

Understanding causes of tree growth response to gap formation: $\Delta^{13}\text{C}$ -values in tree rings reveal a predominant effect of light

P. van der Sleen · C. C. Soliz-Gamboa ·
G. Helle · T. L. Pons · N. P. R. Anten ·
P. A. Zuidema

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Abstract

Key message Carbon isotope ratios in growth rings of a tropical tree species show that treefall gaps stimulate diameter growth mainly through changes in the availability of light and not water.

The formation of treefall gaps in closed canopy forests usually entails considerable increases in light and nutrient availability for remaining trees, as well as altered plant water availability, and is considered to play a key role in tree demography. The effects of gaps on tree growth are highly variable and while usually stimulatory they may also include growth reductions. In most studies, the causes of changes in tree growth rates after gap formation remain unknown. We used changes in carbon isotope ^{13}C discrimination ($\Delta^{13}\text{C}$) in annual growth rings to understand growth responses after gap formation of *Peltogyne* cf. *heterophylla*, in a moist forest of Northern Bolivia. We compared growth and $\Delta^{13}\text{C}$ of the

7 years before and after gap formation. Forty-two trees of different sizes were studied, half of which grew close (<10 m) to single treefall gaps (gap trees), the other half more than 40 m away from gaps (controls). We found variable responses among gap trees in growth and $\Delta^{13}\text{C}$. Increased growth was mainly associated with decreased $\Delta^{13}\text{C}$, suggesting that the growth response was driven by increased light availability, possibly in combination with improved nutrient availability. Most trees showing zero or negative growth change after gap formation had increased $\Delta^{13}\text{C}$, suggesting that increased water stress did not play a role, but rather that light conditions had not changed much or nutrient availability was insufficient to support increased growth. Combining growth rates with $\Delta^{13}\text{C}$ proved to be a valuable tool to identify the causes of temporal variation in tree growth.

Keywords Carbon stable isotopes · Gap formation · Tree growth · Light availability · Water availability · *Peltogyne*

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P. van der Sleen (✉) · P. A. Zuidema
Forest Ecology and Forest Management, Centre for Ecosystems,
Wageningen University, Droevendaalsesteeg 3, 6708 PB
Wageningen, The Netherlands
e-mail: peter.vandersleen@wur.nl

P. van der Sleen
Instituto Boliviano de Investigación Forestal (IBIF), Km 9
carretera al norte, Santa Cruz de la Sierra, Bolivia

C. C. Soliz-Gamboa
Programa de Manejo de Bosques de la Amazonía Boliviana
(PROMAB), Universidad Autónoma del Beni, Riberalta, Bolivia

C. C. Soliz-Gamboa · N. P. R. Anten
Ecology and Biodiversity, Institute of Environmental Biology,
Utrecht University, Padualaan 8, 3584 CH Utrecht,
The Netherlands

G. Helle
Section 5.2 Climate Dynamics and Landscape Evolution,
Helmholtz-Centre Potsdam. Deutsches GeoForschungsZentrum,
Telegrafenberg C127, 14473 Potsdam, Germany

T. L. Pons
Plant Ecophysiology, Institute of Environmental Biology,
Utrecht University, Padualaan 8, 3584 CH Utrecht,
The Netherlands

Present Address:
N. P. R. Anten
Centre for Crop Systems Analysis, Department of Plant
Sciences, Wageningen University, Droevendaalsesteeg 1,
6708 PB Wageningen, The Netherlands

Introduction

The formation of treefall gaps in closed canopy forests can cause a radical change in environmental conditions for neighbouring trees, and is generally believed to play a key role in tree demography (Whitmore 1989; Clark and Clark 1992; Condit 1995). Gap formation can strongly increase light availability for juvenile and suppressed trees (Canham 1988; Canham et al. 1990) and improve nutrient availability (Denslow et al. 1998; Burgess and Wetzel 2000; Muscolo et al. 2007). In addition, water availability close to canopy gaps may be improved by reduced transpiration of canopy trees and reduced root competition (Breda et al. 1995; Bladon et al. 2006). However, increased irradiance and temperature in and around gaps can also increase evaporation from the soil surface and thus reduce moisture content of the upper soil (Barg and Edmonds 1999; Olander et al. 2005). Furthermore, increased crown exposure to light and wind in and close to a gap may increase transpirational demand and thus increase water stress even if gap formation itself does not change soil water availability (Bladon et al. 2006, 2007). Thus, the changes of environmental conditions after gap formation can be complex and may affect tree growth in complex ways.

Empirical studies in tropical forests show that gap formation often increases diameter growth rates of nearby trees (Brokaw 1985; Brown 1996; Hérault et al. 2010). However, not all trees exhibit growth stimulation after gap formation: growth may remain unchanged or even decline in the years following gap formation (Poorter 1999; Miya et al. 2009; Soliz-Gamboa et al. 2012; Hérault et al. 2010). Increased growth rates of understory trees are often assumed to be caused by increased light availability (Hartshorn 1978; Martinez-Ramos et al. 1988; Clark and Clark 1992), whereas a positive growth response of adult trees that have reached the forest canopy may also result from improved water and nutrient availability. While these are the generally expected causes, the actual drivers of growth changes after gap formation remain unknown in most studies.

The measurement of stable carbon isotopes in tree rings may make it possible to determine whether growth changes after gap formation are mostly due to changes in light conditions or changes in water availability (Saurer et al. 1997; Hartmann et al. 2008; Powers et al. 2009, 2010). From the carbon isotope composition of plant material ($\delta^{13}\text{C}$), the discrimination against $^{13}\text{CO}_2$ during CO_2 assimilation can be derived ($\Delta^{13}\text{C}$). This can be used as a proxy for the intercellular CO_2 concentration (C_i) in the absence of changes in the atmospheric CO_2 concentration (C_a , currently ca. 395 ppm) using the model of Farquhar et al. (1982):

$$\Delta = \delta^{13}\text{C}_a - \delta^{13}\text{C}_{\text{plant}} = a + (b-a)C_i/C_a, \quad (1)$$

where $\delta^{13}\text{C}_a$ is the $\delta^{13}\text{C}$ of atmospheric CO_2 (currently ca. -8.3 ‰), a (4.4 ‰) refers to the slower diffusion of $^{13}\text{CO}_2$

compared to $^{12}\text{CO}_2$ through the stomata, and b (27 ‰) to the discrimination by the CO_2 -fixing enzyme Rubisco. A change in C_i can be caused by changes in photosynthetic rates (A) and/or stomatal conductance (g_s). Increased light intensity increases A more than g_s , whereas decreased water availability decreases g_s more than A . Nutrient availability relative to the growth potential of the plant has an effect similar to light intensity and is thus difficult to disentangle from light effects (Ehleringer et al. 1986; Cernusak et al. 2009).

Although changes in $\Delta^{13}\text{C}$ alone are not conclusive with respect to the causes of tree responses to altered environmental conditions, their combined analysis with tree growth data that can be used as a proxy for A , allows the identification of the main drivers of growth changes. For example, if light availability increases after gap formation, it may increase the growth potential of a remaining tree by increasing photosynthetic rates. This can lead to increased growth when the availability of water and nutrients is sufficient. Increased growth is then associated with decreased $\Delta^{13}\text{C}$. If water stress hampers a growth increase after gap formation or even reduces growth, then $\Delta^{13}\text{C}$ is also expected to decrease. An absence of changes in growth and $\Delta^{13}\text{C}$ after gap formation indicates either insufficient increase of light availability or a simultaneous decrease in nutrient availability and an increased growth potential due to higher light availability.

In a previous publication, we reported on a highly variable growth response to gap formation for the shade-tolerant tree *Peltogyne* cf. *heterophylla* in a Bolivian moist forest (Soliz-Gamboa et al. 2012). Growth rates of some trees increased after gap formation, while growth of others decreased or did not change (mostly small juvenile trees). In the current study, we aimed to identify the causes of observed diameter growth responses using the combined analyses of changes in growth and stable carbon isotopes. Specifically, we use $\Delta^{13}\text{C}$ values obtained from tree rings to investigate (1) whether increased tree growth after gap formation is a consequence of increased light (and/or nutrients) or water availability and (2) whether increased water stress after gap formation causes a reduction of growth rates in some trees. We measured tree-ring width and carbon isotope ratios in growth rings in trees of different sizes before and after gap formation.

Materials and methods

Study area and species

The study was carried out in the logging concession “Los Indios” ($10^\circ 26' \text{S}$, $65^\circ 33' \text{W}$) located 86 km northeast of the town of Riberalta, Bolivia. Forests in the region are semi-

deciduous with a dense canopy at 30–35 m height and some emergent trees up to 45 m. Density of stems >10 cm diameter at breast height (dbh) is 423 ha⁻¹ (Toledo et al. 2008). The study area was selectively logged from May to September 2001, at an intensity of 1.4 trees ha⁻¹. After logging, no further disturbances took place.

Mean annual precipitation is 1,690 mm and mean annual temperature is 27 °C (Soliz-Gamboa et al. 2012). We checked if average annual precipitation in the growing season (October–May) differed between the 7-year periods before and after logging (the study period) using climatic data for Riberalta from the database of the KNMI Climate Explorer (Trouet and Van Oldenborgh 2013). No significant difference in average annual precipitation was found between the years before and after gap formation (ANOVA: $F = 0.670$, $p = 0.428$). Unfortunately, no temperature data were available to determine if there were differences in growth season temperatures.

Our study species, *Peltogyne* cf. *heterophylla* (Fabaceae, Caesalpinioideae; hereafter referred to by its genus name), is a shade-tolerant tree, which is evergreen as a juvenile and brevi-deciduous as an adult (Soliz-Gamboa et al. 2012). Tree-ring studies have been conducted on this species and the annual nature of growth rings has been established (Soliz-Gamboa et al. 2011; Brienen and Zuidema 2005). *Peltogyne* is a relatively slow growing species, especially in the juvenile phase. Sampled trees of ca. 25 cm dbh were often more than 100 years old.

Data collection and tree-ring measurements

We sampled 21 trees at <10 m from single treefall gaps or from similar-sized canopy openings formed by skidder trails (gap trees) and 21 trees at more than 40 m away from gaps (control trees). The trees ranged in size from 5 to 25 cm dbh, with a similar size distribution in gap and control trees. The average age of the control trees was 104 years (range 55–158 years) and 102 years in the gap trees (range 32–162 years). Even though *Peltogyne* trees can attain sizes of >100 cm dbh, we did not collect trees larger than 25 cm, because gap effects were expected to be stronger for juvenile—sub-adult trees. We avoided sampling trees that were badly damaged or severely liana infested.

For each tree sampled, we determined the Canopy Closure Index (CCI) (Lieberman et al. 1989, 1995). The CCI is an estimate of the level of shade cast upon the crown of a focal tree based on the density and heights of neighbouring trees that are taller than the focal tree. A low CCI indicates a low density of taller trees surrounding the focal tree and thus, a higher light availability. For all trees up to 20 cm dbh, cross-sectional stem discs were collected using a chain saw. Five of the larger trees were sampled in three different directions using a 22-mm increment borer

mounted on a motor (Stihl BT42). All samples were collected at 50 cm height. Cores and discs were air-dried and polished using grits up to 1,000. Tree rings in the discs and cores were dated and ring widths were measured using a LINTAB 6 and TSAPWin software (Rinntech, Germany). Tree-ring widths (annual increment in cm year⁻¹) were converted to Basal Area Increment (BAI; cm² year⁻¹) as this gives a good estimate of biomass growth (Baker et al. 2004). Individual tree growth responses were determined by comparing the average annual BAI in the 7 years after (2001–2007) to the average annual BAI in the 7 years before (1994–2000) gap formation. Periods of 7 years were chosen as logging took place 7 years before wood samples were taken (in 2008). The year 2001 was included in the period after gap formation because logging occurred prior to the onset of the growing season.

Isotope analyses

Wood material was cut from each of the 14 annual rings (in accordance with the above-mentioned periods 1994–2000 before and 2001–2007 after gap formation) of every tree. Complete growth rings were sampled. Cellulose extraction was performed on the raw wood samples using the adapted Jayme-Wise method (Wieloch et al. 2011). Holocellulose samples were subsequently homogenized in a demi-water solution by a mixer mill (Retsch MM301, Germany) and oven-dried at 70 °C. This novel homogenization procedure gave good results as multiple $\delta^{13}\text{C}$ measurements on subsamples from the same cellulose gave very similar results (maximum difference of 0.04 ‰). All cellulose samples were analysed in a continuous flow mode with an element analyzer coupled to a mass spectrometer at the Geo Forschungs Zentrum in Potsdam, Germany. The carbon isotope composition ($\delta^{13}\text{C}$, in ‰) was then calculated as:

$$\delta^{13}\text{C}_{\text{tree-ring}} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000, \quad (2)$$

where, R_{sample} is the $^{13}\text{C}/^{12}\text{C}$ ratio of a sample and R_{standard} the $^{13}\text{C}/^{12}\text{C}$ ratio of an internationally recognized standard material (V-PDB). Discrimination (Δ) against the heavier ^{13}C can be calculated by:

$$\Delta^{13}\text{C} = (\delta^{13}\text{C}_a - \delta^{13}\text{C}_{\text{tree-ring}}) / (1 + \delta^{13}\text{C}_{\text{tree-ring}}), \quad (3)$$

where $\delta^{13}\text{C}_a$ is the $\delta^{13}\text{C}$ of atmospheric CO_2 . As $\delta^{13}\text{C}_a$ decreased by 1.5 ‰ since the onset of the industrial revolution due to the burning of fossil fuels that are depleted in ^{13}C , we used year-specific values for each of the 14 years of ring formation (McCarroll and Loader 2004). We excluded one large control tree from the analyses, which exhibited significantly lower $\Delta^{13}\text{C}$ values over the entire 14-year period studied.

We examined $\Delta^{13}\text{C}$ instead of the estimate of the intercellular CO_2 concentration in leaves (C_i), which can be derived from $\Delta^{13}\text{C}$, because in the period covered by our study (1994–2007), atmospheric CO_2 concentration (C_a) increased by 7 % (from 359 to 384 ppm). If plants do not respond by changing stomatal conductance and/or assimilation, a 7 % increase in atmospheric CO_2 will result in a similar 7 % increase of C_i . This so-called passive response (McCarroll et al. 2009) may obscure effects on C_i caused by gaps. We therefore used $\Delta^{13}\text{C}$ which is based on the ratio between C_i and C_a , and has been shown to be less influenced by the rise of C_a than C_i [e.g. Hietz et al. (2005), (2011); Loader et al. (2011), but also see Brienen et al. (2011)]. In addition, our experimental setup corrects for this potential confounding factor by including proper controls.

Statistical analyses

Growth rates (BAI) and $\Delta^{13}\text{C}$ often vary over the size range of trees (e.g. Clark and Clark (1992) and Gagen et al. (2007)). This ontogenetic variation could potentially obscure any gap-related effects and might be especially problematic in our data set, as we collected trees of different sizes (5–25 cm dbh). We therefore standardized BAI and $\Delta^{13}\text{C}$ series for each tree by dividing annual values by their 14-year average value. In this way, annual BAI and $\Delta^{13}\text{C}$ values are expressed as proportional deviations from the 14-year average. We subsequently analysed the overall effect of gap formation on standardized BAI and $\Delta^{13}\text{C}$ with a mixed-effects model. Mixed-effects models are well suited for the repeated measures structure of tree-ring and isotope data series. We included ‘gap-formation’ as a fixed factor and ‘individual tree’ as a random factor. Tree size (dbh at the time a gap was formed) was included as a covariate. We also tested if there was an interaction between the effect of gap formation and tree size. Gap and control trees were analysed separately.

Pearson’s correlations were used to test the relation between changes in BAI and changes in $\Delta^{13}\text{C}$. Proportional change (in %) in BAI and $\Delta^{13}\text{C}$ were calculated as this allows for a better comparison of the responses of individual trees than absolute changes, which are, especially for BAI, much greater in large than small trees. We used an ANCOVA to test if there was a difference between gap and control trees in light levels (the inverse of CCI), including tree size as a covariate. Log-transformed CCI was taken to obtain linear relations. We analysed the relation between CCI and BAI and between CCI and $\Delta^{13}\text{C}$ with a multiple linear regression, using log-transformed BAI and $\Delta^{13}\text{C}$ (again to obtain linear relationships). We also included trees size (dbh) as a covariate in the regression analysis, because BAI and $\Delta^{13}\text{C}$ are strongly size dependent, but

furthermore, because CCI also decreases with tree size. All analyses were performed using IBM SPSS Statistics, version 19.0.

Results

Effect of gap formation on growth and $\Delta^{13}\text{C}$

Among the individual *Peltogyne* trees, we found increased, decreased and unchanged growth in basal area (BAI) after gap formation (Fig. 1). Of these gap trees, 14 out of 21 trees showed an increased growth of >25–700 % (Fig. 2). Among control trees, which were located far away from gaps, 8 out of 21 trees showed an increased BAI of >25–200 % (Fig. 2). Given the high variability of responses in the group of gap trees, it is not surprising that we did not find an overall effect of gap formation on standardized BAI in a linear mixed-effects model (Table 1). Nevertheless, we did find a significant interaction between dbh and gap formation ($p < 0.001$; Table 1), suggesting that the response to gap formation depends on tree size. In particular, several medium-sized trees (dbh ca. 15 cm) showed strong positive growth changes after gap formation, which were larger than most of the growth changes in small trees (Fig. 2).

No significant effect of gap formation was found on $\Delta^{13}\text{C}$ in a mixed-effects model analysis (Table 1). Again, the response of the $\Delta^{13}\text{C}$ values to gap formation was highly variable (Figs. 1, 2). It is possible that very old trees do not respond as vigorously to gap formation as similar-sized but younger trees. We checked if age is a stronger driver of the responses to gap formation than size. However, this does not seem to be the case, as there is no significant relation between tree age and its capacity to respond (as for tree size, we only found a significant interaction between gap formation and tree age in the gap trees: $F = 7.988$, $p = 0.005$).

Understanding growth changes

To interpret the causes of growth changes, we related the proportional change (in %) in BAI to the change in $\Delta^{13}\text{C}$ (Fig. 3). In both control and gap trees, changes in BAI correlated significantly with changes in $\Delta^{13}\text{C}$ (Pearson’s $r^2 = 0.237$ ($p = 0.013$) and 0.469 ($p < 0.001$), respectively). Among the trees (both gap and control) showing increased growth, 16 out of 22 were associated with a decrease in $\Delta^{13}\text{C}$ (Fig. 3), whereas 12 out of 19 trees with no or a negative growth change showed an increase in $\Delta^{13}\text{C}$ (Fig. 3).

Because our study is retrospective, we have no data on the changes in light, nutrient and water availability

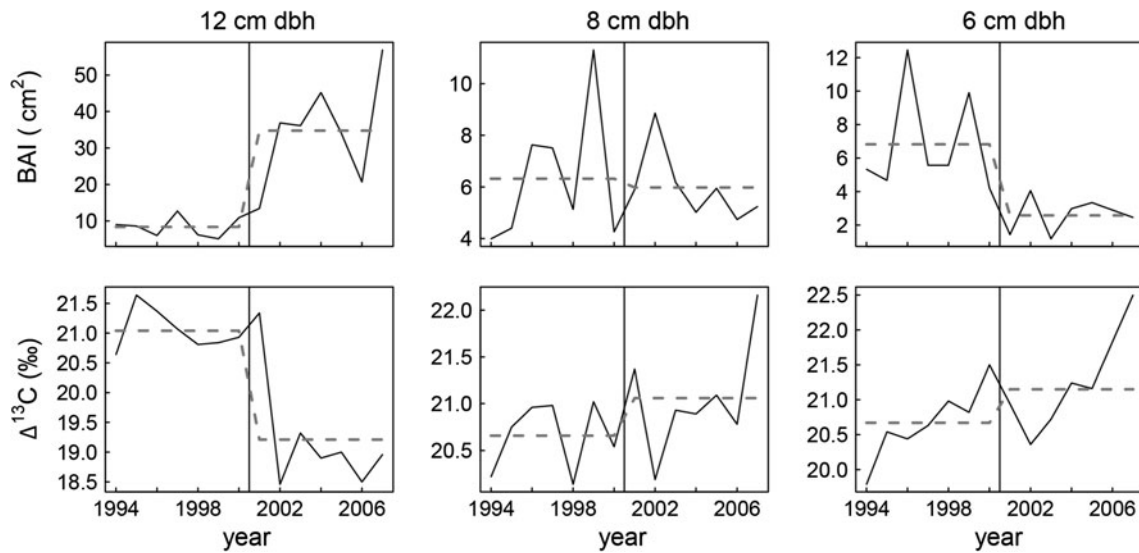


Fig. 1 Three examples of annual Basal Area Increment (BAI) and ¹³C discrimination ($\Delta^{13}\text{C}$) for individuals of *Peltogyne* cf. *heterophylla* that grew <10 m from a logging gap. The black vertical reference line shows the time of gap formation, the dashed grey lines the average BAI and $\Delta^{13}\text{C}$ pre- and post-gap formation

Fig. 2 Changes in Basal Area Increment (BAI) [top panel] and ¹³C discrimination ($\Delta^{13}\text{C}$) [bottom panel] for *Peltogyne* cf. *heterophylla* after gap formation with respect to tree size (dbh) at the time of gap formation. Proportional changes (in %) were taken to account for potential size effects on growth and $\Delta^{13}\text{C}$

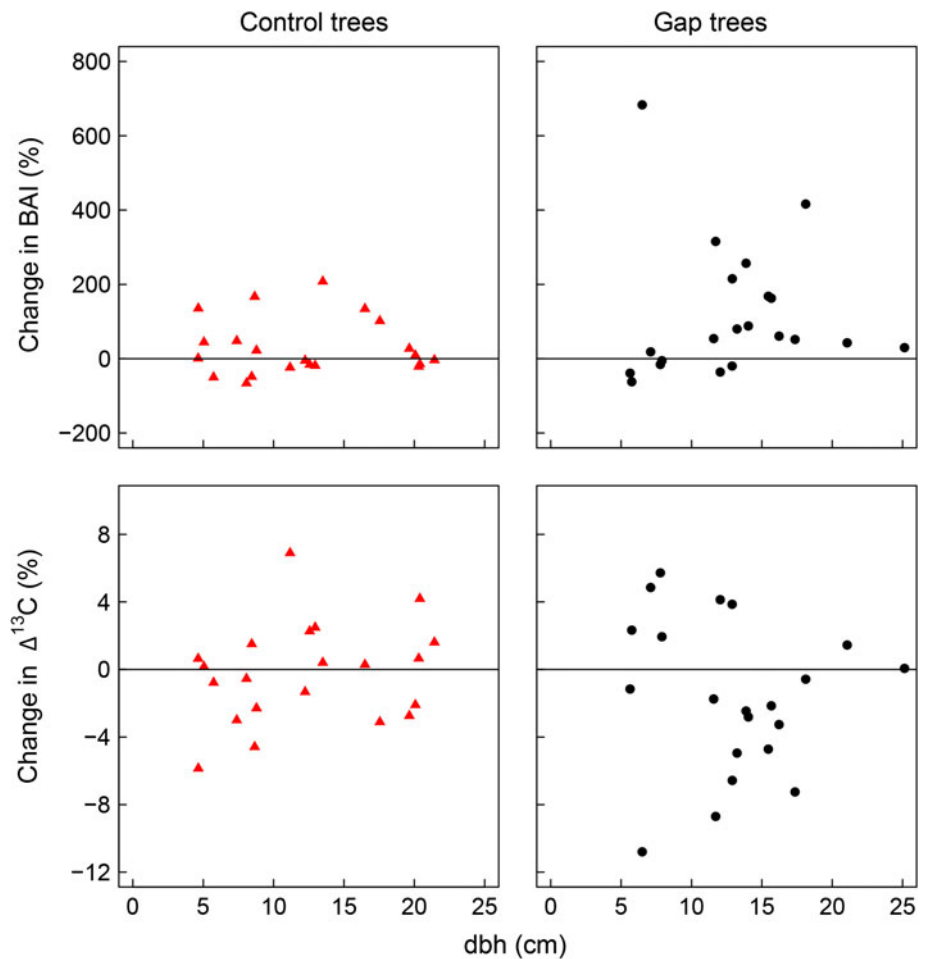


Table 1 Results of the mixed-effects model analyses with standardized Basal Area Increment (BAI) and $\Delta^{13}\text{C}$ as dependent variables and gap formation, tree size (dbh at the time of

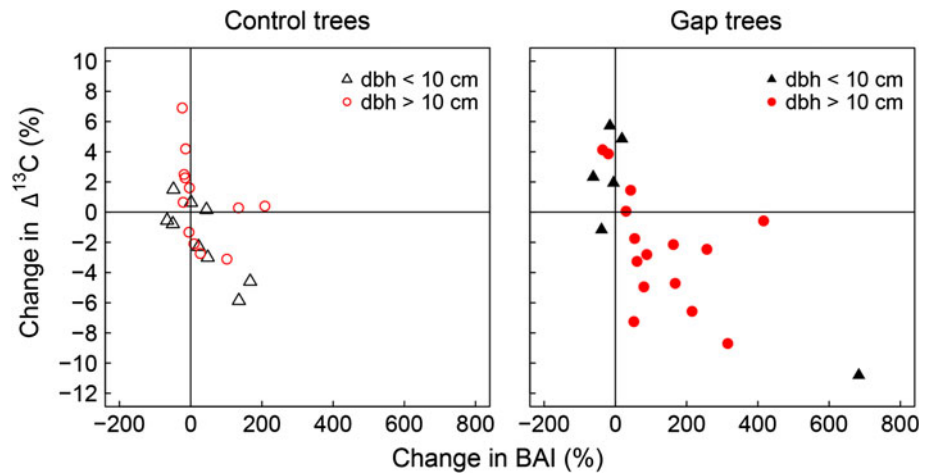
gap formation; inserted as covariate) and the interaction between gap formation and dbh (gap*dbh) as factors

Fixed effects	Control trees			Gap trees		
	df	F value	p value	df	F value	p value
BAI						
Gap formation	258.438	0.023	0.879	238.066	1.487	0.224
dbh	233.512	2.536	0.113	250.492	0.358	0.550
gap*dbh	233.512	0.051	0.821	250.492	18.390	0.000
$\Delta^{13}\text{C}$						
Gap formation	226.851	0.196	0.658	250.057	0.041	0.839
dbh	210.051	0.185	0.667	231.386	0.796	0.373
gap*dbh	210.051	0.026	0.871	231.386	2.930	0.088

Bold value indicates $p = 0.00003$ (or state $p < 0.001$)

df denominator degrees of freedom (numerator d.f. = 1 in all cases)

Fig. 3 Changes in Basal Area Increment (BAI) with respect to $\Delta^{13}\text{C}$ discrimination ($\Delta^{13}\text{C}$) for *Peltogyne cf. heterophylla* after gap formation for control trees [left panel] and gap trees [right panel]. In both control and gap trees, changes in BAI correlated significantly with changes in $\Delta^{13}\text{C}$ (Pearson's $r^2 = 0.237$ ($p = 0.013$) and 0.469 ($p < 0.001$), respectively)



occurring during gap formation. However, we measured canopy closure index (CCI: the inverse of light availability) once in 2007, 7 years after gap formation. We found that, even 7 years after logging, gap trees were, on average, growing at higher light conditions than control trees (ANCOVA: $F = 10.804$, $p = 0.002$; Fig. 4). For both gap and control trees, CCI decreased with tree size [Pearson's $r^2 = 0.301$ ($p = 0.009$) and 0.740 ($p < 0.001$), respectively]. Logically, larger trees experienced, in general, higher light levels. We also related CCI to the averaged BAI and $\Delta^{13}\text{C}$ of the last 5 years (2003–2007) using a linear regression analysis. As tree size also has a strong effect on BAI and $\Delta^{13}\text{C}$, we included tree size as a covariate in the analyses. We found a highly significant increase of BAI with decreasing CCI ($r^2 = 0.680$, $p < 0.001$; Fig. 5) and a significant increase of $\Delta^{13}\text{C}$ with increasing CCI ($r^2 = 0.480$, $p < 0.001$; Fig. 5). Hence, trees with a low CCI, meaning a low density of taller neighbouring trees and thus, receiving abundant light, grew faster and had a lower $\Delta^{13}\text{C}$.

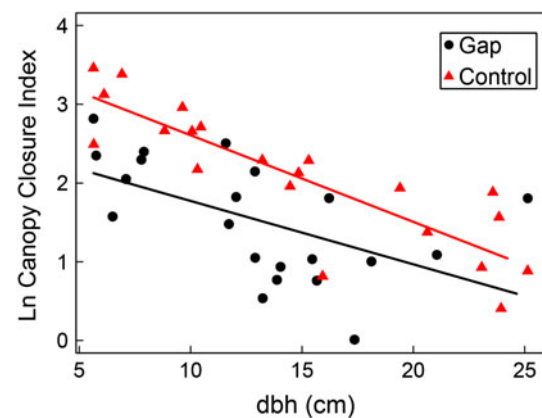


Fig. 4 Light availability (the inverse of Canopy Closure Index; CCI) for gap and control trees in relation to tree size (dbh). Log-transformed CCI was taken to obtain linear relations. Gap trees grew, on average, in higher light conditions than control trees even after 7 years of gap formation (ANCOVA: $F = 10.804$, $p = 0.002$). CCI significantly decreases with tree size in both gap and control trees (Pearson's $r^2 = 0.301$ ($p = 0.009$) and 0.740 ($p < 0.001$), respectively)

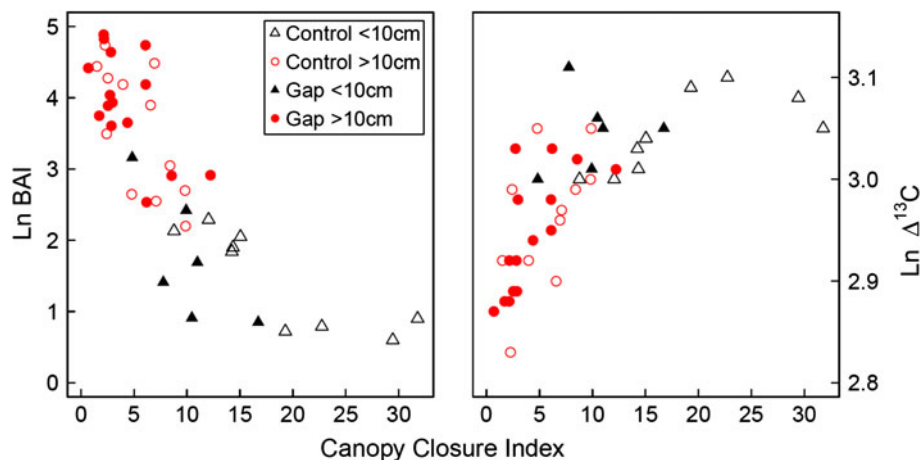


Fig. 5 The relationship between Basal Area Increment (BAI) and Canopy Closure Index (CCI) [left panel] and between ^{13}C discrimination ($\Delta^{13}\text{C}$) and CCI [right panel] for *Peltogyne cf. heterophylla*. For BAI and $\Delta^{13}\text{C}$, we arbitrarily took the average of the last 5 years (2003–2007), CCI was measured only once in 2007. Log-transformed

BAI and $\Delta^{13}\text{C}$ were used to obtain linear relationships. Data were analysed with a multiple linear regression (including tree size as a covariate); $r^2 = 0.680$ ($p < 0.001$) and 0.480 ($p < 0.001$), respectively

Discussion

We used stable carbon isotope ratios in annual growth rings to study the causes of growth changes after gap formation in a common shade-tolerant tree, *Peltogyne cf. heterophylla*, in North-eastern Bolivia. No general effect of gap formation on growth rates (BAI) and ^{13}C discrimination was found ($\Delta^{13}\text{C}$; see Table 1). The lack of an overall effect of gap formation can be explained by the large variability in responses: BAI and $\Delta^{13}\text{C}$ showed increased, zero and negative changes after gap formation (Fig. 1). However, for BAI, but not for $\Delta^{13}\text{C}$, we did find a significant interaction between gap formation and tree size (Table 1), suggesting that the growth response to gap formation depends on tree size. In particular, the medium-sized trees (dbh ca. 15 cm) seem to respond to gap formation by increasing growth rates, but most of the small trees showed negative to zero growth responses (Fig. 2).

What explains the variation in responses to gap formation? Trees showing increased growth rates after gap formation were mainly associated with a decrease in ^{13}C discrimination (Fig. 3). Such a decrease in plant $\Delta^{13}\text{C}$ can be caused by both changes in light/nutrient and water availability (Ehleringer et al. 1986; Cernusak et al. 2009). Improved light and, to a lesser extent, increased nutrient availability, can increase assimilation rates relative to stomatal conductance and therefore, decrease $\Delta^{13}\text{C}$ (Ehleringer et al. 1986; Cernusak et al. 2009). Indeed, we found a significant negative relation between light availability (the inverse of CCI) and $\Delta^{13}\text{C}$ (Fig. 5), a relationship that has already been well documented (Ehleringer et al. 1987; Zimmerman and Ehleringer 1990). The observed decrease in $\Delta^{13}\text{C}$ can also point to increased water stress because

reduced water availability decreases stomatal conductance and therefore, C_i (McNulty and Swank 1995; Saurer et al. 1995; Cernusak et al. 2009). But in the latter case, one would expect a concomitant decrease in growth (as reduced water availability slows down growth). Hence, the increase of growth rates in combination with reduced $\Delta^{13}\text{C}$ after gap formation, as observed in our study, is likely caused by increased light availability, possibly in combination with a proportionally increased nutrient availability.

Growth rates can also increase by a lowering of water stress after gap formation, e.g. by reduced root competition. However, if increased growth rates are the results of improved water availability, we expect to find increased C_i and hence $\Delta^{13}\text{C}$, or no change in C_i and $\Delta^{13}\text{C}$ when occurring in synchrony with increased light/nutrient levels. This is opposite to what we found. Our results thus suggest that changes in water availability after gap formation were less important than changes in light and nutrients for the stimulation of growth.

It was surprising that we did not find a growth response to gap formation in most of the smaller trees (Fig. 2). These trees are expected to benefit the most from increased light availability after gap formation, given their shaded position in the forest understory. Poorter (1999), working in the same region, found no strong growth response of seedlings of some species in high light conditions and suggested this might be a result of increased water stress. This does not seem to apply to our study system, as we found no indications of increased water stress, i.e. no significant decrease in $\Delta^{13}\text{C}$ was observed in combination with decreased growth rates. On the contrary, growth reduction was mainly associated with increased $\Delta^{13}\text{C}$ (Fig. 3), which suggests decreasing light availability. When comparing the

gap trees with the control trees (Figs. 2, 3), it is noteworthy that the latter show a temporal variation in growth and $\Delta^{13}\text{C}$ that is not very different from the gap trees. This indeed suggests that the effect of gap formation (e.g. on understory light levels) might not have been very strong for most trees. However, even 7 years after gap formation, gap trees were, on average, still growing in higher light condition than control trees (Fig. 4). This was especially the case for the medium-sized trees.

A lack of growth stimulation after gap formation is also possible if excessive irradiance during the first years after gap formation causes a strong photo-inhibition, which reduces photosynthetic rates and thereby, increased $\Delta^{13}\text{C}$. For shade-tolerant species, like *Peltogyne* cf. *heterophylla*, photo-inhibition might be a severe problem in high light environments (Krause et al. 1995; Krause and Winter 1996; Houter and Pons 2005). Still, the greatest increase in growth after gap formation (nearly 700 %) in combination with the strongest observed decrease in $\Delta^{13}\text{C}$ (−11 %) was found in one of the smallest trees (Fig. 3). This tree also had a very high light availability ($\text{CCI} = 4.83$) when measured in 2007, suggesting that at least some small *Peltogyne* trees are able to take advantage of gap formation and do not experience strong photo-inhibition. Long-term tree-ring studies also indicate that small trees of this species are able to undergo strong growth spurts (Brienen and Zuidema 2006; Soliz-Gamboa et al. 2011).

Growth stimulation in response to gap formation may also have been hampered by a lowered nutrient availability, which may be caused by the increased growth and nutrient absorption of nearby larger trees or by a reduced leaf litter fall (lower nutrient input) due to the removal of a dominant tree from the canopy. A reduced nutrient availability can lower photosynthetic rates and as such, increases C_i and $\Delta^{13}\text{C}$. Although we do not fully understand why several small trees did not respond to gap formation, our data show that this lack of response was not caused by prolonged water stress, but rather that light availability did not sufficiently increase or that, particularly when $\Delta^{13}\text{C}$ increased, nutrient availability decreased.

We exclude the possibility that the results presented here are strongly affected by ontogenetic (i.e. developmental) changes in growth and tree-ring $\delta^{13}\text{C}$. For carbon isotopes, a ‘juvenile effect’ has often been observed in the early years of tree growth (Freyer 1979; McCarroll and Loader 2004) and has been attributed to ^{13}C -depleted CO_2 near the ground from soil respiration, as well as to other environmental changes (e.g. light) during development (Leavitt 2010). Such ontogenetic changes can potentially interfere with changes caused by gap formation. We, however, expect that ontogenetic effects are very small to absent in our data because: (1) the studied trees were relatively old (minimum tree age was 31 years), (2) the small trees

studied had their leaves at least several meters above the forest floor, excluding an effect of ^{13}C -depleted CO_2 near the ground, (3) the study period was relatively short and ontogenetic changes in growth are gradual for this species (Rozendaal et al. 2010, 2011) and thus cannot explain the abrupt growth changes observed in some trees (Fig. 1), and (4) our experimental setup includes proper controls, i.e. gap trees were compared to control trees that, if present, have similar ontogenetic patterns in growth and $\delta^{13}\text{C}$, but did not experience nearby gap formation (Figs. 2, 3).

The combined analyses of tree growth and carbon isotopes can help to identify some of the possible causes of strong growth decreases (suppressions) or increases (releases) in tree-ring series. It is often assumed that these patterns are mainly caused by periods of low and high light, respectively, and therefore reflect canopy dynamics (Wright et al. 2000; Brienen and Zuidema 2006; Baker and Bunyavejchewin 2006). However, in a Mexican dry forest, some releases could also be related to reduced temperatures, likely causing reduced water stress (Brienen et al. 2010). Carbon isotope ratios in growth suppressions and releases can reveal whether growth changes are mainly driven by shifts in water or light availability and hence, distinguish between the effects of climate and forest dynamics.

We conclude that for *Peltogyne*, the shade-tolerant species studied, growth increase after gap formation is mainly governed by increased light availability and not by increased water availability. Although such light-mediated gap effects have often been proposed, our analyses of carbon isotope ratios indeed point to an effect of light, probably in combination with increased nutrient availability.

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Conflict of interest Authors declare that they have no conflict of interest.

References

- Baker PJ, Bunyavejchewin S (2006) Suppression, release and canopy recruitment in five tree species from a seasonal tropical forest in western Thailand. *J Trop Ecol* 22:521–529
- Baker TR, Phillips OL, Malhi 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. *Philos Trans R Soc Lond B Biol Sci* 359(1443):353–365

- Barg AK, Edmonds RL (1999) Influence of partial cutting on site microclimate, soil nitrogen dynamics, and microbial biomass in Douglas-fir stands in western Washington. *Can J For Res* 29:705–713
- Bladon KD, Silins U, Landhäusser SM, Lieffers VJ (2006) Differential transpiration by three boreal tree species in response to increased evaporative demand after variable retention harvesting. *Agric For Meteorol* 138(1–4):104–119
- Bladon KD, Silins U, Landhäusser SM, Messier C, Lieffers VJ (2007) Carbon isotope discrimination and water stress in trembling aspen following variable retention harvesting. *Tree Physiol* 27(7):1065–1071
- Breda N, Granier A, Aussenac G (1995) Effects of thinning on soil water balance and tree water relations, transpiration and growth in oak forest (*Quercus petraea* (Matt) Liebl.). *Tree Physiol* 15:295–306
- Brienen RJW, Zuidema PA (2005) Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. *Oecologia* 146(1):1–12
- Brienen RJW, Zuidema PA (2006) Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. *J Ecol* 94(2):481–493
- Brienen RJW, Zuidema PA, Martínez-Ramos M (2010) Attaining the canopy in dry and moist tropical forests: strong differences in tree growth trajectories reflect variation in growing conditions. *Oecologia* 163(2):485–496
- 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 Structure Function* 25(1):103–113
- 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. *For Ecol Manage* 82:239–244
- Burgess D, Wetzel S (2000) Nutrient availability and regeneration response after partial cutting and site preparation in eastern white pine. *For Ecol Manage* 138:249–261
- Canham CD (1988) Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69(3):786–795
- Canham CD, Denslow JS, Platt WJ (1990) Light regimes beneath closed canopies and tree fall gaps in temperate and tropical forests. *Can J For Res* 20:620–631
- Cernusak LA, Winter K, Turner BL (2009) Physiological and isotopic ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) responses of three tropical tree species to water and nutrient availability. *Plant Cell Environ* 32:1441–1455
- Clark DA, Clark DB (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol Monogr* 62(3):315–344
- Condit R (1995) Research in large, long-term tropical forest plots. *Trends Ecol Evol* 10(1):18–22
- Denslow JS, Ellison AM, Sanford RE (1998) Tree fall gap size effects on above- and below ground processes in a tropical wet forest. *J Ecol* 86:597–609
- Ehleringer JR, Field CB, Lin ZF, Kuo CY (1986) Leaf carbon isotope ratio and mineral composition in subtropical plants along an irradiance cline. *Oecologia* 70:520–526
- Ehleringer JR, Lin ZF, Field CB, Sun GC, Kuo CY (1987) Leaf carbon isotope ratios of plants from a subtropical monsoon forest. *Oecologia* 72(1):109–114
- Farquhar GD, O’Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. *Aust J Plant Physiol* 9:121–137
- Freyer HD (1979) On the ^{13}C record in tree rings. Part I. ^{13}C variations in northern hemispheric trees during the last 150 years. *Tellus* 31(2):124–137
- Gagen MH, McCarroll D, Loader NJ, Robertson I, Jalkanen R, Anchukaitis KJ (2007) Exorcising the ‘segment length curse’: summer temperature reconstruction since AD 1640 using non-trended stable carbon isotope ratios from pine trees in northern Finland. *Holocene* 17:433–444
- Hartmann H, Wirth C, Messier C, Berninger F (2008) Effects of above- and belowground partial harvest disturbance on growth and water status of residual sugar maple. *Tree Physiol* 28:1851–1862
- Hartshorn GS (1978) Tree falls and tropical forest dynamics. In: Tomlinson PB, Zimmermann MH (eds) *Tropical trees as living systems*. Cambridge University Press, New York, pp 617–638
- Héroult B, Ouallet J, Blanc J, Wagner F, Baraloto C (2010) Growth responses of neotropical trees to logging gaps. *J Appl Ecol* 47:821–831
- Hietz P, Wanek W, Dünisch O (2005) Long-term trends in cellulose $\delta^{13}\text{C}$ and water-use efficiency of tropical *Cedrela* and *Swietenia* from Brazil. *Tree Physiol* 25(6):745–752
- Hietz P, Turner BL, Wanek W, Richter A, Nock CA, Wright SJ (2011) Long-term change in the nitrogen cycle of tropical forests. *Science* 334(6056):664–666
- Houter NC, Pons TL (2005) Gap size effects on photoinhibition in understorey saplings in tropical rainforest. *Plant Ecol* 179(1):43–51
- Krause GH, Winter K (1996) Photoinhibition of photosynthesis in plants growing in natural tropical forest gaps. A chlorophyll fluorescence study. *Botanica Acta* 109:456–462
- Krause GH, Virgo A, Winter K (1995) High susceptibility to photoinhibition of young leaves of tropical trees. *Planta* 197(4):583–591
- Leavitt SW (2010) Tree-ring C–H–O isotope variability and sampling. *Sci Total Environ* 408(22):5244–5253
- Lieberman M, Lieberman D, Peralta R (1989) Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70(3):550–552
- Lieberman M, Lieberman D, Peralta R, Hartshorn GS (1995) Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. *J Trop Ecol* 11(2):161–178
- Loader NJ, Walsh RPD, Robertson I, Bidin K, Ong RC, Reynolds G, McCarroll D, Gagen M, Young GHF (2011) Recent trends in the intrinsic water-use efficiency of ringless rainforest trees in Borneo. *Philos Trans R Soc Lond B Biol Sci* 366(1582):3330–3339
- Martinez-Ramos M, Alvarez-Buylla E, Sarukhan J, Pinero D (1988) Treefall age determination and gap dynamics in a tropical forest. *J Ecol* 76(3):700–716
- McCarroll D, Loader NJ (2004) Stable isotopes in tree rings. *Quatern Sci Rev* 23(7–8):771–801
- 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. *Geochim Cosmochim Acta* 73(6):1539–1547
- McNulty SG, Swank WT (1995) Wood $\delta^{13}\text{C}$ as a measure of annual basal area growth and soil water stress in a *Pinus strobus* forest. *Ecology* 76(5):1581–1586
- Miya H, Yoshida T, Noguchi M, Nakamura F (2009) Individual growing conditions that affect diameter increment of tree saplings after selection harvesting in a mixed forest in northern Japan. *J For Res* 14(5):302–310
- 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. *For Ecol Manage* 242:412–418
- Olander LP, Bustamante MM, Asner GP, Telles E, Prado Z, Camargo PB (2005) Surface soil changes following selective logging in an eastern Amazon forest. *Earth Interact* 9:1–19
- Poorter L (1999) Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Funct Ecol* 13(3):396–410

- Powers MD, Pregitzer KS, Palik BJ, Webster CR (2009) Water relations of pine seedlings in contrasting overstory environments. *For Ecol Manage* 258(7):1442–1448
- Powers MD, Pregitzer KS, Palik BJ, Webster CR (2010) Wood $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and radial growth responses of residual red pine to variable retention harvesting. *Tree Physiol* 30(3):326–334
- Rozendaal DMA, Soliz-Gamboa CC, Zuidema PA (2010) Timber yield projections for tropical tree species: the influence of fast juvenile growth on timber volume recovery. *For Ecol Manage* 259(12):2292–2300
- Rozendaal DMA, Soliz-Gamboa CC, Zuidema PA (2011) Assessing long-term changes in tropical forest dynamics: a first test using tree-ring analysis. *Trees Struct Funct* 25(1):115–124
- Saurer M, Siegenthaler U, Schweingruber F (1995) The climate-carbon isotope relationship in tree rings and the significance of site conditions. *Tellus Series B* 47 B(3):320–330
- Saurer M, Borella S, Schweingruber F, Siegwolf R (1997) Stable carbon isotopes in tree rings of beech: climatic versus site-related influences. *Trees Struct Funct* 11(5):291–297
- Soliz-Gamboa CC, Rozendaal DMA, Ceccantini G, Angyalossy V, van der Borg K, Zuidema PA (2011) Evaluating the annual nature of juvenile rings in Bolivian tropical rainforest trees. *Trees Struct Funct* 25(1):17–27
- Soliz-Gamboa CC, Sandbrink A, Zuidema PA (2012) Diameter growth of juvenile trees after gap formation in a Bolivian rainforest: responses are strongly species-specific and size-dependent. *Biotropica* 44(3):312–320
- Toledo M, Poorter L, Peña-Claros M, Leano C, Bongers F (2008) Diferencias, en las características edáficas y la estructura del bosque, de cuatro ecoregiones forestales de Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental* 24:11–26
- Trouet V, Van Oldenborgh GJ (2013) KNMI Climate Explorer: a web-based research tool for high-resolution paleoclimatology. *Tree Ring Res* 69(1):3–13
- Whitmore TC (1989) Canopy gaps and the two major groups of forest trees. *Ecology* 70(3):536–538
- Wieloch T, Helle G, Heinrich I, Voigt M, Schyma P (2011) A novel device for the batch wise isolation of α -cellulose from small-amount wholewood samples. *Dendrochronologia* 29(2):115–117
- Wright EF, Canham CD, Coates KD (2000) Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Can J For Res* 30(10):1571–1580
- Zimmerman JK, Ehleringer JR (1990) Carbon isotope ratios are correlated with irradiance levels in the Panamanian orchid *Catasetum viridiflavum*. *Oecologia* 83(2):247–249