Long-term growth and Δ^{13}C trends in *Hura crepitans* do not show changes in growth, climatic and environmental drivers in a Neotropical forest concession in Eastern Bolivia.

Gideon Terburg

Summary

Permanent plot studies in moist Neotropical forests reported that growth and dynamics have increased since the 1980's resulting in an increased carbon sink capacity. These results are gathered over relative short time scales and do not give any insight in possible drivers steering the growth and dynamic changes. Therefore research is needed on long-term growth trends and long-term changes in climatic and environmental drivers. We researched long-term growth trends with tree ring analysis and used stable carbon isotopes ratios (^{13}C discrimination) as a proxy to determine the driving factors behind the growth changes. This research was conducted on *Hura crepitans* a dominant long-lived pioneer tree species from a semi-deciduous moist forest in Eastern Bolivia. Ninety-seven *H. crepitans* individuals were sampled and analysed within similar diameter sections to correct for diameter dependent and age related growth effects. The results show decreased growth in the small diameter sections (5-20cm) over the last 70 years and no change in the bigger diameter sections. We found a decreased trend in Δ^{13}C in the smallest diameter section (5-10cm), but no trends in the bigger sections. With the analysis of the growth and Δ^{13}C trends in the 5-10cm section it is determined that the juvenile selection effect is the driving factor steering these trends. The juvenile selection effect, an effect caused by higher survival of rapid growing individuals, makes the trends in the 5-10cm section biased. Therefore there is no evidence found for changes in growth, dynamics and drivers over long time-scales. The combination of long-term growth and isotope trends showed to be a promising tool to create more insight in long-term changes in growth and the climatic and environmental drivers.

Introduction

Permanent plot studies in South America have reported increased forest biomass, growth and dynamics since the 1980's (Baker *et al.*, 2004; Laurance *et al.*, 2004; Phillips *et al.*, 2008), and therefore an increased carbon sink capacity for mature humid tropical rainforest (Phillips *et al.*, 1998; Phillips *et al.*, 2008; Laurance *et al.*, 2009). Mature humid tropical rainforest might therefore acts as a mitigating factor on the [CO$_2$] increase and thereby the magnitudes of climate changes (Bonan, 2008).

   The changes in Neotropical forests have only been recorded for short time scales starting from the 1980's (Phillips *et al.*, 2008), and it is unknown if these changes are temporal fluctuations or long term changes. Tree ring studies have shown to be useful in studying long term growth and climate trends (Soulé and Knapp, 2006; Sun *et al.*, 2010; Sidvora *et al.*, 2010; Gebrekirstos *et al.*, 2009; Brienen *et al.*, 2011), and can so contribute to creating insight in long-term growth changes in Neotropical forests.

Drivers and growth

   Although still under heavy debate, several drivers are hypothesized to have influenced the observed changes in tropical forests. These include: increased temperature, increased precipitation, increased nutrient depositions, recovery from (past large scale) disturbances and CO$_2$ fertilisation

(Chambers and Silver, 2004; Lewis *et al.*, 2004; Phillips *et al.*, 1998). Increased temperature, as is reported to be on-going on a global scale (IPCC, 2007), and increased nutrient depositions (Holland *et al.*, 1999) both potentially increase the photosynthesis on the leaf level. Temperature rise may increases the chlorophyll and carotenoid concentrations together with increased electron transport (Lewis *et al.*, 2004), where increased nutrient availability stimulates the levels of complexes used for photosynthesis (Evans, 1989). Increased temperature can also have an inhibiting effect on photosynthesis by increasing transpiration and photorespiration (Long, 1991). Rising [CO_2] can decrease the inhibiting effects of temperature rise (Drake *et al.*, 1997; Lewis *et al.*, 2004), by increasing the optimum and maximum temperature at which leaves photosynthesise (Shue and Lin, 1999; Long, 1991), and decreases in stomatal closure leading to less transpiration (Chambers and Silver, 2004). Since temperature and CO_2 both have increased (IPCC, 2007), a change in response of leaves to temperature together with a higher CO_2:O_2 ratio will minimize the inhibiting effects of temperature on photosynthesis (Drake *et al.*, 1997; Lewis *et al.*, 2004).

The occurrence of recent disturbances will increase the nutrient and light availability for the surrounding trees (Canham, 1988; Denslow *et al.*, 1998; Muscolo *et al.*, 2007), and thereby also increase the photosynthesis (Brokaw, 1985; Brown, 1996; Herault *et al.*, 2010). The increases in photosynthetic activity can result in higher growth rates. Increased growth of the Neotropical forests can also be caused by recovery from past large scale disturbances, either caused naturally or by human activity (Phillips *et al.*, 1998; Denevan, 1992). In the case of large scale past disturbances the forests increase in total biomass as a result of succession. Precipitation and CO_2 fertilisation on the other hand can increase growth by influencing the stomatal conductance. Increased precipitation can make it possible for the plants to maintain a high stomatal conductance, which can results in higher carbon sequestration rates (Davies and Zhang, 1991). The on-going increase in atmospheric carbon dioxide concentrations (c_a) (IPCC, 2007), can lead to a CO_2 fertilisation effect in plants due to higher light- and water-use efficiencies (Nock *et al.*, 2010; Lewis *et al.*, 2004). This CO_2 fertilisation can manifest due to increased water-use efficiency by the physiological response of the plant by lowering the stomatal conductance (g_s) under higher CO_2 concentrations (Drake *et al.*, 1997; Nock *et al.*, 2010, Brienen *et al.*, 2011). Reduced g_s leads to less transpiration by which the plant loses less water per unit carbon sequestrated (Feng, 1999). The increase of CO2 can also lead to a lower photorespiration rate which leads to a higher resource-use efficiency in the plant (Drake *et al.*, 1997) and lead to a higher carbon sequestration rate per unit light, hence higher light-use efficiency (Saxe *et al.*, 1998; Drake *et al.*, 1997). The physiological responses of the stomata to precipitation and CO_2 respectively can lead to and is caused by an increased supply of CO_2 to the internal carbon dioxide concentration (c_i) and can therefor change growth. The establishment of c_i is caused by the supply in CO_2 through the stomata and the demand of CO_2 by photosynthesis (Farquhar, 1982).

Conceptual model

The analysis of stable carbon isotopes over long timescales can show changes in physiological processes in the plants (McCaroll and Loader, 2004). The ^{13}C:^{12}C ratio of cellulose in the wood of growth rings can be used as a proxy for the discrimination against ^{13}C ($\Delta^{13}C$) and the internal carbon dioxide levels in the leaves (ci) (Farquhar *et al*,. 1982). Combining growth trends, obtained by tree ring analysis, with stable carbon isotope analysis can therefor determined which drivers influence the growth over long timescales. As discussed above the possible drivers all influence growth in different ways, by either directly adjusting the assimilation rate (A) or indirectly by affecting stomatal conductance (g_s). The conceptual model illustrated in Fig. 1 shows the possible changes in growth and isotope trends and the most likely driving factor behind this combination of trends.
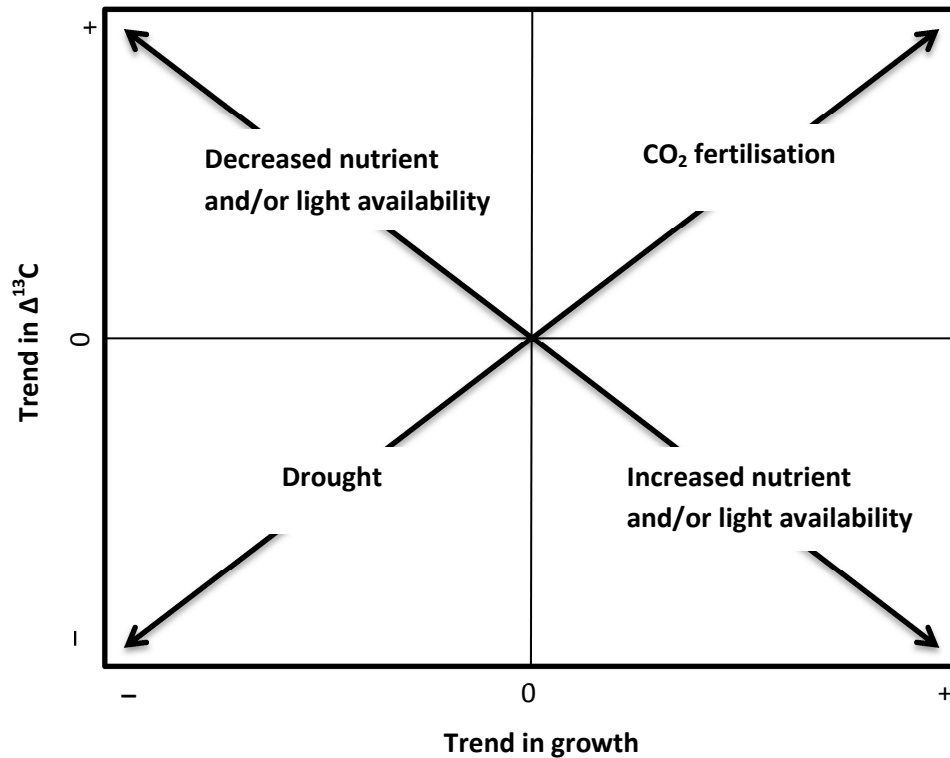
Fig. 1 Conceptual model of driving forces behind possible negative or positive trends in growth and carbon isotope discrimination ($\Delta^{13}C$). $\Delta13C$ is proportional to ci/ca.

Drivers and isotopes

The CO_2 fertilisation effect and occurrence of disturbances or increased nutrient availability can both stimulate growth over time but influence c_i in different ways. In the case of CO_2 fertilisation $\Delta^{13}C$ will show a positive trend due to increasing c_i levels as a consequence of the rise in c_a. With the occurrence of disturbances the nutrient and light availability for surrounding trees will increase (Canham, 1988; Denslow *et al.*, 1998; Muscolo *et al.*, 2007), which will results in higher assimilation rates and a reduction in c_i, hence a negative $\Delta^{13}C$ trend. Similar changes will occur when the nutrient availability will increase by for example increased nitrogen deposition. Decreasing growth trends can be caused by reduced light and/or nutrient availability, selection in juvenile trees and drought, shown by increasing and decreasing trends in $\Delta^{13}C$ respectively. Decreased light and/or nutrient availability will cause a reduction in the photosynthetic rate, leading to a lower demand of c_i and a positive trend in discrimination. Juvenile selection is caused by the skewed distribution of fast and slow growing individuals throughout the data and will cause similar trends as reduced light and/or nutrient availability. The older trees which will be sampled exist almost solemnly out of juvenile fast growing individuals which have had the least cumulative mortality risk during the growth process to reaching the canopy (Rozendaal *et al.*, 2010). In contrast the data of young trees consists of rapid and slow growing trees. As a consequence the growth trend will be declining over time, and the $\Delta^{13}C$ trend will increase. Since the low growth in young trees will most likely be caused by low levels of light, they will have lower photosynthetic rates and higher $\Delta^{13}C$. Negative $\Delta^{13}C$ trends co-occurring with negative growth trends can be explained by drought, either caused by less water availability and/or a rise in temperature. Reduced water availability and rising temperature will cause a reduction in g_s to limit the evaporative loss of water. By reducing the stomatal aperture the supply of CO_2 to c_i is reduced, resulting in a decreased discrimination trend.

Given that the increased growth in Neotropical forest is recorded throughout the Amazon basin (Phillips *et al.*, 2008), it is hypothesized that tree growth rates have increased over long time-scales caused by the CO2 fertilisation effect leading out of increased internal carbon dioxide concentrations. Our main research questions in this research are; (1) Has tropical tree growth changed over longer timescales (70-100 years)? (2) Can long term isotope trends explain the change in long-term growth trends? The tree ring and isotope analysis were conducted on 97 trees of a dominant tree species, *Hura crepitans,* in eastern Bolivia.

Material and Methods

Study site and species

The study has been conducted in the semi-deciduous tropical moist forest Agroindustria Forestal La Chonta (15°47' S, 62°55' W) in eastern Bolivia. This is a transitional forest between Chiquitano dry forest and moist Amazonian forests (Peña-Claros *et al.*, 2008). The amount of average annual rainfall is 1580 mm, with a 4 month period with less than 100 mm/month^{-1} (Peña-Claros *et al.*, 2008). The studied species is *Hura crepitans* from the Euphorbiaceae family. *H. crepitans* is a long lived semi-deciduous pioneer species which is partially shade tolerant (Francis, 1990).

From the 2011 logging quadrant (216 ha), 97 *H. crepitans* individuals with a diameter from 5 up to 73 cm were sampled. From every individual tree the canopy closure index (CCI) was determined, from the amount of overshadowing by neighbouring trees, to estimate the amount of overshadowing (Lieberman *et al.*, 1989). The CCI (inverse of light availability) of the crown is calculated by the difference in crown height and stem distance of taller neighbouring trees in a 10m radius to the sampled individual. Sampling was done by either harvesting a disc at dbh with a chain saw or by taking increment cores at dbh in three directions with a Hagelöf increment borer (40 cm with 5 mm diameter). The sampled individuals were spatially selected by putting a 300 by 300m raster over the quadrant. We sampled every *H. crepitans* individual within randomly assigned circles of 50m radius within each 300x300 grid. This sampling strategy has been followed in order to decrease autocorrelation and to get a distribution in size categories which is representative for the forest.

Tree ring measuring and analysis

After air-drying all tree samples were sanded in order to determine where the rings start and end. After rough sanding, the top layer of the increment cores was cut off with razor blades. The annual growth of every tree was measured over three different radii to determine and correct for false and wedging rings and get a good approximation of the average annual growth. The annual increments of the discs were measured with Tsapwin (Rinntech, Germany), and the increment cores with Windendro (Regent Instruments, Canada).

H. crepitans is a new species in the field of dendroclimatology. In the fire scar study of López-Callejas (2003) it was determined that *H. crepitans* produces rings on annual basis (López-Callejas, 2003).

In order to correlate for the differences in growth rates of different sized and aged trees we transformed ring width to basal area increment
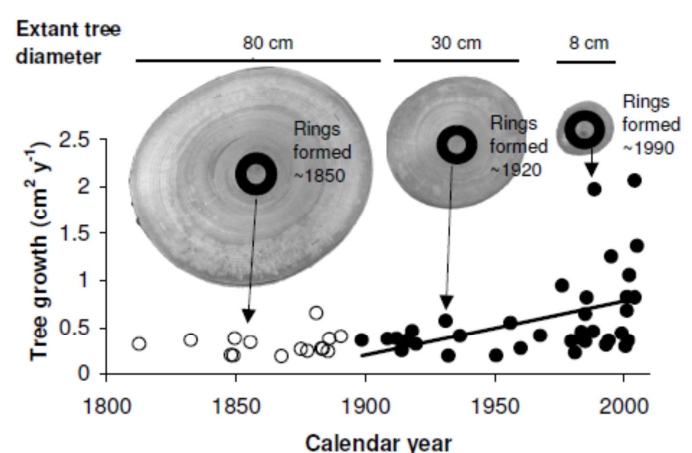

Fig. 2 Example of sampling strategy from *Pseudolmedia Igevis* in Bolivia. The black circles show correlated diameter sections which represent tree growth for different diameter trees for comparable tree ages. These results show an increase in tree growth (cm^2 y^{-1}) during the 20th century (black dots) but none for the 19th century (Rozendaal *et al.*, *unpublished results*).

(BAI). The BAI was analysed within four diameter sections to obtain growth trends in comparable growth stages over time. The diameter sections were: 5-10cm; 10-20cm; 20-30cm and 30-40cm. The use of diameter sections corrects the growth rates for diameter dependent and age related growth effects. The comparison of diameter sections can reveal long-term trends in growth rates which are not related to ontogeny (Fig. 2; Brienen and Zuidema, 2006).

Isotope measuring

Wood samples were taken in fixed bulk samples of five proceeding years. By using bulk samples the year to year variation is dampened in the data which makes the long-term trends become more pronounced (Hietz et al., 2005). Cellulose extraction was performed on the raw wood samples using the adapted Jayme-Wise method (Wieloch et al., 2011). The extracted cellulose has been homogenised in a demi-water solution using a vortex and oven dried at 50°C. The homogenised cellulose was measured by a Sercon ANCA element analyser coupled to a Sercon Hydra 20-20 mass spectrometer at the department of Geography of the University of Leicester, UK.

Isotope data analysis

The measured isotope ratios of the samples have been referenced to a set standard (VPDB) (Coplen, 1995; McCarroll and Loader, 2004). By referencing the isotope ratios the isotope signature is obtained

$$\delta^{13}C_{cellulose} = \left(\frac{R_{cellulose}}{R_{standard}} - 1\right) * 1000 \tag{1}$$

where R is the ratio between ^{13}C and ^{12}C of a cellulose sample and the international standard value, and $\delta^{13}C_{cellulose}$ is the isotope signature of the cellulose in parts per thousand (‰) (McCarroll and Loader, 2004). It should hereby be noted that the carbon isotope signature of the cellulose differs between 1-2‰ compared to the δ^{13}C of the leaf sugars (Badeck *et al.*, 2005). Any further calculations with the $\delta^{13}C_{cellulose}$ values deflect relative changes and not absolute values.

   Variation in the carbon isotope ratio is controlled by the discrimination factor against $^{13}CO_2$ (Δ^{13}C). Δ^{13}C Establishes through two fractionation factors which favour $^{12}CO_2$ over $^{13}CO_2$ due to different physical, chemical and biological properties (McCarroll and Loader, 2004). The first fractionation process is a physical fractionation and takes place when the CO_2 diffuses into the stomata (ε_D). The second fractionation is a biochemical fractionation when CO_2 binds to Rubisco (ε_c). Both fractionation processes are influenced by the ratio between c_i and c_a (Farquhar *et al.*, 1982; Helle and Schleser, 2004). From $\delta^{13}C_{cellulose}$ the Δ^{13}C and the c_i can be calculated using

$$\Delta^{13}C = \delta^{13}C_{atm} - \delta^{13}C_{cellulose} = -\varepsilon_D\left(1 - \frac{c_i}{c_a}\right) - \varepsilon_c\left(\frac{c_i}{c_a}\right) \tag{2}$$

In which Δ^{13}C is the fractionation factor in parts per thousand (‰), $\delta^{13}C_{atm}$ is the isotopic signature of the atmosphere (currently around -8‰), ε_D is physical fractionation when CO_2 diffuses into the stomata (-4.4‰) and ε_c is the biochemical fractionation by rubisco (-27‰) (Farquhar *et al.*, 1982; Helle and Schleser, 2004).   Due to the burning of fossil fuels, which are depleted in ^{13}C, the isotopic composition of the atmosphere has been decreasing since the industrial revolution (Suess effect) (McCarroll and Loader, 2004). Therefore the $\delta^{13}C_{cellulose}$ has been corrected to pre-industrial levels (-6.4‰) by calculating $\delta^{13}C_{corr}$ (McCarroll *et al.*, 2009)

$$\delta^{13}C_{corr} = \delta^{13}C_{cellulose} - (\delta^{13}C_{atm} + 6.4) \tag{3}$$

The discrimination factor was calculated with equation (2) by using $\delta^{13}C_{corr}$ as $\delta^{13}C_{cellulose}$ and a stable pre-industrial $\delta^{13}C_{atm}$ of -6.4‰.

Statistical Analysis

The changes in growth and discrimination over time have been tested with the Pearson's correlations. The correlations between discrimination rates and BAI with CCI were also tested with Pearson's correlations.

Results

Growth and isotope patterns within the diameter sections

A decrease in annual growth over time has been found in the two smallest diameter sections (Fig. 4a & 4b) (r=-0.29 and -0.28; p=0.005 and 0.015, respectively). In the diameter sections 20-30cm and 30-40cm we did not find any trend over time (Fig. 4c & 4d).

We found a significant decreasing trend in $\Delta^{13}C$ in the smallest diameter section 5-10cm (Fig. 5a) (r=-0.27; p=0.025). Within the other diameter sections no clear trend was observed (Fig. 5b, 5c and 5d).
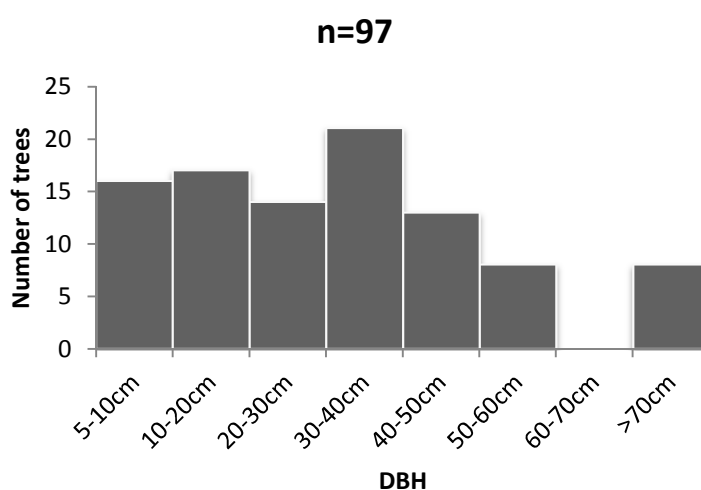

Fig. 3 Distribution of the sampled trees over the size catagories.

The correlation between CCI and average annual growth within in the smallest diameter section (5-10cm), grown in 2001 or later, is shown in Fig. 6. This correlation states the influence of light availability on growth rates in extant small trees. We found a strong negative relation between the CCI in the growth season 2010 and the plotted average growth rates (r=-0.61; p<0.001). Looking at the same trees within the same diameter section as included in Fig. 6 we observed a strong positive relation between the discrimination level and CCI (Fig. 7) (r=-0.61; p=0.020).

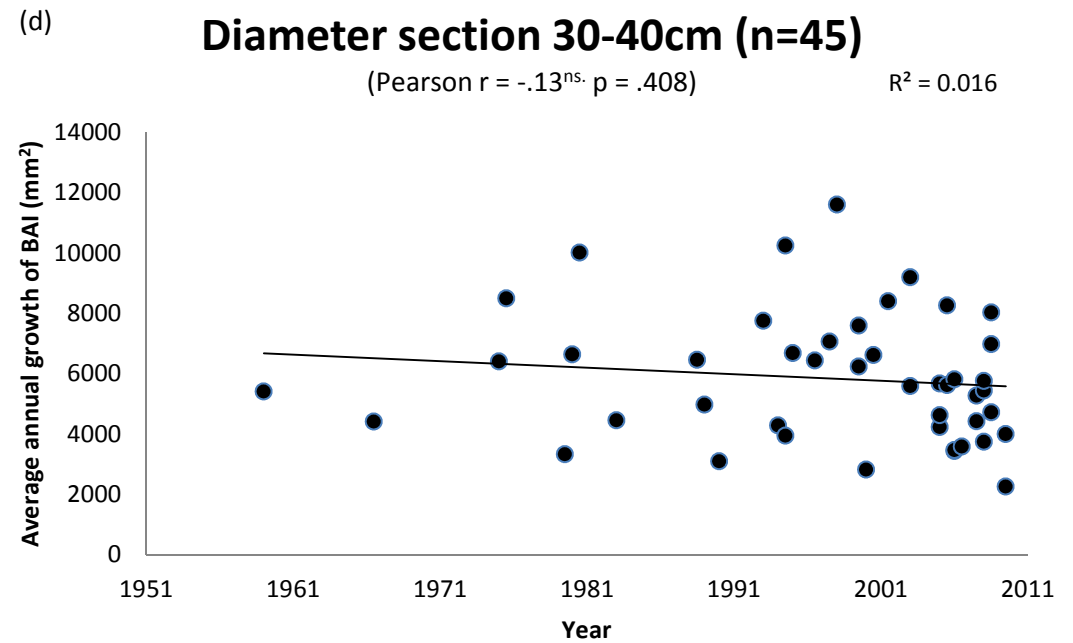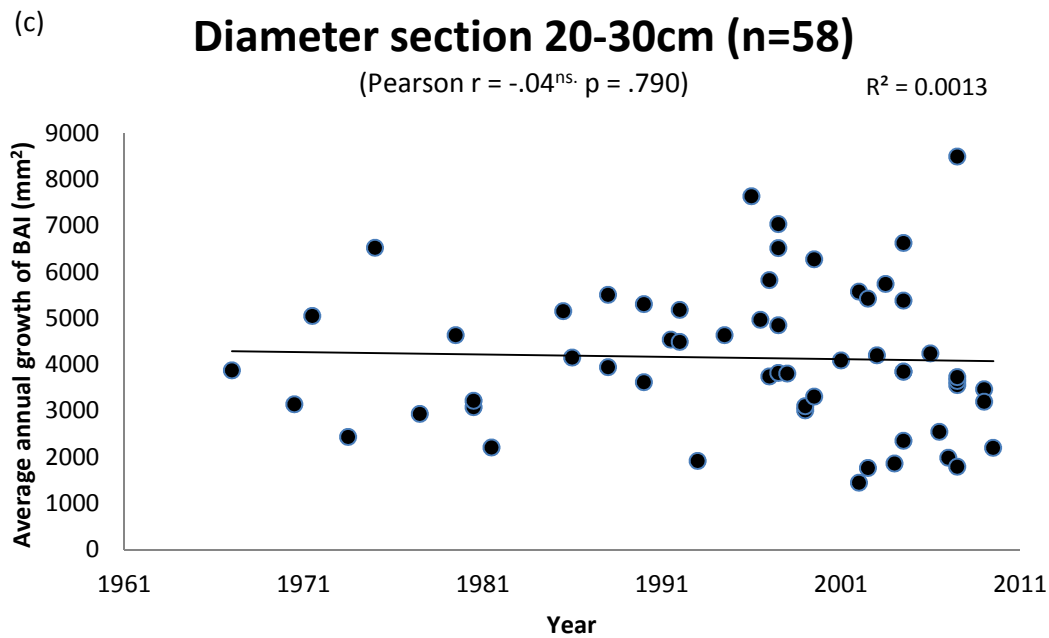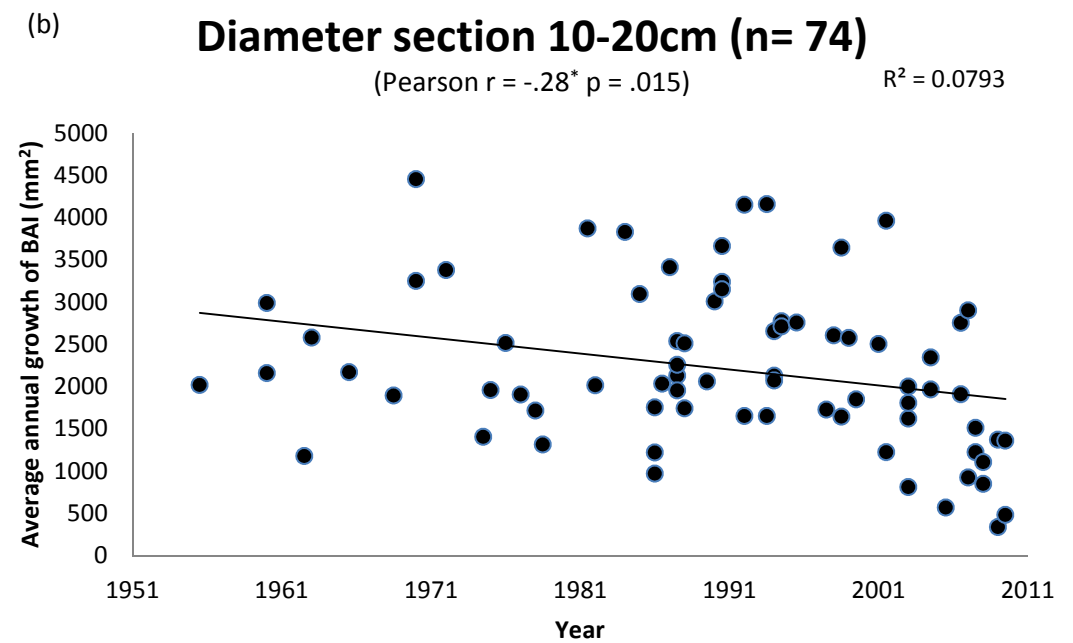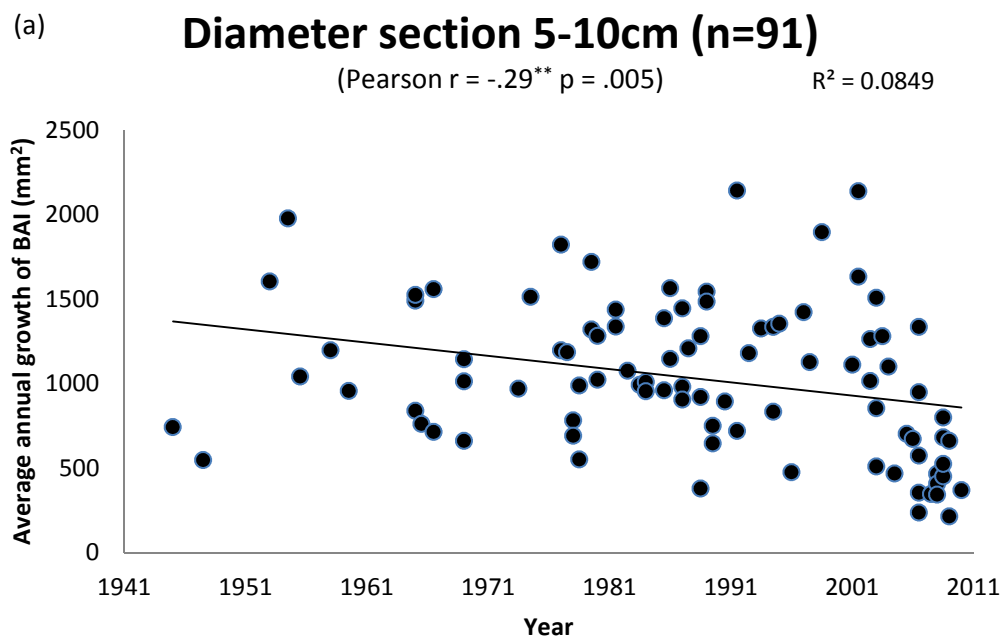**Fig. 4** Average annual growth of basal area of increment (BAI) within the diameter sections over time of *Hura crepitans*; (a) 5-10cm, (b) 10-20cm, (c) 20-30cm, (d) 30-40cm.
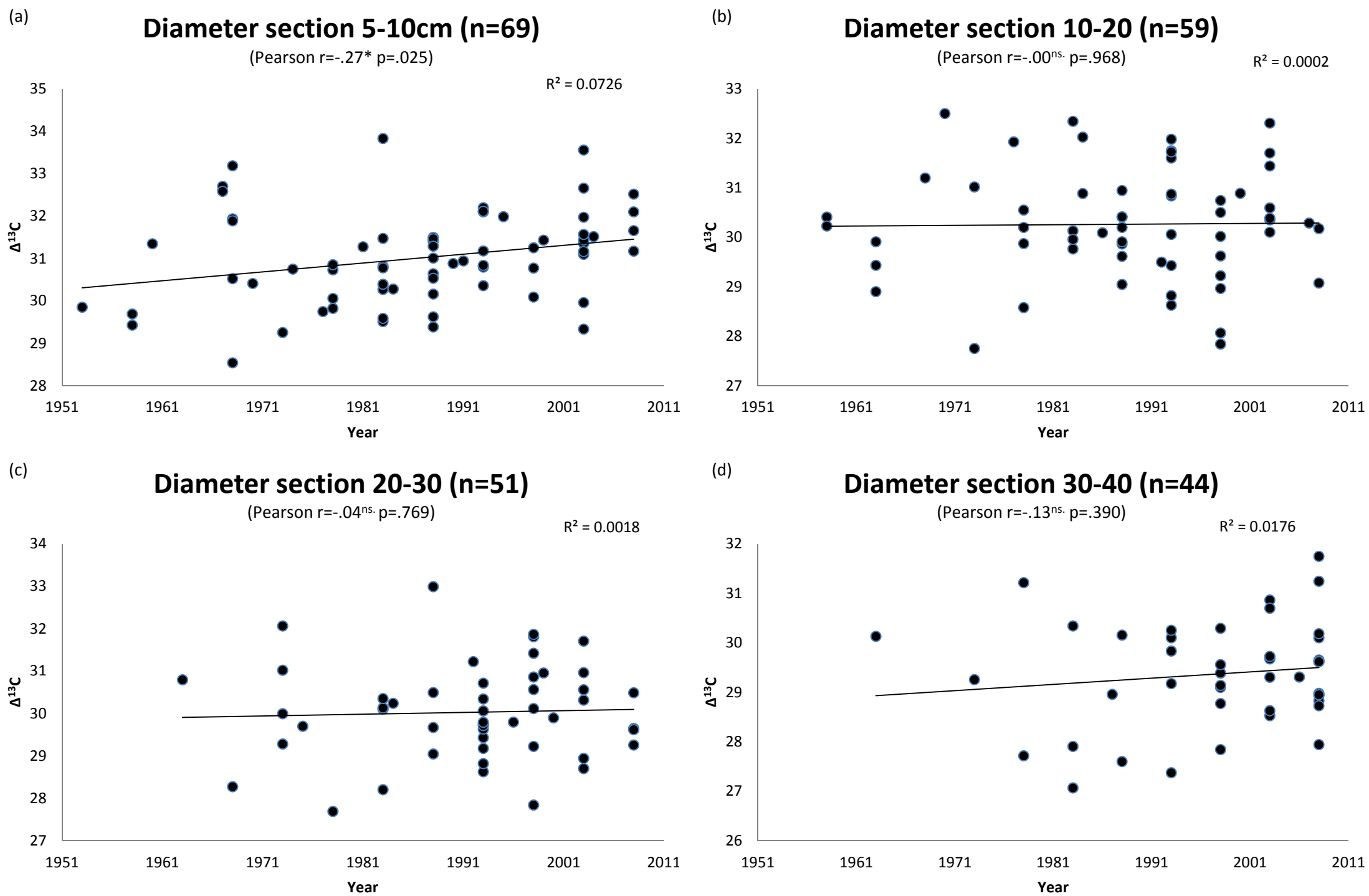
Fig 5. Discrimination factor ($\Delta^{13}C$) within the diameter sections over time of *Hura crepitans*; (a) 5-10cm, (b) 10-20cm, (c) 20-30cm, (d) 30-40cm.

Trees which grew diameter section 5-10cm in 2001 or after (n=28)

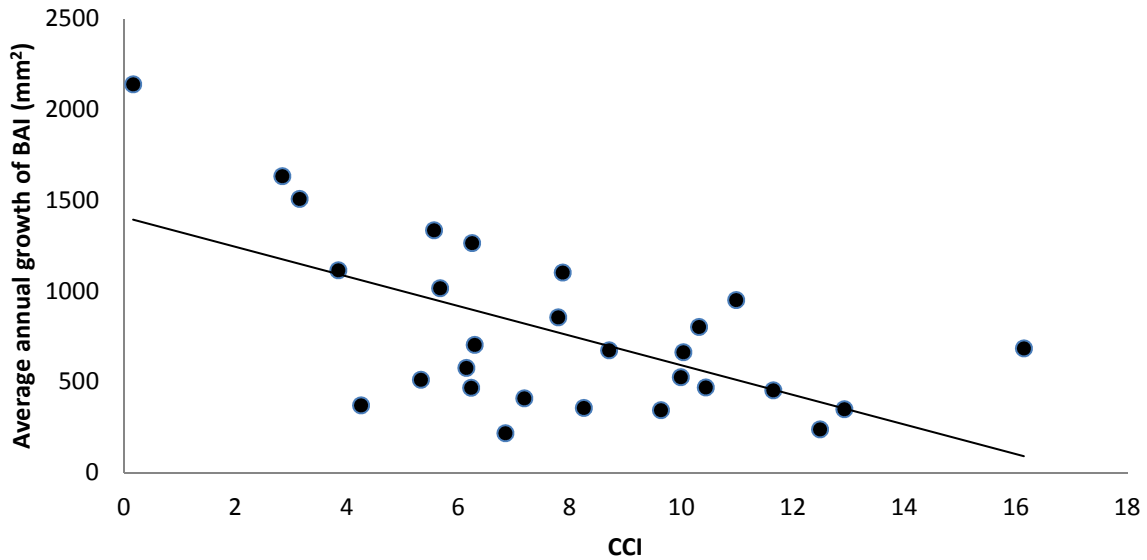(Pearson r=-.61*** p<.001) $R^2 = 0.3689$

Fig 6. Average annual growth of BAI within the diameter section 5-10cm of the trees which grew this diameter section in or after 2001, plotted against the corresponding canopy closure index (CCI).

Trees which grew diameter section 5-10cm in 2001 or after (n=14)

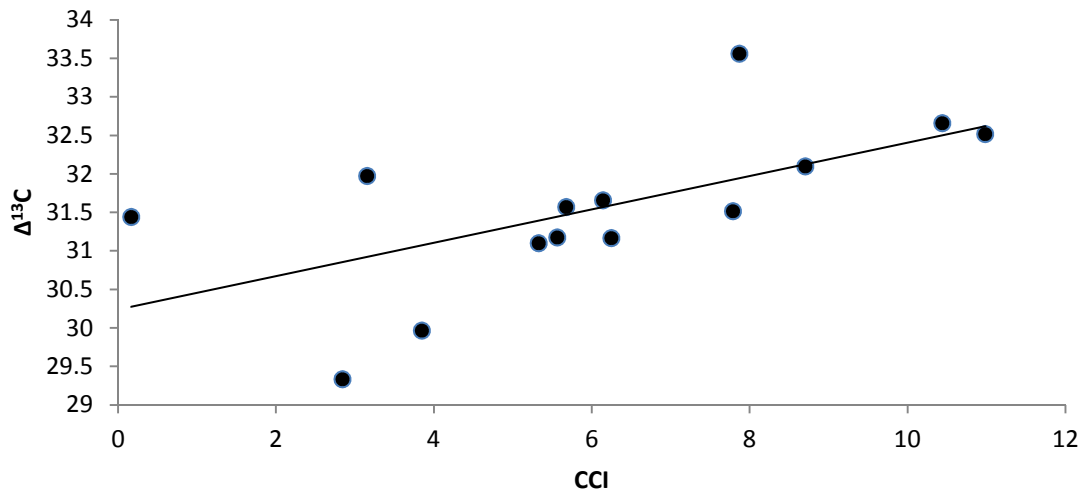(Pearson r=-.61* p=.020) $R^2 = 0.3727$

Fig 7. $\Delta^{13}C$ within the diameter section 5-10cm of the trees which grew this diameter section in or after 2001, plotted against the canopy closure index (CCI).

Discussion

Long-term growth trends

We found a trend of decreased growth for small trees (dbh 5-20 cm) over the last 70 years, but not for larger trees (dbh 20-40 cm) (Fig. 5). This result can be caused by two main reasons: drying of the top soil layer and a reduction in light and/or nutrient availability. Global increased temperature (IPCC, 2007), and decreasing precipitation amounts observed in model studies over the Amazon (Betts *et al.*, 2004) lead to the reported drying trends in Neotropical forests (Burke *et al.*, 2006). Gradual drying in the Neotropical forests will lead to increased respiration and a decline in soil moisture (Davidson *et al.*, 1998). The most pronounced effect of drying will be found in the top soil layer, where deep soil layers remain more stable under climatic changes (Li *et al.*, 2008). This makes that the drying trends will have the greatest effect on small relatively shallow rooted, hence smaller trees. The second possible explanation is the reduction in light and/or nutrients availability. This effect most likely establishes by the earlier discussed juvenile selection effect, where the extant slow growing small individuals cause a decreasing growth trend and an increasing discrimination trend due to the amount of overshadowing.

Drivers steering long term growth trends determined by isotope analysis

By analysing the growth trends together with the discrimination trends clarity can be given about the driving process for the observed growth trends. The conceptual model in Fig. 1 shows the explaining drivers for the four different sets of possible growth trends. We found a negative growth trend combined with a positive $\Delta^{13}C$ trend for the diameter section 5-10cm (Fig. 5a & 6a), where the bigger diameter sections did not show a trend in $\Delta^{13}C$ (Fig. 6b, c, d). The trends caused by decreased light and/or nutrient availability in the smallest diameter section suggest that a juvenile selection effect causes reducing growth rates. Due to the inclusion of extant slow growing juvenile individuals the assimilation rate will decrease over time and c_i will rise, causing the observed trends. The juvenile selection effect is most likely to appear only in smaller diameter sections due to the inclusion of extant small trees in these sections. The same trends can be found if decreased light availability, caused by increased cloud cover, is the main driving force. Decreased light availability over time will cause a decreasing assimilation rate and thereby increases discrimination rates by lowering the demand from c_i. However, if the light availability has indeed decreased, these trends should become apparent in all diameter sections and not only the smaller ones. In addition, research has not clearly showed changes in cloud cover (Wylie *et al.*, 2005) or even a slight decrease in cloud cover anomalies over the tropics (Warren *et al.*, 2007). The same explanation why reduced light is not thought to be the controlling driver accounts for reduced nutrient availability. A reduction in nutrient availability in the forest should become apparent in all diameter sections, and in addition the evidence points to a global increased nutrient deposition (Holland *et al.*, 1999).

The juvenile selection effect is thought to be mainly established by differences in light availability between trees (Rozendaal *et al.*, 2010). The CCI (inverse of light availability) of extant small trees (diameter 5-10cm grew after 2001) shows a negative correlation with growth (Fig. 7). This correlation supports the idea that among the smaller trees, slow growing individuals are present and therefore also the juvenile selection effect in the dataset is present. The same accounts for the positive correlation between $\Delta^{13}C$ and CCI of these trees (Fig. 8), which shows the presence of individuals with high c_i values due to lower assimilation rates, hence slow growing juveniles.

When using isotope signatures to determine the driving factors behind found growth trends we strongly recommend to use $\Delta^{13}C$ values and not changes in c_i or intrinsic water-use efficiency (iWUE= $(c_a-c_i)/1.6$) over time. The changes in c_i and iWUE over time are mainly influenced by rising c_a, where $\Delta^{13}C$ is shown to be less influenced by rising c_a (Loader *et al.*, 2011; Hietz *et al.*, 2005; Nock *et al.*,

2010). As a consequence the $\Delta^{13}C$ changes over time contain a stronger signal of the various possible drivers than c_i and iWUE.

Implications of the found trends

As we interpret the observed overall trends, taking into account that the juvenile selection effect causes a bias in the trends for the small diameter classes, no change is observed in either growth or discrimination. These findings conflict with the hypothesis and the findings in permanent plot studies at comparable sites as this study (Phillips *et al.*, 1998). The permanent plot studies showed, although on short time scales, increased growth and dynamics throughout the Amazon region which led to the idea that the Amazon, in recent decades has acted as a carbon sink (Phillips *et al.*, 1998; Phillips *et al.*, 2008; Laurance *et al.*, 2009). Increased dynamics coincide with higher turn-over rates which causes higher disturbance levels in the forest (Phillips and Gentry, 1994). Increased disturbances will lead to increased light and nutrient availability (Canham, 1988; Denslow *et al.*, 1998; Muscolo *et al.*, 2007), causing higher assimilation rates leading to increased growth and decreased c_i. The increased occurrence of disturbances would therefore match the increase in light and/or nutrient line in the conceptual model. The absence of a trend in discrimination rates shows that there is no change in environmental and climatic drivers which influence the growth patterns. Due to the absence of trends in growth and discrimination rates there is no evidence for increased disturbances and therefore dynamics.

Several possible methodological errors in permanent plot studies have been stated (Sheil, 1995; Clark, 2002). Errors which lead to an overestimation of growth in basal area are immature forest bias, buttress creep and basal area inflation (Phillips *et al.*, 2002). The immature forest bias establishes by sampling forest plots which are recovering from recent disturbances. These plots will contain higher diversity and will decrease in stem density over the years (self-thinning) and the basal area will increase, caused by succession (Clark, 2002; Phillips *et al.*, 2002). Basal area inflation and buttress creep both overestimate growth of basal area by respectively measuring at heights containing bole irregularities and measuring at a fixed height at which, over time, bole irregularities creep up (Sheil, 1995; Clark, 2002). These potential biases can explain the found difference in our research with the Neotropical permanent plot studies.

Also our research is subject to possible biases, caused by unevenly distributed five year bulk samples for the cellulose extraction. Ideally five year bulk samples should be concentrated around a fixed diameter section, with 2 year before and after the corresponding growth year of sampling. By conducting this strategy the year to year variation is dampened out without embedding any ontogenetic trend in the data. Due to the absence of this evenly distribution in the samples it is possible to get an under or over estimation of the isotope signature due to possible ontogenetic effects. The ontogenetic effect can establish by over representation of years before or after the year that the specific DBH is reached. In our data there is no systematically over representation of years before or after the set sample year, which in combination with the substantial sample size is not expected to lead to an ontogenetic bias in the trends.

Conclusively, the trends observed in growth and discrimination rates of *H. crepitans* do not show evidence for changed growth patterns or growth drivers over time. These findings conflict with the observations from Neotropical permanent plots and show that those results could be short term fluctuations. By combining long term growth and isotope data a better insight can be created in the growth of forest stands and the environmental drivers causing growth trends.

References

Badeck FW, Tcherkez G, Nogués S, Piel C, Ghashghaie J (2005) Pos-photosynthetic fractionation of stable carbon isotopes between plant organs – a wide spread phenomenon. *Rapid Communications in Mass Spectrometry*, **19**, 1381-1391.

Baker TR, Phillips OL, Mahli Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Monteagudo A, Neill DA, Núñez Vargas P, Pitman NCA, Silva JNM, Vásquez Martínez R (2004) Increasing biomass in Amazonian forest plots. *Philosophical Transaction of The Royal Society Biological Science*, **359**, 353-365.

Betts RA, Cox PM, Collins M, Harris PP, Huntingford C, Jones CD (2004) The role of ecosystem-atmosphere interactions in simulated Amazonian precipitation decrease and forest dieback under global climate warming. *Thearetical and Applied Climatology*, **78,** 157-175.

Bonan G (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, **320**, 1444-1449.

Brienen RJW, Wanek W, Hietz P (2011) Stable carbon isotopes in tree rings indicate improved water use efficiency and drought responses of a tropical dry forest tree species. *Trees*, **25**, 103-113.

Brienen RJW, Zuidema PA (2006) Lifetime growth patterns and age of Bolivian rain forest trees obtained by tree ring analysis. *Journal of Ecology*, **94**, 481-493.

Brokaw NVL (1985) Gap-phase regeneration in a tropical forest. *Ecology*, **66**, 682-687.

Brown N (1996)A gradient of seedling growth from the centre of a tropical rain forest canopy gap. *Forest Ecology and Management*, **82**, 239-244.

Burke EJ, Brown SJ, Christidis N (2006) Modeling the recent evolution of global drought and projections for the twenty-first century with the Hadley Centre Climate Model. *Journal of Hydrometreology*, **7**, 1113-1125.

Canham CD (1988) Growth and canopy architecture of shade-tolerent trees: response to canopy gaps. *Ecology*, **69**, 786-795.

Chambers JQ, Silver WL (2004) Some aspects of ecophysiological and biogeochemical responses of tropical forests to atmospheric change. *Philosophical Transaction of The Royal Society Biological Science*, **359,** 463-476.

Clark DA (2002) Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecological Applications*, **12**, 3-7.

Coplen TB (1995) Discontinuance of SMOW and PDB. *Nature*, **375**, 285.

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology*, **4**, 217-227.

Davies W, Zhang J (1991) Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Plant Molecular Biology*, **42**, 55-76.

Denevan WM (1992) The pristine myth: the landscape of the Americas in 1492. *Annals of the Association of American Geographers*, **82**, 369-385.

Denslow JS, Ellison AM, Sanford RE (1998) Treefall gap size effects on above- and bellow-ground processes in a tropical wet forest. *Journal of Ecology*, **4**, 597-609.

Drake BG, Gonzàlez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2? *Annual review of plant physiology and plant molecular biology*, **48**, 609-639

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia*, **78**, 9-19.

Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, **9**, 121-137.

Feng X (1999) Trends in intrinsic water-use efficiency of natural trees for the past 100-200 years: a response to atmospheric CO_2 concentration. *Geochimica et Cosmochimica Acta*, **63**, 1891-1903.

Francis JK (1990) Hura crepitans L. Sandbox, molinillo, jabillo. Euphorbiaceae. Spurge family. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry, SO-ITF-SM; 38, 5.

Gebrekirstos A, Worbes M, Teketay D, Fetene M, Mitlöhner R (2009) Stable carbon isotope ratios in tree rings of co-occurring species from semi-arid tropics in Africa: Patterns and climatic signals. *Global and Planetary Change*, **66,** 253–260.

Helle G, Schleser GH (2004) Interpreting climate proxies from tree-rings. *Towards a synthesis of Holocene proxy data and climate models*. In: The KIHZ project: *Towards a synthesis of Holocene proxy data and climate models* (eds Fischer H, Floeser G, Kumke T, Lohmann G, Miller H, Negendank JFW, von Storch H). ISBN: 978-3-540-20601-9, 129-148.

Herault B, Ouallet J, Blanc L, Wagner F, Baraloto C (2010) Growth responses of neotropical trees to logging gaps. *Journal of Applied Ecology*, **47**, 821-831.

Hietz P, Wanek W, Dünisch O (2005) Long-term trends in cellulose ^{13}C and water-use efficiency of tropical *Cedrela* and *Swietenia* from Brazil. *Tree Physiology*, **25**, 745-752.

Holland EA, Dentener FJ, Braswell BH, Sulzman JM (1999) Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry*, **46**, 7–43.

IPCC (2007) Summary for Policymakers. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Laurance SGW, Laurance WF, Nascimento HEM, Andrade A, Fearnside PM, Rebello ERG, Condit R (2009) Long-term variation in Amazon forest dynamics. *Journal of Vegetation Science*, **20**, 323-333.

Laurance WF, Oliveira AA, Laurance SG, Condit R, Nascimento HEM, Sanchez-Thorin AC, Lovejoy TE, Andrade A, D'angelo S, Ribeiro JE, Dick CW (2004) Persvasive alteration of tree communities in undisturbed Amazonian forests. *Nature*, **428**, 171-174.

Lewis SL, Mahli Y, Phillips OL (2004) Fingerprinting the impact of global change on tropical forests. *Philosophical Transaction of The Royal Society Biological Science*, **359**, 437-462.

Li S, Lü S, Ao Y, Shang L (2008) Annual variation in the surface radiation budget and soil water and heat content in the upper Yellow River area. *Environmental Geology*, **57**, 389-395.

Lieberman M, Lieberman D, Peralta R (1989) Forests are not just swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology*, **70**, 550-552.

Loader NJ, Walsh RPD, Robertson I, Bidin K, Ong RC, Reynolds G, McCarroll D, Gagen M, Young HF (2011) Recent trends in the intrinsic water-use efficiency of ringless rainforest trees in Borneo. *Philosophical Transaction of The Royal Society Biological Science*, **366**, 3330-3339.

Long SP (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO2 concentrations: Has its importance been underestimated? *Plant, Cell and Environment*, **14,** 729-739.

López-Callejas L (2003) Estudio de los annilos de crecimiento en once especies forestales de Santa Cruz, Bolivia. *Unpublished Master thesis*, Universidad autónomia Gabriel René Moreno, Santa Cruz, Bolivia.

McCarroll D, Gagen MH, Loader NJ, Robertson I, Anchukaitis KJ, Los S, Young GHF, Jalkanen R, Kirchhefer A, Waterhouse JS (2009) Correction of tree ring stable carbon isotope chronologies for changes in the carbon dioxide content of the atmosphere. *Geochemica et Cosmochimica Acta*, **73**, 1539-1547.

McCarroll D, Loader NJ (2004) Stable isotopes in tree rings. *Quarternary Science Reviews*, **23**, 771-801.

Muscolo A, Sidari M, Mercurio R (2007) Influence of gap size on organic matter decomposition, microbial biomass and nutrient cycle in Calabrian pine (*Pinus laricio, Poiret*) stands. *Forest Ecology and Management*, **242**, 412-418.

Nock CA, Baker PJ, Wanek W, Leis A, Grabner M, Bunyavejchewin S, Hietz P (2010) Long-term increase in intrinsic water-use efficiency do not lead to increased stem growth in a tropical monsoon forest in western Thailand. *Global Change Biology*, **17**, 1094-1063.

Phillips OL, Gentry AH (1994) Increasing turnover rates through time in tropical forests. *Science*, **263**, 954-958.

Phillips OL, Mahli Y, Higuchi N, Laurance WF, Nuniez PV, Vasquez RM, Laurance SG, Ferreira LV, Stern M, Brown S, Grace J (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science*, **282**, 439-442.

Phillips OL, Mahli Y, Vinceti B, Baker T, Lewil SL, Higuchi N, Laurance WF, Núñez Vargas P, Vásquez Martinez R, Laurance S, Ferreira LV, Stern M, Brown S, Grace J (2002) Changes in growth of tropical forests: evaluating potential biases. *Ecological Applications*, **12**, 576-587.

Phillips OL, Lewis SL, Baker TR, Chao K, Higuchi N (2008) The changing Amazon forest. *Philosophical Transaction of The Royal Society Biological Science*, **363**, 1819-1827.

Peña-Claros M, Fredericksen TS, Alarcón A, Blate GM, Choque U, Leaño C, Licona JC, Mostacedo B, Pariona W, Villegas Z, Putz FE (2008) Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management*, **256**, 1458-1467.

Rozendaal DMA, Brienen RJW, Soliz-Gamboa CC, Zuidema PS (2010) Tropical tree ring reveal preferential survival of fast-growing juveniles and increased juvenile growth rates over time. *New Phytologist*, **185**, 759-769.

Saxe H, Ellsworth DS, Heath J (1998) Tree and forest functioning in an enriched CO_2 atmosphere. *New Phytologist,* **139**, 395-436.

Sheil D (1995) A critique of permanent plot methods and analysis with examples from Budongo forest, Uganda. *Forest Ecology and Management*, **77**, 11-34.

Shue B, Lin C (1999) Photosynthetic response of seedlings of the sub-tropical tree *Schima superba* with exposure to elevated carbon dioxide and temperature. *Environmental and experimental botany*, **41**, 57-65.

Sidvora OV, Siegwolf RTW, Saurer M, Naurzbaev MM, Shaskin AV, Vaganov EA (2010) Spatial patterns of climate changes in the Eurasian north reflected in Siberian larch tree-ring parameters and stable isotopes. *Global Change Biology*, **16**, 1003-1018.

Soulé PT, Knapp PA (2006) Radial growth rate increases in naturally-occurring ponderosa pine trees: a late 20th century CO2 fertilization effect? *New Phytologist*, **171,** 379-390.

Sun F, Kuang Y, Wen D, Xu, Z, Li J, Zuo W, Hou E (2010) Long-term tree growth rate, water use efficiency and tree ring nitrogen isotope composition of *Pinus massoniana L.* in response to global climate change and local nitrogen deposition in Southern China. *Soils Sediments*, **10**, 1453-1465.

Warren SG, Eastman RM, Hahn CJ (2006) A survey of changes in cloud cover and cloud types over land from surface observations, 1971-96. *Journal of Climate*, **20**, 717-739.

Wieloch T, Helle G, Heinrich I, Voigt M, Schyma P (2011) A novel device for batch-wise isolation of α-cellulose from small-amount wholewood samples. *Dendrochronologia*, **29**, 115-117.

Wylie D, Jackson DL, Menzel WP, Bates JJ (2005) Trends in global cloud cover in two decades of HIRS observation. *Journal of Climate*, **18**, 3021-3031.