

# Climate is a stronger driver of tree and forest growth rates than soil and disturbance

Marisol Toledo<sup>1,2\*</sup>, Lourens Poorter<sup>1,2</sup>, Marielos Peña-Claros<sup>1,2</sup>, Alfredo Alarcón<sup>2</sup>, Julio Balcázar<sup>2</sup>, Claudio Leaño<sup>2</sup>, Juan Carlos Licona<sup>2</sup>, Oscar Llanque<sup>3</sup>, Vincent Vroomans<sup>2</sup>, Pieter Zuidema<sup>3,4</sup> and Frans Bongers<sup>1</sup>

<sup>1</sup>Forest Ecology and Forest Management Group, Centre for Ecosystem Studies, Wageningen University, PO Box 47, 6700 AA Wageningen, the Netherlands; <sup>2</sup>Instituto Boliviano de Investigación Forestal (IBIF), Casilla 6204, Santa Cruz, Bolivia; <sup>3</sup>Asociación PROMAB, Av. Del Ejército Final, Campus Universitario, Beni, Bolivia; and <sup>4</sup>Ecology and Biodiversity, Institute of Environmental Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, the Netherlands

## Summary

1. Essential resources such as water, nutrients and light vary over space and time and plant growth rates are expected to vary accordingly. We examined the effects of climate, soil and logging disturbances on diameter growth rates at the tree and stand level, using 165 1-ha permanent sample plots distributed across Bolivian tropical lowland forests.
2. We predicted that growth rates would be higher in humid than in dry forests, higher in nutrient-rich than nutrient-poor forests and higher in logged than non-logged forests.
3. Across the 165 plots we found positive basal area increases at the stand level, which agree with the generally reported biomass increases in tropical forests.
4. Multiple regression analysis demonstrated that climate variables, in particular water availability, were the strongest drivers of tree growth. More rainfall, a shorter and less intense dry period and higher temperatures led to higher tree growth rates.
5. Tree growth increased modestly with soil fertility and basal area growth was greatest at intermediate soil fertility. Surprisingly, tree growth showed little or no relationship with total soil nitrogen or plant available soil phosphorus.
6. Growth rates increased in logged plots just after logging, but this effect disappeared after 6 years.
7. *Synthesis.* Climate is the strongest driver of spatial variation in tree growth, and climate change may therefore have large consequences for forest productivity and carbon sequestration. The negative impact of decreased rainfall and increased rainfall seasonality on tree growth might be partly offset by the positive impact of increased temperature in these forests.

**Key-words:** Bolivia, climate, disturbance, growth rate, logging, plant–climate interactions, rainfall, soil, temperature, tropical forest

## Introduction

All plants depend on the availability of water, nutrients and light as essential resources for growth. In tropical rain forests, these resources vary over spatial and temporal scales and, as a result, tree growth varies with resource availability. In general, tree growth increases with rainfall (Murphy & Lugo 1986; Dauber, Fredericksen & Peña-Claros 2005) and decreases with drought (Nath *et al.* 2006; Lola da Costa *et al.* 2010). Independently of rainfall, soil fertility can also affect

tree growth rate (Lu, Moran & Mausel 2002; Malhi *et al.* 2004) with better growth on more nutrient-rich soils (Russo *et al.* 2005). Many tropical forests differ from temperate forests in their stocks and flows of biologically important nutrients both within and from biomass resources. In particular, humid tropical ecosystems are relatively rich in available N (Vitousek 1984; Sollins 1998) and growth rate is likely to be limited by P or other rock-derived nutrients (Vitousek & Denslow 1986, 1987; Tanner, Vitousek & Cuevas 1998). While there are studies of the effects of either climate (Bullock 1997; Clark *et al.* 2003; Feeley *et al.* 2007) or soil (Vitousek & Standford 1986; Davies 2001; Russo *et al.* 2005) on growth rate, there are very few studies simultaneously considering the

\*Correspondence author. E-mail: mtoledo@ibifbolivia.org.bo

effects of both environmental factors on tree growth (but see Baker, Burslem & Swaine 2003a).

Vieira *et al.* (2004) found no relationship between growth rates and soils in Amazonian rain forests, and suggested that human disturbance may have overruled more subtle environmental differences. Disturbances initiate the forest growth cycle through the creation of canopy gaps. These gaps or vertical holes in the canopy open up space, increase light-, nutrient- and, probably, water availability, and thus create possibilities for recruitment of new plants and species (Van der Meer, Sterck & Bongers 1998). Therefore, both natural disturbances (e.g. strong winds, landslides) and anthropogenic disturbances (e.g. fires, logging) are important drivers of forest dynamics (Hartshorn 1980). Although logging has several negative impacts on forest ecosystems and forest functions (e.g. forest degradation and associated fires; Nepstad *et al.* 1999), it also creates conditions that stimulate the growth of the remaining trees, thus accelerating the growth of previously suppressed individuals (Carvalho, Silva & Lopes 2004). Similarly, growth rates also increase with increasing logging intensity (Finegan & Camacho 1999; Peña-Claros *et al.* 2008a; Villegas *et al.* 2009).

In many tropical countries forest management for timber harvesting is an important economic activity. In Bolivia, the current Forestry Law provides a strong stimulus for sustainable forest management (Snook *et al.* 2007). An important aspect of this law is the establishment and monitoring of a network of permanent sample plots in the lowland forestry areas. The Bolivian network also presents an appropriate system in which to examine the relationship between forest components and environmental conditions, since plots cover different forest types, from humid evergreen Amazon forests to dry deciduous Chiquitano forests (Navarro & Maldonado 2002; Toledo *et al.* in press). Lowland Bolivia is also characterized by large differences in geomorphology and geological history: in the west the relatively young and nutrient-rich landscapes of the Pre-Andean predominate rather than the ancient rocks and nutrient-poor soils of the Brazilian Shield found in the east (Killeen *et al.* 2006).

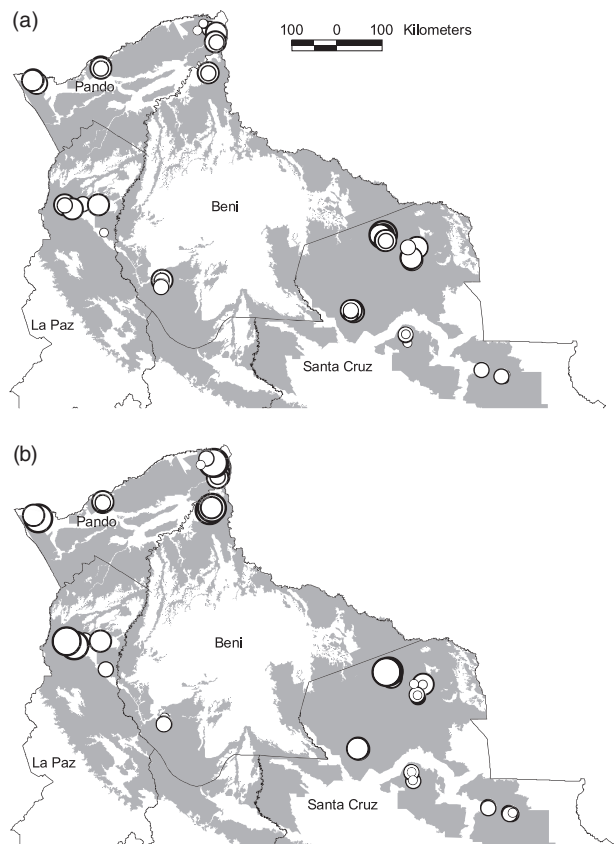
In this study we used 165 1-ha permanent plots of this Bolivian network to describe individual tree and stand level growth rates, and to determine how climate, soil and logging affect them. This is one of the few broad-scale comparative studies of tree and forest growth in the Neotropics that considers both environmental gradients and disturbance factors. We addressed the following questions. (1) How do rates of individual tree (diameter) and stand level (basal area) growth vary across lowland Bolivia? (2) What are the effects of climate, soil and disturbance on these growth variables? We expected tree growth to be highly variable due to the high heterogeneity of environmental conditions in Bolivia (Navarro & Maldonado 2002; Ibisch & Mérida 2003). Considering that growth increases with resource availability, we predicted that growth rates would be higher in moist than in dry sites, higher in nutrient-rich than nutrient-poor forests, and higher in disturbed than non-disturbed forests (Swaine, Lieberman & Hall 1990; Carvalho, Silva & Lopes 2004; Dauber, Fredericksen & Peña-Claros 2005).

## Material and methods

### STUDY AREA

For this study a total of 165 1-ha plots were selected from the Network of Permanent Plots in lowland Bolivia (Fig. 1). These plots were established in old-growth forests by various projects and forestry concessionaries (see Acknowledgements for more details). To date this network and its database has been coordinated and managed by the Instituto Boliviano de Investigación Forestal (IBIF). The plots are located between 10–18° S and 59–69° W, in upland forests (*terra firme*; the 5% of plots found in areas of seasonal flooding were also included in the analysis), generally on flat terrain (20% on sloping ground in hilly areas), and in an altitude range from 100 to 500 m asl. These plots are distributed over the main environmental gradients of climate and soil and 52% of them have been affected by logging.

Lowland Bolivia is characterized by two rainfall gradients: a south–north gradient where rainfall increases towards the equator with mean annual precipitation ranging from 1100 to 1900 mm and an east–west gradient where mean rainfall increases from 1600 to 2200 mm due to orographic uplift towards the Andes. However, the precipitation in individual years can vary from 600



**Fig. 1.** Variation in (a) average diameter ( $DGR_{avg}$ ) and (b) stand basal area ( $BAGR_{stand}$ ) growth rates of 165 permanent plots located in four departments (Pando, La Paz, Beni and Santa Cruz) of lowland Bolivia. The size of the symbols scales proportional with the growth rate. Potential forest cover of areas assigned to timber production is indicated in grey. The white areas in Pando pertain to floodplains, in Beni and north of La Paz to savannas, and in Santa Cruz to the Cerrado and Chaco vegetation.

to 3000 mm per year from the driest to wettest areas (based on at least 30 years data, 1970–2007, Servicio Nacional de Meteorología e Hidrología-SENAMHI, unpublished data). In general, the lowlands in Bolivia experience a 4–7-month dry season (with precipitation < 100 mm per month) from about April to September, corresponding to the austral winter. Mean annual temperature is between 24.2 and 26.4 °C. Additionally, lowland Bolivia is characterized by differences in geomorphology and geological history (Montes de Oca 1997; Suárez-Soruco 2000), leading to strong gradients in soil characteristics. The soils vary considerably in fertility, from acid Acrisols in the Amazon forest in the north, via Acrisols and Luvisols in the centre, to Cambisols and Arenosols in the south (Gerold 2003).

#### DATA COLLECTION AND ANALYSIS

The 165 selected plots were all established between 1995 and 2005 and measurement periods varied between 2 and 11 years, with the last measurements taking place in 2007. Plots were typically square (100 × 100 m), with only 11 of them being rectangular (20 × 500 m). In each plot, every tree ≥ 10 cm diameter at breast height (DBH; measured at 130 cm, or higher when buttresses were present) was measured with diameter tape, painted at the measurement point, tagged and identified, following standard protocols (Alder & Synnott 1992; Contreras *et al.* 1999). Re-censuses were mostly carried out in the same season or month as the plots were established, thus minimizing the effect of intra-annual variation in DBH change. In most of the total of 85 plots that were affected by logging activities, logging started immediately after their establishment; 80 plots were not logged.

The annual diameter growth per individual was calculated as:  $(D_f - D_i)/t$  where  $D_f$  is the final diameter and  $D_i$  is the initial diameter at the start of the interval. Based on this diameter growth rate (hereafter DGR) we calculated five variables per plot, representing the growth rate at the individual level: average (DGR<sub>avg</sub>), median (DGR<sub>50</sub>), 90th (DGR<sub>90</sub>), 95th (DGR<sub>95</sub>) and 99th percentile (DGR<sub>99</sub>) of annual diameter growth. Values for the 90th and 95th diameter growth rate percentile are not included in the results because they were highly correlated with the DGR<sub>avg</sub>, DGR<sub>99</sub> and between themselves (see Table S1 in Supporting Information). The DGR<sub>50</sub> and DGR<sub>99</sub> were calculated to provide information on median and upper levels of growth rate. Additionally, we calculated the basal area growth rate at the stand level (hereafter BAGR<sub>stand</sub>) as the net yearly basal area change per plot. The BAGR<sub>stand</sub> was calculated as:  $(BA_f - BA_i)/t$ , where  $BA_f$  is the final total plot basal area and  $BA_i$  is the plot basal area at the start of the measurement interval (for control plots) or just after logging (for logged plots). In both formulae,  $t$  is the time, in years, between the two measurement dates. Note that BAGR<sub>stand</sub> includes the effects of growth, recruitment and mortality, while DGR is based upon individuals that survived the whole monitoring period.

For each plot 20 soil samples were collected from the first 30 cm of soil with an auger, and a pooled sample of 500 g was analysed within a week after collection at the Center of Tropical Agricultural Research (CIAT-Santa Cruz, Bolivia). The analyses included 12 edaphic variables: percentage of clay, silt and sand, measured with the Bouyoucos hydrometer; exchangeable Ca, Mg, Na, K (in 1 M ammonium acetate at pH 7); cation exchange capacity (CEC, sum of cations plus acidity); acidity (in 1 M KCl); plant available phosphorus (P, Olsen method); organic matter (OM, Walkley-Black method) and total nitrogen (N, micro-Kjeldahl method). For each plot we obtained five climatic variables, interpolated from available data

from 45 weather stations in the region, and 12 edaphic variables obtained from sampled soils. To summarize these environmental variables we performed two independent Principal Component Analyses, (PCAs, see Table S2 in Supporting information). The PCA was done for 220 1-ha plots that are part of the Network of Permanent Plots in lowland Bolivia, and included the 165 plots that are analysed here for their dynamics. The climatic PCA considered annual temperature, annual precipitation, precipitation of the three driest months, length of the dry period (# months < 100 mm), and length of the drought period (# months < 50 mm). The first two axes of the climatic PCA explained 94% of the variation. The first axis (65%) correlated positively with annual precipitation and negatively with dry period length (henceforth referred to as the rainfall axis). The second axis (29%) correlated positively with mean annual temperature and negatively with the precipitation of the driest months (hereafter temperature axis). The edaphic PCA considered the 12 edaphic variables. The first two axes of the edaphic PCA explained 68% of the variation. The first axis (48%) correlated positively with variables related with soil fertility (CEC, Ca, Mg, Na, K, P, OM and N), and negatively with acidity (hereafter soil fertility axis). The second axis (20%) represented variation in soil texture and correlated positively with clay and silt and negatively with sand (hereafter soil texture axis) (Table S2).

Four logging-related variables were used to describe forest disturbance in each plot. Two dummy variables were created: Logging Presence (LP) to describe whether logging occurred (1) or not (0) in the plots and Logging Impact (LI), which describes whether the impact was high (1) or low (0) in logged plots (based on the number and location of logged trees and number of additional trees that died due to logging operations). Other continuous variables representing logging disturbance were the Logged Basal Area (LBA, in m<sup>2</sup> ha<sup>-1</sup>, based upon the number and diameter of the trees logged) and the Time After Logging (TAL, in years).

The four growth variables were first correlated (Pearson correlation) with the individual environmental variables to evaluate what components of these composite axes were most important. Each of the four growth rate variables were subsequently regressed on the four main environmental axes and the four disturbance variables (including interactions and their quadratic terms, when necessary) using a series of multiple backward regressions. We used the PCA axes for this regression analysis, rather than the original individual environmental variables, to avoid problems with multicollinearity and over fitting. Quadratic terms were included in the models because non-linear relationships between growth rates and predictors were observed in scatter plots. Because the increases in explained variation as a result of including interaction effects in the models were very low, we re-ran the analyses without the interactions and present only the latter results. For each variable the Kolmogorov–Smirnov test for normal distribution was applied and, if necessary, the data were logarithmic (log<sub>10</sub>), square root or arcsine-transformed. All statistical analyses were performed with SPSS 15.0 for Windows (SPSS Inc., Chicago, IL, USA).

## Results

### VARIATION IN TREE AND FOREST GROWTH RATES

Growth variables showed relatively high variation across plots, with the largest variation in DGR<sub>50</sub> and BAGR<sub>stand</sub> (Table 1). On average, BAGR<sub>stand</sub> was 0.49 m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>. Mean

**Table 1.** Mean  $\pm$  standard deviation (SD) and ranges (minimum–maximum) of tree and forest growth variables from 165 1-ha permanent plots across lowland Bolivia

Variables	Mean	SD	Minimum	Maximum	Ratio
DGR <sub>avg</sub> (cm year <sup>-1</sup> )	0.31	$\pm 0.10$	0.12	0.70	5.8
DGR <sub>50</sub> (cm year <sup>-1</sup> )	0.20	$\pm 0.08$	0.07	0.59	8.0
DGR <sub>99</sub> (cm year <sup>-1</sup> )	1.77	$\pm 0.63$	0.63	3.82	6.1
BAGR <sub>stand</sub> (m <sup>2</sup> ha <sup>-1</sup> year <sup>-1</sup> )	0.49	$\pm 0.21$	0.17	1.22	7.2

The ratio was calculated by dividing the maximum value by the minimum value. DGR = Diameter growth rate, BAGR = basal area growth rate, Avg = average. DGR<sub>50</sub> and DGR<sub>99</sub> refer to the 50th and 99th percentile of tree growth rates in a 1-ha plot.

DGR<sub>avg</sub> was 0.31 cm year<sup>-1</sup>, with the lowest value in a plot with low rainfall and the highest value in a plot with intermediate rainfall. In relation to the median and upper growth rate limits (DGR<sub>50</sub> and DGR<sub>99</sub>), highest values were found in plots of higher rainfall and lowest values in plots of lower rainfall. Although low DGR<sub>avg</sub> was found mostly in plots with lower rainfall (Figs 1a and 2a) low BAGR<sub>stand</sub> was found in plots with both low and high amount of rainfall (Figs 1b and 2b).

#### FACTORS AFFECTING TREE AND FOREST GROWTH

All four growth variables had, in general, qualitatively similar relationships to the environmental axes and variables, except for the texture axis, drought period, P, acidity, and LBA (Table 2). Most of the significant relationships were found for DGR<sub>avg</sub>, DGR<sub>50</sub> and BAGR<sub>stand</sub>. Growth variables were always positively and significantly correlated with climate axes and, in most of the cases, negatively and non-significantly to the soil axes (although BAGR<sub>stand</sub> had a significant negative relationship with the soil fertility axis).

When related to individual environmental variables, growth variables increased significantly with annual precipitation and temperature and decreased with the dry period (Table 2). Soil variables generally had negative relationships to growth variables but OM content was the only one where this was consistently significant. All disturbance variables were positively related to the four growth variables except TAL (Table 2, Fig. 2g,h).

The backward regression models indicated the relative importance, and explained the effects of, environmental axes and disturbance variables on growth rates (Table 3). The total variation explained by the models ranged between 23 and 54%. Variation in DGR<sub>avg</sub> was explained best (54%), and was affected by most of the predictors, while variation in BAGR<sub>stand</sub> was explained least (23%) and was affected by fewer predictors. Rainfall was the most important axis, affecting all growth rates significantly and positively (Fig. 2a, b). Similarly, temperature and soil fertility had positive effects,

**Table 2.** Pearson correlation coefficients of four tree growth variables with four environmental axes, four disturbance and 18 environmental variables from 165 1-ha plots located in Bolivian lowland forests

	DGR <sub>avg</sub>	DGR <sub>50</sub>	DGR <sub>99</sub>	BAGR <sub>stand</sub>
Rainfall axis	0.35**	0.22**	0.33**	0.27**
Temperature axis	0.26**	0.21*	0.29**	0.26**
Fertility axis	-0.14	-0.16	-0.17	-0.23**
Texture axis	-0.04	-0.02	-0.04	0.10
Annual precipitation (mm)	0.41**	0.22**	0.48**	0.37**
Driest months (mm)	0.12	0.04	0.09	0.06
Temperature (°C)	0.44**	0.35**	0.40**	0.39**
Dry period (# of months < 100 mm)	-0.48**	-0.31**	-0.46**	-0.33**
Drought period (# of months < 50 mm)	-0.06	-0.04	0.02	-0.02
Ca (cmol kg <sup>-1</sup> )	-0.12	-0.16	-0.14	-0.23**
Mg (cmol kg <sup>-1</sup> )	-0.15	-0.12	-0.26**	-0.33**
Na (cmol kg <sup>-1</sup> )	0.05	0.03	-0.03	-0.09
K (cmol kg <sup>-1</sup> )	-0.08	-0.01	-0.25**	-0.19*
CEC (cmol kg <sup>-1</sup> )	-0.21*	-0.28**	-0.12	-0.14
Acidity (cmol kg <sup>-1</sup> )	-0.03	-0.05	0.13	0.30**
P (cmol kg <sup>-1</sup> )	0.09	0.08	0.17*	-0.03
Organic matter (%)	-0.33**	-0.27**	-0.26**	-0.23**
N (%)	-0.15	-0.15	-0.15	-0.17*
Sand (%)	0.06	0.05	0.09	0.01
Silt (%)	-0.18*	-0.24**	-0.09	-0.02
Clay (%)	0.05	0.14	0.08	0.02
Logging presence (yes/no)	0.28**	0.34**	0.08	0.06
Logging impact (yes/no)	0.31**	0.31**	0.14	0.12
Logged basal area (m <sup>2</sup> ha <sup>-1</sup> )	0.26**	0.30**	0.09	-0.01
Time after logging (year)	-0.16	-0.08	-0.09	-0.05

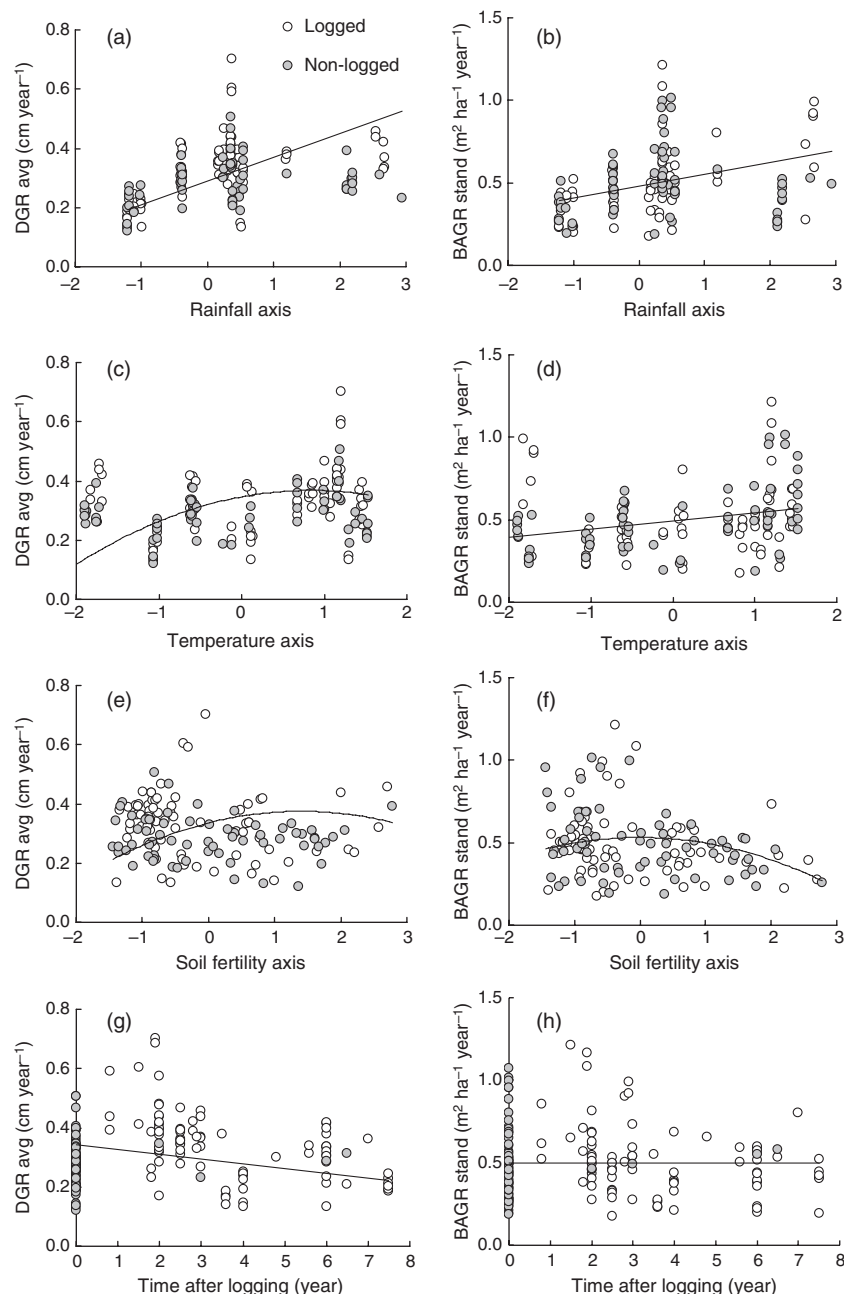
\* $P \leq 0.05$ , \*\* $P \leq 0.01$ . DGR = diameter growth rate, BAGR = basal area growth rate, CEC = cation exchange capacity, Avg = average.

although sometimes with a plateau (Fig. 2c–e), while BAGR<sub>stand</sub> declined again at higher soil fertility levels (Fig. 2f). The soil texture axis had significant negative effects only on growth rates at tree level. Disturbance variables ‘logging’ and ‘logging intensity’ had a significant positive effect on DGR<sub>avg</sub> and DGR<sub>50</sub> whereas time after logging (TAL) had a significant negative effect (Table 3, Fig. 2g).

## Discussion

In this study we describe how tree growth at individual and stand level differ among Bolivian forests, showing that both environmental and disturbance factors have effects on growth rates, and that climate is the strongest driver. Rainfall, temperature, soil fertility and logging-related disturbance generally had positive effects on tree and stand growth.





**Fig. 2.** Relationships between average tree diameter growth rate ( $DGR_{avg}$ ) and stand basal area growth rate ( $BAGR_{stand}$ ) with environmental axes: (a, b) rainfall, (c, d) temperature, (e, f) soil fertility and (g, h) time after logging (TAL) of 165 logged (white circles) and non-logged (grey circles). Environmental axes are multivariate composite PCA axes with high scores indicating plots with high rainfall, high temperature, and high soil fertility. Regression lines are according to the backward multiple regression models and were plotted by keeping all other significant environmental variables constant (at the grand mean value across all 165 plots), while varying alone the variable of interest. Coefficients of determination and significance levels are shown in Table 3. There are a few plots that were not logged (grey symbols) but that nonetheless had a TAL larger than 1 because they were affected by low impact of logging of the surrounding area.

#### VARIATION IN TREE AND FOREST GROWTH

We found high variation in tree growth rates at individual and at stand level in lowland Bolivia, in line with our hypothesis. The  $DGR_{avg}$  of  $0.31 \pm 0.10 \text{ cm year}^{-1}$  and its range ( $0.12\text{--}0.70 \text{ cm year}^{-1}$ ) is within the range ( $0.08\text{--}0.80 \text{ cm year}^{-1}$ ) of diameter growth rates reported for other tropical forests

(Manokaran & Kochummen 1987; Chambers, Higuchi & Schimel 1998; Finegan & Camacho 1999; Alder *et al.* 2002; Pereira da Silva *et al.* 2002). The average of  $BAGR_{stand}$  ( $0.49 \pm 0.21 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$ ) was similar, but the range ( $0.17\text{--}1.22 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$ ) was larger than for other tropical forests ( $0.25\text{--}0.92 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$ ) (Lieberman *et al.* 1990; Nebel *et al.* 2001; Lewis *et al.* 2004). While several factors may be

**Table 3.** Backward multiple regression analysis of forest and tree growth variables on environmental (climatic and soil axes and their quadratic terms, as indicated by the squares) and disturbance variables for 165 1-ha permanent plots in lowland Bolivia

Variables	Environmental axes							Disturbance variables				
	Rainfall		Temperature		Soil fertility		Soil texture	LP	LI	TAL	F	R <sup>2</sup>
	Rain	Rain <sup>2</sup>	Temp	Temp <sup>2</sup>	Fertil	Fertil <sup>2</sup>	Text					
DGR <sub>avg</sub>	0.89***		0.61***	−0.33**	0.61***	−0.27**	−0.28**	0.37**	0.18**	−0.39***	16.53	0.54
DGR <sub>50</sub>	0.38***		0.34**		0.24*		−0.26**	0.53***		−0.29*	10.25	0.32
DGR <sub>99</sub>	1.03***	−0.78***			0.15*		−0.29***				26.09	0.44
BAGR <sub>stand</sub>	0.38***		0.29***		−	−0.23**			−		13.28	0.23

Only for significant predictors the standardized regression coefficient (Beta) are included into the model. *F*-value and coefficient of determination (*R*<sup>2</sup>) are provided. Texture<sup>2</sup> and Logged basal area were in none of the regressions significant, and therefore not shown in the table. Significance levels are shown \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001. DGR = Diameter growth rate, BAGR = basal area growth rate, Avg = average, Temp = Temperature, Fertil = Fertility, Text = Texture, LP = logging presence, LI = logging impact, TAL = Time after logging. Note that all PCA axes vary from negative to positive. A negative slope for Fertility<sup>2</sup> results therefore in a bell-shaped curve for BAGR<sub>stand</sub> vs. soil fertility (Fig. 2f), with an optimum.

responsible for this variation in growth rates, we considered that climatic, edaphic and disturbance factors have an important role in explaining this variation.

#### CLIMATIC EFFECTS ON GROWTH RATES

In general, our study supports the hypothesis that growth rates increase with water availability (Table 2, Fig. 2a). In lowland Bolivia, the lowest annual growth rate at tree level occurred at the drier end of the rainfall gradient (Fig. 2a), and these dry forest values are in line with studies for other dry tropical forests (Swaine, Lieberman & Hall 1990; Uslar, Mostacedo & Saldias 2004). Tropical dry forests are likely to have lower annual growth rates than moist forests due to their shorter growing period occasioned by lower rainfall (Murphy & Lugo 1986; Phillips *et al.* 1998; Condit *et al.* 2004). In addition, studies focusing on temporal variation in rainfall have shown that lower annual rainfall, or a more intense drought period, decreases growth rates and affects forest dynamics (Condit, Hubbell & Foster 1995; Williamson *et al.* 2000; Nath *et al.* 2006; Clark, Clark & Oberbauer 2010). This has also been clearly demonstrated by experiments in mature old-growth Amazonian forests where rainfall was excluded (Nepstad *et al.* 2002; Lola da Costa *et al.* 2010). Water availability thus influences tree growth rates, particularly in seasonal forests, where it determines both the inter- and intra-annual growth patterns (Baker, Swaine & Burslem 2003b; Vieira *et al.* 2004).

While research on growth rates related to temporal variation (Manokaran & Kochummen 1987; Swaine, Lieberman & Putz 1987; Felfili 1995) and at species level (Finegan, Camacho & Zamora 1999; Clark *et al.* 2003) has received considerable attention, spatial patterns in growth rates among forests with different rainfall patterns have been less investigated (but see Condit *et al.* 2004; Vieira *et al.* 2004; Dauber, Fredericksen & Peña-Claros 2005). In addition, much research on tropical forest dynamics has focused on moist forests rather than on dry forests (but see Swaine, Lieberman & Hall 1990; Bullock 1997; Uslar, Mostacedo & Saldias 2004; Nath *et al.* 2006). While

basal area growth was positively correlated with rainfall, some moister forests were found to have lower growth (Fig. 2d), possibly due to lower stem density or to a high abundance of slow-growing species. Species composition varies markedly along the rainfall gradient studied here (M. Toledo, unpublished data), and the forests at drier end of the gradient are characterized by (inherently) slow-growing, drought-adapted species. These dry forest species may grow slowly because they are either drought-deciduous, and photosynthesize and grow for only part of the year, or they are evergreen and drought tolerant, and the adaptations that come along with drought tolerance (narrow vessels and dense wood) come at the expense of a reduced hydraulic conductance and slow growth (Markesteijn 2010). Similarly, along a Panamanian rainfall gradient growth rate differences amongst forests could be explained by differences in species composition and successional status among the plots (Condit *et al.* 2004).

Basal area can be directly translated into biomass (Phillips *et al.* 1998; Chave, Riéra & Dubois 2001), and the positive basal area growth found in this study agrees with the general finding that biomass has increased in tropical forests of South America (Phillips *et al.* 1998; Baker *et al.* 2004; Laurance *et al.* 2004; Lewis *et al.* 2004). In contrast, Central American forests showed decreasing growth rates at both species (Clark *et al.* 2003) and stand levels (Feeley *et al.* 2007).

We also found significant positive effects of temperature on all growth variables (Table 2, Fig. 2c, d) which is surprising, given the small difference in mean annual temperature between sites (24.2–26.4 °C). Increased growth can be caused by plants getting closer to their photosynthetic optimum. However, it is more likely that our average temperature is a good reflection of the minimum temperatures perceived. Bolivian forests are situated at the southern margin of the tropical forest biome, and experience regular cold fronts ('surazos') coming from Patagonia, in which the temperature may drop in a few hours by 15 degrees, to 12–15, and even 6 °C (Montes de Oca 1997). These cold fronts may last from 2 days up to 2 weeks, and the frequency, duration and intensity are higher in the south than

in the north, and they are even felt up to the centre of the Amazon basin, near Manaus. Across nine Bolivian lowland weather stations with longer term climatic records, the minimum monthly temperature recorded varied from 13.8 to 17.3 °C, and these minimum monthly temperatures are highly correlated with the average annual temperature (Pearson's  $r = 0.87$ ,  $P < 0.01$ ,  $n = 9$ ). Such cold fronts may lead to reduced photosynthetic activity and chilling injury of tropical trees (Feng & Cao 2005), and therefore to reduced growth. In contrast, in a Costa Rican rainforest, Clark *et al.* (2003), Clark, Clark & Oberbauer (2010) found that annual diameter increment of six species, and productivity of 0.5 ha plots, was significantly reduced in warmer years and that such an effect could already be detected with a 1–2 degrees temperature increase. The authors concluded that tropical forest productivity is reduced in years with warmer night time temperatures because of increased stem respiration. Feeley *et al.* (2007) used long-term data from 50-ha forest plots located in Panama and Malaysia to examine changes in relative basal area growth rates excluding mortality and recruitment data. They found that growth rates in these two forests had decelerated dramatically, with negative effects of temperature, over the past two decades. Temperature increases over the past several decades have been more pronounced in Southeast Asia and Central America than through much of the Amazon basin, where some regions have actually experienced a net cooling since 1960 (Malhi & Wright 2004). Whether these findings, in contrast to our positive effects on growth rates, reflect regional differences in climate or climate change remains to be studied. Differences in the part of the rainfall- and temperature gradient that has been considered, and differences in design and analyses used may also contribute to the observed differences.

Our results highlight the importance of comparisons of forests under a wide range of climatic regimes for documenting the range of growth rates and for understanding responses to environmental variation, given that climate change is not only predicted but is already being experienced in some tropical forests (Malhi & Wright 2004; Boisvenue & Running 2006; Phillips *et al.* 2009). The negative effects of predicted increased seasonality, however, may be partly offset by the positive effects of temperature on tree growth, at least for our study region. To be able to understand the adverse impacts of reduced rainfall it is therefore important to determine the response of trees and forests to climate change, through annual and long-term monitoring of ecosystem performance.

#### EDAPHIC EFFECTS ON GROWTH RATES

We hypothesized that growth rates would increase with soil fertility, as found in other forests (Swaine, Lieberman & Hall 1990; Russo *et al.* 2005). Instead, non-significant or even weak negative correlations were found between growth rates and individual and composite soil variables (Table 2). Perhaps the edaphic effect was so weak, and the climatic effect was so strong because soils were sampled at a small scale at one point in time, whereas the climate was based on a long-term average and averaged out over large spatial scales. However, we

consider that the weak edaphic effects are more likely to be partly due to the confounding effects of water availability in our study: some plots in high rainfall areas were characterized by both higher growth rates and highly weathered and nutrient-poor soils. The multiple regression analysis removed this confounding effect and showed that tree growth did indeed increase with soil fertility (Table 3, Fig. 2e), in line with the hypothesis, while stand basal area growth showed was optimum at intermediate values of soil fertility (Fig. 2f). Variation in nutrients and water availability can have complex interacting effects on tree growth at different spatial and temporal scales. For example, Baker, Burslem & Swaine (2003a) studied tree diameter growth in semi-deciduous and evergreen forests in Ghana and found that, with relatively high soil water availability, growth was higher in semi-deciduous than in evergreen forest. This difference between the two forests was only apparent under sufficient rainfall levels, and was attributed to the higher soil nutrient availability in the semi-deciduous forest. While variation in soil fertility appears to be important for determining variation in the growth rates of some species (Veenendaal *et al.* 1996; Davies 2001; Baker, Burslem & Swaine 2003a), its role in controlling growth patterns at stand-level is smaller than the role of water availability. This warrants future studies using combined analyses of both climate and soil.

Most lowland forest soils have relatively large amounts of N but relatively small amounts of available P (Vitousek & Stanford 1986; Sollins 1998). It is generally assumed that P should limit plant growth in tropical forests but we found surprisingly weak relationships between growth, N and P, either in the bivariate correlation analysis (Table 2), or in a backward multiple regression analysis where all individual environmental variables were taken into account (data not shown). One reason might be that our N and P gradients were not long enough to pick up the growth stimulating effect. Alternatively, nutrient pool sizes may not be a good indicator of the nutrients that are available to plants, and plant responses might be more tightly related to nutrient mineralization rates (cf. Ordoñez *et al.* 2009). Nutrient limitation might be avoided by dynamic and fast nutrient cycling in tropical ecosystems (Lathwell & Grove 1986; Vitousek & Stanford 1986). Our results are, therefore, more consistent with the hypothesis that plants in tropical forests may obtain nutrients directly from litter fall rather than after they enter the soils (Scott, Proctor & Thompson 1992), from the atmosphere (Jordan 1982) or from mycorrhizal fungi that obtain nutrients from litter and soils (Jordan & Herrera 1981; Onguene & Kuyper 2005). Consequently, nutrients may also be available sources other than those measured by soil analysis alone (Clinebell *et al.* 1995).

In our forests, at the lower end of the rainfall gradient (1100–2200 mm year<sup>-1</sup>) water is clearly a limiting factor, and soils may play a minor role. The situation might be different in wetter Amazonian forest, where the climate is more uniform, and when a larger variation in soil types is sampled. Aragao *et al.* (2009), for example, did find a positive correlation between total above- and belowground net primary productivity and soil phosphorus for 10 Amazonian forests on very

contrasting soils. Correlations are only the first step in understanding causal relations between soil variables and plant growth rates. Fertilization experiments in tropical montane forest show that tree growth increases in response to N and P (Tanner, Kapos & Franco 1992; Tanner, Vitousek & Cuevas 1998). However, experimental fertilization studies with large trees on nutrient-poor lowland forests found no significant increase in tree growth (Mirmanto *et al.* 1999; Gleason *et al.* 2010) or leaf litter production (Kaspari *et al.* 2008; but see Mirmanto *et al.* 1999) to added N and/or P, probably because lowland forests are less nutrient limited than montane forests. Consequently, more experimental studies on tree growth of lowland forests are required with special emphasis on deficiency of P and other important nutrients (Lathwell & Grove 1986; Sollins 1998).

In general, individual soil variables were negatively related to growth rates with few significant relationships; organic matter (OM) showing the strongest negative correlations with all the growth rates (Table 2). Plots in the drier areas tended to have lower growth rates, at tree and stand level, and higher OM. This may be related to slow rates of litter decomposition under low rainfall (Lugo & Murphy 1986; Powers *et al.* 2009). More variables (Ca, Mg, K and N) were negatively and significantly related to growth rate at stand level. We expect the confounding effect of water availability to play a similar role to that described above. Similarly, no significant correlations between soil nutrient availability and tree growth variation were found in Borneo (Ashton & Hall 1992), Costa Rica (Clark, Clark & Read 1998) and Brazil (Vieira *et al.* 2004). The Brazilian study showed that Manaus, the site with slowest growth, also had the lowest amount of total base cations, while Rio Branco, the site with relatively fast growth rates, had soils with the lowest OM and cation exchange capacity. Vieira and co-workers suggested that selective logging and extractive management may have affected the differences on growth rates (Vieira *et al.* 2004).

#### DISTURBANCE EFFECTS ON GROWTH RATES

In lowland Bolivia, growth rates increased in logged plots, especially those which had a high logging impact, and decreased with time after logging (Table 3, Fig. 2g). This is in accordance with our hypothesis that opening up of the canopy enhances light availability and hence photosynthetic carbon gain and tree growth. In tropical ecosystems, logging removes mainly larger trees, thus increasing canopy openness with associated changes in micro-environmental conditions that affect forest growth rates (Schulz 1960; Van Dam 2001). Our analyses show that significantly higher  $DGR_{avg}$  occurred in logged plots ( $0.34 \pm 0.12$  cm year<sup>-1</sup>; range 0.13–0.70) than in non-logged plots ( $0.28 \pm 0.08$  cm year<sup>-1</sup>; range 0.12–0.51; *t*-test, *t* = 13.7, *P* ≤ 0.05) (Fig. 2g). These results are consistent with higher growth rates in logged vs. non-logged plots in Brazilian (Carvalho, Silva & Lopes 2004) and Peruvian Amazonian forests (Nebel *et al.* 2001). Our average  $BAGR_{stand}$  ( $0.49 \pm 0.21$  m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>) across the 165 plots was very similar to the average value ( $0.51 \pm 0.04$  m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>)

found across 50 plots in Amazonian forests (Lewis *et al.* 2004). Both basal area growth rates increased through time. However, the variation in our plots was larger, probably due to the larger environmental gradient considered or due to the logging effects. Plots in logged forests had a similar  $BAGR_{stand}$  ( $0.51 \pm 0.21$  m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>) compared to non-logged plots ( $0.48 \pm 0.20$  m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>), probably because the enhanced growth of surviving trees in logged plots was balanced by an enhanced logging-induced mortality.

The amount of logged basal area (LBA) did not affect  $BAGR_{stand}$ , probably because of the small variation in logging intensity among our plots. Conventional logging intensity in Bolivia usually is low (1–3 trees per ha) compared to other countries: in Costa Rica 4–15 trees per ha are felled (Finegan, Camacho & Zamora 1999), in French Guiana ca. 10 trees per ha (Gourlet-Fleury & Houllier 2000), and in Borneo more than 10 trees per ha (Sist *et al.* 2003). Logging affected mainly the  $DGR_{avg}$  and  $DGR_{50}$  (Table 3), which emphasizes the effects on the small and suppressed trees that directly benefit from canopy opening by logging. In contrast,  $DGR_{99}$  was not affected by logging, probably because these fast-growing individuals receive high light conditions and/or are already in the forest canopy.

Time after logging (TAL) had negative effects only on growth rate at tree level (Table 3); diameter growth peaked after 2 years and returned to background levels 6 years after logging (Fig. 2g), most likely because the forest canopy closed again with time. Silvicultural experiments in the Brazilian Amazon found that the growth stimulus caused by logging lasts for only 3 years, declining thereafter following canopy closure (Silva *et al.* 1995). Similar results were found in plots with increasing logging intensity, in Costa Rica (Finegan & Camacho 1999), Surinam (De Graaf, Poels & Rompaey 1999), and Brazil (Carvalho, Silva & Lopes 2004).

We have found current disturbances to be an important source explaining the variation of growth rate, but it is likely that there are others. Field observations found that past logging affected some plots in the Bolivian network, which led to an opening up in the canopy and the establishment of (long-lived) pioneer species. Plots that showed the highest growth rate also had a high density of (long-lived) pioneer species. Higher growth rates due to higher abundance of pioneer species have also been reported in Ghana (Hall & Swaine 1981) and Panama (Condit *et al.* 1999). Fast-growing species complete their life cycle more rapidly and they have higher mortality rates, resulting in higher gap formation rates, which in turn create suitable conditions for the establishment of light-demanding species (Van der Meer, Sterck & Bongers 1998; Peña-Claros *et al.* 2008b) and competitive lianas (Schnitzer & Bongers 2002). Lowland forests of Bolivia vary considerably in liana density (Pérez-Salicrup, Sork & Putz 2001; Toledo *et al.* 2008); thereby lianas can overtop trees and reduce light availability for tree growth (Putz 1984). It has been demonstrated that trees without lianas have higher growth rates (Peña-Claros *et al.* 2008a; Villegas *et al.* 2009). Thus variation in floristic composition and forest structure, related to some extent with disturbances, can also affect forest growth.



## CONCLUDING REMARKS

Results from this study demonstrated that both environment and disturbance significantly explained growth rate variation in Bolivian lowland forests. This variation was most strongly determined by climate and water availability. More rainfall, a shorter and less intense dry period and higher temperatures lead to higher growth rates. Soil fertility and soil texture alone, however, did not show strong effects. While growth rates increased with logging-related disturbances, the positive stimulus of logging disappeared after 6 years.

We related growth rate to composite environmental PCA axes, to avoid problems with collinearity and over fitting. However, in some cases individual climatic variables such as the length of the dry period, annual precipitation and temperature showed stronger correlations to growth rates than the multivariate climatic axes (Table 2), suggesting that they were driving the observed patterns. Similarly, Mg, CEC and OM were more strongly correlated to growth rates than the multivariate soil axes (Table 2). Climate change scenarios for the tropics predict a future decrease in rainfall and increase in temperature. The high sensitivity of tree growth to these climatic factors may have large consequences for forest productivity and carbon sequestration. The negative effects of increased seasonality on tree growth, however, may partly be offset by the positive effects of higher temperature in these Bolivian forests. Finally, from a forest management perspective, the high variation in growth rates in different lowland forests should be taken into account. Our results strongly suggest that forest management should be fine tuned to local site conditions and forest characteristics.

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## Supporting Information

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

**Table S1.** Correlations between tree growth parameters in Bolivian lowland forests.

**Table S2.** Mean and range of climate and soil parameters of the Bolivian 1-ha forest plots and their correlations with the environmental PCA axes.

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