light	leaf count	+	0.19	**	0.03
Calophyllum	soil temp.	longevity	+	0.45	*	0.10
	air temp.	appearance	+	**0.90**	**	0.01
	evaporation	appearance	–	**0.89**	*	0.06
	soil temp.	leaf fall	–	0.38	**	0.01
	air temp.	leaf fall	–	0.29	**	0.04
	humidity	leaf fall	+	0.28	**	0.04
	evaporation	leaf fall	+	0.22	*	0.09
	air temp.	leaf number	+	0.12	*	0.08
Clusia	evaporation	leaf fall	+	0.38	**	0.02
	light	leaf number	+	0.19	**	0.03
Eugenia	soil temp.	leaf number	+	0.30	***	<0.01
	rain	leaf number	+	0.21	**	0.03
	evaporation	leaf number	–	0.25	**	0.02
Lysianthus	light	longevity	–	0.24	*	0.07
	humidity	longevity	+	0.25	*	0.07
	air temp.	leaf fall	–	0.24	*	0.07
	soil temp.	leaf number	+	0.21	**	0.02
	rain	leaf number	+	0.38	***	<0.01
	light	leaf number	–	0.12	*	0.09
	evaporation	leaf number	–	0.47	***	<0.01
	rain	blade length	+	0.38	**	0.03
	air temp.	blade length	+	0.47	***	<0.01
	light	blade length	–	0.29	**	0.05
	evaporation	blade length	–	0.49	***	<0.01
Hedyosmum	light	blade length	+	0.31	**	0.04
Ardisia fert.	evaporation	longevity	–	**0.58**		0.13
	humidity	leaf fall	+	0.45	*	0.07
	evaporation	leaf fall	–	**0.62**	*	0.06
	soil temp.	leaf number	–	0.12	***	<0.01
Clusia fert.	soil temp.	leaf number	–	0.33	***	<0.01
	rain	leaf number	–	0.21	**	0.03
	light	leaf number	+	0.17	**	0.04
	evaporation	leaf number	+	0.19	**	0.05
	rain	blade length	+	0.42	**	0.02
	humidity	blade length	+	0.37	**	0.04
Hedyosm. fert.	soil temp.	leaf number	+	0.24	*	0.09
	air temp.	leaf fall	+	0.22		0.11
	soil temp.	leaf number	–	**0.53**	***	<0.01
	evaporation	leaf number	+	0.20	*	0.09
	humidity	blade length	–	0.44	**	0.01

*** $P < 0.01$
** $P < 0.05$
* $P < 0.1$

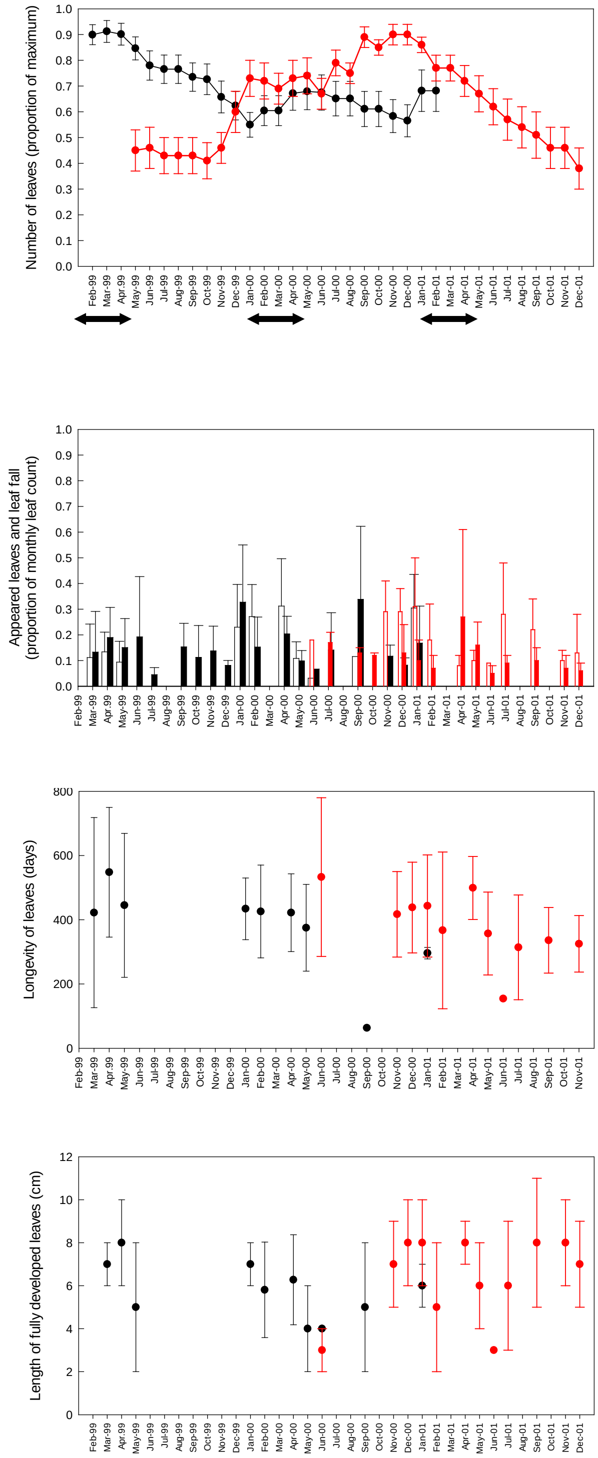

Fig.16 Monthly number of leaves as a proportion of the maximum, leaf appearance (open bars) and leaf fall (closed bars) as a proportion of the monthly leaf count, longevity of leaves and leaf blade lenght of fully developed leaves for control (black) and fertilized (red) *Ardisia* plants. Error bars represent standard error for the number of leaves and standard deviation for all other parameters. Arrows indicate dry season period.

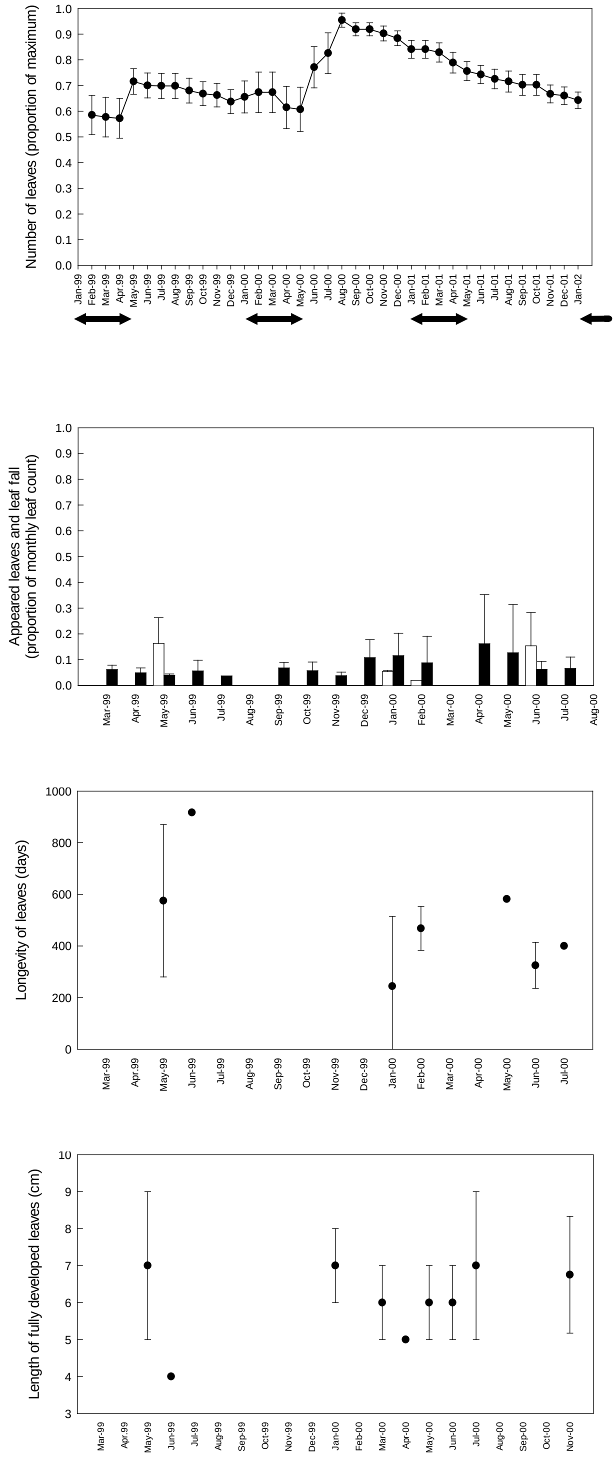

Fig.17 Monthly number of leaves as a proportion of the maximum, leaf appearance (open bars) and leaf fall (closed bars) as a proportion of the monthly leaf count, longevity of leaves and leaf blade lenght of fully developed leaves for *Calophyllum* plants. Error bars represent standard error for the number of leaves and standard deviation for all other parameters. Arrows indicate dry season period.

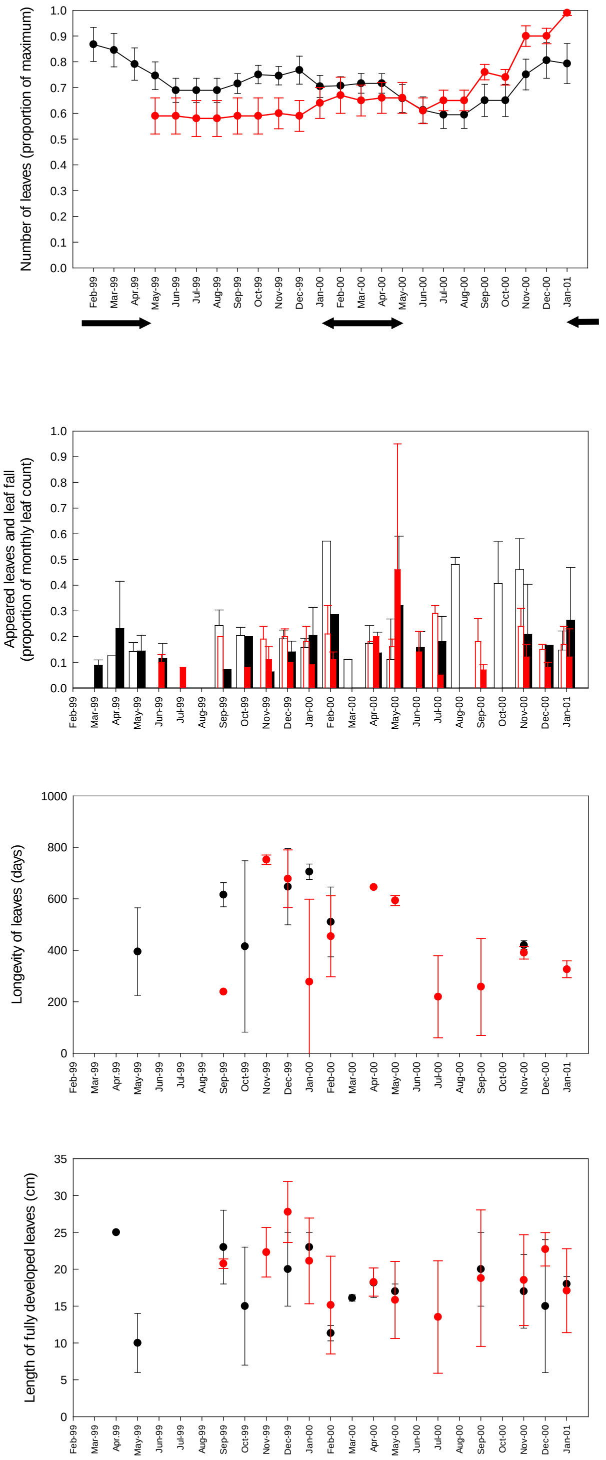

Fig.18 Monthly number of leaves as a proportion of the maximum, leaf appearance (open bars) and leaf fall (closed bars) as a proportion of the monthly leaf count, longevity of leaves and leaf blade lenght of fully developed leaves for control (black) and fertilized (red) *Clusia* plants. Error bars represent standard error for the number of leaves and standard deviation for all other parameters. Arrows indicate dry season period.

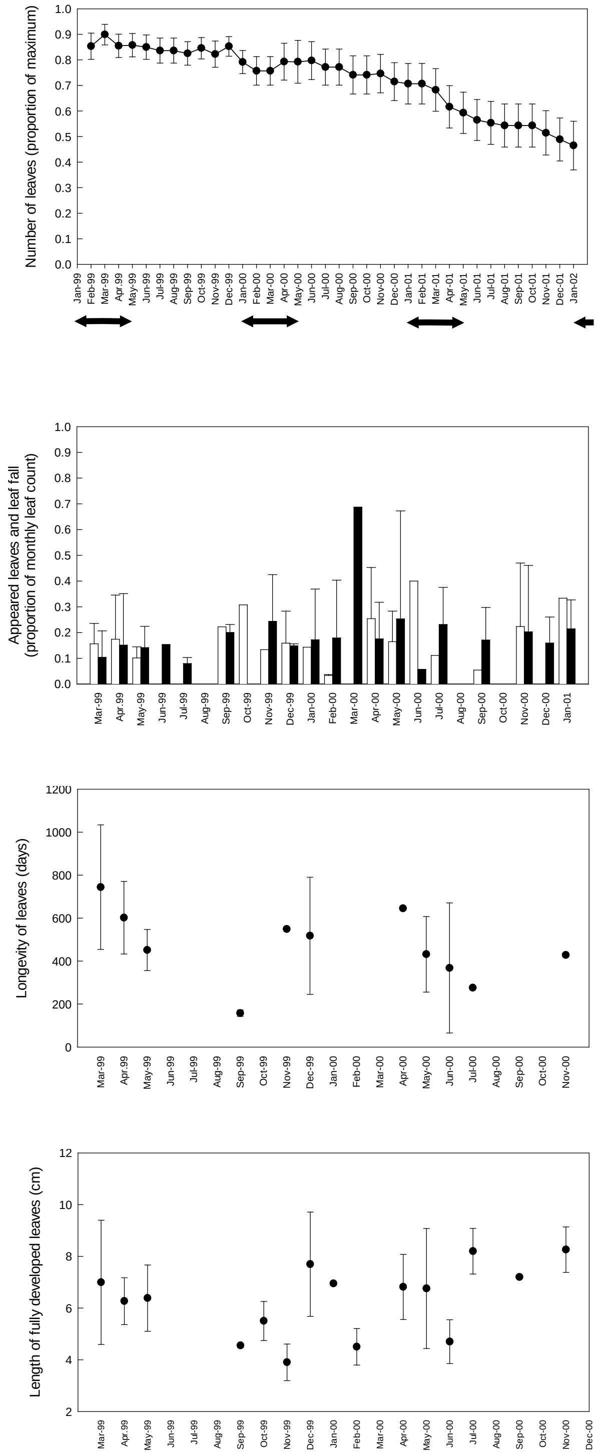

Fig.19 Monthly number of leaves as a proportion of the maximum, leaf appearance (open bars) and leaf fall (closed bars) leaves as a proportion of the monthly leaf count, longevity of leaves and leaf blade lenght of fully developed leaves for *Eugenia* plants. Error bars represent standard error for the number of leaves and standard deviation for all other parameters. Arrows indicate dry season period.

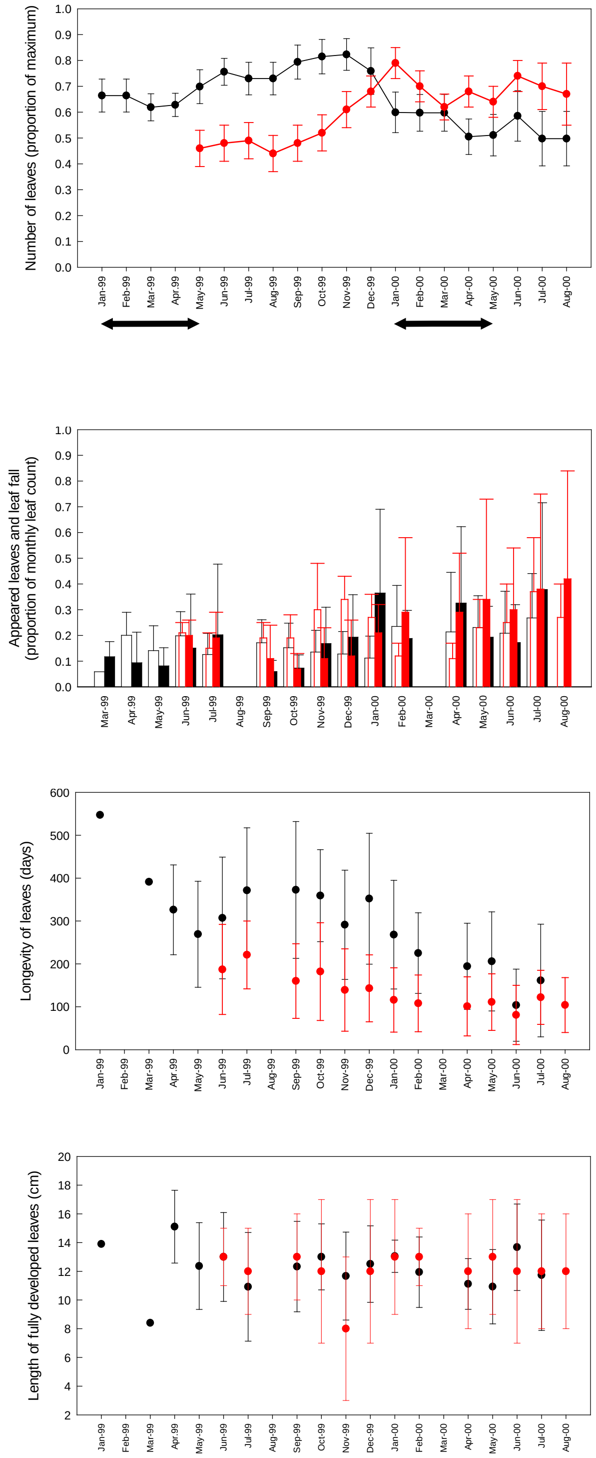

Fig.20 Monthly number of leaves as a proportion of the maximum, leaf appearance (open bars) and leaf fall (closed bars) as a proportion of the monthly leaf count, longevity of leaves and leaf blade lenght of fully developed leaves for control (black) and fertilized (red) *Hedyosmum* plants. Error bars represent standard error for the number of leaves and standard deviation for all other parameters. Arrows indicate dry season period.

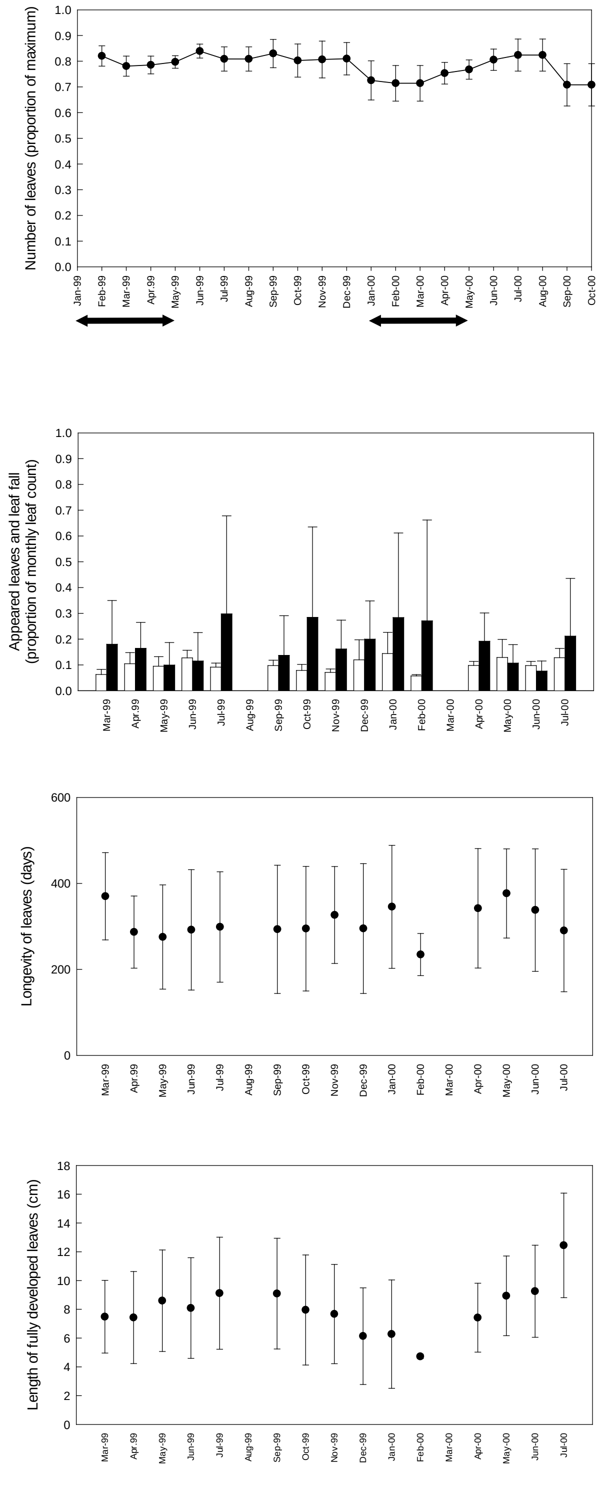

Fig.21 Monthly number of leaves as a proportion of the maximum, leaf appearance (open bars) and leaf fall (closed bars) as a proportion of the monthly leaf count, longevity of leaves and leaf blade lenght of fully developed leaves for *Lysianthus* plants. Error bars represent standard error for the number of leaves and standard deviation for all other parameters. Arrows indicate dry season period.

4.4 Discussion

4.4.1 Meteorological relations

Generally, climatological parameters clearly show a distinct dry season at the montane study site. Despite the strong horizontal precipitation, mainly at night (personal observation), there were differences in integrated water related parameters. Soil water content was measured on 14 Nov. 1999 (rainy season) and 11 Apr. 2000 (dry season). It did not show significant differences (data not shown), however a slight trend of lower water content in the upper soil layer could be registered during the dry season.

Most of the significant relations between meteorological parameters obtained in this study are self-explaining and there is no need to discuss them further. Examples are the increase in soil temperature with increasing air temperature, decrease of rainfall and minimum humidity with higher light (PPFD) levels and increased evapotranspiration.

However, some relations are not completely clear at the first sight. Soil temperature increased with rainfall, and decreased with minimum humidity and evapotranspiration. A similar picture is evident from increasing air temperatures with higher rainfall and lower evapotranspiration. These phenomena could be related to the stronger and more frequent cloud cover during rainy periods, on the one hand hindering increased cooling during cloudless night periods, on the other hand enhanced storage of heat in water-saturated soils during day periods and slow release at night. Furthermore, soil and air temperature were strongly positively correlated with daylength, suggesting that extended time of daylight have a stronger positive influence on temperature parameters than the possibly negative effect of an increased cloud cover.

4.4.2 Leaf phenological characteristics

4.4.2.1 Control plants

The dry season in the Cerro Jefe montane cloud forest was not very pronounced compared to seasonally dry lowland forest sites in Panama but still exerted an influence on leaf phenology of tree species. Trees were all of evergreen habit, nevertheless some significant relations of meteorological and phenological characteristics could be found. Rooting characteristics of the single species was not examined, but the general observation was that most of the species are shallow rooters extending their roots only into the upper few centimeters of the soil profile. In contrast, root systems of evergreen trees are generally described to reach deeper soil layers. However, within evergreen species smaller trees showed a larger decline in predawn water potential than larger trees during the dry season (Eamus 1999). A possible explanation for the shallow rooting of evergreens at Cerro Jefe, could be the anaerobic conditions in the finely structured clayish soil, due to water logging and the lack of N (data not shown) in deeper soil layers. Thus, roots mats were mainly concentrated on the soil surface, resulting in a possible drying of roots during extended rainless periods. Drought exerted a negative influence on leaf phenology of semi-deciduous plant species in ecosystems with more extensive dry periods, like in some lowland tropical forests and savannas (Schaik et al. 1993, Eamus 1999, Eamus and Prior 2001). For such ecosystems, any seasonality of rainfall (from one to eight months) has been demonstrated to have the most significant impact on structure and function of these ecosystems. It determines phenology, growth patterns and physiological behavior of the vegetation (Eamus 1999). A similar impact can at least be suggested for *Calophyllum*, *Lysianthus* and *Eugenia*, as supported by the significant correlations of leaf phenological and water related parameters (Tab.6). On the other hand, no clear relation of such kind could be found for *Clusia* and *Hedyosmum* plants, pointing to other mechanisms regulating leaf fall and flush. Furthermore, in *Ardisia* even a negative effect of water related parameters on leaf phenology and a positive influence of light was evident suggesting stronger a dependency on levels of irradiance than on water status (Wright and van Schaik 1994). Temperature related parameters also had an effect on phenology of *Ardisia*, *Calophyllum*, *Lysianthus* and *Eugenia*. In a Mexican tropical lower montane forest, increasing air temperature triggered leaf flush of deciduous species (Williams-Linera 1997, 1999). A similar effect was only observed for *Calophyllum* plants. However, this effect could also be related to an extended daylength inducing leaf production that covaried with temperature. *Lysianthus* showed increased leaf fall with decreasing temperatures and shortened daylength and *Ardisia* exhibited the opposite pattern. Leaf appearance was diminished with rising air temperatures, again suggesting another parameter as determinant for leaf phenology for this species. This phenomenon is probably linked to a significant decrease of the number of leaves (proportion of maximum) with extended daylength.

There exists an extensive discussion in the literature about what could be the most important abiotic, biotic or endogenous factor determining phenology of plants. The more uniform the conditions are, the clearer clusters of phenologies are developed. In a wet tropical forest, light is probably the most apparent trigger for leaf production, as described for understory plants (Barone 1998). In strong seasonally dry habitats, water will become the factor controlling most of the phenological processes. It is obvious, that there are several possibilities of combinations in between such extremes. The more diverse the environments (between such climatic opposites) are, the more different combinations of phenological characters occur in the same ecosystem.

The cause of such variation in timing and intensity of leaf dynamics has been much debated (Reich et al. 1995b, Wright 1996). Day length (Opler et al. 1976, Bullock and Solis-Magallanes 1990), temperature (Specht 1986), vapour pressure deficit (Wright and Cornejo 1990, Duff et al. 1997) and irradiance (Wright and van Schaik 1994, Wright 1996) have all been identified as environmental triggers controlling leaf fall and leaf flush. However, Reich and Borchert (1982, 1984), Borchert (1991, 1994a, b) and Reich (1995) strongly argue for endogenous control of plant phenology that is secondarily subject to environmental perturbation and modulation.

The results allow suggestions on phenological patterns being internally programmed, but triggered by external factors like the here in this study examined climatic ones, but possibly also by biotic factors as the in the literature described herbivoral pressure (Schaik et al. 1993). This plasticity would also represent the most effectively strategy to persist non-periodic environmental fluctuations like hurricanes or the “El Niño” phenomenon (Scatena 2001).

At the Cerro Jefe montane cloud forest site, light seems not to be the major restricting or triggering factor as in more closed lowland forests (Wright and van Schaik 1994), however some effects of light were statistically significant. Water status and temperature are rather the triggers for leaf phenological processes, as indicated by cumulated influence in all examined tree species (Tab.6). It has to be considered that the temperature effect could also be a masked effect of an extended daylength inducing leaf production in some of the analysed plants. Inductive low-energy phytochrome control of development was demonstrated to have an effect on phenological processes, however the detailed mechanisms of phytochrome action are incompletely understood (Jones 1992). In spite of additional water supply through horizontal precipitation especially in the drier periods, some species seem to be affected by drying topsoil, having an effect on these trees due to the especial situation of the soil and resulting physiognomy of the roots.

In some plants however, endogenous leaf phenology patterns can persist external influences and those follow relatively static leaf appearance and fall dynamics. This is evident in the genus *Hedyosmum* that flushes and drops leaves throughout the year, apparently independent of the site climatic characteristics or other influences. The only positive effect on leaf appearance was found to be related to increased daylength. *Hedyosmum mexicanum* in Mexico has the same leaf phenological pattern as *Hedyosmum bomplandianum* (this study) and *Hedyosmum arborescens* in Jamaica, despite growing at climatically different sites, especially concerning precipitation (Mexico, approximately 1500 mm; Panama, approximately 3500 mm) (Williams-Linera 1997, 1999, 2000). At the Cerro Jefe montane forest site, different strategies of leaf phenology occur side by side. Internal mechanisms are proposed as determinants for the phenology (as shown for *Hedyosmum*), which are in some cases triggered or modulated by water related parameters (as demonstrated for *Calophyllum*, *Eugenia* and partly for *Lysianthus*), or temperature related parameters (*Calophyllum*, *Lysianthus* and the opposite effect at *Ardisia*) and for some species irradiance was a additional weak factor influencing specific leaf phenological parameters (*Clusia*, *Lysianthus* and indirectly *Ardisia*).

The presented relations of climatic factors and leaf phenology were statistically significant, however some results were relatively weak and also changed markedly after fertilization of three species (*Ardisia*, *Clusia* and *Hedyosmum*). Moreover, it has to be considered that climatic parameters were strongly interrelated, therefore some relations with leaf phenology could also be masked or resulting from such interrelations.

4.4.2.2 Fertilized plants

Leaf phenology patterns of the three fertilized species significantly changed compared to control plants. Fertilization increased leaf appearance of *Ardisia* and *Hedyosmum*, while leaf fall rates remained more or less unchanged. The leaf count reached a distinct maximum followed by an increase of leaf fall, subsequently decreasing the number of leaves. A possible explanation is an induction of leaf production due to a relieve of a nutrient limiting situation, followed by an increased leaf turnover apparent in a higher rate of leaf fall. Leaf phenology of fertilized *Ardisia* plants was furthermore characterized by an increase in leaf blade length linked to a higher SLA. A faster leaf turnover as a result of an increased nutrient supply can be perceived in the significant lower leaf longevities of fertilized *Hedyosmum* plants. Fertilized *Clusia* plants showed a similar trend in the number of leaves pattern, during the experimental time as the control plants. The increase of number of leaves with both treatments towards the end of the study however, could be a reaction to increased leaf flushing and reduced leaf fall due to higher light levels with beginning of the dry season.

After fertilization, mainly temperature related factors had an effect on leaf phenology of *Hedyosmum* plants and water-related parameters correlated significantly with leaf fall of fertilized *Ardisia* plants. In contrast, in control *Ardisia* plants leaf appearance was correlated with temperature and water related parameters. This suggests that after relieving nutrient limitation, which also affects leaf production, climatic triggers began to control fall of leaves that became increasingly overshaded.

Eamus (1999) published a cost-benefit analysis for evergreen and deciduous species. This approach assumes that plant structures have costs and benefits associated with them. Leaves are costly to produce and maintain, however, the benefit is a positive leaf lifetime carbon gain. Leaves on lower branches are often shed when shaded as cost-benefit balance becomes negative. It was also postulated that when leaf longevity increases, construction costs of the more resistant leaf also rise. Photosynthetic capacity of leaves with extended longevities is usually lower but on a lifetime scale do not differ from short-lived species. This analysis could possibly be applied to the fertilized trees of this study. All three species together showed fertilizer responses that could be interpreted as representing a shift in cost-benefit relationship after reducing the cost of N acquisition in fertilized plants. SLAs increased at all three species, leaf longevity of *Hedyosmum* decreased, trends in induced photosynthetic capacity could be observed at least for *Hedyosmum*, a trend to increasing leaf blade length was evident in *Ardisia*, leaf appearance was enhanced for certain periods in two species, followed by an increased rate of leaf fall due to overshading. Although, the results show only trends, it is detectable that a small-scale shift in cost-benefit relations, after N cost relief, occurred. Fertilization possibly had an effect on endogenous processes of the studied species, changing the affinity of phenology being triggered by specific climatic parameters. This is suggested as a supplementary evidence for the endogenous control of phenology at plants. Further experiments of that kind on a longer time scale are necessary to test whether and to what extent it is possible to model the cost-benefit balance of leaves in relation to phenological patterns and its intrinsic controls.

5. Conclusion

5.1 Prediction of carbon gain from short-term photosynthesis and leaf N

Diel leaf carbon gain and maximum potential photosynthetic capacity of the three studied montane species were similarly significantly correlated as for 8 tropical lowland species in Panama (Zotz and Winter 1993). This was, due to the low light saturation points of the montane plants, reaching maximum photosynthesis levels most time of the day.

Annual carbon gain of the studied montane species was also high significantly correlated with average leaf nitrogen. It was even possible to fit the data points of this study to the correlation of the seasonal lowland forest plants (Zotz and Winter 1994c). Explanation for this close linear relationship was the similar long-term N-use efficiencies of montane and lowland site plants.

These two prediction methods could therefore be applied to the montane species, confirming the general validity of these concepts. However, similar relationships from other sites in the tropics would be useful to reinforce the efficacy of these advantageous methods.

5.2 Photosynthetic capacity and nutrient relations

Photosynthetic capacity of plants at the montane site was not influenced by leaf nutrients other than N and P. This two elements did significantly determine photosynthetic capacity, however the extended results allow further more detailed conclusions about which of this nutrients had the stronger effect on primary production of plants. A new projection using N:P ratios relations with photosynthetic capacity and thereafter quantifying the influence of the single nutrient within such a ratio, provided strong evidence that N was limiting plant productivity at the studied montane site compared to two lowland sites. This was further supported by the more negative $\delta^{15}N$ values in leaves of montane plants mirroring the situation in the younger ^{15}N depleted and N poor soils at this site. In contrast, no clear relation between the analysed parameters at the two compared lowland sites could be found. The only exception was that at the primary lowland site photosynthetic capacity was significantly related with potassium, suggesting this nutrient as a possible limiting factor at this site. Other analysed nutrients did not show any relationship with photosynthetic capacity and are therefore excluded from nutrient limitation discussions.

5.3 Carbon balance and nitrogen content during leaf ontogeny

Photosynthetic parameters at *Clusia* plants were significantly related with PPFD and leaf N content. Carbon gain of *Hedyosmum* correlated significantly with PPFD, suggesting irradiance levels as an additional important determinant for photosynthesis at Cerro Jefe montane plants. Light became a stronger photosynthesis determining factor in fertilized plants after the influence of possibly restricting N levels was excluded. However, N was luxuriously accumulated in the leaves of fertilized plants without a significant increase of photosynthetic parameters, changing the relationship of leaf N and annual carbon gain, but not affecting the possibility of predicting carbon gain from short term photosynthesis measurements (A_{max}).

5.4 Adaptations of leaf phenology to seasonality

Generally, leaf phenology of the evergreen tree species seems to be endogenously determined. However, the examined montane site plants show a seasonal pattern and some climatic factors apparently trigger leaf phenological mechanisms depending on the different species. Water related parameters (monthly rainfall, evapotranspiration and min. relative humidity) triggered leaf phenological patterns of *Calophyllum*, *Eugenia*, *Clusia* and *Lysianthus*, temperature related parameters (air and soil temperature) influenced leaf phenology of *Ardisia*, *Calophyllum*, *Lysianthus* and *Eugenia* and light levels had an effect on the phenology of *Clusia*, *Lysianthus* and *Ardisia*. *Hedyosmum*, as described before for that genus, was the only plant that showed continuous leaf production and fall without any pattern caused by climatic factors, suggesting a solely internal regulated leaf phenology. This genus belongs to the family of the Chloranthaceae and order of the Laurales representing an ancient taxonomical group. This could be a possible explanation for the relatively indifferent leaf phenological pattern, but also for the photosynthetical and leaf nutrient characteristics corresponding to a pioneer plant pattern. Fertilization did not induce major changes the leaf production characteristics of the analysed tree species. However, results were not completely clear, nutrient limitation of leaf phenology at least for *Ardisia* and *Hedyosmum* were carefully discussed. This two studied tree species reacted to fertilization with increased SLA and faster leaf turnover. *Ardisia* showed trends in increased leaf blade length and leaf longevity of *Hedyosmum* plants was reduced as a result of fertilization. A further indication for internal determination of primary production adapted to prevailing conditions was the pronounced accumulation of N in leaves of all fertilized species, with hardly any quantitative response in photosynthetic and leaf phenological parameters.

5.5 Synopsis

The Cerro Jefe tropical montane forest represents a valuable and worth preserving ecosystem that occurs comparably on surrounding mountain ridges. As mentioned above such landscapes are important as water sources for rivers, but also act as refuges for organisms from lower surrounding and more intensively anthropological exploited areas.

This study showed that short term photosynthetic capacity of plants at the Cerro Jefe site is influenced by the amount of leaf N concentrations mirroring the N available in the system. On a long term photosynthetical parameters (A_{max} and A_{24h}) were also influenced by leaf N concentrations for two out of three tree species and light was additionally a determining factor. Light did also influence leaf phenology of some of the studied tree species along with water related parameters and temperature. However, despite fertilization, growth of trees did not significantly respond to the higher availability of nutrients, except with a pronounced accumulation on N in leaves, without a detectable change in leaf productivity in study periods. Only one species (*Hedyosmum*) responded to fertilization with slightly higher photosynthetic capacity and carbon balance in very young leaves, but with decreased leaf longevity. Moreover leaf phenological traits were altered following fertilization, indicating a possible shift in the leaf cost-benefit balance towards light and water related parameters after mainly N limitation relief.

No intrinsic single factor could be detected that was strongly limiting leaf productivity of the studied plants. It was rather a compound effect of several different parameters on plant growth. Relationships of abiotic factors and productivity could however, only be demonstrated on leaf basis. In the future, it will be necessary to perform similar studies on whole plant level to find out about sink and sources and their influence on plant growth. Additionally, scaling up to ecosystem level is essential to understand the interactions and structure of the montane vegetation. Furthermore the effect of others, not in this study included abiotic and biotic parameters as wind, horizontal precipitation, herbivory, mycorrhizae and microbial soil activity will allow more detailed conclusions on plant productivity of tropical montane forests. However, this study already pointed some ecophysiological particularities of such systems out, hence, there is no doubt about the conservation and protection value of such tropical montane forests.

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7. Summary

An ecophysiological approach on a montane tropical forest on Cerro Jefe (Panama) was performed, to describe the photosynthetical characteristics, nutrient relations and leaf phenological patterns of typical plants on different time scales.

The first part of the study was dedicated to the potential photosynthetical capacity of montane plants and their relation to leaf nutrient characteristics, compared with two lowland forest sites, differing in succession and water availability. A new and more precize method in detecting nutrient limitation was developed, using correlations of photosynthetic capacity with nutrient ratios and quantifying the influence of the single nutrient within such ratios. A combination of the results with soil mineral analyses and nitrogen isotope ratios, indicating that the montane site is depleted in ^{15}N, give strong evidence, that plants at the studied montane site are primary nitrogen limited. Applying the from the literature already established method of the correlation significance of photosynthetic capacity with a single nutrient, photosynthesis at the montane site and the secondary lowland forest would thereafter be N and P, and the primary lowland site be N and K co-limited. Some of these results are contradictory to general models of nutrient limitation in the tropics and are therefore discussed carefully.

A second part of the study was dedicated to the photosynthetic capacity, carbon gain and leaf N concentrations of three tropical montane tree species on an ontogenetic basis. The results obtained, confirmed two methods of predicting carbon gain of plants, with much less time consuming measurements, for the first time for tropical montane plant species. Annual carbon gain can be predicted from mean leaf N concentration although on montane forest trees at a natural stand, and daily carbon assimilation can be predicted with short-term measurements of photosynthetic capacity. There is evidence that leaf N has an influence on photosynthetic parameters at least for two analysed tree species. Light was related to photosynthetic parameters of *Clusia* and *Hedyosmum* especially after a possible N limitation was removed. However, photosynthesis was saturated at very low light levels, resulting in the highly significant correlation of photosynthetic capacity and daily carbon and the confirmed prediction method. Fertilized plants showed a luxurious accumulation of leaf N, without significant response in photosynthesis.

The third aspect of the study dealt with the leaf phenology of six tree species and their dependence on climatic triggers. All studied species were evergreen, but nevertheless showed some fluctuation in leaf production and fall. *Calophyllum*, *Lysianthus* and *Eugenia* leaf phenology was negatively influenced by drought parameters suggesting the dry season period as a trigger for leaf fall and the rainy season for leaf production. *Ardisia* showed the opposite

pattern concerning water related parameters, additionally there was a significant positive influence of light on the number of leaves, suggesting this parameter as a positive trigger for this species. Increasing of air and soil temperature were positive triggers for production of *Calophyllum* leaves and a decrease of air temperature enhanced leaf mortality of *Lysianthus* plants. However, potential geographical daylength was positively related to air and soil temperature and could have a masked influence on leaf phenology. Leaf phenology is suggested to be internally programmed, in addition triggered by external factors. Some climatic influences changed markedly after fertilization for the single plant species. However, a single factor that was valid for a majority of the analysed tree species could not be found. Nonetheless, a shift in leaf cost-benefit balance after fertilization can be suggested Apparently, the interrelation of these climatic parameters and the relatively weak seasonality masked a clear effect on the leaf phenology of this montane forest species.

8. Abbreviations

$\delta^{13}C$	ratio of $^{13}C/^{12}C$
$\delta^{15}N$	ratio of $^{15}N/^{14}N$
$^{13}CO_2$	carbon dioxide with ^{13}C carbon
^{15}N	stable isotope of nitrogen
A_{24h}	carbon gain, netto diel CO_2 assimilation
Al	aluminum
A_{mass}	CO_2 assimilation on leaf mass basis
m.a.s.l.	meters above sea level
Fig.	figure
Tab.	table
A_{max}	photosynthetic capacity, maximum CO_2 assimilation under saturating light
ANOVA	analyses of variance
B	boron
C	carbon
C_3	plants performing CO_2 assimilation via the ribulose bisphosphate (phosphoglyceric acid) pathway
Ca	calcium
CAM	crassulaceae acid metabolism, CO_2 fixation at night via the phosphoenolpyruvate pathway
CO_2	carbon dioxide
Cu	copper
Fe	iron
H	hydrogen
HP	horizontal precipitation, condensing mist
IGN	Instituto Geográfico Nacional
IRGA	ifra red gas analyser
ITCZ	inter tropical convergence zone
J_{max}	light-saturated rate of electron transport
K	potassium
LAR	leaf area ratio
LED	light emitting diode
Mg	magnesium
Mn	manganese
Mo	molybdenum
N	nitrogen
Na	sodium
P	phosphorus
PFD	photon flux density
p_i/p_a	ratio of partial intercellular/ambient CO_2 pressure
PNM	Parque Nacional Metropolitano
PNUE	photosynthetic nitrogen use efficiency
PPFD	photosynthetic photon flux density
PPUE	photosynthetic phosphorus use efficiency
Rubisco	ribulose bisphosphate carboxilase/oxigenase
S	sulfur
SD	standard deviation
SLA	specific leaf area
TMCF	tropical montane cloud forest
UV-B	ultra violet light of 280-350 nm
Vc_{max}	maximum rate of carboxylation
Wt	weight

9. Zusammenfassung

Zur ökopysiologischen Charakterisierung eines montanen tropischen Regenwaldes wurden Photosyntheseaktivität, Blatt-Mineralstoffgehalte und Blattphänologie ausgesuchter typischer Bergregenwaldarten untersucht.

Der erste Teil der Studie beschäftigte sich mit der potentiellen Photosynthese-Kapazität montaner Pflanzen und ihrer Abhängigkeit von den Blattmineralstoffgehalten, wobei auch ein Vergleich mit Pflanzen zweier Tieflandstandorte gezogen wurde. Dabei wurde eine neue, sensiblere Methode zur Erfassung von Nährstofflimitierungen entwickelt, die darauf abzielt aus Korrelationen der Photosynthesekapazitäten mit den Nährstoffverhältnissen den Einfluss der einzelnen Nährstoffe zu quantifizieren. Eine Kombination dieser Aussagen mit Ergebnissen von Bodenmineralstoffanalysen sowie mit den N-Isotopen Verhältnissen in den Blättern, die eine Abreicherung an ^{15}N anzeigen, deuten stark auf eine N Limitierung des montanen Standortes hin. Nach dem in Literatur bekannten Korrelationsverfahren der Photosynthesekapazität mit den Gehalten der einzelnen Mineralstoffen in den Blättern würden der montane und der sekundäre Tiefland-Standort durch N und P limitiert und der primäre Tieflandwald durch N und K kolimitiert sein. Einige dieser Ergebnisse widersprechen allerdings etablierten Nährstofflimitierungsmodellen und werden deshalb mit Vorsicht diskutiert.

Im zweiten Teil der Studie wurden die Photosynthesekapazität, der Kohlenstoffgewinn und die Blatt-Stickstoffkonzentrationen von drei tropischen Bergregenwaldbaumarten für die gesamte Blattlebensdauer bestimmt. Die Ergebnisse bestätigen die Verwendbarkeit zweier Methoden zur Bestimmung des Kohlenstoffgewinnes anhand von Kurzzeitmessungen erstmalig an einem Montanstandort: So können einerseits Jahreskohlenstoffbilanzen aus Blattstickstoffbestimmungen und andererseits Tageskohlenstoffbilanzen durch Korrelationen mit Photosynthesekapazitäten erhalten werden. Die Blatt-Stickstoffkonzentrationen scheinen einen Einfluss auf die Photosynthesekapazitäten von zwei der untersuchten Baumarten zu haben. Nachdem eine mögliche N-Limitierung durch Düngung abgeschwächt wurde, wuchs der Einfluss von Licht auf die Photosynthese von *Clusia* und *Hedyosmum*. Gedüngte Pflanzen hatten höhere N-Konzentrationen in den Blättern, die Photosyntheseraten blieben jedoch unverändert.

Der dritte Teil der Studie beschäftigte sich mit dem Einfluss von Klimafaktoren auf die Blattphänologie von 6 Bergeregenwaldarten. Alle Arten waren immergrün, zeigten aber dennoch saisonale Schwankungen in der Blattproduktion und im Laubabwurf.

Während bei *Calophyllum*, *Lysianthus* und *Eugenia* durch Trockenheit der Laubabwurf hervorgerufen wurde, war andererseits die Blattproduktion von *Ardisia* in der Trockenzeit angeregt und es bestand eine Abhängigkeit der Blattproduktion vom Licht. Höhere Temperaturen hatten einen positiven Einfluss auf die Blattproduktion von *Calophyllum*. Generell scheint die Blattphänologie endogen gesteuert zu sein, allerdings hatten klimatische Parameter teilweise signifikante Einflüsse auf die Blattproduktion. Einige dieser Einflüsse veränderten sich bei den gedüngten Pflanzen. Dies deutet auf eine Verschiebung der Kosten-Nutzen Bilanz nachdem eine Nährstofflimitierung durch Düngung ausgeschlossen wurde.

10. Curriculum vitae

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Studium:

89-90	Maschinenbau an der Technischen Universität Wien
90-98	Biologie an der Universität Wien, Studienzweig Ökologie**,** Schwerpunkt Tropenbiologie
97-98	Diplomarbeit**:** "*Kohlenstoff- und Stickstoffhaushalt tropischer Bäume bei unterschiedlichen Lichtverhältnissen*", an der Abteilung Chemische Physiologie der Pflanzen, Institut für Ökologie und Naturschutz der Universität Wien, Erlangung des Titels Mag. rer. nat.
06/97-08/97	Feldarbeit in Panama für die Diplomarbeit Stipendium der Universität Wien für kurzfristige Arbeiten im Ausland
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Wien, im September 2002 Mag. Richard Gottsberger