

Different patterns of biomass allocation of mature and sapling host tree in response to liana competition in the southern temperate rainforest

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Abstract Lianas can negatively affect their host tree. The evidence comes from studies in tropical forests, where lianas decrease the growth rate and reproduction of their host tree. This is primarily a consequence of water and nutrient competition, two limiting factors in tropical forests. In contrast, for some areas of southern temperate rainforests the competition for these resources could be less severe, because of the high rainfall and fertile soils. But so far, no study has determined the effect of liana competition over their host tree in southern temperate rainforests. The aim of this study was to evaluate, in field conditions, the effect of liana *Cissus striata* (Ruiz & Pavon) competition over the growth rate of mature *Nothofagus obliqua* (Bidr Egefam) host tree. In an experimental approach, we determined whether above- and/or below-ground competition is more important in this interaction. We also looked for compensatory strategies that would allow trees to respond to liana competition. In field conditions, we found that infested trees have a decrease in their relative growth rate of 26% and a reduction of the leaf area index (LAI) of 20% compared with control trees. In the greenhouse experiment, we found that saplings were water stressed and that there was light competition. Neither competition for water nor light had a significant effect on the growth rate of infested saplings. This could be explained because saplings showed compensatory strategies in response to competition. These strategies were based in the biomass distribution between organs (leaf area, slenderness index) and within leaves (LMA). In conclusion, we found that *C. striata* has a negative effect over the growth of mature and sapling *N. obliqua* host trees. This was a consequence of above-ground and below-ground competition, but we cannot disentangle which type of competition is more important. Trees respond to liana competition, mature host trees change the canopy architecture and saplings allocate resource between and within organs, which allows them to optimize resource capture.

Key words: biomass allocation, liana–host interaction, plant competition, temperate rainforest, vines.

INTRODUCTION

Lianas are woody climbing plants that, unlike trees and shrubs, need other plants for physical support to reach the forest canopy (Gentry 1991; Schnitzer & Bongers 2002; Phillips *et al.* 2005). Lianas allocate few resources to structural support, so they can assign more resources to stem and root elongation, and develop a higher ratio of leaf mass to stem area (Putz 1984). All these traits allow them to have a higher growth rate in relation to other growth forms (Schnitzer & Bongers 2002; Schnitzer 2005a). This growth rate advantage enables lianas to reach great abundance and richness throughout the world. In tropical forests lianas represent 44% of the woody species diversity, a species abundance of 17 species per 0.1 ha and a density of 70 individuals per 0.1 ha (Schnitzer & Bongers 2002) while in temperate forests

lianas represent 10% of the woody species diversity, with 5 species per 0.1 ha and 30 individuals per 0.1 ha (Gentry 1991; Schnitzer & Bongers 2002). Even with this low representation in temperate forests, they achieve a high infestation rate. In the southern temperate rainforest of Chile 54% of mature trees were infested by the massive liana *Hydrangea serratifolia* (Jiménez-Castillo & Lusk 2009). This high abundance and infestation rate ensure that lianas have an important role in the forest's dynamics, as they suppress tree regeneration and increase tree mortality (Putz & Mooney 1991; Schnitzer & Bongers 2002).

Different studies show that in tropical ecosystems, there is strong resource competition in the liana–host interaction (Putz 1980, 1984; Clark & Clark 1990; Gentry 1991; Hegarty 1991; Dillenburg *et al.* 1993a,b, 1995; Schnitzer *et al.* 2000; Schnitzer 2005b). Lianas compete efficiently for light, as they develop a large leaf biomass (Schnitzer *et al.* 2000; Schnitzer & Bongers 2002; Gallenmuller *et al.* 2004). Thus they shade their host and achieve a higher light interception

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than trees and shrubs of similar basal area (Putz 1984). Also, lianas have deeper root systems than other growth forms (Holbrook & Putz 1996; Tyree & Ewers 1996). This lets them access deeper sources of water and therefore avoid water stress during dry periods (Pérez-Salicrup & Barker 2000; Restom & Nepstad 2001). All these traits enable lianas to compete efficiently for light, water and nutrients, and therefore sustain a high growth rate, which is their main competitive advantage in relation to other growth forms.

The principal consequences of liana competition are the decrease in growth rate and fecundity of the host tree (Putz 1980, 1984; Stevens 1987; Gentry 1991; Dillenburg *et al.* 1993a,b, 1995; Ingwell *et al.* 2010). This has been demonstrated in studies of liana removal from mature host trees (Pérez-Salicrup & Barker 2000) and in experiments of saplings in different competition treatments (Dillenburg *et al.* 1993a,b, 1995; Schnitzer 2005b). In both cases, trees without lianas have a higher growth rate (saplings) and fecundity (mature trees) compared with infested trees. Until now, no studies has evaluated the effect of competition over the fitness of mature trees or disentangled which type of competition is more important in temperate forests. Also, an experiment with saplings allows the assessment of compensatory strategies, which to our knowledge, has not been considered in previous studies of the liana–host interaction.

Moreover, different studies that quantify the impact of above-ground (AGC) and below-ground competition (BGC) of lianas over the host tree had contrasting results. It has been shown that in tropical seasonal forests, BGC is the major mechanism by which lianas affect tree growth (Dillenburg *et al.* 1993a,b, 1995; Pérez-Salicrup & Barker 2000; Schnitzer 2005b; Toledo-Aceves & Swaine 2008). For example, in a seasonal dry tropical forest in Bolivia, Pérez-Salicrup and Barker (2000) showed that the pre-dawn water potential of the host tree *Senna multijuga* became significantly less negative one day after the cutting of lianas from around the tree, suggesting strong BGC for water. In contrast, studies developed in aseasonal tropical forests, showed that BGC of lianas does not have a significant effect on the growth rate of trees, possibly due to the high rainfall and fertile soils (Denslow *et al.* 1998; Ostertag 1998). As well as the difference between seasonal and non-seasonal forests, it is widely acknowledged that AGC (light) is the major factor that limits plant performance in wet and nutrient-rich forests (Coomes & Grubb 2000). The AGC could be especially intense in the liana–host interaction, because lianas develop a great canopy over their host tree, which reduces the photosynthetically active radiation (PAR) by 30–50% and the canopy openness by 10–20% (Pérez-Salicrup 2001). In seasonal forests AGC has a negative effect on the host tree growth rate only in combination with below-

ground competition (Dillenburg *et al.* 1993a,b, 1995; Schnitzer 2005b). But in the southern temperate rainforest, which is a mainly wet and nutrient rich forest, AGC would be the principal mechanism by which lianas would reduce the fitness of the host tree.

In response to competition plants can develop different compensatory strategies, adjusting the biomass allocation, branching pattern, leaf morphology or enzyme activity (Coomes & Grubb 2000). Because resources allocated to one organ are not available to other organs, allocation implies tradeoffs and therefore strategies of plants in response to environmental stress (Weiner 2004). Thus differences in biomass allocation appear to be more important than differences in physiological mechanisms (Schwinning & Weiner 1998; Weiner 2004). In this sense, a general response of plants to limited resource conditions is the increase of biomass allocated to organs that allows them a higher resource capture (Chapin 1991). In response to BGC the biomass allocation to roots can increase (Chapin 1991; Dillenburg *et al.* 1995). In the case of AGC, plants can change the biomass distribution between organs, increasing leaf area and/or leaf biomass at the expense of a lesser root biomass, stem diameter or height (Dillenburg *et al.* 1995; Schnitzer 2005b). Other compensatory mechanisms include the biomass distribution within organs, for example in poor environments plants can change the density (dry mass per unit of volume) and/or thickness of a leaf, with a higher leaf mass per area (LMA; Castro-Díez *et al.* 2000; Wright *et al.* 2002). Leaf mass per area is an important trait, because it correlates positively with net assimilation capacity per unit area, leaf longevity and defence function (Ellsworth & Reich 1992). These and others biomass distributions could be compensatory mechanisms that would be essential for trees prone to liana infestation.

Most of the studies on liana–host interactions have been made in tropical ecosystems (Schnitzer & Bongers 2002), with little research in temperate ecosystems (Muñoz *et al.* 2003; Carrasco-Urra & Gianoli 2009; Jiménez-Castillo & Lusk 2009). These two ecosystems differ in their resource availability; tropical forests, despite their high productivity, are characterized as restrictive systems because, in general, they have poor soils and severe droughts (Brown & Lomolino 1998). This could be the main reason why competition studies in tropical seasonal forests demonstrate that BGC is more important than AGC in the liana–host interaction (Putz 1980, 1984; Stevens 1987; Gentry 1991; Dillenburg *et al.* 1993a,b; Schnitzer 2005b). In fact, BGC of the liana decreases tree growth-rate by 50–55% (Ladwing & Meiners 2009; Schnitzer & Carson 2010). On the other hand, most areas of the southern temperate rainforest, are characterized as a less restrictive system due to the high rainfall and fertile soils (di Castri & Hajek 1976;

Muñoz 1980; González *et al.* 1997). Until now, no studies have evaluated the effect of the liana competition with their host trees in the temperate rainforest or the importance of above and BGC. Due to the characteristics of this ecosystem, we hypothesized that competition between liana and host tree would not be as intense as that observed in tropical seasonal forests. We also expected that AGC would be more important in this interaction. So the aim of this study was: to evaluate the effect of liana competition over the growth rate of mature host trees in the southern temperate rainforest; to disentangle the effect of above and BGC in the liana–host interaction, and to examine how trees respond to liana competition in this ecosystem.

METHODS

Correlational patterns

To achieve our goals we established two methodological approaches, one in field conditions with mature host trees and an experimental approach in greenhouse condition using saplings in different competition treatments. Our research considers as study models the deciduous tree species *Nothofagus obliqua* (Bidr. Egfam) and the liana *Cissus striata* (Ruiz & Pavon). We choose these species due to the high relative abundance of both species and their frequent association in the study site (unpubl. data, 2010).

The field work was carried out in San Martín Experimental Forest (39°38'S, 73°7'W), located 20 km northeast of Valdivia, southern Chile. The climate is rainy temperate, with a mean annual precipitation of 2240 mm and 2 months of summer droughts. The mean temperature in winter is 7.3°C and 17.5°C in summer (di Castri & Hajek 1976). Soil conditions are characterized by nitrogen availability, deep and well drained soils, derived from volcanic ash overlying moraine and fluvio-glacial deposits (González *et al.* 1997). In this study site we select 30 mature *N. obliqua* trees, all with a similar diameter (31.1 cm ± 10 cm; ANOVA $F(1, 29) = 1.9934$; $P = 0.16$), and all were located at the forest edge. Half of these trees were infested by the liana *C. striata* (termed 'Liana infested') and the other half was liana free ('Control'). In the case of the infested trees, all the liana

reached the tree canopy and had similar diameters (3–5 cm). For all these trees the leaf area index (LAI) was measured as a proxy of leaf biomass, through the use of hemispherical photographs taken with a fish-eye lens of 180° field of vision (FCE8, Nikon). To measure the LAI of the trees (infested and control) hemispherical photographs of each tree were taken in summer, when trees and lianas have a full expanded canopy. Then, in winter, photographs were taken when this deciduous species had lost its leaves allowing easy access to the liana canopy for measurement. Finally, the winter measurement was subtracted from the summer measurement, and the value of the tree's LAI was obtained. The photographs of the canopy were analysed using the software Hemiview, version 2.1 (Delta-T Devices Ltd, UK). The relative growth rate of all the mature trees was measured, using the widths of the tree-rings of the last five years as a proxy. Cores samples were taken from each host tree using an increment borer, the samples were photographed and analysed using software SigmaScan pro5 (SPSS Inc.). Each tree-ring was standardized by the diameter of each tree at breast height. The average of the last 5 years was used to ensure that all the trees studied had been infested by a liana during this period of time.

Experimental approach

For the experimental approach, in greenhouse conditions 56 saplings of *N. obliqua* were used, all of which were 2 years old and 40–50 cm in height. Thirty-eight individuals of the liana *C. striata* were obtained from the study site. With all these individuals, we create four competition treatments (Fig. 1). These included: (i) Control (C) 18 saplings were planted in individual pots without lianas; (ii) BGC where 18 saplings were planted with a liana in the same pot, maintaining only the roots in contact and the canopy remained separated by using an external support for the liana canopy; (iii) AGC where the canopies of ten saplings were placed in contact with liana canopies, maintaining the roots separated in individual pots; and (iv) above- and below-ground competition (ABGC) 10 saplings were planted with a liana in the same pot maintaining roots and canopy in contact. In the BGC and C treatments the sample size was of 18 individuals per treatment (as opposed to 10 in the other two treatments), the extra individuals were used for measuring the leaf water potential at the end of each watering period. These

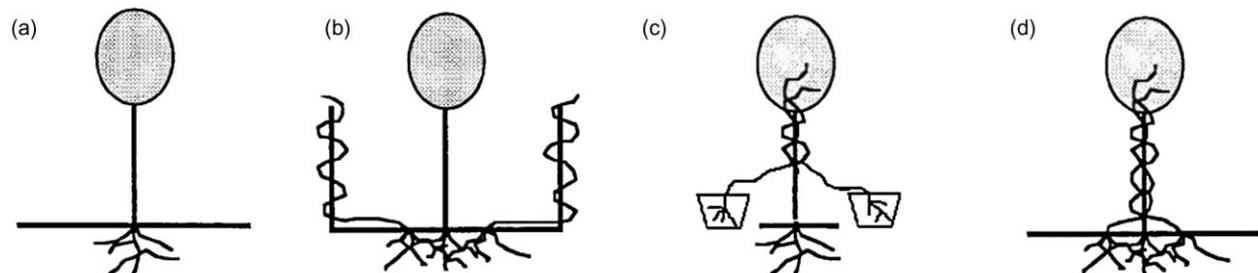


Fig. 1. Experimental design of the competition treatments. We set four competition treatment, considering as study models the tree *Nothofagus obliqua* and the liana *Cissus striata*. The treatments are: (a) control, (b) below-ground competition, (c) above-ground competition and (d) above- and below-ground competition. More details of the treatments in *Methods* section.

individuals were discarded from the measurement of biomass increment, to avoid the effect of branch removal, so 10 individuals were counted per treatment for all the biomass allocation measurements. Treatments were performed by planting saplings in pots of two litre capacity for all treatments. In the case where the saplings and the liana were placed together, the volume of soil was maintained to generate competition (exploitation and/or interference, Begon *et al.* 1996, Goldberg 1996). The C : N ratio of the soil used in all treatments was 14.8:1, so nitrogen was available. The experiment was conducted over a period of three months, corresponding to the growth season and pre-senescence of the host tree.

The experiment was proposed to investigate the above (light) and below-ground (water and nutrient) competition. In relation to BGC, we created water competition in the BGC treatment, with the establishment of three watering periods. In the first month all the pots were watered with 200 mL of water (full soil capacity) every 4 days, in the second month they were watered with 200 mL of water every 6 days and in the third month they were watered with 200 mL of water every 12 days. During the experiment the temperature in the greenhouse was 7.5°C to 31.5°C and relative humidity was 82% on average. To detect if plants were under water stress, midday leaf water potential (MPa) of four individuals per BGC and C treatments were measured, at the end of each watering period, using a pressure chamber (PMS 600, PMS Instruments). To determine the foliar nutritional status of saplings in BGC and C treatments, at the end of the experiment the nitrogen, phosphorus and potassium concentration in the leaves were quantified. Foliar samples were analysed in the Laboratorio de Suelos of the Facultad de Ciencias Agrarias in the Universidad Austral de Chile, using the methodology proposed by Sadzawka *et al.* (2007) and the results were expressed as percentage of nutrients (kg per 100 kg dry biomass). In relation to AGC, the light interception index (LII) of lianas was estimated as the difference between the incident light ($\mu\text{mol s}^{-1} \text{m}^{-2}$) above the liana canopy and the remaining light under the canopy. This measurement was performed using a photometer (sensor quantum Li-Cor 250).

Finally, to determine the effect of liana competition, the growth rate of saplings was measured by calculating the total increase in plant biomass (g). To identify compensatory mechanisms the biomass distribution between organs was determined by separately measuring the biomass allocated to leaves, branches, stems and roots. In addition the lengths (cm) of the stems, branches and petioles were measured. To estimate the biomass allocation within organs, different indexes of biomass distribution and foliar parameters were measured, such as (i) *slenderness index* (SI) as the proportion between stem length and diameter of stem base, indicating the resource allocation to elongation and thus to light capture; (ii) *branching index* (BI), as the proportion between stem length and total branch length, which indicates the allocation of resources to lateral growth to avoid the liana shading; and (iii) *shoot : root ratio* (S/R) was calculated as the total above-ground biomass divided by the below-ground biomass, indicating the allocation of biomass to obtain light, water or nutrients. Foliar parameters were also measured as number of leaves, foliar area (cm^2) and LMA (g cm^{-2}).

Statistical analysis

All data were tested for normal distribution and homogeneity of variance. In relation to the correlational patterns (field condition), the difference in the relative growth rate and LAI was analysed between infested and control trees with a one-way ANOVA. Relative growth rate and LAI were considered as dependent variables and the presence or absence of liana as an independent variable. In the experimental approach, the data were analysed using one-way ANOVA and for those parameters that did not show a normal distribution non-parametric Kruskal–Wallis analyses were estimated. Treatments were set as independent variables and the sapling biomass, biomass index and foliar parameters were set as the dependent variables (SAS Institute Inc., Cary, NC, USA). In the case of significant differences in the models, Tukey HSD tests were used to determine which of the treatments differed significantly from the others (SAS Institute 2000). To determine the relationship between light interception of the liana and morphometric parameters of the host tree, a correlation test was carried out, the significance level of the relationship was determined with a bivaried analysis. For the response variable ‘water stress’ a two-way ANOVA was performed with the independent variables being ‘watering periods’ and ‘liana infestation’. All analyses were performed with the statistical program STATISTICA (StatSoft V.7).

RESULTS

In field conditions, we found that infested mature *N. obliqua* trees have a significant decrease in their relative growth rate. Infested trees presented a reduction of 25.6% in the relative growth rate, in relation to trees free of lianas ($P = 0.01$; Fig. 2). These infested trees also had a 20% decrease in the LAI in relation to control trees ($P = 0.05$; Fig. 3).

In the experimental approach, significant differences in the water potentials between treatments were observed, where the BGC treatment showed more negative water potential than C saplings ($P < 0.001$;

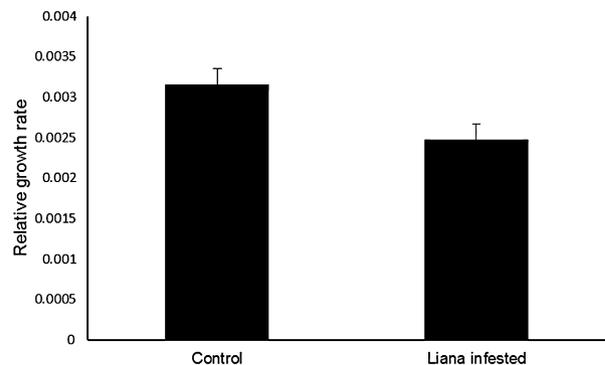


Fig. 2. Relative growth rate (ring width/breast height) of mature trees of *N. obliqua* infested by *C. striata* versus control trees, ANOVA $F(1, 28) = 6.70$, $P = 0.0124$. Bars represent standard error of the mean.

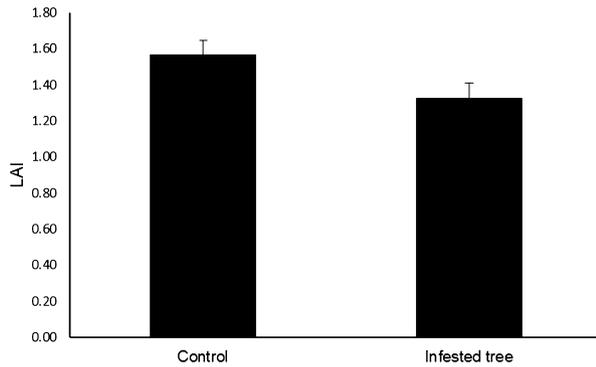


Fig. 3. Leaf area index (LAI) of adult trees of *N. obliqua* infested by *C. striata* and control trees. ANOVA $F(1, 28) = 42.13$, $P = 0.05$. Bars represent standard error of the mean.

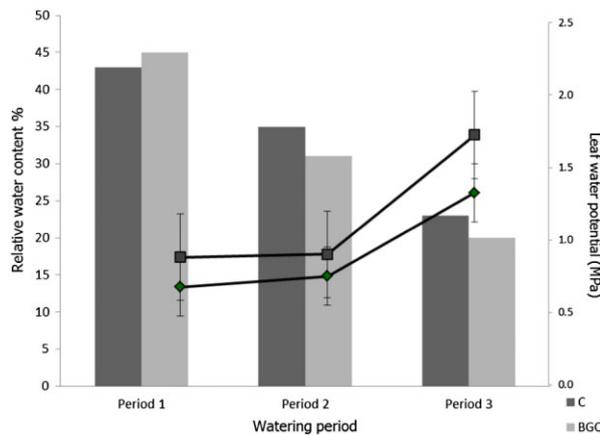


Fig. 4. Two-way ANOVA for the difference in leaf water potential (MPa) of saplings in below-ground competition (BGC; square dots) and control (C; diamonds) treatment, in relation to the watering period and the relative water content of soil (grey and black bars). Both parameters were significant different between treatment and periods ($P < 0.001$) and ($P < 0.001$) respectively. Bars represent standard error of the mean.

Fig. 4). This means that saplings in BGC have higher water stress. Differences between watering periods ($P < 0.001$) were also detected, where the third watering period presented more negative water potential in relation to the other watering periods. No effect was found in the interaction between competition treatment and the watering period ($P = 0.26$; Fig. 4). The analysis of nutrient concentration in foliar tissue did not show significant differences for nitrogen, phosphorus or potassium between treatments (Table 1). In relation to AGC, the LII of the liana was negatively correlated with leaf area of saplings ($r^2 = 0.53$; $P = 0.04$), but was positively correlated with the BI ($r^2 = 0.43$; $P = 0.02$) of saplings in the AGC treatment (Fig. 5), and did not have a significant relationship with other biomass allocation traits.

Even though, we showed water stress and light competition, saplings in different competition treatment did not differ in the total plant biomass. No significant differences were found in the relative biomass of leaf, root or stem, either for the number of leaves and specific leaf area ($\text{cm}^2 \text{g}^{-1}$) among treatments (Table 1). However, biomass allocation within leaves as shown by LMA, showed significant differences between the AGC-C treatments ($P = 0.03$; Fig. 6) and between AGC-ABGC ($P = 0.05$). Biomass distribution within stems observed in the SI showed significant differences between treatments, where ABGC saplings had a higher value of the parameter compared with the C treatment and the BGC treatment. Branching index and S/R did not show any significant differences among treatments (Table 1).

DISCUSSION

Correlation pattern: liana reduces the relative growth rate of mature trees

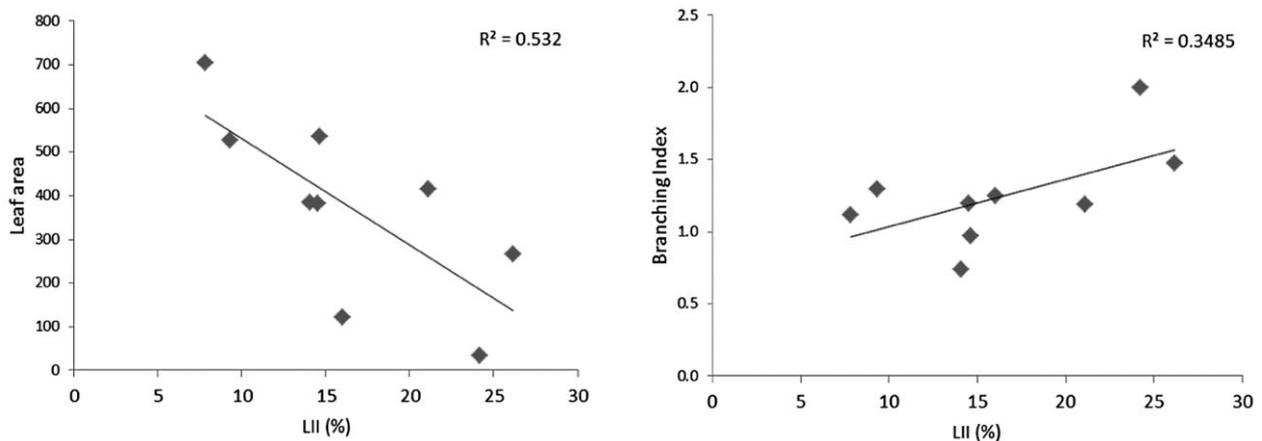
In the field condition the liana reduced the growth rate of the mature tree by approximately 26% (Fig. 2). This negative relationship has also been observed in studies carried out in tropical forests, but in that ecosystem the effect of liana competition was twice that observed in our study. In tropical forests it has been shown that the relative growth rate of mature trees without lianas was 50% greater than infested trees (Pérez-Salicrup & Barker 2000; Ladwing & Meiners 2009). Also, liana competition decreases growth rate in the diameter of infested saplings by nearly 56% (Dillenburg *et al.* 1993a). These results support our prediction that liana–host competition is lower in the temperate rainforest than that observed in tropical forests, which could be due to the greater availability of resources in this ecosystem (Denslow *et al.* 1998). Even with a great amount of evidence, particularly in the tropical ecosystem, most of the studies have only considered a few species so all the findings should be taken with this consideration.

The decrease in growth rate could be related to the lower LAI of the infested trees (Fig. 3). As these trees have a lower leaf biomass or lower leaf layers in the canopy (Chen & Black 1992; Selaya 2008), this would result in a reduced primary productivity and therefore explain the lower growth rate of infested trees. The sensitivity of leaf area and leaf biomass to light, water and nutritional competition has been widely reported (Selaya 2007, 2008). Chapin (1991) suggests that change of foliar parameters operate as ‘warning systems’ for the tree that allow them to change the biomass allocation before the stress causes a negative balance on carbon gain. Moreover Selaya (2007) reported that shade intolerant trees respond to light

Table 1. ANOVA table for variables: relative biomass (BMR), length of different organs, leaf area, specific leaf area (SLA), shoot/root ratio (S/R), slenderness index and branching index, between treatments

| | d.f. | F | P |
|-------------------|------|-------|--------|
| BMR leaf | 3 | 1 | 0.271 |
| BMR stem | 3 | 0.506 | 0.6807 |
| BMR branch | 3 | 1.62 | 0.2007 |
| BMR root | 3 | 1.35 | 0.271 |
| Stem length | 3 | 15 | 0.2356 |
| Branch length | 3 | 1 | 0.556 |
| Petiole length | 3 | 14 | 0.2466 |
| Leaf area | 3 | 0.95 | 0.4234 |
| SLA | 3 | 12 | 0.3261 |
| S/R | 3 | 17 | 0.1888 |
| Slenderness index | 3 | 4 | 0.0197 |
| Branching index | 3 | 1 | 0.3386 |
| Foliar nitrogen | 1 | 35 | 0.07 |
| Foliar phosphorus | 1 | 0.04 | 0.8 |
| Foliar potassium | 1 | 0.037 | 0.8498 |

Also shown are tests of the difference in foliar nitrogen, phosphorus and potassium in leaf tissue between BGC and C treatments. BGC, below-ground competition; C, control.

**Fig. 5.** Correlation between light interception index (LII) of liana *C. striata* over leaf area ($r^2 = 0.53$, $P = 0.04$) and branching index ($r^2 = 0.43$, $P = 0.02$) of *N. obliqua* saplings in AGC treatment. AGC, above-ground competition.

competition by producing shallow canopies, with leaves concentrated at the top of the canopy, to avoid shading by other plants. In our study, infested trees of *N. obliqua* responded in a similar way with lower LAI, which indicates a reduction of the layers of canopy and therefore a lower photosynthetic biomass. This species is deciduous, so it has to optimize the efficiency of light interception during the growth period. Therefore a shallow canopy could be a strategy to escape the liana shading and therefore avoid light competition.

Experimental approach: above and below ground competition

Below-ground competition of the liana had a significant negative effect over the water status of sapling

hosts. In BGC treatments saplings showed a more negative water potential, which became even more negative in the watering periods with less water availability (third period) (Fig 4). Actually, our results suggest that even with water availability, liana had a negative effect on water acquisition of the saplings. An effect of liana over the water status of the host tree has also been reported in other studies (Dillenburg *et al.* 1993a,b; Barberis & Tanner 2005; Schnitzer 2005b; Toledo-Aceves & Swaine 2008). For example, Barker and Pérez-Salicrup (2000) in tropical dry forests showed that leaf water potential of the host tree in pre-dawn conditions, was much less negative just one day after the removal of the lianas, which means a decrease in the water stress. This type of competition would be most important in the liana–host interaction (Dillenburg *et al.* 1993a,b; Schnitzer 2005b), because

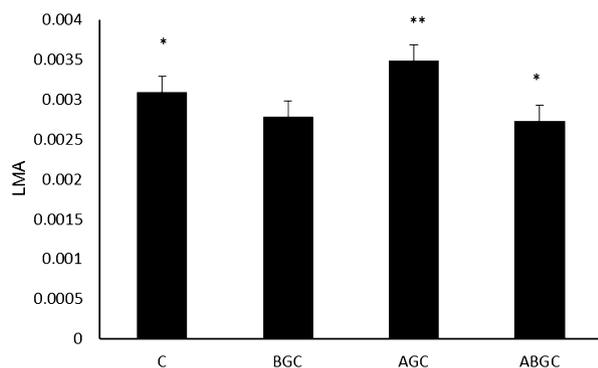


Fig. 6. Leaf mass per area (LMA) of *N. obliqua* saplings show significant differences between treatments ($P = 0.03$), AGC (**) treatment have a higher LMA and differ significantly from C (*) and ABGC (*) (Tukey, $P < 0.05$). Bars represent standard error of the mean. ABGC, above- and below-ground competition; AGC, above-ground competition; BGC, below-ground competition; C, control.

it has been shown that trees do not just decrease their water stress after liana cuttings, but also double their growth rate (Pérez-Salicrup & Barker 2000). Also, Toledo-Aceves and Swaine (2008) reported that liana BGC had a strong negative effect on the growth rate of various sapling species (−58%) even under high water availability. However, this evidence comes from tropical dry forests, where this type of competition is more important due to the seasonal characteristic of the precipitation regime. Our study shows that even with water availability lianas generate water stress to the host trees.

We did not find evidence for nutrient competition. Saplings in BGC did not show a decrease in phosphorus and potassium concentration in foliar tissue (Table 1). We found just a slight difference in which saplings in the BGC had a lower leaf nitrogen concentration than the C treatment, but this was not statistically significant. Contrary to our results, Dillenburg *et al.* (1993b) showed that BGC was generated by limiting nitrogen availability, which negatively affected the growth rate of sapling hosts. A lower nitrogen concentration in the leaf may reflect a lower nutritional status of trees or a higher rate of leaf senescence. In our study, given the same age and relative biomass of leaves between saplings, the trend of lower nitrogen concentration could be due to the greater ability of the liana to acquire nutrients (Lambers *et al.* 1998). We expected nutrient competition because this could be related to the water stress of BGC treatment, which could cause a lower rate of nutrient acquisition, since the ability to acquire nutrients is closely related to the ability to transport them (Casper 1997; Lambers *et al.* 1998).

Saplings show strategies different than expected in response to AGC of the liana. In AGC treatment,

saplings did not increase their leaf area in response to the liana LII. However, they did respond by increasing the length of the branches in relation to the stem length (Fig. 5). So saplings increase their lateral growth to avoid liana shading.

Even with above and below ground competition, saplings did not show a decrease in total biomass as a result of liana competition. Further, there was no significant difference in the relative biomass or length of organs between treatments (Table 1). Similar to our results, Toledo-Aceves and Swaine (2008) showed that infested trees did not show differences in relative biomass distribution between organs. This could be due to the extent of the experiment (3 months), which only considered one growth period and perhaps more time is needed to observe responses at a whole plant level. Even when they do not respond at a whole plant level, they change the biomass allocation at different levels: between or within organs. This could be a compensatory response (see below) of saplings to allocate more resource to the organs that enhance the capture of the most limiting resources (Dillenburg *et al.* 1995) and diminish the effect of liana competition.

Compensatory response based on biomass distribution

We observed different compensatory mechanisms associated mainly to biomass allocation within organs. At the leaf level, individuals of AGC have greater LMA in relation to other treatments (Fig. 6). These results show us that saplings do not increase leaf expansion but increase the density and/or thickness of the leaf, indicating an adjustment to achieve a greater photosynthetic capacity (Lambers *et al.* 1998). Different studies show that trees in stressful environments have a greater LMA (Castro-Díez *et al.* 2000; Wright *et al.* 2002), which allows them to keep the photosynthetic state of leaves close to the optimal values (Reich *et al.* 1999). Moreover, it has been shown that species in poor environments produce leaves with higher LMA because it is positively correlated with net assimilation capacity per unit area (Ellsworth & Reich 1992), a greater concentration of photosynthetic compounds per unit area, less self-shading and greater leaf longevity (Niinemets 2001). So, this higher LMA observed could give them a competitive advantage due to greater photosynthetic potential.

Furthermore, saplings in the AGC treatment showed a greater elongation of stems and branches, as another compensatory mechanism. In the ABG treatments saplings increased the SI, so they allocated more resources to stem elongation and less to diameter increase (Table 1). Similar to our findings, it has been

shown that in AGC saplings have longer stems with smaller diameters (Dillenburg *et al.* 1993a; Schnitzer 2005b). Additionally, saplings in BGC have the lowest SI, which means that these saplings generate a shorter and thicker stem, giving biomass allocation priority to the roots.

All these compensatory mechanisms, could explain why we did not observe a decrease in total biomass in different competition treatments. Most of these mechanisms were observed in the AGC treatment, so this could be a sign that light competition is more important than water competition. The capacity to respond to changes in resource availability is critical for plant success, and results in a growth advantage under heterogeneous conditions (Chapin 1991; Grime & Mackey 2002; Sack *et al.* 2003; Bloor & Grubb 2004). A large morphological plasticity in biomass allocation, in response to change in resource supply, generates a lower variation in the growth rate of a plant (Lambers *et al.* 1998). So there is a small variation in total biomass between different environments. This enables the plants to continuously explore new resource patches. We examined different levels of response, based on the biomass allocation at the whole plant level, between and within organs. The change in parameters like LMA, SI and BI between treatments (Fig. 6 and Table 1) was generated in response to the shading of the liana. All this evidence suggests that, the capacity to allocate biomass within and between organs is a key mechanism by which saplings can cope with liana infestation.

To conclude, our results show that lianas decrease the relative growth rate and LAI of mature hosts. These results are in accordance with our expectation, that the negative effect of lianas over their host trees would be less than that observed in tropical forests. On the other hand, even with light and water competition there was not decrease of the total biomass of saplings. We propose that short-term compensatory mechanisms are the main reason why saplings showed little response at the whole plant level. This, mechanism was based on biomass distribution between and within organs, which in general involve the response to light competition, and to our knowledge there is no study that has previously reported the response of saplings to competition with lianas. Both mature trees and saplings respond to liana competition with changes in traits that allow them a higher light interception or a decrease of leaf shading. To our knowledge this is the first study of the liana–host competition in the temperate rainforests, and one of the few studies that involves the effect of liana over mature host trees and saplings. More studies are needed to involve a higher number of species and evaluate the impact of liana–host competition over the forest dynamics in the temperate rainforest.

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