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Stand structure and tree increment of a tropical lowland rainforest in Costa Rica

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ABSTRACT

Given the proceeding change in global climate little is known yet on how tropical forest ecosystems will react - ecosystems which are known for storing large amounts of carbon in their vegetation and soils because of their high productivity. Latest results differed whether tropical forests will still act as carbon sinks or on the contrary will become carbon sources under global change. Analyzing growth patterns and therefore carbon accumulation in different forest sites along with climatic parameters is one possible strategy to find out more about future scenarios of tropical rainforest responses. This study focused on diameter at breast height (dbh) and aboveground biomass (AGB) growth at three sites differing in topographic and successional conditions. A secondary slope forest, a primary slope forest and a primary ridge forest in the Esquinas Rainforest, Costa Rica were investigated for differences in dbh and AGB increments, forest structure and microclimate. Stand structure turned out not to be significantly different while microclimate differed in minimum soil temperature being lowest in the primary ridge forest and lowest maximum air temperature in the primary slope site. Tree growth rates according to sites, family level, dbh and height size classes, months, years and various climatic factors such as rainfall, air temperature, number of dry days or multivariate ENSO index were analyzed with data collected over 5 years. Mean annual dbh increment (averaged over 5 years) in the Esquinas rainforest was very high, i.e. 3.72 ± 0.23 mm for trees with $\text{dbh} > 10$ cm and 1.22 ± 0.07 mm for trees with $\text{dbh} < 10$ cm. Successional stage played a considerable role as the secondary site showed significantly higher gain in tree increment than the primary sites due to large contributions of fast growing pioneer species. Interactions between growth patterns and interannual climate were investigated but no significant correlation between tree increment and ENSO phases could be demonstrated. A time delay of the effect of rain fall and dry days per month on AGB increments could be proved, while air temperature had little effect. The data therefore indicate that forests in different topographic positions are differently sensitive to intra- and interannual changes in climate, and therefore are expected to differently respond to future climate change.

KEYWORDS

Climate change, diameter growth rate, tropical rainforest, AGB increment, ENSO, forest structure, microclimate

1. GENERAL INTRODUCTION

1.1 “The climate and the primate” - Global climate change effects in the tropics

The Intergovernmental Panel on Climate Change (IPCC) describes the ongoing climate change amongst others as follows:

Global mean surface temperature has increased by +0,74 °C over the past century, while the concentration of carbon dioxide in the atmosphere rose 35 %, namely from 280 ppm in the year 1750 to 379 ppm in the year 2005. It increased 78 % because of using fossil fuels and 22% because of changes in land use e.g. forest clearance (http://www.awi.de/de/aktuelles_und_presse/ausgewaehlte_themen/klimawandel/ipcc_bericht_2007/zusammenfassung/ 28.06.2010).

The latter is a major source not only of carbon dioxide but also of other greenhouse gases like methane and nitrous oxide- all of them principle causes of global warming (2004, Houghton, 1991, Fearnside, 2000). Future scenarios predict that precipitation is likely to rise in higher latitudes, while in the tropics and subtropics (plus Mediterranean regions) climate change probably leads to decreasing rainfall (http://www.awi.de/de/aktuelles_und_presse/ausgewaehlte_themen/klimawandel/ipcc_bericht_2007/zusammenfassung/ 28.06.2010). And actually for the global tropical land region an anticorrelation of mean surface temperature and precipitation has been found over the past two decades: years of peaks in temperature were also years of abnormally low rainfall (Keeling et al., 2005, Los et al., 2001). However, within the tropics long-term rainfall trends vary strongly (Malhi and Wright, 2004), and so finally does the relationship between rainfall and temperature. Wet forests with low seasonality for example showed peak temperatures during strong El Nino events but no change in precipitation (Clark, 2004). Additionally, studies have shown that temperature increased mostly because the daily minimum temperature rose, the increase being about twice as fast as the daily maximum temperature since 1950, which in fact leads to a diminished diurnal temperature range (Easterling et al., 1997, Vose et al., 2005).

Little is known about the change of total amount or quality of photosynthetically active radiation (PAR) in tropical rainforests, although light was found to be the main controller of CO₂ exchange, accounting for 48% of the variance in net ecosystem CO₂ exchange (Goulden et al., 2004) and in

forests with very mild drought stress (La Selva, CR) variations in PAR have been found to be tightly associated to interannual variation in stem growth (Clark and Clark, 1994).

Data from ground stations indicated declining global incoming solar radiation at land surfaces from 1960 to 1990, due to increased aerosols and cloud cover, a phenomenon known as global dimming and considered to have counterbalanced the greenhouse effect (Roderick and Farquhar, 2002). But during the 1990s global dimming did not continue and it changed on the contrary in global brightening until now and may currently influence the greenhouse effect as well as the surface temperature, the hydrological cycle and ecosystems (Wild et al., 2005).

Both, studies over normal dry seasons (Huete et al., 2006) and anomalous interannual drought in addition to seasonally low precipitation (Saleska et al., 2007), found widespread greening in Amazonia. Leaf flushing and increased photosynthesis are attended by seasonal peaks of PAR, due to decreased cloudiness, suggesting that sunlight is more influential than rainfall on rainforest phenology and productivity, assumed that access to deep soil water is given. The study of Goulden et al. (2004) based on eddy covariance also showed greater rates of carbon accumulation during the dry season. An explanation for the counterintuitive pattern could be that during dry periods reduced litter decomposition is occurring, leading to decreased soil and litter respiration, while canopy photosynthesis apparently wasn't suffering from drought stress, probably because of deep rooting. However, increased diffuse light resulting from increased aerosols and cloud cover has also been found related to enhanced efficiency of forest carbon uptake (Clark, 2004).

To date current global terrestrial biosphere models and empirical measurements differ widely in their predictions of biosphere-atmosphere interactions and responses of ecosystems to changing climate and atmospheric CO₂ concentration.

However, the large spatial and temporal scales in area and time make direct experimentation nearly impossible and predictions therefore depend on either complex models or direct experimentation at smaller scales (Moorcroft, 2006).

El Niño/Southern Oscillation (ENSO) events for example have large effects on tropical precipitation and surface temperature and are restricted in seasonal and spatial dimensions.

Although it can't be excluded that reductions in regional rainfall are related to proceeding deforestation, a strong correlation has been found between ENSO events and increasingly severe drought episodes in Amazonian moist tropical forests (Nepstad et al., 2002).

Hartmann (2002) also discovered large variations in the tropical atmospheric energy budget which was related to El Niño and La Niña events (Chambers and Silver, 2004). El Niño/Southern Oscillation events occur on average every 3 to 7 years and influence the climate mainly of equatorial pacific-

coastal countries in South America and Asia. They are part of large-scale, complex interactions between air (changes in atmospheric pressure and winds, called Southern Oscillation) and sea (changing ocean temperatures and currents, called El Niño) leading to higher rainfall, warmer than normal sea surface temperature and less-nutrient-rich water in coastal South America and to droughts and cooler surface water in coastal Southeast Asia. Climatic effects during strong ENSO phases are even evident in areas very distant from the tropical Pacific. Recent studies found additional El Niño seasons characterized by sea surface temperatures anomalies in the Central Pacific presuming it as a consequence of global warming (Ashok and Yamagata, 2009, Larkin and Harrison, 2005, Di Lorenzo et al., 2010). Modeling and statistical analyses indicated that seasonal droughts in the Neotropics may increase as ENSO events develop more frequent and severe in the future as affected by global warming (Trenberth and Hoar, 1997, Timmermann et al., 1999).

One major issue of global change research is how tropical vegetation will respond to future climatic changes and how this feeds back on regional and global climate and carbon cycles. Although climatic effects on tropical forests and their ecological functions may be potentially large, these effects are far from being fully understood (Nepstad et al., 2002). As short-term events like ENSO bring periodic climatic changes similar to those predicted for global climate change in much of the tropics, research on ecosystem responses to ENSO have been widely used as a proxy for the climate sensitivity of tropical ecosystems to long-term changes. For instance, field data point to decreased forest productivity and increased tree mortality through strong ENSO events with high temperatures and drought (Condit et al., 1995, Laurance et al., 2001, Rolim et al., 2001, Clark, 2004).

The range of potential terrestrial ecosystem responses to global changes i.e. rising atmospheric CO₂ concentration, the increase in land surface temperature, changes in precipitation and ecosystem moisture status, and altered disturbance regimes, varies from the physiological scale of e.g. leaves and fine roots which are very short-termed and immediate, to ecosystem scales like changes in tree community structure and shifts in carbon allocation and storage in long-lived woody tissues or slow-cycling soil organic matter.

(1) Leaves respond to changes in atmospheric CO₂ concentration via increases in the photosynthetic carbon assimilation, while the increased carbon gain often does not lead to increased plant growth. Much of this extra carbon gain intermittently increases plant carbon storage and root exudation and is lost via autotrophic and heterotrophic respiration, and therefore hardly has an effect on long-term carbon balance (Chambers and Silver, 2004).

On the one hand, given that the availability of water, nutrients and light as well as air temperature are in an optimal range, increasing atmospheric CO₂ can stimulate plant growth and act as kind of a

fertilizer. Exposing leaves to doubled atmospheric CO₂ leads to an increase in photosynthetic rate by 30 to 50% (Curtis and Wang, 1998), which has been assumed to be an explanation for biomass increases of tropical forests through the last 300 years (Clark et al., 2010). In contrast, other experiments showed that tropical rainforests under enhanced atmospheric CO₂ conditions will respond by little or no increases in net primary production (Clark, 2004). On the other hand enhanced atmospheric CO₂ leads to global warming and possibly increased drought frequency and severity in some very productive areas, which both are likely to have negative effects on vegetation and ecosystems because of decreased water availability and heat damage to those plant parts where photosynthesis takes place. Plant physiology of tropical trees occurs close to the temperature maximum. Measurements at the leaf-level demonstrated reduced net carbon assimilation at higher daytime temperatures (Doughty and Goulden, 2008). Small increases in air temperature (particularly night temperatures) therefore had negative effects on plant C gain because of increased respiration and growth in many studies of tropical rainforests (Doughty and Goulden, 2008, ClarkPiper et al., 2003). Moreover, the increase of respiration by plants (Amthor and Baldocchi, 2001) and also microbes (Holland et al., 2000) with temperature has been shown to follow an exponential relationship.

(2) Changes in tree community structure may occur due to shifts in species compositions when drought tolerance limits of certain species are exceeded, followed by increased mortality (Condit et al., 1995, Williamson et al., 2000) and reduction of reproduction of some species.

By investigating large canopy gaps and forest fragments, researchers demonstrated that tree community structure can change faster than previously anticipated i.e. over annual to decadal periods (Lugo and Scatena, 1996, Laurance et al., 1997, LauranceLaurance et al., 1998, LauranceFerreira et al., 1998, Dale et al., 2001).

1.2 “Pardon? Carbon?” - The global carbon cycle and tropical rainforests

One important link between forests and the atmosphere is carbon dioxide exchange.

Not only the climate is influencing forests, but also forests influence the climate by physiological processes involving CO₂. Atmospheric CO₂ is one of the major radiatively active gases, contributing 60 % of the total global warming potential of greenhouse gases (Hansen et al., 1998), and absorbing 90 % of the long wave radiation the Earth surface emits. The part of the absorbed energy that is reradiated in the same form back to the Earth surface is responsible for the greenhouse effect and causes enhanced warming as the fraction of these gases in the atmosphere increases (Chapin et al., 2002, p19). Anthropogenic emissions of CO₂ in the 1990s were estimated to be 6.3 Pg C/year (1 Pg= 10¹⁵ g or 1 Gt) – according to latest IPCC 2007 data 7.8 Gt/year by now-, but only 3.2 Pg C/year were accumulated in the atmosphere and 2 Pg C/year were found dissolved into the ocean according to Keeling et al. (1995), Keeling et al. (1989) and Schimel et al. (1996) as cited in Mohamed et al. (2004) and Schimel (1995). (http://www.awi.de/de/aktuelles_und_presse/ausgewaehlte_themen/klimawandel/ipcc_bericht_2007/zusammenfassung/ 28.06.2010). The missing carbon is supposed to be stored by terrestrial vegetation and soils (Ciais et al., 1995, Keeling et al., 1996), including tropical rainforests because of their high productivity (Clark, 2002). Estimates therefore indicate that the terrestrial biosphere currently sequesters 20 to 30 % of global anthropogenic CO₂ emissions (Gurney et al., 2002).

Shifts in carbon allocation and storage, which can impact upon atmospheric CO₂ concentrations, have been more intensely studied in temperate, boreal and arctic ecosystems than in tropical ecosystems (Chambers and Silver, 2004), although tropical forests fix and store a greater amount of carbon in their vegetation and soils than the other biomes (Dixon et al., 1994). Or in the words of Nepstad et al. (2002): „In Amazonia alone, forest biomass is equivalent to more than a decade of net human-induced carbon emission worldwide.“

Of the global biomass carbon pool 37 % is found in tropical forests, more than half - 53 % according to Chave et al. (2001) - of which is in the Neotropics. In numbers, the tropical forest carbon pool is 428 Pg, while the world's living terrestrial carbon pool is 1146 Pg (Dixon et al., 1994).

Although they only account for 22 % of potential vegetation by area (Melillo et al., 1993), tropical forests contribute approximately 35 % of the global net primary production (global NPP is estimated at 60 PG C/year according to http://www.ipcc.ch/ipccreports/sres/land_use/index.php?idp=24 (10.03.2011)), while tropical savannas and grasslands represent a further quarter of global NPP (Saugier et al., 2001). Estimations across a broad spectrum of different tropical rainforests resulted in a total NPP range from 1.7 to 21.7 Mg C ha⁻¹ yr⁻¹ (ClarkBrownKicklighterChambersThomlinsonNi et al., 2001). Interestingly tropical primary forests store more carbon (384 ± 56 Mg C ha⁻¹) than secondary forests (228 ± 13 Mg C ha⁻¹). However less thereof is stored in soils, i.e. 59 % of total ecosystem carbon stock is found in primary forests soils to 4 m depth, compared to 84 % in secondary forests soils. Respectively 29 % of the carbon in primary forests is stored in aboveground biomass and 10 % in belowground biomass. Only 9 % of ecosystem C is found in aboveground and 5 % in belowground biomass in secondary forests (Sierra et al., 2007). In the tropics large stocks of carbon are preserved in soil organic matter for centuries and longer (Trumbore et al., 1995, de Camargo et al., 1999, Bernoux et al., 2002), stabilized on mineral surfaces (Telles et al., 2003). Therefore short-term responses in carbon storage occur due to changes in the mass of wood and woody debris (Phillips et al., 1998), because carbon in living tree biomass is assumed to stay for only a few decades (Potter et al., 1993).

1.3 “Sources or sinks?” – The carbon balance of tropical forests

Forests are sinks for CO₂ through photosynthetic activity and sources because of autotrophic and heterotrophic respiration. The rates of ecosystem photosynthesis, respiration and decomposition vary diurnally and seasonally, depending on the physical environment like soil moisture, irradiance and air temperature and the biota's physiology including plant phenology and microbial basal metabolism (Goulden et al., 2004). Small shifts between these carbon fluxes of an ecosystem can have great effects on atmospheric CO₂ concentrations, while changing climate and atmospheric composition are assumed to be causing changes in forest NPP themselves (ClarkBrownKicklighterChambersThomlinsonNi et al., 2001). Net primary production therefore is a common variable to measure forest photosynthetic activity and carbon uptake. It is defined as the difference between carbon fixed in new organic material produced by the vegetation of an ecosystem during photosynthesis and the carbon released during plant respiration over a specified time interval, or simply as the sum of daily net growth or gross primary production (GPP) less autotrophic respiration (Chambersdos Santos et al., 2001). Autotrophic respiration means plants are losing photo-assimilates because of the energy costs of growing and maintaining living tissue (Luyssaert et al., 2007). Old growth primary Forests in the climax state are considered to be in equilibrium in terms of CO₂ with the atmosphere (Waring and Schlesinger, 1985). However, results in the current literature are diverging whether rainforests are carbon sources or sinks and data depend on which site and method was used.

Interestingly most studies in mature Paleotropical forests didn't find evidence of a net biomass change (exception: Lewis et al. (2009)), but some old growth neotropical lowland rainforests indeed showed increasing biomass (Clark, 2002, Phillips et al., 2008). Studies based on eddy covariance (Fan et al., 1990, Grace et al., 1995, Malhi et al., 1998) and long-term forest inventory records (Phillips et al., 1998, Phillips et al., 2002, Baker et al., 2004, Lewis et al., 2004) demonstrated that mature tropical moist forests act as net carbon sinks due to increasing biomass (ClarkBrownKicklighterChambersThomlinsonNi et al., 2001, Rolim et al., 2005), . Grace et al. (1995) found a moderate carbon sink (-1.0 Mg C ha⁻¹ yr⁻¹), Malhi et al. (1998) a large sink (-5.9 Mg C ha⁻¹ yr⁻¹), so did Andreae et al. (2002) with -3 to -7 Mg C ha⁻¹ yr⁻¹ and Phillips et al. (1998) reported a smaller sink of -0.6 ± 0.4 Mg C ha⁻¹ yr⁻¹ (Miller et al., 2004). Other studies based on measurements of tree growth ,(Chave et al., 2003, Clark, 2002, Laurance et al., 2004, Chave et al., 2008) as well as eddy covariance studies in conjunction with detailed field data (Saleska et al., 2003, Chambers and Silver, 2004) come to the conclusion that at least some neotropical forests have to be described as in a state

of dynamic equilibrium (Rolim et al., 2005), or suggest that local biomass increases because forests are recovering from past disturbances (Chave et al., 2008, Fisher et al., 2008).

Again other studies predicted that because of decreasing soil moisture (Tian et al., 1998) and/or increasing temperatures (Kindermann et al., 1996) NPP will decrease and tropical forests will therefore become net carbon sources to the atmosphere (ClarkBrownKicklighterChambersThomlinsonNi et al., 2001, ClarkClark et al., 2003). Data from above-canopy towers in Brazil and Costa Rica, measured by eddy covariance, detected reduced carbon uptake in the warmest daytime periods (Loescher et al., 2003, Goulden et al., 2004, Doughty and Goulden, 2008). Measurements of tree growth in Costa Rica, Malaysia and Panama also showed negative correlations between biomass increment and temperature (ClarkClark et al., 2003, Feeley et al., 2007). Tree growth in a Costa Rican tropical wet forest for example was very sensitive to variations in mean annual night-time temperature, but also to a range of dry season conditions (Clark et al., 2010). In a dry-down experiment in an Amazonian forest (Brando et al., 2008) major reductions in forest productivity followed rainfall exclusion, which confirms observations during severe droughts linked with record temperatures brought by extreme El Nino events (Clark, 2004, McDowell et al., 2008).

Miller et al. (2004) also found a moist tropical forest in Brazil to be a source of CO₂ or, at most, a modest carbon sink ($+0.8 \pm 2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; a positive flux indicates carbon loss by the forest, a negative flux indicates carbon gain) for the period from 1984 to 2000. Moreover, strong tropical land CO₂ emissions in years of enhanced temperatures and decreased precipitation were found tightly negatively correlated with interannual tree growth variations in a forest in Costa Rica (ClarkClark et al., 2003, Breitsprecher and Bethel, 1990). All these arguments show that a noticeable fraction of these emissions derive from shifts in tropical forest carbon balance due to climatic changes (Clark et al., 2010).

In summary, eddy covariance measurements in tropical forests showed a higher uncertainty of carbon balance estimates than in temperate forests. In many cases biometric and micrometeorological data in tandem demonstrated that different neotropical forests are hardly one strong persistent carbon sink (Miller et al., 2004), and some of them in contrast may show severely reduced biomass production in future climates that are only slightly drier and/or warmer (Clark et al., 2010).

1.4 Measurement of Net Primary Production: “Still under construction”

Growth analyses in moist and wet tropical forests have to be based on direct measurements because of the lack of reliable annual tree-ring chronologies (Clark et al., 2010). And because age is difficult to measure, size is the main attribute to describe the dynamics of natural forests. Long-term records with frequent re-measurements of biomass stocks at one site in short time intervals e.g. monthly to annual are important (and even more important as they hardly exist) to identify the forests' responses to environmental drivers and inter-annual climatic variations (Clark et al., 2010). Terrestrial NPP is actually impossible to measure directly in the field, NPP being the difference between gross primary production (GPP) and total plant respiration. Therefore NPP has been alternatively defined as all new organic material produced during a specified interval, based on measurements of all below- and above-ground components including the increments and losses of forest biomass throughout a time period (ClarkBrownKicklighterChambersThomlinson and Ni, 2001). The methods still have to be improved and adjusted to obtain stable, reliable and comparable data for different tropical rainforests.

Measurable NPP fractions, where losses represent material that was produced and then lost during the interval:

	increments	losses
aboveground	•Aboveground biomass increment (net increases in wood in stems and branches and in foliage)	•fine litterfall (shed leaves, twigs, flowers, fruits)
		•losses to consumer (herbivory, frugivory, sap-sucking)
		•volatile and leached organics
belowground	•net coarse root increment	•dead coarse roots
	•net fine root increment	•dead fine roots
		•root losses to herbivores
		•root exudates
		•carbohydrate exports to symbionts (root nodules, mycorrhizae)

TABELLE 1 ADAPTED FROM CLARK BROWN KICKLIGHTER CHAMBERS THOMLINSON AND NI, 2001

Depending on forest structure, edaphic conditions, successional stage and other parameters the amount of each fraction is differing. Aboveground biomass (AGB) seems to be the largest and certainly the easier to measure fraction of NPP. But concentrating only on aboveground increments and losses leads to serious underestimation of total NPP, because in some forests root exudates and CHO exports to symbionts were found accounting for 15-30 % of NPP (Norton et al., 1990, Darrah, 1996, Vogt et al., 1982) and fine root dynamic is also likely to account for large fractions of NPP, at least in some Nordic forests (Ruess et al., 1996). A global examination of tropical forests showed a range of 0.3 to 3.8 Mg C ha⁻¹ yr⁻¹ of AGB increment, and annual litterfall was measured in several studies to account for 0.9-6.0 Mg C ha⁻¹ yr⁻¹ (ClarkBrownKicklighterChambersThomlinsonNi et al., 2001). For sites with relatively low fertility a ratio of 2:1 between leaf/twig production and coarse wood productivity has been found, already including 12 % consumption of soft NPP, leaf production apparently being the higher priority for plants then stem production (Malhi et al., 2004). Therefore fine litterfall is one of the largest components of NPP and of consumption classes only herbivory has been quantified and found accounting 12-30 % of leaf biomass (Lowman, 1995). Hard to measure components such as carbon allocation to belowground plant growth and reproductive organs, as well as losses through herbivory, emissions of volatile organic compounds (VOC) and CH₄ and root exudates were estimated to account for 20 % of NPP in tropical forests (11 % in global average) (Luyssaert et al., 2007). Because plant biomass contains approximately 50 % carbon (Drake et al., 2003) and stem biomass dominates the aboveground carbon pool dynamics, AGB plays a prominent role in most carbon dynamic studies. However, stem increment constitutes only one but not the major fraction of total NPP (Malhi et al., 2004). Aboveground biomass is the total amount of biological material present above the soil surface in a specified area (Drake et al., 2003), and the increment and therefore AGB productivity is mostly estimated over the growth rate of existing trees plus the recruitment of new trees (ChambersHiguchi et al., 2001). Dry mass increment (DMI) is defined as AGB increment or stand mass increment (ClarkBrownKicklighterChambersThomlinson and Ni, 2001, ClarkBrownKicklighterChambersThomlinsonNi et al., 2001, Chambersdos Santos et al., 2001), and represents one important and easy-to-measure component of NPP, describing the change in the mass of surviving trees over time in an inventory plot (Rolim et al., 2005). In contrast, dry mass stand (DMstand) represents the total change in tree stand mass over time, which is the sum of recruitment and DMI less mortality. For calculating forest carbon balance DMstand is the most important variable. DMstand is also more variable than DMI because of highly episodic tree mortality (Rolim et al., 2005). Disturbance events are typically followed by an increase in AGB as the forest recovers (Drake et al., 2003). Keeling and Phillips (2007) found a global relationship between above-ground net primary production (ANPP) and AGB: AGB peaks at ANPP of 15-20 Mg ha⁻¹ yr⁻¹ ANPP, plateaus at ANPP > 20-25 Mg ha⁻¹ yr⁻¹ and is likely to decline at higher ANPP. Growth rates of tropical

trees vary in relation to age, season and microclimatic conditions and, dependent on the environment, also between and within species (cf. (Ferri, 1979) as cited in (da Silva et al., 2002). Also climatic, edaphic and other environmental factors lead to different spatial distribution of AGB and NPP; nutrient-rich areas for example tend to support more AGB than nutrient-poor sites, the latter showing higher belowground biomass allocation according to Oliver and Larson (1990) and Kimmins (1997) as cited in Drake et al. (2003). Negative correlations of tree annual diameter increments with annual means of daily minimum temperature have been found and were again found elevated in record-hot El Niño years (ClarkPiper et al., 2003). Tree growth is also negatively correlated to annual means of daily mean temperature, whereas mean monthly dry season volumetric soil moisture and dry season rainfall is positively correlated. Annual means of atmospheric CO₂, annual means of daily maximum temperature, estimated daily annual irradiance and total annual rainfall on the other hand were not found significantly related to net primary productivity. It seems yet unclear if the very strong relationship between enhanced productivity and dry season rainfall is a kind of side product of an unconsidered factor conditional upon rainfall (Clark et al., 2010). According to Schuur (2003) a linear increase exists between NPP and increased temperature, but not between NPP and mean annual precipitation (MAP) in tropical ecosystems. Instead of that NPP peaks with MAP of 2500 mm and decreases with higher rainfall (Schuur, 2003). High precipitation in already wet areas may cause decreasing NPP because of diminished radiation inputs, increasing nutrients leaching or reducing soil oxygen availability (Schuur, 2003).

Tree growth is mostly measured as the change in tree diameter at breast height (dbh) between years, and biomass is calculated based on allometric equations. Precision of re-measurements of tree dbh is low (± 5 % uncertainty). For higher temporal resolution and greater accuracy dendrometer bands are used. They are easy to install and use, cheap and they don't harm the measured trees. But they are only applicable for trees greater than dbh of 10 cm. As trees with dbh < 10 cm and lianas are also an important fraction in AGB, smaller diameter woody plants are directly measured using calipers (da Silva et al., 2002).

Accurately chosen allometric equations are needed to relate tree diameter to biomass and to avoid harvesting and weighing of the measured trees getting this relation. In temperate as well as in tropical areas studies have shown a strong correlation between the aboveground dry biomass (AGTB) of a tree and its dbh (Overman et al., 1994, Bunce, 1968, Brown et al., 1997, Rapp et al., 1999, Whittaker and Woodwell, 1968, Lescure et al., 1983). Different kinds of allometric equations have been developed, tested and published: equations which estimate AGB from dbh data only, which use dbh and tree height data and equations which consider dbh as well as wood density data. Tree Height is hardly recommended though for estimating AGB (Chave et al., 2001). Three-parameter regressions though show higher correlations than two-parameter ones even if one of the variables is

the fault-prone height (Chave et al., 2001). Some allometric equations are meant to be locally derived best-fit equations (Brown et al., 1997); others are approaches to cover a larger range of tropical rainforest types (Chambersdos Santos et al., 2001). And there also have been models developed depending on primary and secondary forests as well as different ones for palms and lianas, as is used in Sierra et al. (2007). According to Chave et al. (2001) in many cases well fitting equations using only dbh are depending on the form

$$\ln(AGTB) = a + b \ln(D)$$

with *AGTB* meaning the aboveground dry biomass of a tree in kg, *a+b* being the coefficients depending on equation and area and *D* is the dbh (in cm);

Another important component of above-ground NPP is leaf, twig, flower and fruit production. And assuming a quasi-equilibrium system where the production is equivalent to the losses within a measured period, the leaf, twig, flower and fruit production can be estimated through litterfall collections. Losses to consumers can't be measured with this method and according to (ClarkBrownKicklighterChambersThomlinson and Ni, 2001) these losses account up to 12 % of measured litterfall.

Litterfall collection in case of fine litterfall (which includes mostly leaves, small twigs, flowers and fruit parts and is more uniformly distributed (Dent et al., 2006)) is simple with the use of well replicated litter traps installed above the soil surface. To minimize losses through herbivory and decomposition the collections have to be frequent and regularly (ClarkBrownKicklighterChambersThomlinson and Ni, 2001). Coarse litter (palm and other big leaves, big fruits, big twigs and dead wood- very heterogeneous in space and time (Clark, 2002)) is collected within marked transects frequently, but not as often as the fine litter. Both fractions of litter are dried and weighed. Coarse woody debris can be subdivided in standing and fallen dead wood. Dbh, height and density is measured from each piece of dead wood- the last variable is gained from core samples- to finally get the mass of CWD.

Vitousek (1984) compared annual litterfall in different tropical areas and found a minimum of 2.5 Mg ha⁻¹ dry mass litterfall in a drought-deciduous forest in Puerto Rico and a maximum of 12.6 Mg ha⁻¹ dry mass in a mixed deciduous forest in Belize and 12.0 Mg ha⁻¹ dry mass for an evergreen seasonal forest in Colombia.

Root production, fine root increment and turnover usually is measured by ingrowth cores, minirhizotron, sequential coring and ¹⁵N labeling (Hendricks et al., 2006, Hendricks et al., 1997). The indirect carbon balance method is calculating the difference between soil respiration and litterfall to

obtain the sum of root respiration and belowground net primary production and is well fitted for total belowground C allocation estimations (Raich and Nadelhoffer, 1989).

1.5 Study aims

Knowing the structure of different neotropical rainforests and knowing how the aboveground biomass changes or not is very important for understanding more about global carbon dynamics. To decipher the internal and external drivers of growth in different forest sites may enable to understand responses of these ecosystems to future climatic shifts.

As shown above existing data vary strongly between sites, which points to the complexity of this question and that THE neotropical rainforest doesn't exist. Therefore measurements at regional scales become very important as well as to establish a set of reliable data from all over the world using well-founded methods.

This study examined the controls of wood increment in a humid tropical lowland rainforest in Province Puntarenas, Costa Rica. Three different sites in the Esquinas forest, which is part of the National Park Piedras Blancas, were established, differing in topographic and successional conditions (a secondary ravine forest, a primary ravine forest and a primary ridge forest were measured), to answer the following questions:

- Does the forest structure and microclimate of the sites differ?
- Are there correlations between DBH increment and topographic, tree family or tree size parameters?
- Is tree growth fluctuating between years and months? Are seasonal and therefore climatic differences in AGB increment detectable, notably in relation to ENSO? And which controls are dominating in a tropical moist forest with no clear dry season: the internal (seasonal) or external (interannual) triggers?

Microclimatic parameters at the forest sites such as PAR (photosynthetic active radiation), soil and air temperature and air moisture were analyzed for one year. Precipitation and air temperature as well as wood increment were measured over a period of 5 years; coarse woody debris and forest site structure were investigated once.

2. Manuscript for publication

2.1 Introduction

Tropical rainforests are commonly known because of their capacity to store high amounts of atmospheric carbon as a result of their high productivity (Clark, 2002). The largest fraction of the carbon pool is stored in soil organic matter bound to mineral surfaces, being sequestered there for centuries (Trumbore et al., 1995, de Camargo et al., 1999, Bernoux et al., 2002, Telles et al., 2003). And therefore for short-term responses in carbon storage the attention has to be turned on changes in the living tree biomass (Phillips et al., 1998, Potter et al., 1993). As stem biomass dominates the above-ground carbon pool dynamics, above-ground biomass plays a prominent role in most carbon dynamic studies. Clark et al. (2010) suggested to establish long-term records with frequent re-measurements of biomass stocks at sites and to measure biomass stock changes in short time intervals to finally identify the forests' responses to environmental drivers and inter-annual climatic variations. Little is known about the temporal variation of tree growth in the tropics because of the lack of reliable annual tree-ring chronologies (Clark et al., 2010). Growth analyses in tropical rainforests have to be based on direct measurements. By installing dendrometer bands around the tree trunk at breast height, tree increments can be read frequently. Although growth rates vary significantly between and within tree species, most growth analyses took place on ecosystem or forest stand level (da Silva et al., 2002). The extremely high species diversity combined with local rarity of most of the tree species has so far hindered efforts in these directions (Clark and Clark, 2001, Clark and Clark, 1999) , and this study therefore analyzed how tree increments vary on family level.

Growth rates of tropical trees vary also in relation to age, season, microclimatic and edaphic conditions, (cf. (Ferri, 1979) as cited in (da Silva et al., 2002). And according to Clark and Clark (2000) there are even more factors that might be called responsible for differences in diversity, vegetation structure and growth rates among sites: length and intensity of dry seasons, light availability, differences in soil characteristics, topographic position, differences in disturbance, differences in species composition (due to successional status) and hydrologic regime.

Finding out which of these factors affect growth in different tropical forest sites may help to understand how these forests will respond to climatic changes. Monitoring tree increments during short-time climatic variation as ENSO phenomenon is a chance to obtain deeper insight. Existing data point towards a decline of forest productivity and enhanced tree mortality in strong El Niño years with high temperatures and drought. (Condit et al., 1995, Laurance et al., 2001, Rolim et al., 2001, Clark, 2004)

Regional precipitation patterns can have different effects on sites with different topographic and edaphic conditions and for example ridge and slope sites may not respond the same way to changing rainfall. However, Chave et al (2001) found in French Guiana no clear evidence of significant influences of soils on spatial variability of biomass and nor did Clark (2002) in La Selva. Nepstad et al. (2002) started a throughfall exclusion experiment and provoked small soil water reductions. Comparing these increments with those on the undisturbed reference site Nepstad et al. (2002) suggested that stem diameter growth is very sensitive to drought. Too much precipitation on the other hand can also affect tree growth rates. Photosynthesis in already wet areas could be slowed down not only because of limited root respiration due to saturated soils but also because of high cloudiness associated with rainfall (Vieira et al., 2004), increased nutrient leaching or reduced soil oxygen availability (Schoor, 2003).

A study comparing above-ground coarse wood productivity on a wider scale of over 100 plots throughout the neotropics didn't find obvious correlations between wood productivity and rainfall, dry season length or sunshine. The only relationship seemed to be a negative correlation of tree increments with minimum temperature (Malhi et al., 2004), which was verified by Clark and Piper et al. (2003) for El Niño years. Moreover Clark et al. (2010) found mean monthly dry season volumetric soil moisture and dry season rainfall positively correlated to growth.

This study aimed at elucidating controls of growth at three forest sites in the Esquinas Rainforest in the Pacific lowlands of Costa Rica. The sites differed in topographic and successional condition and tree increment data were collected for 5 years in order to (1) examine how forest structure and microclimate differ dependent on succession and topography, (2) detect possible correlations between diameter growth pattern and topography, tree family and tree size and (3) study AGB fluctuations in relation to climatic conditions and ENSO phenomena over years and months.

2.2 Materials and methods

2.2.1 Study site

This study was conducted in the Esquinas Forest (Piedras Blancas National Park), which is located in the south of Costa Rica near the border to Panama. The protected area covers altogether 148 km² with an altitudinal range from 0 to 579 m above sea level. Situated on the western side of the Cordillera de Talamanca, the National Park is not really conterminous to the Pacific Ocean but to a shallow bay named Golfo Dulce, shielded from the Pacific Ocean through the peninsula of Osa with the Corcovado National Park.

In the area old grown primary forests alternate with secondary forest growing on former cacao plantations, pastures and logging areas. Near the village La Gamba and the Tropical Research Station of the University of Vienna in the Northeastern edge of the National Park, the research sites (8°42'46'' N, 83°12'90'' W) were situated, divided into three permanent plots.

The mean annual rainfall sum in this very humid study site is 5.913 mm (measured in the years from 1998 to 2010 in the biological station of La Gamba, Huber W. & Weissenhofer A., unpublished data). This area is showing mild seasonality with driest months January until March and wettest from September until November. In the measured period from 2006 to 2011, the years with lowest and highest precipitations were 2009 and 2010 with annual rainfall sums of 4.789 mm and 7.373 mm, which makes the measured area a classified wet forest according to the Holdridge life zone system. Mean annual temperature inside the forest was 24.9°C, while at the tropical research station La Gamba (TRSLG) mean annual temperature was 28.8°C. The hottest year during the study period was 2009, showing a mean annual temperature of 29.6°C and a mean annual maximum temperature of 35.1°C. Mid day sum per month of PAR outside the forest reached 10.426 µE and soil temperature and relative humidity inside the forest averaged 24.6°C and 96.3 % over 2006 – 2007. In the investigated region the soil types are Inceptisols and Ultisols. Ultisols are the dominant soils of ridges and are highly weathered, strongly acidic and clayey. Due to erosion, the soils of ravines and lower slopes are represented by the younger and less weathered Inceptisols (Huber, 2005).

To obtain a representative profile of the forest types differing in edaphic and topographic conditions, microclimate, disturbance regime and species composition, three sites were chosen for the establishing of permanent plots:

A secondary ravine forest, a primary ravine forest and a primary ridge forest.

The primary ridge forest is characterized by greater species richness compared to the secondary ravine forest, and microclimatic differences (a lower relative air humidity e.g.) compared to the

ravine sites because of its greater canopy openness and exposure. The secondary ravine forest has been growing undisturbed for the past at least 20 years on a former cacao plantation and is dominated by the pioneer species *Vochysia ferruginea*.

2.2.2 Study design

In each of these three forest types permanent plots of 0.12 ha were installed, each divided in 3 subplots with 4 x 0.01 ha. All of the trees and palms > 10cm dbh in all of the plots and all of the trees and palms < 10 cm dbh in just one of the 4 x 0.01 ha areas in each of the subplots were taxonomically identified to species level. They were tagged, height and dbh were measured. Data about coarse woody debris and fine litter were recorded to gain AGB stock information. Microclimate data loggers were installed in the understory and soil of each forest stand for recording soil and air temperature and air humidity. At the field station PAR and precipitation data were collected continuously. Installations for measuring throughfall and stemflow, litter stock and decomposition, root production and turnover were established in the same plots.

In the present study the attention was directed to dbh increment, BA and AGB stocks and AGB increments and to several factors possibly influencing differences like microclimate, site, size, phylogenetics and interannual climatic variations.

2.2.3 Forest structure

For forest structure analysis all of the dbh data collected was separated into 5 size classes: dbh < 10 cm, dbh 10-20 cm, dbh 20-30 cm, dbh 30-50 cm and dbh > 50 cm. Size class distribution of numbers in stems were calculated counting them in each of the 3 plots of 400 m² respectively, for trees with dbh smaller than 10 cm in just one of the 4 subplots á 100 m², then calculating the number of stems per ha and taking the means of the plots for representing the whole site. Total BA and AGB were calculated for the different forest types as described in the corresponding chapter and AGB respectively BA per ha were calculated in the same way as stem distribution.

Coarse woody debris (CWD) was analyzed and separated into standing and fallen coarse woody debris but considering only trees showing diameters above 10 cm. Diameter at breast height of every standing CWD higher than 1.3 m was measured in each subplot and height was estimated with a telescope bar. Volume in cm³ was calculated using a model for truncated cones from (Harmon, 1996):

$$V=L*(Ab+(AbAt)^{0.5+At})/3$$

L represents height; Ab means area of the base and is a result of the measured dbh. At means area of the top and the radius for At was calculated with:

$$d=1.59*D*(h^{-0.091})$$

Where d is the new diameter at the top, D the original one at the base of the trunk and h is the height (Clark et al., 2002);

From every fallen CWD with dbh>10 cm length was determined using a tape measure, and diameter was measured 3 times per tree (at the base, in the middle and at the top) using an adequate large caliper. The volume formula was a different for fallen CWD, namely Newton's formula, but also taken from (Harmon, 1996) and with Am = area of the middle section as new value:

$$V= L*(Ab+4*Am+At)/6$$

Standing as well as fallen CWD was divided up into 3 decay classes:

- Sound which means more than 75 % of the volume is intact and hard
- Fully decomposed, which means more than 75 % of the wood is soft and rotten
- Partially decomposed: intermediate between sound and fully decomposed

With a small drill for wood a sample from every piece of dead wood was taken, oven dried and weighed. Mean density in each decay class was calculated and used for those pieces of coarse woody debris where it was impossible to take a wood sample. After all mass of standing, fallen and total CWD was calculated for each site multiplying density and volume.

Losses of measured trees were counted and summed for the different sites and years and expressed in %. Input of annual coarse woody debris was also gathered from losses of measured trees- they were extrapolated per ha (with the examined area and for trees < 10 cm and with the number of trees per ha in the accordant area for trees > 10 cm) and the mean over 5 years was taken for every site. For correlations with climate the means for every year was taken over all sites.

2.2.3.1 Tree Increment

In each site and size class (dbh 10-20 cm, dbh 20-30 cm, dbh > 30 cm) 10 trees were chosen (adding up to a total number of 90 measured trees) which fulfilled the criteria of regular growth and accessibility. The bark round the trunk of those trees was cleaned and smoothed with a steel brush at breast height- carefully to avoid injuring phloem and cambium. If trees had buttress roots at breast height the procedure was carried out above them where the stem shape was again cylindrical. Each

stem of multi-stemmed trees was handled separately. After this preparation dendrometerbands were installed and each tightened with a spring. After finishing the installation dbh was noted directly, but recollected several times within 1 month before the bands showed stable values and the actual measuring could be started. After that dbh-data were measured every month from March 2006 to April 2011.

This method does not fit for trees with dbh 2.5-10 cm, so the small trees were marked at breast height with color spray to identify a steady point of measure and dbh was measured with a caliper. The diameter was read with an accuracy of 0.5 mm. Then at the same height but shifted 90° a 2nd measurement was carried out. Both values were noted and later the mean value was calculated. Small tree diameters were measured every 3 months from March 2006 to March.

Dbh increment for each tree was calculated using

$$\Delta dbh = dbh(t_{12}) - dbh(t_0) \text{ as well as } \Delta dbh = dbh(t_x) - dbh(t_{x-1})$$

With $dbh(t_0)$ being the first measurement in the new period and $dbh(t_{12})$ the 12th measurement afterwards in case of the dendrometerband measured trees and the March measurement in the subsequent year in case of the caliper measured trees to obtain annual increments. For monthly increment-data the dbh of one month was subtracted from the dbh of the previous month, which equates to the second equation. Small trees measured with caliper produced 3-months increments this way and were considered separately in ANOVA calculations. For getting adequate and unbiased increment results within dbh classes also mm increments per mm tree diameter were calculated dividing yearly increments of trees by the accordant dbh.

For analyses trees at all three sites were divided into 4 dbh size classes (dbh 2.5-10 cm, dbh 10-20 cm, dbh 20-30 cm and dbh > 30 cm) and families with more than 3 measured trees in the plots were identified. Height of all trees had been measured using a telescope bar and height-classes (0-5 m, 5-10 m, 10-20 m and > 20 m) were established- looking for differences amongst all those factors in connection with tree increments in sites and years using ANOVA- statistics.

2.2.4 BA and AGB increment

For estimating basal area (BA) a circular cross-section of all trees was assumed, and with the formula of circle areas: $a = d/2 * \pi$ calculated.

As finding the right AGB calculation proved to be more difficult according to recent literature, different AGB formulas were tested and compared and out of 12 models in the present study for trees with dbh > 10 cm the tropical moist forest model, published by (Brown et al., 1997), has been chosen:

$$Mass=42.7-12.8Db+1.24Db^2$$

Db=dbh in cm, mass is measured in kg (dry biomass)

This model gave comparable results to most of the others and seemed therefore to provide comparable values. It was especially formulated and tested for moist tropical rainforests and Chambers and dos Santos et al. (2001) too attested this model solid results in their study on allometric relationships in different forest types. Allometric estimations tend to overestimate AGB of large trees with dbh > 60 cm but this model does so to a lesser degree according to Brown et al. (1997) and also Chambers and dos Santos et al. (2001).

For trees with dbh 2.5-10 cm another model was chosen, published in this form by Chambers and dos Santos et al. (2001):

$$\ln[mass]=-2.30+2.67*\ln[Db]$$

The estimation of lianas with an own equation was neglected because of a very small number of this life-form having diameters > 10 cm. To obtain AGB increments the procedure was the same as for dbh increments. Absolute AGB increments in Mg/ha were projected multiplying increment means of the measured trees for each site with the related tree number in this site. Trees that died in a census interval were ignored because their dbh increment was assumed to be zero (ClarkBrownKicklighterChambersThomlinson and Ni, 2001). They were calculated separately as coarse woody debris. For stand increment calculations it would have been necessary to measure also the ingrowths of trees (trees that reach the minimum size for measuring) and to consider both, ingrowths and losses, in the number of trees per ha with which the increment means were multiplied.

Investigating the intra annual fine structure of possible climate effects AGB was calculated with the sum of tree increments for each site in each month for one year and then correlated to monthly means of maximum temperature, minimum temperature, mean temperature, the monthly rain sum, numbers of dry days per month and to the multivariate ENSO index (MEI)- not only to the according months, but also to past climatic conditions. Increments and according climatic conditions were moved against each other to detect possible influences of past climate on biomass up to 12 months back. Considering that typically ENSO cycles last from May to April, AGB increments had to be calculated in the same interval to relate them to ENSO phenomena and compare the ENSO years to mean annual precipitation (MAP), dry days per year, months with less than 200 mm precipitation, dry season precipitation (sum from January till March), mean annual mean, maximum and minimum temperature and ENSO index. The latter was taken and summed for the measured years from

<http://www.esrl.noaa.gov/psd/enso/mei/table.html> (03.08.2011). ENSO index was also related to tree losses and input of new pieces of CWD.

2.2.5 *Microclimate data*

At the biological station precipitation (as daily sum), air temperature (minimum, maximum and means of the day) and PAR (sum every 30 min) were recorded with a Vaisala weather station in an open place. Additionally in all 3 forest sites 2 HOBO data loggers were installed in the understory measuring air temperature and humidity. Two data loggers in each site were buried 10 cm in the soil to monitor soil temperature. All the logger data were recorded in intervals of 15 minutes. Unfortunately the data of PAR and the microclimate loggers at the different sites turned out to be incomplete and full of gaps. Data gaps were filled using regressions between microclimatic variables.

Air temperature measured in the station was used for monthly mean minimum, maximum and mean calculations during the years from 2006 to 2011, as well as the monthly and annual precipitation sum, which was calculated from station data too. The quality of microclimate data from the plots was dependent on the lifespan of each of the loggers. At least a set of microclimate data for one year for each site was retrieved. Microclimate data from the loggers were read out with Greenline and BoxCar software.

2.2.6 *Data analysis*

Data were analyzed using One-Way and Multifactor ANOVA for detecting differences of tree increment between sites, years, size-classes, height classes, families and interactions amongst them. Simple Regressions were done to correlate especially climate factors with tree growth in terms of AGB increment. Levene test was used to check variance homogeneity, in some few other cases Kruskal Wallis test was first choice.

ANOVA results were further investigated with multiple range tests. The Scheffe test was chosen because of differences in data numbers in the different cases.

2.3 Results

2.3.1 *Forest structure and microclimate*

For different dbh size classes of trees the abundance of trees in the different sites was determined. Mean stem density was apparently highest in the primary ridge forest, for small trees as well as for bigger ones. Noticeable less small trees could be found in the primary slope forest compared to the other sites, whereas the fraction of trees with dbh 10-20 cm was remarkable high with 43.8 % compared to 25.2 % and 28.6 % in the secondary slope forest and the primary ridge forest respectively (Table 1).

Stem density did not differ significantly at the different sites and size classes at the 95 % confidence level, nor did mean basal area (Table 2). Mean basal area was quite similar at all sites ranging between 31 and 33 m² ha⁻¹. Total above ground biomass was lowest in the primary slope forest, which is considered to be the nutrient richest, but the differences between all three sites were not significant. The AGB of small trees at primary ridge was significantly higher compared to both other sites (Table 2).

The most input of coarse woody debris in all sites during the measured years occurred in the secondary slope forest. Belowground biomass measured as living fine roots was highest in the primary ridge forest; litter stock in contrast showed highest values in the secondary slope forest (Table 1).

To demonstrate microclimatic conditions in forest stands compared to an open area values of mean monthly air temperature were measured in each of the three forest sites and additionally at the biological station. Results are presented for the year 2006. In comparison to the station climate the mean temperature in the forest sites was significantly lower (~4°C) and all sites differed significantly from the station values, but not among each other (Table 2). From the different sites the primary ridge forest indicated the largest fluctuations in both directions and was the one with the highest mean value (24.7°C) while the primary slope forest was the coolest with 24.5°C, but differences here were marginal (Figure 1, Table 2).

Soil temperature at a depth of 10 cm below the surface was in large parts bounded between the minimum and maximum air temperature. Of all factors the different forests differed only significantly in maximum air and minimum soil temperature. The secondary slope forest and the primary ridge forest had significantly higher maximum temperatures (27.9°C and 28.4°C) than the primary slope (27.0°C). Minimum soil temperature was lowest in the primary ridge forest with 23.2° and therefore

contrary to air temperature. Sometimes it was even lower than minimum air temperature, which was differing from the other sites. The two slope sites were quite similar with 23.7°C (secondary slope) and 23.8°C minimum soil temperature (primary slope). Considering minimum air humidity no significant difference between the sites could be found, only primary slope forest was more humid than the ridge site (90 % air humidity compared to 84 %). The former exhibited a noticeable and sharp decline of both mean and minimum air humidity in May where also maximum air temperature was highest (Figure 2, Table 2).

2.3.2 Analyses of dbh increment

2.3.2.1 Family

Vochysiaceae as a family of pioneer trees is worth mentioning because of its remarkably high annual growth increment (mean over 5 years being 7.4 mm) and *Arecaceae* as representative of palms without significant secondary growth on the other hand because of very small increments (0.55 mm per year). *Rubiaceae* and *Moraceae* had significantly smaller increments compared to *Vochysiaceae*; *Annonaceae*, *Tiliaceae* and *Fabaceae* showed significantly higher increments compared to *Arecaceae* (Figure 3).

2.3.2.2 Height and dbh classes

Trees were divided into 4 height classes, i.e. < 5 m (0), 5-10 (1), 10-20 (2) and > 20 m (3). The highest measured tree was 53 m. As analysis of the relations of relative tree increments ($\text{mm mm}^{-1} \text{ year}^{-1}$) showed, growth in the smallest height class was highest (Figure 4). In fact the secondary forest showed higher relative increments in height class 0 and 1 compared to the primary forests (Table 2). The primary forests showed quite similar values in all height classes.

Comparing dbh size classes to height size classes, results were looking similar, i.e. in the secondary forest size class 0 showed significantly higher values as in the primary forests (Table 2).

The result of a two way ANOVA of relative annual dbh increments was that the factor site was not significant while size class and the interaction of size class and site were highly significant. The factors height class and site were both highly significant in a two way ANOVA (Table 2).

2.3.2.3 Dbh classes, sites, years

Annual tree increment was by far highest in the secondary slope forest ($0,035 \text{ mm mm}^{-1} \text{ dbh year}^{-1}$) compared to primary ridge ($0,017 \text{ mm mm}^{-1} \text{ dbh year}^{-1}$) and slope forest ($0,015 \text{ mm mm}^{-1} \text{ dbh year}^{-1}$). Not using the mm increment/mm dbh values would have led to an underestimation of small trees which would have been expressed in a smaller increment-rate in the primary ridge forest, because of its large abundance of small trees (Table 2).

2008/09 and 2009/10 were smallest in terms of increments ($0,017$ and $0,018 \text{ mm mm}^{-1} \text{ dbh year}^{-1}$). 2006/07 and 2007/08 showed intermediate growth rates and all of them were significantly different from 2010/11 which had highest relative increment growth rates ($0.032 \text{ mm mm}^{-1} \text{ dbh year}^{-1}$).

Size class 0 showed highest relative increment growth rates ($0.028 \text{ mm mm}^{-1} \text{ dbh year}^{-1}$) compared to the other size classes. Values declined quasi constantly with size class (Figure 5).

Site and dbh class appeared to highly significantly affect increment, followed by strong effects of year. The interaction between dbh size class and site was also highly significant, but none of them showed significant interactions with the factor year. Overall, size class was the dominant factor controlling relative increment growth (Table 2).

In the secondary forest site size class null emerged as the one with highest increment growth. Primary slope forest showed higher growth rates in size only in year five but in this year not only in size class 0 but also in size class 3. Primary ridge forest showed also high increment growth in size class 3, though in year one (Figure 5).

Considering the coefficients of variation (CV) of size classes and sites, size class 0 had most inconsistency among the sites (with a CV of 63 %) due to larger increments at the secondary site. Size class 1 and 2 had small CV's. A CV of 25 % was found in the biggest size class. Comparing the CV of size classes and years (interaction not significant) size class 0 showed largest variation over the years (Table 2, Figure 5).

2.3.2.4 Dbh classes, sites, years, months

Only trees with dbh greater than 10 cm were considered in statistical analyses of seasonal and annual patterns of increment growth, because smaller trees had not monthly but 3-monthly measurement intervals. Increments in diameter were no longer taken as mm per mm dbh because size classes were disregarded in this part of the analysis. Monthly increment did not significantly interact with sites or dbh classes, but strongly with years, meaning that increment in some months

differed significantly between years. Statistical output pointed to months having little more influence on differences in increments than years (Table 2).

June, May and April showed on average the highest increments (0.45, 0.43 and 0.39 mm), December the lowest and November and January the second lowest (0.17 and 0.19 mm). A strong relationship between monthly increments and mean temperature or rain sum could not be figured out (Figure 6).

Small trees were only measured in intervals of three months, so analysis is based on this kind of data. Combining increments for sites, years and months led to highly significant effects of all components (Table 2). Comparing the F- ratios (data not shown), sites turned out to have most influence, then years and last the factor month. On average the months AprilMayJune (0.44 mm) and JulyAugustSeptember showed higher dbh increment than JanuaryFebruaryMarch and OctoberNovemberDecember (0.27 mm). Year five was on average the most (0.51 mm), year four the least productive one (0.21 mm). From the different sites secondary slope forest was the one with highest growth rate (0.53 mm) and the primary slope forest the one with the lowest, showing increments of 0.19 mm (Table 2, Figure 8).

Climatic parameters as mean monthly rain sum and mean monthly maximum and minimum temperature in comparison showed that 2009/10 was a hot and dry year (mean monthly minimum temperature was 24.7°C, annual rain sum 5322 mm), while 2010/11 was rich in precipitation (7750 mm) but intermediate in temperature (mean monthly minimum temperature was 23.8°C). Also 2006/07 was a hot and dry year with most mean dry days per months of all years (8.4). At the scale of MEI 2006/07 and 2009/10 were classified as El Niño years with positive values (0.57, 0.92), the other years represented the cold ENSO phase La Niña (Table 2).

Mean monthly precipitation sum showed for all years the wettest months from September till November and the driest from January till March. Altogether year 2010/11 was wettest with much more rain during the wetter months and 2009/2010 the hottest year with higher minimum temperatures during most months. Year 2008/09 and 2009/10 had each one peak in the category number of dry days per months, namely in the months January and February respectively, and a smaller one in April.

2.3.3 Analyses of AGB growth

2.3.3.1 Intra annual growth

Over one annual cycle effects of climatic conditions on AGB increment were examined up to twelve months after they occurred (Figure 9). Monthly rain sum and on the other hand the number of dry days per months had apparently the strongest influence on growth. A modest negative correlation could be observed after two to five months for the secondary slope forest and the primary ridge forest in case of monthly rain sum, whereas a positive long term effect was detected after eight to twelve months. Especially the primary ridge forest showed strong significant correlations, secondary slope forest showed smaller effects and for primary slope forest effects were largely non-significant. Increments in the primary slope forest seemed to be most independent from monthly rainfall. Dry days affected growth strong and positive after three to six months in the secondary and the ridge forest. Nine months after the dry days were measured a contrary reaction started, quite similar to the effect of rain sum and especially strong at the Ridge site. Effects by monthly maximum temperature on AGB were barely existent, only the secondary slope forest showed one significant weak negative correlation after eight months. Mean temperature seemed not to have that much influence either. Both secondary and primary slope forest exhibited a slightly positive correlation with mean minimum temperature after one month. The primary slope forest instead showed another positive correlation after twelve months. Once more the primary ridge forest showed a strong and highly significant positive correlation after twelve months. Therefore minimum temperature could be considered as having more influence on growth than maximum or mean temperature, but temperature had very low effect at all. Multivariate ENSO Index (MEI) had little effect on tree increments (Figure 8).

2.3.3.2 Inter annual growth and ENSO

Aboveground biomass increment showed significant differences between the sites where the primary ridge site was lowest (11.2 Mg/ha) compared to 16.3 and 18.8 Mg/ha in the primary and secondary slope forest, but not between years. Nonetheless the years 2010/11 and 2006/07 showed highest increments of biomass (17.8 and 17.3 Mg/ha) compared to the years 2008/09 and 2009/2010 with 13.2 and 13.6 Mg/ha (Table 2).

Comparisons between AGB increment and various climatic parameters resulted in no significant relations (table 3). This is probably due to only 5 annual measurements being too few to detect significant interannual effects on tree growth.

2.4 Discussion

2.4.1 Site differences in forest structure, AGB and increment

Mean annual dbh increment (averaged over 5 years) in the Esquinas rainforest was high, i.e. 3.72 ± 0.23 mm for trees with dbh > 10 cm and 1.22 ± 0.07 mm for trees with dbh < 10 cm, compared to results found in Brazil with 1.62 ± 0.21 mm per year for trees > 10 cm (da Silva et al., 2002) and another Brazilian study where results for trees > 10 cm ranged between 1.48 ± 0.20 mm and 3.98 ± 0.33 mm per year (Vieira et al., 2004). In La Selva (Caribbean coast of Costa Rica) dbh increments for 6 nonpioneer species with dbh > 1 cm ranged between 0.6 mm in a low year to 12.6 mm in a top year (Clark and Clark, 1994).

Aboveground biomass increment was 15.4 ± 1.03 MG ha⁻¹ a⁻¹ for all trees measured over 5 years, which also ranged on the higher part of reported values. Chave et al. (2003) for example found 7.05 ± 0.32 Mg⁻¹ ha⁻¹ as highest value of various 5 year periods on Barro Colorado Island in Panama.

Total above-ground biomass stock (including trees with dbh > 10 cm and dbh < 10 cm) was highest at the ridge site with large contribution of biomass by small trees. The different sites showed statistically similar aboveground biomass (352, 335 and 357 Mg⁻¹ ha⁻¹) and the values were comparable to other neotropical sites (Chave et al. (2001): 309 Mg⁻¹ ha⁻¹ in French Guiana for trees dbh > 10 cm, Nascimento and Laurance (2002): 326 Mg⁻¹ ha⁻¹ trees > 10 cm and 21.1 Mg⁻¹ ha⁻¹ < 10 cm), and respectively higher than in a site quite similar to La Gamba- Barro Colorado Island, where Chave et al. (2003) found 281 Mg⁻¹ ha⁻¹ for trees > 1cm. Estimates of AGB stock for trees dbh > 10 cm in La Selva, Costa Rica ranged from 161 to 186 Mg/ha and Clark and Clark (2000) did not find that topographic position had any influence on AGB distribution as we found. Significantly higher biomass accumulation in secondary forests were found by Alves et al. (1997) and Lugo and Brown (1992), while Nelson et al. (1999) stated that AGB equations developed for primary forests tend to overestimate biomass of secondary forests because of higher wood density in primary forests. Even the highest coarse woody debris stock in this study i.e. at the ridge site was low in comparison to 24.8 Mg⁻¹ ha⁻¹ in Brazil (Nascimento and Laurance, 2002). Standing coarse litter was highest at the ridge site which is most likely because of its exposure and increasing winds causing tree gaps. Fine litter fall was one of the highest recorded so far for moist or wet tropical rainforests, which is an evidence for generally nutrient-rich conditions (Drage, 2007), while belowground biomass was clearly the highest at the ridge site being caused by lower nutrient availability (Ratzer Bruno, 2006).

2.4.2 Phylogenetic effects

On the family level, *Vochysiaceae* as representatives of long-lived pioneer trees were highly abundant in the secondary forest. According to this study *Vochysia spp.* showed highest increment growth rates, which could be explained by its status as pioneer plant on disturbed areas (Finegan et al., 1999). Palms (*Arecaceae*) on the other hand in most cases don't have secondary growth in girth, and therefore showed lowest increments. The family of *Rubiaceae* with subcanopy trees and treelets were here represented by understory species which by low light conditions hold low increment growth. From the measured trees of the family of *Moraceae* both *Brosimum spp.* and *Castilla tunu* were found. The former is considered as k- strategist, the latter as r- strategist and as more of the *Brosimum spp.* trees were in the measured group the result points in the direction of low increment growth rates. *Tiliaceae* also is considered to be a family of r- strategists with fast-growing and light wood trees, and here showed greater increments.

2.4.3 Height and dbh class

Other than the family-level, the relative increments in height classes showed significant differences at the three sites, probably due to differences in species composition, light climate and stem density between the sites. The sudden decline of tree increment from height class 1 to 2 at the secondary site could be caused by rapidly growing pioneers which are later shade suppressed at a certain height (competition for light during early years) or small mature shadow tolerant species in height class 2 (which is more likely). Small trees in all sites showed highest growth also in the dbh class comparison, which points to an under storey composition of mostly fast growing young sub canopy species.

The primary slope forest had lowest numbers in small trees, but had the highest proportion of intermediate trees (size-class 2) and trees over 30 cm dbh and this site is considered as the nutrient-richest site. Complexity was added for the primary slope forest consulting dbh size class instead of height class, because this forest showed lower increments (though not significantly) in size class 1 and 2 than in size class 3 which might point at slow growing shade tolerant species in the middle storey and light demanding, fast growing tree species in the canopy or shade-suppression. The youngest site- the secondary forest- contained many trees of fast growing *Vochysiaceae* and also a high abundance of small trees. However, the greatest fraction of small-sized trees and lowest stem density in bigger size classes was found in the primary ridge forest. We found no significant difference in relative increment growth at this site, which indicated that light wasn't the determining factor in this site with relatively high canopy openness. It may also be a hint for the presence of long-lived, slow-growing K-strategists at sites with more stressful climatic conditions like strong winds, lower air humidity and greater temperature amplitude like in the ridge site, and lower nutrient availability and greater soil acidification at the ridge site.

The lower increments in bigger height classes at all sites could also result from increased maturity. There is a phase of growth decline with advanced age, dependent on species. Trees with a dbh maximum of 15 cm can be considered already mature with a dbh of 10 cm whereas a tree of dbh 60 cm but a maximum of 90 cm shows more increment because of a more juvenile stadium (Finegan et al., 1999).

For further analyses it would be interesting to look at the combination of family and height class, because shadow tolerant species of the under- and middle storey can be found at the slow growing end of the spectrum, whereas light demanding trees of the sub canopy, canopy and emergent species are fast growing (Finegan et al., 1999), and therefore tree family or tree species growth as dependent on tree height would be worthwhile to be investigated. Lieberman et al. (1985) found four types of growth: under storey trees with slow maximum growth and short lifespan resulting in small size, sub canopy trees with similar growth rates to under storey trees but with a lifespan twice as long, canopy and sub canopy species that are tolerant of shade but with an opportunistic response to increased light levels and therefore a high maximum growth rate and long lifespan and the fourth group with shade-intolerant canopy and sub canopy trees with fast maximum growth rates and shorter lifespan. Keeling et al. (2008) in addition found a correlation between wood tissue density and light demand, meaning that shade tolerant trees gain more density than diameter. A long-term study, not necessarily at species level but with these four groups, would be highly recommended in combination with response to climate change.

2.4.4 Dbh class, site, year

Size class 0 of the secondary slope forest showed constantly high growth during all 5 measured years, but especially in year 2010/11- a La Niña year with high precipitation during the whole year, least dry days per months and highest rainfall during the dry season. Vieira et al. (2004) and Chave et al. (2003) also detected largest increments in the smallest size class with highest amounts reaching up to 56 % of annual aboveground biomass increment, but the smallest size class in case of Vieira was from 10-30 cm, in the other study from 1-25 cm. Vieira et al. (2004) furthermore mentioned that small trees show less seasonal response in the Amazon, which could not be confirmed in this study. Size classes and years didn't significantly interact and if anything then size class 0 showed most variance during the different years. If a buffered microclimate in the under storey would have influence on small trees in comparison to exposed canopy trees with more variable climatic conditions (cf. diagram with microclimate of different sites and the biological station as an open area in comparison), big trees

would have shown more variance in dbh increment between years than smaller ones. At the primary ridge site the trend of size class 0 was opposite in direction to other size classes, which could indicate that small trees are eventually more sensitive to climatic influences than bigger trees at a site that is low in nutrient supply and more exposed. Vieira et al. (2004) assumed that the smallest size class is experiencing the least water in dry periods and therefore is undergoing more likely drought stress, due to rooting depth being shallower than of large trees. Actually the small trees of the ridge site had lower growth rates in the year 2006/07 and 2008/09 which were the years with the least rainfall during the dry period from January till March, the greatest number of dry days per year and the most months that showed precipitation less than 200mm. Moreover, they exhibited highest growth in 2010/11- the year with outstanding rainfall during these months. Bigger trees seemed to fluctuate less in growth rate in the slope forests and insofar dealt better with the hot and dry climatic conditions in 2009/10, which showed highest minimum, maximum and medium temperatures of all measured years, least rainfall, highest MEI- index and by the way least increment values at all sites. The primary slope site was found to be the coolest and the site with the highest air moisture, as well as with highest soil water content. However, no significant correlation was found for inter annual climate variability or MEI and dbh increment either. A study carried out by da Silva et al. (2002) also found no significant differences between increments in slope and ridge sites.

The site with highest increment growth was the secondary forest. Brown and Lugo (1990) found secondary forests characterized by high litter fall and biomass production especially during the first 15 years. The secondary site in the measured area is approximately in its twenties and its high litter fall and stock and high dbh growth rate in comparison to the mature sites suggest still secondary forest activity probably due to the high amount of pioneers found in the species composition (e.g. *Vochysia*). It also showed highest rates of biomass losses due to mortality during the measured period, which points towards a very dynamic site. Pioneer species also show a higher mortality in smaller size classes (Condit et al., 1995), which is reflected here very well by the amount of losses in the secondary site. In Chave et al. (2001) the secondary forest site had third highest increment out of seven different observed habitats. At small tree sizes pioneer species showed markedly higher maximum growth than non-pioneer species, but this growth advantage was lost with increasing tree size and at most other sizes all species displayed the same range of growth increment (Clark and Clark, 1999). This could be an explanation for highest growth rates occurring in the smallest size class in the secondary forest in this study.

2.4.5 Internal and external trigger of dbh and AGB growth

Intra annual climatic influences on tree increments weren't very clear. It could be shown that the fastest growth of trees smaller and bigger than a dbh of 10 cm did take place neither in the rainy nor in the dry season. April to June had on average highest dbh increments while November to January showed lowest. The typical "dry season" lasted from January till March and was characterized by little rainfall and many dry days per month. The months April to June showed ascending increments with more distance to the dry season and increasing precipitation. Drage (2007) observed a peak of leaf litterfall at the end of the "dry period" at the same study sites. Higher nutrient availability due to enhanced litter decomposition in the transition from "dry" to wet season may lead to higher dbh increments in the following months. However, Vieira et al. (2004) discussed that variation in stem water content could overlay seasonal differences in growth and that seasonal variations were less distinctive in smaller size classes, which could not be confirmed in this study.

Diameter Increments of both small and bigger trees did not show a correlation to years of different ENSO phases; even though at least 2009/10 was quite a strong El Niño year and differed as such significantly in maximum and minimum temperature at the study site and increments were highest 2010/11- the strongest La Niña year of all measured years. This could be due to lag times of more than a year after strong events, which is however difficult to assess with this short time series of five years.

Comparing AGB increments at the different sites in response to previous rainfall, dry days, ENSO index or air temperature the primary slope forest turned out to be most independent from previous monthly rainfall (while rainfall and dry days had most influence of all other factors in the other forest types), which might be pointing to an enhanced moisture status of this forest. The ridge site showed strongest climate control but shifted by 10-12 months. The site showed a especially strong positive response to rainfall but not until 10 to 11 months later, and negative responses to rainfall 2 to 4 months ago. The inverse response was found to the number of dry days at the ridge site. Too much rain could cause diminished increment because of saturated soils limiting root respiration and therefore slowing photosynthesis. Moreover, high rainfall implies less light because of increased cloudiness: Clark and Clark (1994) found in La Selva daily photosynthetic active radiation (PAR) indeed being weakly negatively correlated with tree growth. The same study found no clear relationship between annual rainfall and tree growth rates.

According to Clark et al. (2010) dry season rainfall has not only a positive effect on tree growth, but even short periods of drought are able to reduce stand wood productivity by 20 % or more even in very wet tropical forests. In Clarks study dry season rainfall was predominate over other related

meteorological factors like radiation and temperature and clearly explained increasing and decreasing increments. Correlations of annual AGB increment against number of dry days and precipitation sum from January till March were not significant in this study, but rain sum and dry days per month had strong effects on future tree increments, i.e. tree dbh growth showed a lag time of approximately 12 months.

Moreover, Clark and Piper et al. (2003) found annual means of daily minimum temperature to be negatively correlated to tree increment, which could not be confirmed in this study, where minimum temperature only affected tree growth 12 months later, but strongly only at the ridge site.

2.5 Conclusion

- Topography had a strong influence on diameter growth, whereas successional status seemed to matter more than microclimatic factors. Secondary slope forest had significantly higher increment rates than the primary sites.
- Small trees with up to 10 cm dbh or < 5 m height showed the highest relative increment growth, especially in the secondary slope forest due to secondary forest species composition, i.e. the high abundance of fast growing pioneer trees.
- 2010/11 was an extreme La Niña year and had highest dbh increment growth of all years, but a significant general correlation between dbh increment and ENSO phases could not be detected. A time delay between effects of rainfall and dry days per month on AGB increments could be proved, while temperature had no or little effect at all.

3. References

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4. Tables and figures

Table1 Forest structure

	Secondary slope forest			Primary slope forest			Primary ridge forest		
Stem distribution [%]									
dbh size class 2.5-10cm			51.9			31.3			54.8
dbh size class 10-20cm			25.2			43.8			28.6
dbh size class 20-30cm			12.2			10.4			13.1
dbh size class 30-40cm			7.6			13.5			1.2
dbh size class >50cm			3.1			1.0			2.4
Stem density [N ha⁻¹]									
dbh size class <10cm	2267	±	208	1000	±	173	3067	±	1405
dbh size class >10cm	525	±	217	550	±	66	717	±	213
Basal area [m² ha⁻¹]									
dbh size class <10cm	3	±	0.5	1.8	±	0.6	4	±	1.6
dbh size class >10cm	30	±	11	29	±	11	29	±	18
Above ground biomass [Mg ha⁻¹]									
dbh size class <10cm	15.7	±	1.8	7.3	±	2.9	46	±	17
dbh size class >10cm	336	±	123	327	±	151	308	±	212
Coarse woody debris [N ha⁻¹]									
standing CWD	25	±	25	8	±	14	58	±	38
fallen CWD	92	±	38	183	±	163	92	±	38
Coarse woody debris mass [Mg ha⁻¹]									
standing CWD	0.25	±	0.27	0.14	±	0.19	7.9	±	7.6
fallen CWD	7.2	±	8.8	11.6	±	9.6	5.2	±	2.3
Input CWD [N ha⁻¹ a⁻¹]									
mean over 5 years	144	±	62	34	±	48	97	±	71
Losses of measured trees [% a⁻¹]									
mean over 5 years			4.5			2			2.6
Belowground biomass[Mg ha⁻¹] (1)									
living fine roots (all diameters) in 0-30 cm soil depth	5.17	±	3.20	4.07	±	1.07	12.59	±	3.98
Litter stock [Mg ha⁻¹] (2)									
fine litter stock	4.74	±	0.82	3.50	±	0.47	4.22	±	0.73
coarse litter stock	6.93	±	3.22	2.69	±	1.03	2.68	±	0.70

All values except percentages with standard deviation

1) data from Ratzer, A. (2007)

2) data from Drage, S. (2007)

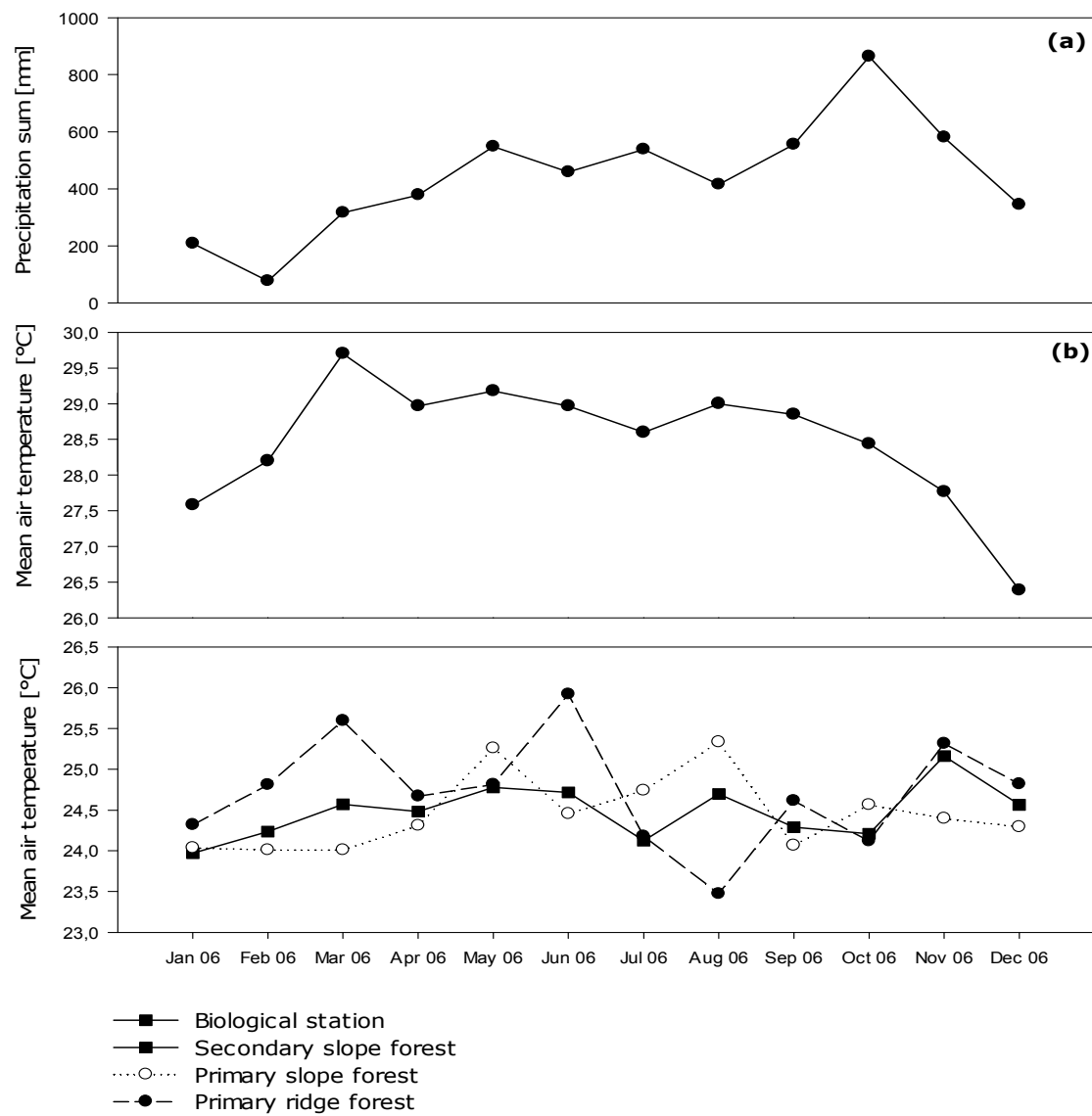


Figure 1 Monthly precipitation sum (a) and monthly mean air temperature (b) provided by measurement stations at the biological station, mean air temperature also provided by additional loggers at the three different forest sites (c), all data from 2006. Forest sites not significantly different at the 95% confidence level, $n=12$.

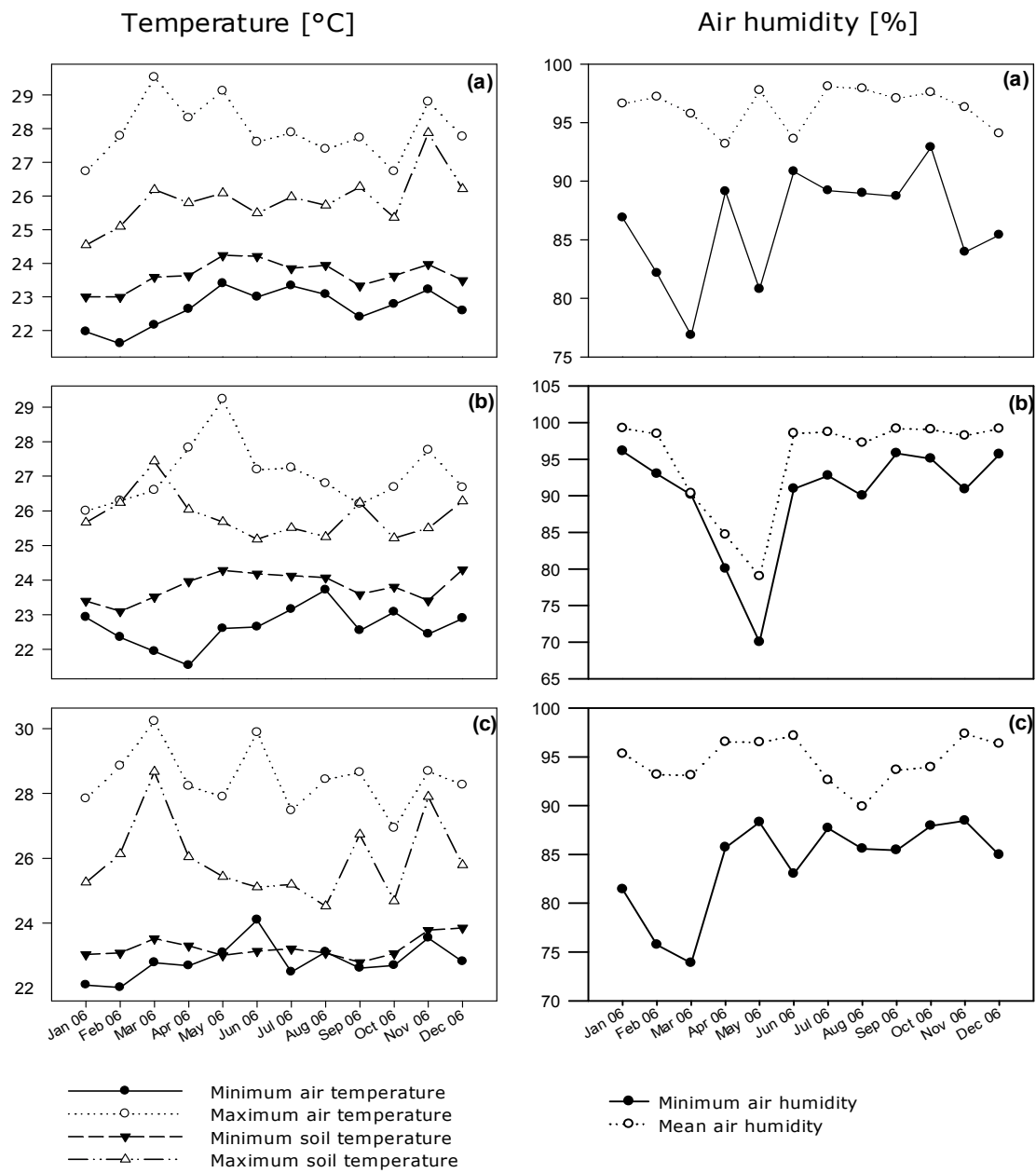


Figure 2 Monthly means of maximum and minimum air temperature, maximum and minimum soil temperature (measured 10cm below surface) and mean and minimum air humidity in the researched secondary slope forest (a), primary slope forest (b) and primary ridge forest (c), all data from 2006. Maximum air temperature and minimum soil temperature significantly different, $P < 0.05$, multiple range test LSD, $n = 12$.

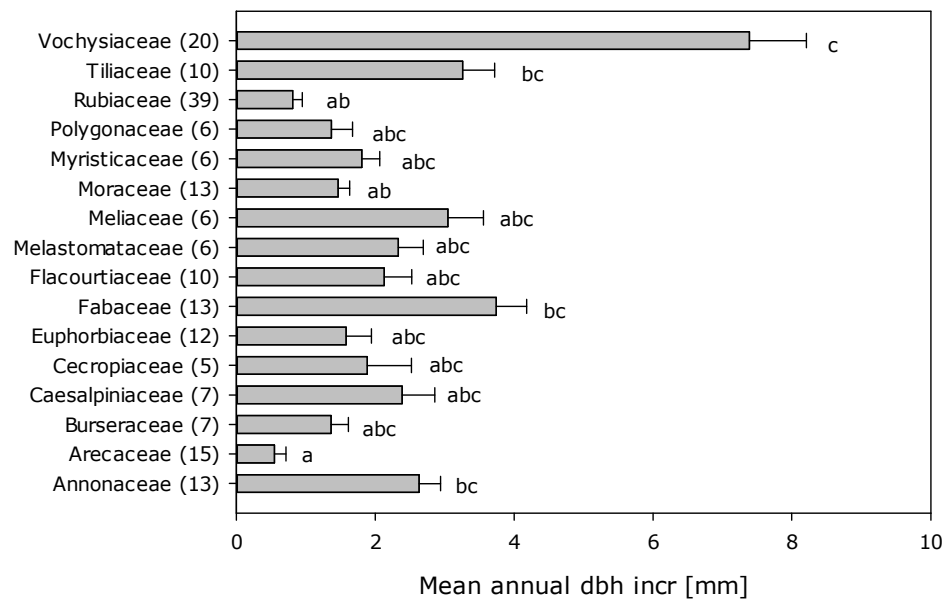


Figure 3 Mean annual dbh increments of different tree families over 5 years, numbers in brackets give numbers of measured trees within families. Mean values sharing the same letter are not significantly different from each other, $P < 0.0001$, Kruskal-Wallis test, multiple range test Scheffe. All bars with SE.

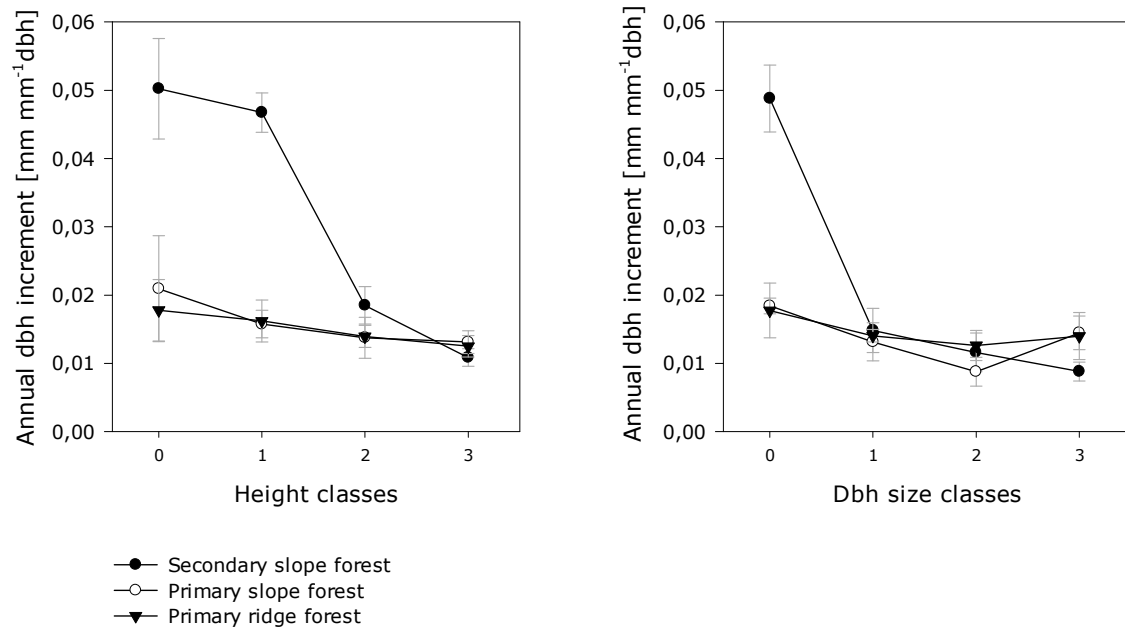


Figure 4 Mean relative annual dbh increment over 5 years for 4 height classes. Class 0: trees < 5m, class 1: 5-10m, class 2: 10-20m, class 3: >20m. Mean dbh increment over 5 years for 4 dbh size classes. Class 0: trees 2.5-10cm, class 1: 10-20cm, class 2: 20-30cm, class 3: >30cm. Secondary forest significantly different from the primary forests in height classes 0 and 1 and in dbh class 0, $P < 0.05$, multiple range test LSD, $n=5$. All means with SE.

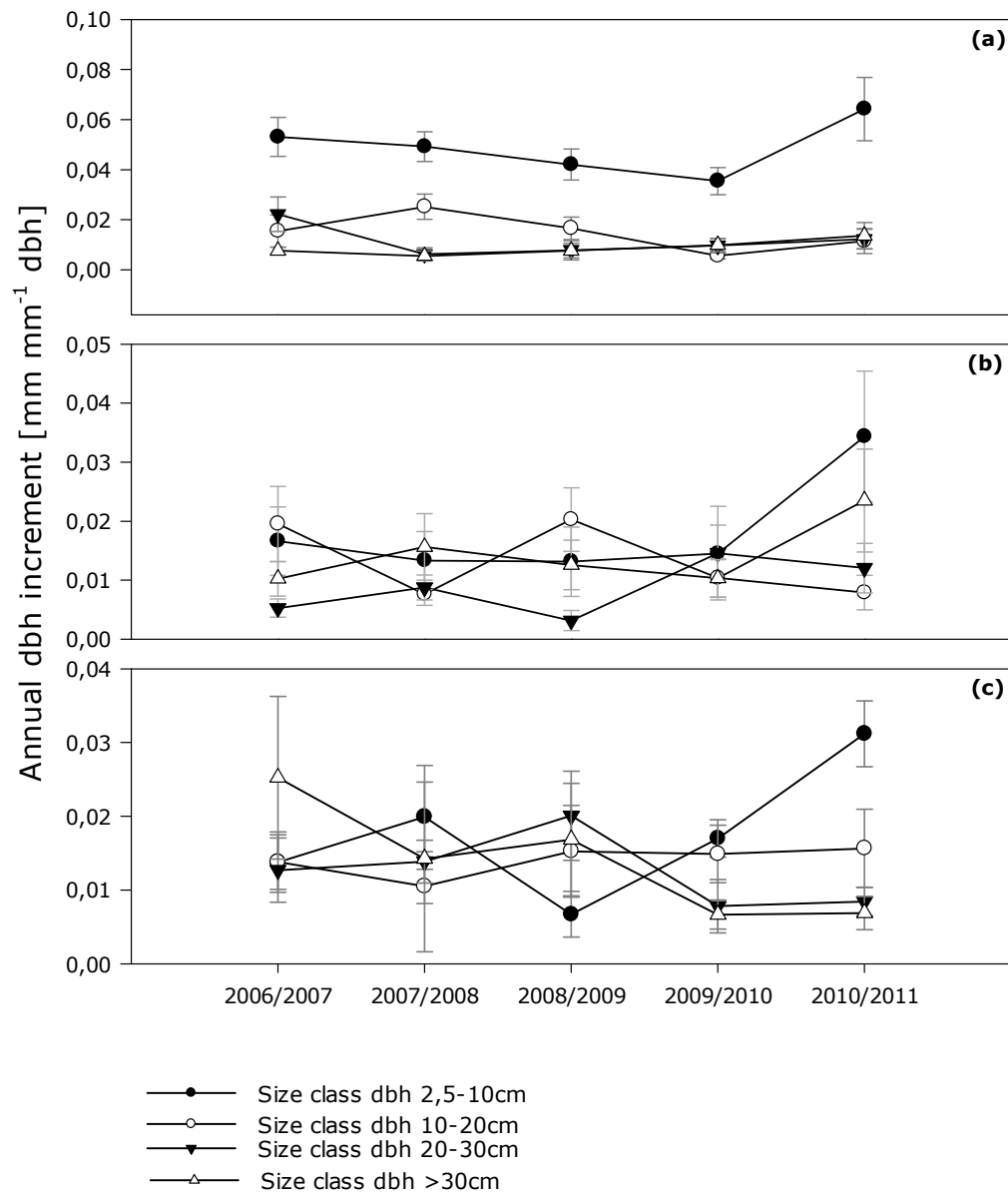


Figure 5 Mean relative dbh increment per measured year for the three different sites secondary slope forest (a), primary slope forest (b) and primary ridge forest (c). All factors highly significant, interaction between sites and dbh classes also significant, $P < 0.05$. Multiple range test Scheffe, Levene and Kruskal-Wallis test, all plots with SE.

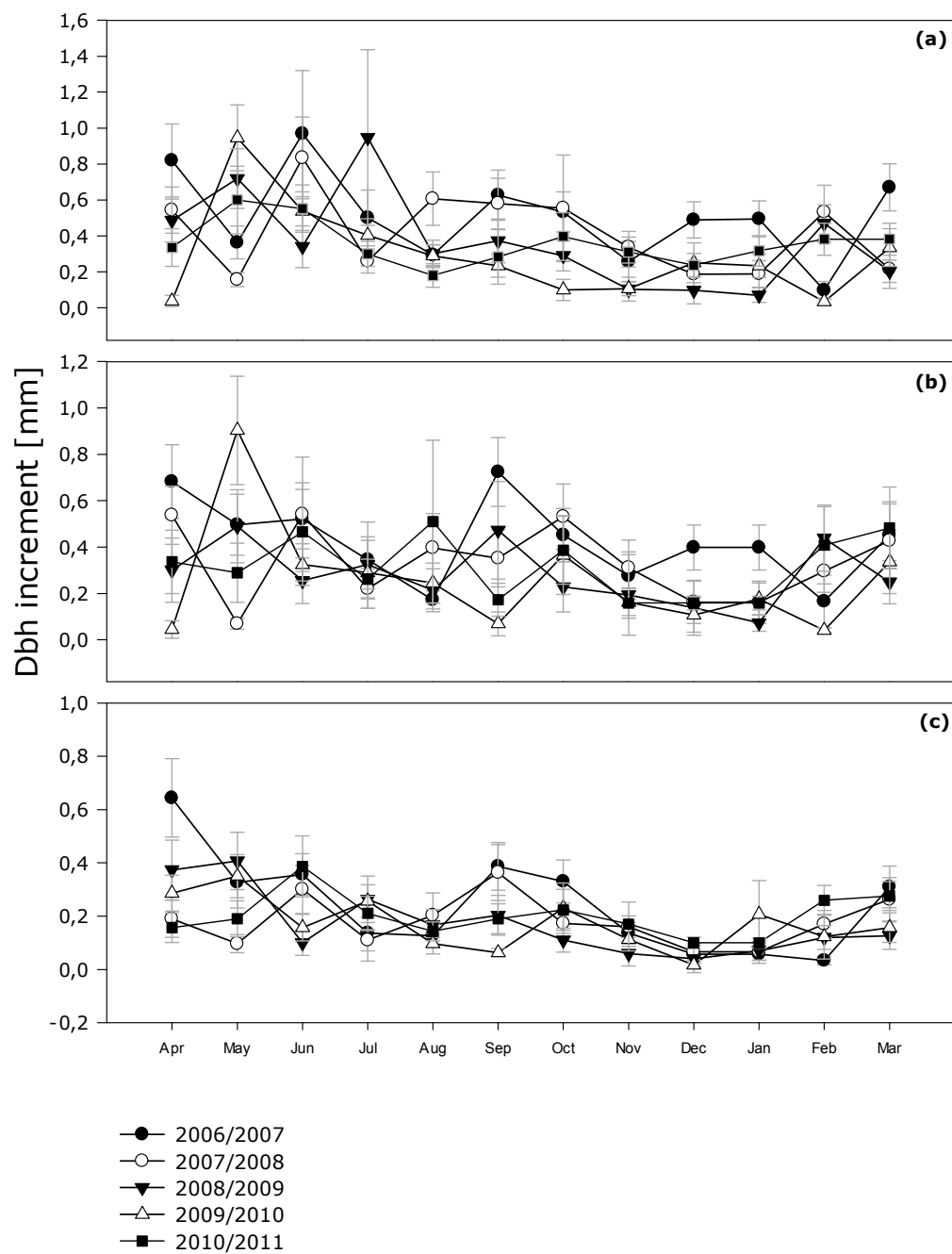


Figure 6 Mean monthly dbh increment for trees with dbh>10cm compared in five measured years and 3 sites: secondary slope forest (a), primary slope forest (b) and primary ridge forest (c). All factors highly significant, but significant interaction only between months and years, and also sites and dbh-classes; $P < 0.0001$. Multiple range test Bonferroni, all plots with SE.

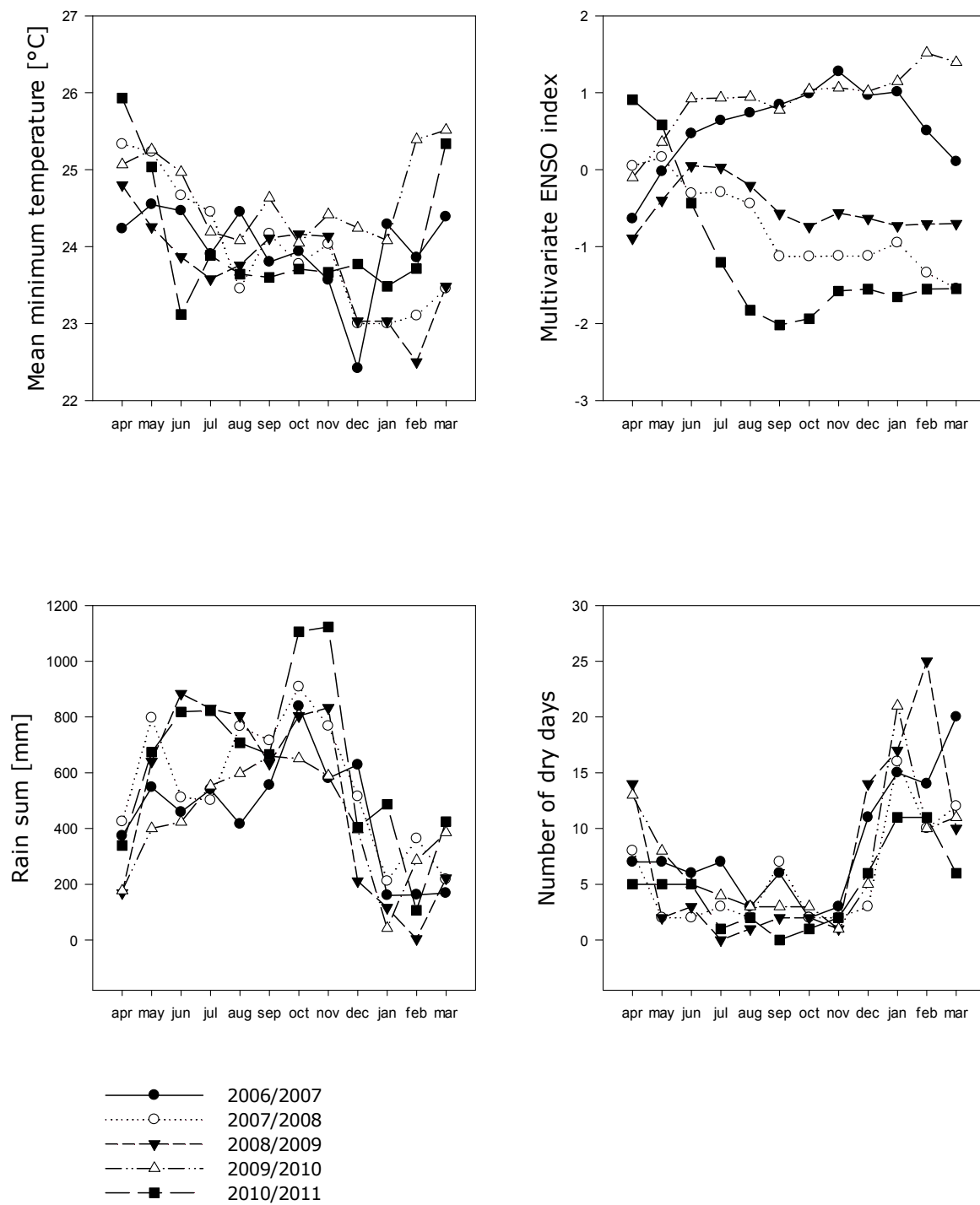


Figure 7 Mean monthly minimum temperature, mean monthly rain sum, multivariate ENSO index and number of dry day for each month compared in five measured years at the tropical research station. Minimum temperature and MEI significant; $p < 0.05$; multiple range test LSD.

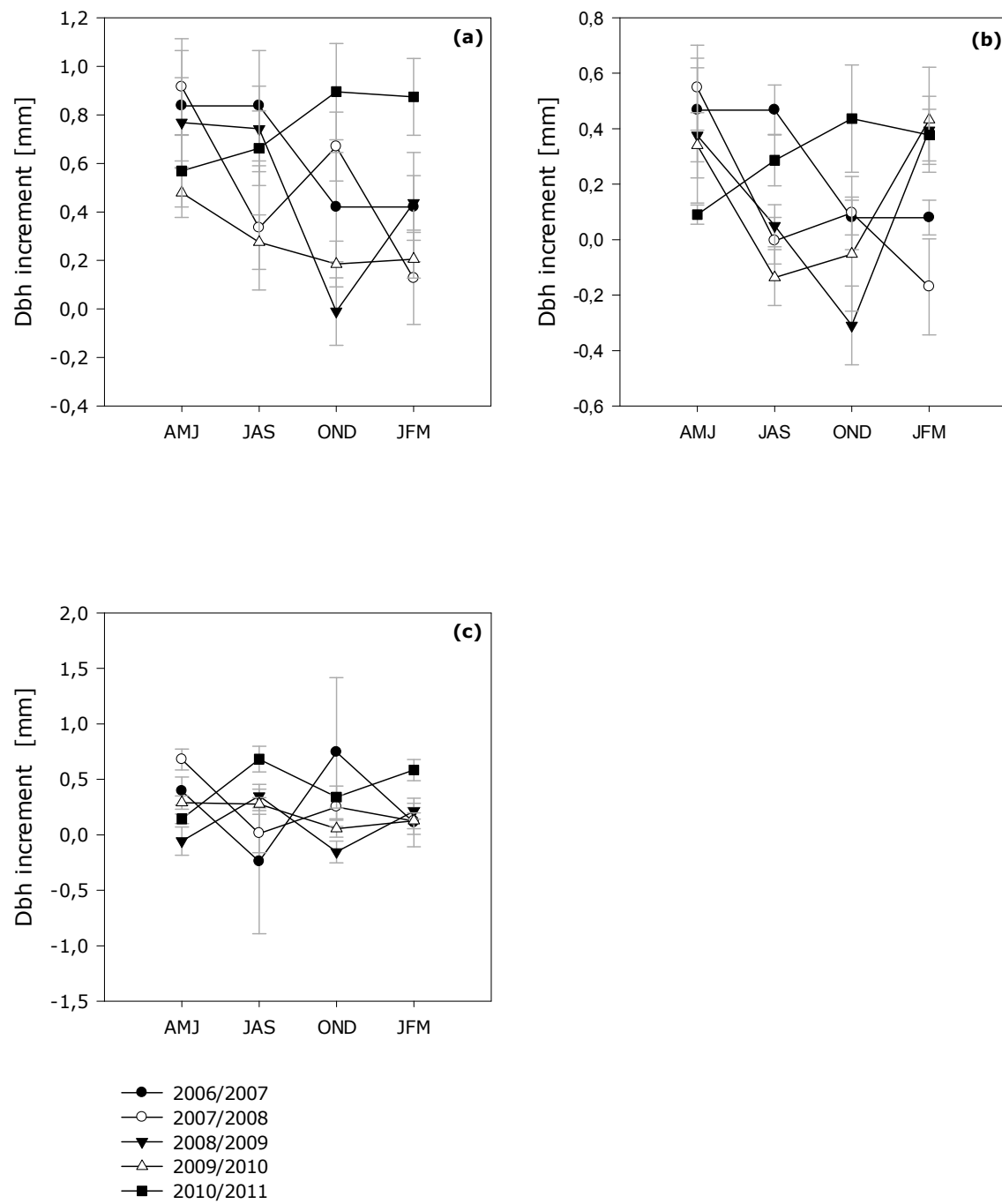


Figure 8 Dbh increments for trees with dbh<10cm measured in sets of months (AMJ= April, May and June; JAS= July, August and September; OND= October, November and December; JFM= January, February and March) for different sites: secondary slope forest (a), primary slope forest (b) and primary ridge forest (c) and years. All factors highly significant, $P < 0.0001$, multiple range test Bonferroni, all plots with SE.

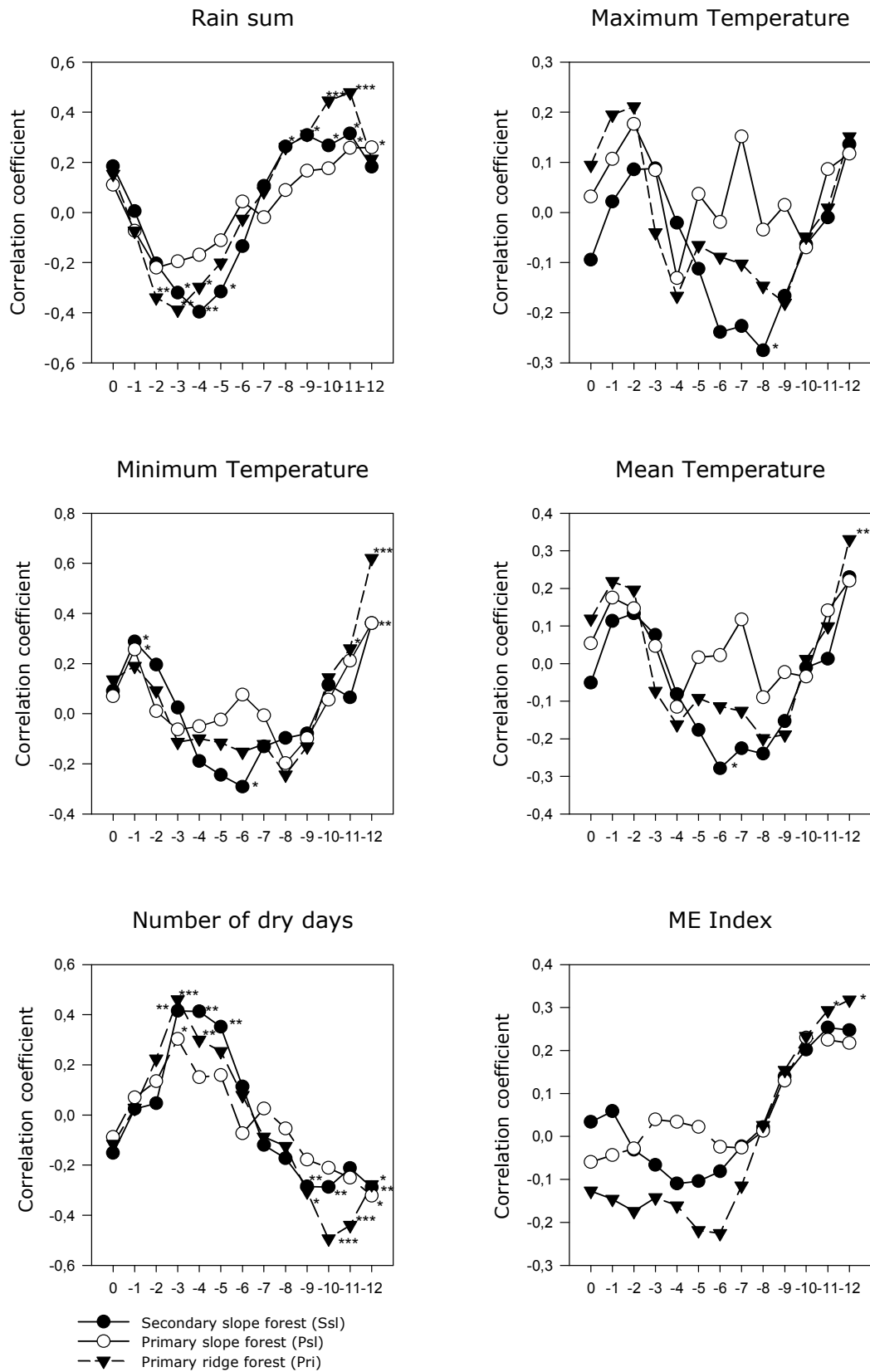


Figure 9 Monthly means of maximum, minimum and medium temperature, monthly rain sum, number of dry days and ME Index per months of 5 years switched against AGB increments of trees with dbh>10cm, x-axis showing number of months before actual increment measurement. Values significant P<0.05 marked with *, values significant P<0.01 marked with **, values significant P<0.001 marked with ***

Table2 Statistics

Forest structure		sites			size classes								
		Ssl	Psl	Pri	Ssl	<10 Psl	Pri	Ssl	>10 Psl	Pri			
Stem density (n=3)	P		0.0788			0.0574			0.4178				
	means (trees ha ⁻¹)	1550	2792	3783	1000	2267	3067	525	550	717			
	sign. Diff (LSD)	A	A	A	A	A	A	A	A	A			
Basal area (n=3)	P		0.9775			0.1657			0.9964				
	means (m ² ha ⁻¹)	33.0	30.8	32.5	3.32	1.79	3.50	29.8	29.0	29.0			
	sign. Diff (LSD)	A	A	A	A	A	A	A	A	A			
Above ground biomass (n=3)	P		0.9869			0.0095			0.9773				
	means (Mg ha ⁻¹)	352	335	357	15.7	7.28	48.5	336	327	308			
	sign. Diff (LSD)	A	A	A	A	A	B	A	A	A			
Microclimate		forest sites			station								
		Ssl	Psl	Pri									
Microclimate (n=12)	P		<0,0001										
	means (°C)	24.5	24.5	24.7	28.5								
	sign. Diff (LSD)	A	A	A	B								
Minimum air temperature (n=12)	P		0.6988										
	means (°C)	22.7	22.7	22.8									
	sign. Diff (LSD)	A	A	A									
Maximum air temperature (n=12)	P		0.0020										
	means (°C)	27.9	27.04	28.4									
	sign. Diff (LSD)	A	B	A									
Minimum soil temperature (n=12)	P		0.0027										
	means (°C)	23.7	23.8	23.2									
	sign. Diff (LSD)	A	A	B									
Maximum soil temperature (n=12)	P		0.9652										
	means (°C)	25.9	25.9	26.0									
	sign. Diff (LSD)	A	A	A									
Minimum air humidity (n=12)	P		0.053										
	means (%)	86.3	90.0	84.0									
	sign. Diff (LSD)	A	A	A									
Mean air humidity (n=12)	P		0.6307										
	means (%)	96.3	95.1	94.6									
	sign. Diff (LSD)	A	A	A									
Height and dbh classes		Height classes											
		Ssl	0 Psl	Pri	Ssl	1 Psl	Pri	Ssl	2 Psl	Pri	Ssl	3 Psl	Pri
Annual dbh increments (n=5)	P		0.0094			<0.0001			0.3538			0.5789	
	means (mm mm ⁻¹ dbh)	0.05	0.02	0.02	0.05	0.02	0,02	0.02	0.01	0.01	0.01	0.01	0.01
	sign. Diff (LSD)	B	A	A	B	A	A	A	A	A	A	A	A
two-way	P												
	site	<0.0001											
	height class	<0.0001											
	interaction	<0.0001											

		Dbh classes												
		Ssl	0 Psl	Pri	Ssl	1 Psl	Pri	Ssl	2 Psl	Pri	Ssl	3 Psl	Pri	
Annual dbh increments (n=5)	P		<0.0001			0.9009			0.5333			0.2851		
	means (mm mm ⁻¹ dbh)	0.05	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	
	sign. Diff (LSD)	B	A	A	A	A	A	A	A	A	A	A	A	
		P												
Two-way ANOVA	site	0.0643												
	height class	<0.0001												
	interaction	<0.0001												
Annual increment														
		Ssl	sites Psl	Pri										
Annual dbh increments	P		<0.0001											
	means (mm mm ⁻¹ dbh)	0.04	0.02	0.02										
	sign. Diff (Scheffe)	B	A	A										
		years												
		2006/07	2007/08	2008/09	2009/10	2010/11								
	P			0.0002										
	means (mm mm ⁻¹ dbh)	0.02	0.02	0.02	0.02	0.03								
	sign. Diff (LSD)	A	A	A	A	B								
		Dbh classes												
		0	1	2	3									
	P		<0.0001											
	means (mm mm ⁻¹ dbh)	0.03	0.01	0.01	0.01									
	sign. Diff (Scheffe)	B	A	A	A									
Multifactor ANOVA	P													
	three way ANOVA													
	interaction level													
	site	<0.0001	0.0728	0.0858										
	dbh-class	<0.0001	<0.0001	<0.0001										
	year	0.0181	0.4424	0.4826										
	site*dbh-class		0.0003	0.0003										
	site*year		0.0852	0.1063										
	dbh-class*year		0.6864	0.5451										
	site*dbh-class*year			0.1052										
Coefficient of Variances	Dbh classes													
		0	1	2	3									
	CV (%) sites	63	6	18	25									
	CV (%) years	32	22	13	19									

Monthly increment		years												
		2006/07	2007/08	2008/09	2009/10	2010/11								
Dbh increment trees >10cm	P			<0.0001										
	mean (mm)	0.39	0.31	0.27	0.25	0.31								
	sign. Diff (Bonferroni)	B	A	A	A	AB								
		jan	feb	mar	apr	may	months	jun	jul	aug	sep	oct	nov	dec
	P						<0.0001							
F- Ratio	mean (mm)	0.45	0.24	0.33	0.39	0.44	0.45	0.33	0.27	0.35	0.33	0.19	0.17	
	sign. Diff (Bonferroni)	AB	ABC	BCD	CD	D	D	BCD	ABC	CD	BCD	AB	A	
	months	9.51												
	years	7.80												
	Multifactor ANOVA	P												
	interaction level	1	2	3										
	year	<0.0001	<0.0001	0.0002										
	month	<0.0001	<0.0001	<0.0001										
	dbh-class	<0.0001	<0.0001	<0.0001										
	site	<0.0001	<0.0001	<0.0001										
	year*month		<0.0001	<0.0001										
	year*dbh-class		0.2239	0.3059										
	year*site		0.9266	0.8208										
	month*dbh-class		0.2830	0.6134										
	month*site		0.7260	0.4124										
	dbh-class*site		<0.0001	<0.0001										
	year*month*dbh-class			0.8045										
	year*month*site			0.5874										
	year*dbh-class*site			0.6560										
	month*dbh-class*site			0.8734										

Dbh increment trees <10cm		months							
		JFM	AMJ	JAS	OND				
P			0.0006						
	mean (mm)	0.28	0.44	0.31	0.27				
	sign. Diff (Bonferroni)	A	B	B	A				
		2006/07	2007/08	2008/09	2009/10	2010/11			
	P			<0.0001					
F- Ratio	mean (mm)	0.38	0.32	0.22	0.21	0.51			
	sign. Diff (Bonferroni)	AB	AB	A	A	B			
		Ssl	Psl	Pri					
	P		<0.0001						
	mean (mm)	0.53	0.19	0.25					
F- Ratio	sign. Diff (Bonferroni)	A	B	C					
	month	7.62							
	year	16.81							
	site	18.68							

Multifactor ANOVA		P				
	interaction level	1	2	3		
	year	<0.0001	<0.0001	<0.0001		
	month	<0.0001	0.0071	0.0157		
	site	<0.0001	<0.0001	<0.0001		
	year*month		<0.0001	<0.0001		
	year*site		0.0075	0.0065		
	month*site		0.0475	0.0160		
	year*month*site			0.0055		
Climate		years				
		2006/07	2007/08	2008/09	2009/10	2010/11
Maximum temperature (n=12)	P			<0.0001		
	mean (°C)	33.2	32.7	32.7	35.9	33.3
	sign. Diff (LSD)	A	A	A	B	A
Minimum temperature (n=12)	P			0.0317		
	mean (°C)	24.0	24.0	23.7	24.7	24.1
	sign. Diff (LSD)	A	A	A	B	A
Rain sum (n=12)	P			0.2454		
	mean (mm)	431	558	515	423	640
	sign. Diff (LSD)	A	A	A	A	A
Number of dry days (n=12)	P			0.5010		
	mean (dry days month ⁻¹)	8.4	5.8	7.6	7.3	4.6
	sign. Diff (LSD)	A	A	A	A	A
Multivariate ENSO index (n=12)	P			<0.0001		
	mean (index)	0.57	-0.76	-0.50	0.92	-1.15
	sign. Diff (LSD)	A	BC	B	A	C
Aboveground biomass		sites				
		Ssl	Psl	Pri		
Annual increments (n=5)	P		0.0014			
	mean (Mg ha ⁻¹)	18.2	16.3	11.2		
	sign. Diff (LSD)	A	A	B		
		years				
		2006/07	2007/08	2008/09	2009/10	2010/11
Annual increments (n=3)	P			0.5766		
	mean (Mg ha ⁻¹)	17.3	15.3	13.2	13.6	17.8
	sign. Diff (LSD)	A	A	A	A	A

Mean values sharing the same letter within a row are not significantly different from each other

Table3 Interannual growth correlations against mean annual climate parameters for 5 years (n=5)

	P-value	Cc	R squared [%]	
AGB Increment Secondary slope forest				
Annual rainsum	0,831	0,13	1,8	
Dry days year ⁻¹	0,525	0,38	14,7	
Months with rainsum <200mm	0,535	0,37	14,0	
Precipitation sum from January - March	0,981	-0,01	0,0	
Mean min temp month ⁻¹	0,539	-0,37	13,8	
Mean max temp month ⁻¹	0,288	-0,60	35,7	
Mean med temp month ⁻¹	0,347	-0,54	29,2	
MEI-index	0,795	-0,16	2,6	
AGB Increment Primary Slope forest				
Annual rainsum	0,400	0,49	24,2	
Dry days year ⁻¹	0,371	-0,52	26,9	
Months with rainsum <200mm	0,555	-0,36	12,8	
Precipitation sum from January - March	0,189	0,70	48,9	
Mean min temp month ⁻¹	0,945	0,04	0,2	
Mean max temp month ⁻¹	0,846	0,11	1,3	
Mean med temp month ⁻¹	0,886	0,09	0,8	
MEI-index	0,777	-0,18	3,1	
AGB Increment Primary Ridge forest				
Annual rainsum	0,197	0,69	47,7	
Dry days year ⁻¹	0,382	-0,51	25,8	
Months with rainsum <200mm	0,533	-0,38	14,1	
Precipitation sum from January - March	0,144	0,76	58,0	
Mean min temp month ⁻¹	0,613	-0,31	9,6	
Mean max temp month ⁻¹	0,625	-0,30	8,9	
Mean med temp month ⁻¹	0,617	-0,31	9,4	
MEI-index	0,394	-0,50	24,7	
MEI Index				
Annual rainsum	0,020	*	-0,93	87,2
Dry days year ⁻¹	0,281		0,60	36,4
Months with rainsum <200mm	0,658		0,27	7,4
Precipitation sum from January - March	0,416		-0,48	22,8
Mean min temp month ⁻¹	0,044	*	0,89	78,9
Mean max temp month ⁻¹	0,139		0,76	57,2
Mean med temp month ⁻¹	0,475		0,43	18,1
% losses of measured trees	0,130		0,77	58,9
CWD ha ⁻¹	0,331		0,56	30,8

Significant values labelled with *

5. Appendix

Summary

Anthropogenic emissions of carbon dioxide are still rising and while parts of them remain and accumulate in the atmosphere contributing to global warming another fraction dissolves into the ocean. The missing carbon is supposed to be stored by terrestrial vegetation and soils. Tropical rainforests fix and store a greater amount of carbon than other biomes and are therefore a very important carbon pool. Only little is known yet on how these sensitive ecosystems will be responsive to global climate change. To date current global terrestrial biosphere models and empirical measurements differ widely in their predictions of biosphere-atmosphere interactions and responses of ecosystems to changing climate and atmospheric carbon dioxide concentration.

Latest results differed whether tropical forests will still act as carbon sinks or on the contrary will become carbon sources under global change. In many cases biometric and micrometeorological data demonstrated that different neotropical forests are hardly one strong persistent carbon sink, and some of them in contrast may show severely reduced biomass production in future climates that are only slightly drier and/or warmer.

In the tropics large stocks of carbon are preserved in soil organic matter for centuries and longer, stabilized on mineral surfaces. Therefore short-term responses in carbon storage occur due to changes in the mass of wood and woody debris, because carbon in living tree biomass is assumed to stay for only a few decades. Forests are sinks for carbon dioxide through photosynthetic activity and sources because of autotrophic and heterotrophic respiration. The rates of ecosystem photosynthesis, respiration and decomposition vary diurnally and seasonally.

While net primary production is a common variable to measure forest photosynthetic activity and carbon uptake, aboveground biomass seems to be the largest fraction of NPP and is easy to measure. As short-term events like El Niño and Southern Oscillation (ENSO) bring periodic climatic changes similar to those predicted for global climate change in much of the tropics, research on ecosystem responses to ENSO have been widely used as a proxy for the climate sensitivity of tropical ecosystems to long-term changes.

This study examined the controls of wood increment in a humid tropical lowland rainforest in Province Puntarenas, Costa Rica. Three different sites in the Esquinas forest, which is part of the National Park Piedras Blancas, were established, differing in topographic and successional conditions: a secondary slope forest, a primary slope forest and a primary ridge forest. Associated studies analyzed litterfall and root dynamics in these forest sites.

Stem distribution, basal area, aboveground biomass (AGB), coarse woody debris and tree losses were determined to compare the forest structure at the research sites. For recording soil and air temperature and air humidity data loggers were installed in the understory and soil of each forest site. At the field station photosynthetically active radiation (PAR), air temperature and precipitation were recorded in an open place. Diameter at breast height (dbh) increment was measured installing dendrometer bands round the trunks or in case of trees smaller than a dbh of 10cm with direct caliper measurements. Data were collected monthly (small trees in intervals of 3 months) and then correlated with topographic, tree family and tree size parameters and analyzed for tree growth fluctuations between months and years respectively. For both small and big trees several allometric equations to calculate AGB were tested and compared. After calculating AGB increments with the finally chosen equations diverse climatic parameters were tested for time-delayed seasonal effects on AGB increment as well as for interannual changes, notably in relation to ENSO. Microclimatic parameters of the forest sites such as PAR (photosynthetic active radiation), soil and air temperature and air moisture were analyzed for one year. Precipitation and air temperature as well as wood increment were measured over a period of 5 years.

Mean annual dbh increment over 5 years was very high with 3.72 ± 0.23 mm for trees with dbh > 10cm and 1.22 ± 0.07 mm for trees with dbh < 10 cm. Results also showed that topography had a strong influence on AGB growth with the ridge site having smaller increments than the slope forests. Successional status seemed to matter more than microclimatic factors: the secondary slope forest had significantly higher increment rates than the primary slope site. Small trees with up to 10 cm dbh or height less than 5 m showed the highest relative growth, especially in the secondary slope forest due to secondary forest species composition i.e. the high abundance of fast growing pioneer trees.

2010/11 was an extreme La Niña year and had highest tree growth of all years, but a significant general correlation between dbh increment and ENSO phases could not be detected. This could be due to lag times of more than one year after strong events, which however is difficult to assess with this short time series of 5 years. A time delay between effects of rain fall and dry days per month on AGB increments could be proved, while temperature had no or little effect at all. The data therefore indicate that forests on different topographic positions are differently sensitive to intra- and inter-

annual changes in climate and therefore are expected to respond differently to future climate change.

Zusammenfassung

Anthropogen verursachte CO₂ Emissionen steigen nach wie vor an und während Teile davon in der Atmosphäre akkumulieren und zur globalen Erwärmung beitragen, nehmen Ozeane einen anderen Anteil davon auf. Der verbliebene Teil jedoch wird aller Wahrscheinlichkeit nach von der terrestrischen Vegetation und ihren Böden gebunden. Tropische Regenwälder fixieren und speichern eine größere Menge an Kohlenstoff als jedes andere Biom und sind daher ein sehr wichtiger Kohlenstoffpool. Bis jetzt ist jedoch wenig darüber bekannt wie diese sensiblen Ökosysteme auf den fortschreitenden globalen Klimawandel reagieren werden. Aktuelle globale terrestrische Biosphärenmodelle und empirische Messungen variieren sehr stark in ihren Voraussagen bezüglich zukünftigen Interaktionen von Biosphäre und Atmosphäre, oder bezüglich Reaktionen des Ökosystems auf den Klimawandel und die ansteigende Kohlendioxidkonzentration in der Atmosphäre.

Neuere Ergebnisse lieferten bis jetzt keine klaren Antworten auf die Frage ob tropische Regenwälder trotz des globalen Klimawandels eine Kohlenstoffsенke bleiben oder sich im Gegenteil zu einer zusätzlichen Kohlenstoffquelle wandeln werden. In vielen Studien zeigten biometrische und mikrometeorologische Daten, dass man in den meisten untersuchten Wäldern in den Neotropen kaum von einer konstant starken Kohlenstoffsенke sprechen kann. Einige von ihnen könnten stattdessen sogar ihre Biomasseproduktion deutlich reduzieren wenn zukünftige Klimaszenarien tatsächlich auch nur wenig trockener und/oder wärmer ausfallen.

Große Mengen an Kohlenstoff lagern in den Tropen über Jahrhunderte hinweg fest eingebunden in mineralische Bodenschichten. Kurzfristige Umlagerungen im Kohlenstoffkreislauf finden in der Biomasse statt, da Kohlenstoff in lebenden Bäumen nur eine vergleichsweise geringe Verweildauer von einigen Jahrzehnten aufweist. Wir sprechen von Wäldern als Kohlenstoffsенken weil sie durch Photosynthese atmosphärischen Kohlenstoff fixieren, und als Quellen, da sie Kohlenstoff im Zuge von sowohl autotropher als auch heterotropher Atmung freisetzen. Die Bilanz von Photosynthese, Atmung und Dekomposition in einem Ökosystem variiert mit den Tages- und Jahreszeiten.

Eine verbreitete Variable um die Photosyntheseaktivität eines Waldes und schließlich auch die Aufnahme von Kohlenstoff durch den Wald zu messen ist die Nettoprimärproduktion (NPP). Unter den Anteilen zur Nettoprimärproduktion sticht die oberirdische Biomasse (AGB) hervor, da sie

mengenmäßig eine wesentliche Rolle spielt und relativ einfach zu ermitteln ist. Auf der anderen Seite sind kurzfristige Ereignisse wie das El Niño and Southern Oscillation (ENSO) Phänomen gut geeignet um die Sensitivität von tropischen Ökosystemen gegenüber klimatischen Veränderungen zu untersuchen, da diese Naturerscheinung periodisch wiederkehrende Klimaschwankungen mit sich bringt, ähnlich denen, die für langfristigen globalen Klimawandel vorausgesagt werden.

Diese Studie untersuchte die Einflüsse auf den Holzzuwachs in einem tropischen Tieflandregenwald in der Provinz Puntarenas in Costa Rica. Dazu wurden drei bereits angelegte Untersuchungsflächen genutzt, die sich in ihren topographischen Eigenschaften und in ihrem Sukzessionsstadium unterscheiden: ein sekundärer Hangwald, ein primärer Hangwald und ein primärer Kammwald.

Anzahl, Grundfläche und Biomasse aller Bäume in verschiedenen Größenklassen, sowie Anzahl und Biomasse von Totholz wurde in den Untersuchungsflächen aufgenommen bzw. ermittelt und verglichen, um einen Einblick in die Waldstruktur zu bekommen. Um Aufzeichnungen über das Mikroklima in den einzelnen Standorten zu erhalten wurden Datenlogger im Unterwuchs und im Boden installiert, die Bodentemperatur, Lufttemperatur und Luftfeuchte erfassten. Auf der Tropenstation La Gamba wurden Werte zu photosynthetisch aktiver Strahlung (PAR), Lufttemperatur und Niederschlag gemessen. Um das Wachstum der Bäume mit einem Durchmesser größer als 10 cm untersuchen zu können wurden Dendrometerbänder in Brusthöhe am Stamm der Bäume installiert und der Durchmesser in Brusthöhe (dbh) monatlich abgelesen. Kleinere Bäume wurden mit einer Schublehre alle drei Monate vermessen. Die so erfassten Zuwachsdaten über einen Zeitraum von 5 Jahren wurden auf ihre Beziehung zu Topographie, Größenklassen der Bäume und Familienzugehörigkeit hin untersucht, beziehungsweise auf Zuwachsschwankungen im Bezug auf verschiedene Monate und Jahre. Für Bäume unter 10 cm Durchmesser und Bäume mit einem Durchmesser über 10 cm wurden diverse allometrische Gleichungen getestet um von ihrem Durchmesser auf die Biomasse hochzurechnen. Diese wurden getestet und verglichen und schließlich für jede der 2 Größenklassen die passendste ausgewählt. Mit den so erhaltenen AGB Datensätzen wurde der Biomassezuwachs auf zeitverzögerte Reaktionen auf saisonale Klimaschwankungen untersucht. Ebenso wurde nach signifikanten Zuwachsschwankungen zwischen den einzelnen Jahren und nach deren klimatischen Auslösern- vor allem im Hinblick auf ENSO- gesucht.

Der jährliche dbh- Zuwachswert, gemittelt über 5 Jahre, war mit 3.72 ± 0.23 mm für Bäume mit dbh > 10cm und 1.22 ± 0.07 mm für Bäume dbh < 10 cm sehr hoch verglichen mit Werten aus der Literatur. Die Ergebnisse zeigten außerdem, dass die Topographie und das Sukzessionsstadium größeren Einfluss auf das Wachstum zu besitzen scheinen als das Mikroklima. Vor allem der Sekundärwald hatte signifikant höhere Zuwachsraten als die Primärwälder. Kleine Bäume bis zu einem Durchmesser

von 10 cm oder einer Höhe bis zu 5 m wiesen das höchste relative Wachstum auf, vor allem im Sekundärwald, was auf die spezielle Artenzusammensetzung mit einer hohen Dichte von schnell wachsenden Pionierbäumen zurückzuführen ist.

2010/11 kann als extremes La Niña Jahr charakterisiert werden und fiel durch besonders hohe Wachstumsraten auf, ansonsten jedoch konnte kein signifikanter Zusammenhang zwischen AGB-Zuwachs und ENSO-Phasen entdeckt werden. Das könnte am zeitverzögerten Reaktionspotential von Ökosystemen von bis zu einem Jahr nach einem starken Klimaereignis liegen, Solche Trends und Zusammenhänge sind jedoch mit dem vorliegenden Datensatz von 5 Jahren nur schwer statistisch signifikant nachweisbar. Was sehr wohl festgestellt werden konnte war ein zeitverzögerter saisonaler Effekt von Niederschlag, sowie der Anzahl der Trockentage pro Monat auf den Zuwachs an Biomasse, während Temperaturschwankungen im Unterschied dazu eine eher geringere Rolle zu spielen schienen.

Zusammenfassend zeigte diese Studie, dass Wälder in verschiedenen topographischen Positionen unterschiedlich sensibel auf klimatische Schwankungen innerhalb eines Jahres und zwischen den Jahren reagieren, und damit wohl auch unterschiedlich auf zukünftige Klimaveränderungen.

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