

## Abundance and diversity of lianas in a Neotropical dry forest: the influence of soil moisture

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**Background and aims** – Based on data across tropical forests, a leading hypothesis posits that lianas are better competitors than trees under water shortage. Evaluating this hypothesis at a local scale may provide insights into its generality. We tested whether the abundance of lianas –relative to trees– decreases with soil moisture in a Neotropical dry forest. We also evaluated the influence of water availability on liana diversity.

**Methods** – Lianas ( $\geq 1$  cm diameter) and trees ( $\geq 1.5$  m height) were counted and identified, and soil moisture was measured, in twenty  $10 \times 10$  m plots at different distances to water sources. Linear regressions assessed the relationships between water availability and relative abundance and diversity of lianas.

**Key Results** – We found a significant and positive relationship between the relative abundance of lianas and water availability. Liana density ranged from 21 to 77 individuals per plot. Soil moisture did not influence liana species richness (S) or Fisher's  $\alpha$ . Eighteen liana species were recorded, from ten families.

**Conclusions** – Our results show that, in contrast with geographic and regional patterns, relative abundance and diversity of lianas at a local scale are not favoured by water shortage. This suggests that different mechanisms may prevail in the liana-tree interaction across water availability gradients.

**Key words** – Lianas, Neotropical dry forest, distribution, trees, water availability, species richness.

### INTRODUCTION

Lianas are an abundant and diverse group of plants that ascend to the forest canopy using other plants as support (Gentry 1991). Because they invest less biomass in structural support, lianas allocate more resources to reproduction, canopy development, and stem and root elongation (Schnitzer & Bongers 2002). Lianas are particularly abundant and diverse in lowland tropical forests, where they can constitute up to 40% of woody stems and more than 25% of woody species (Schnitzer 2005, van der Heijden & Phillips 2008, Schnitzer & Bongers 2011); they also occur in high density in some temperate forests, but with lower diversity (Chettri et al. 2010, Gianoli et al. 2010). Lianas compete with trees both above and below ground, therefore trees infested by lianas show reduced growth, reproduction and survival (Schnitzer & Bongers 2002, 2011, Schnitzer et al. 2011, Tobin et al. 2012); liana infestation may even alter whole-forest carbon storage (Durán & Gianoli 2013, van der Heijden et al. 2015). Overall, the relative abundance of lianas is increasing throughout the Neotropics (Phillips et al. 2002, Schnitzer & Bongers 2011, Schnitzer et al. 2012, Laurance et al. 2014).

Schnitzer (2005) observed that liana abundance was correlated negatively with mean annual precipitation and positively with seasonality across c. 70 lowland tropical forests worldwide, and that –at a regional scale– lianas were more abundant in a dry forest compared to a moist forest and a wet forest. Moreover, at a local scale, height growth in lianas was c. seven times that of trees during the dry season but only twice as much during the wet season. Schnitzer (2005) concluded that lianas are better competitors than trees under water shortage, probably due to their deep roots and efficient vascular system. Furthermore, Schnitzer (2005) put forward that the same mechanism that enables lianas to proliferate in seasonally dry tropical forests may also explain their abundance at the local scale within forests. This hypothesis has received support from several studies (e.g. Swaine & Grace 2007, Cai et al. 2009, Chen et al. 2015, DeWalt et al. 2010), but other studies have reported contrasting results (van der Heijden & Phillips 2008, Malizia et al. 2010, Durigon et al. 2013, van der Sande et al. 2013). Here we test Schnitzer's hypothesis in a tropical dry forest at a very local scale, to provide insights into the generality of this ecological hypothesis. With regard to patterns of liana diversity, DeWalt et al. (2006) found in a Bornean rainforest that liana diver-

sity increased with increasing soil nutrients and water availability. Several studies across tropical and subtropical forests have found that soil moisture or mean annual precipitation are positively related to liana diversity (Ibarra-Manríquez & Martínez-Ramos 2002, Molina-Freaner et al. 2004, van der Heijden & Phillips 2009, Addo-Fordjour et al. 2013).

Liana abundance is not only driven by abiotic factors. A Neotropical study reported that structural features of the forest (availability of host trees and their characteristics) were more important than environmental factors (rainfall, seasonality, soil variables) in determining liana density and basal area (van der Heijden & Phillips 2008). In a temperate rainforest, light availability did not affect liana abundance in forest plots when the study accounted for density and size of host trees (Carrasco-Urra & Gianoli 2009). The link between liana abundance and density of host trees has been further reported in several surveys (e.g. Baars et al. 1998, Madeira et al. 2009, van der Heijden & Phillips 2009). Results of those studies suggest that expressing liana abundance relative to that of trees is ecologically meaningful.

Our goals in this field study, carried out in a tropical dry forest in Northern South America, were to evaluate whether the abundance of lianas – relative to trees – decreases with soil moisture at the within-forest scale, and to determine whether soil moisture is positively associated with liana diversity at the same scale.

## MATERIALS AND METHODS

The study focused on a tropical dry forest (Holdridge 1967) located in an inter-Andean valley close to the Magdalena river in west-central Colombia (3°18'55"N 75°15'40"W), and was carried out between December 2011 and March 2012. The study site has several slopes together with flat areas (altitude range: 470–750 m a.s.l.). Climate is warm year-round, with average annual precipitation of 1346 mm, annual potential evapotranspiration of 1665 mm and 66% of relative humidity (IDEAM 2014). Mean annual temperature is 29°C and mean minimum and maximum temperatures are 22.4°C and 33°C, respectively (IDEAM 2014). This tropical dry forest has two dry seasons: from late December to February and from June to early September. Several forest patches are close to water sources, such as streams or springs (shallow groundwater).

To assess liana abundance, we set up twenty plots (10 m × 10 m) across the study forest (total area of the forest patch: 4.14 km<sup>2</sup>). We included sites close to and far away from water sources in order to maximize the variation in water availability (soil moisture). During the middle of the dry season we measured soil water potential (kPa) at 35 cm depth in twelve points within each of the twenty plots using a tensiometer (IRROMETER Company Inc., Riverside, California, USA). The range of distances among plots was 100–1635 m. The plots were located at the forest interior to avoid edge effects. Soil moisture measurements were taken only once. Although soil moisture should vary across the seasons, the relative ranking of the sampled sites in terms of water availability (dry sites – moist sites) should not vary, thus allowing us to test our main hypothesis.

Within the plots we counted, measured and identified all rooted lianas ≥ 1 cm diameter at 1.30 m from the rooting point (Gerwing et al. 2006, Schnitzer et al. 2008) (plants were not tagged). We followed the nomenclature system of APG III (Stevens 2012) and all species names were verified in The Plant List (2013). In every plot we also counted and identified all trees ≥ 1.5 m height. Field identification of lianas and trees was complemented by identification in the COL herbarium (Universidad Nacional de Colombia), where vouchers were deposited.

We used linear regression analysis to evaluate the relationships between liana diversity and relative abundance (number of lianas / number of trees) and soil moisture (mean of twelve points) in the twenty plots. Species diversity estimates included species richness (S) and Fisher's  $\alpha$ . We included Fisher's  $\alpha$  because it is more robust to sample size than species richness and allows comparisons among study sites (Mascaro et al. 2004). Analyses were conducted in the "vegan" (Oksanen et al. 2010) and "Biodiversity R" (Kindt & Coe 2005) packages of the R software environment (R Development Core Team 2013).

## RESULTS

Within the twenty study plots (0.2 ha) of tropical dry forest there were 861 individual lianas ≥ 1 cm diameter (table 1), with a total basal area of 27.74 m<sup>2</sup>. Liana density and species richness ranged from 21 to 77 individuals and from two to eight species per plot, respectively; soil moisture (soil water potential) ranged from -6.9 MPa to -26.8 MPa across plots.

We found a significant and positive relationship between the relative abundance of lianas (number of lianas / number of trees) and water availability (mean soil water potential, kPa) (linear regression,  $R^2 = 0.27$ ,  $N = 20$ ,  $P = 0.018$ ; fig 1). The increase in liana relative abundance with soil moisture resulted from a concomitant decrease in tree abundance ( $R = -0.584$ ,  $R^2 = 0.341$ ,  $N = 20$ ,  $P = 0.007$ ) because liana abundance was unaffected by water availability in the plots ( $R^2 = 0.002$ ,  $N = 20$ ,  $P = 0.848$ ).

We did not find a significant relationship between soil moisture and liana species richness (S) ( $R^2 = 0.05$ ,  $N = 20$ ,  $P = 0.163$ ) or Fisher's  $\alpha$  ( $R^2 = 0.03$ ,  $N = 20$ ,  $P = 0.474$ ). Eighteen liana species were recorded (89% of them were determined at least to genus) representing sixteen genera and ten families (table 1). The most abundant families were Sapindaceae, Fabaceae, and Bignoniaceae, which comprised half of the species in the study area. The dominant liana species in terms of number ( $N = 179$ ) was *Serjania grandis* Seem. (Sapindaceae), accounting for 20.8% of all individuals and with presence in all the plots. The range of Fisher's  $\alpha$  was 17.9–69.8 per plot.

## DISCUSSION

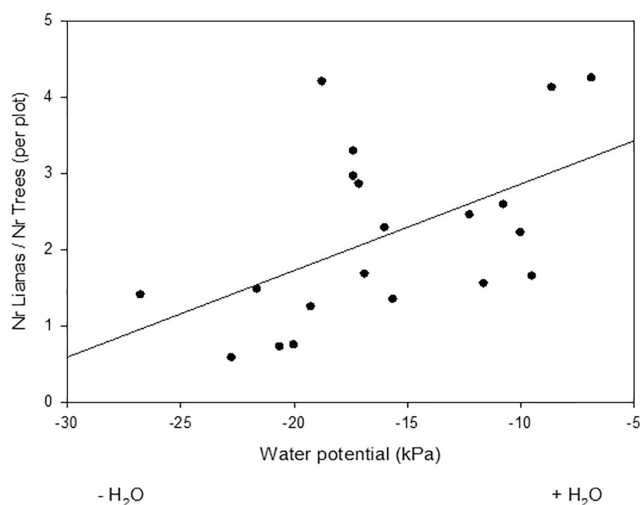
In this tropical dry forest the relative abundance of lianas was higher in microsites with higher soil moisture. Our results do not support the general hypothesis that compared to trees lianas are favoured by water availability (Schnitzer 2005). Liana abundance in other tropical forests has been positively

**Table 1 – Liana species found in 0.2 ha of a tropical dry forest in northern South America.**Diameter of lianas (mean  $\pm$  SE; cm) measured at 1.30 m from rooting point.

Species	Family	N	Diameter
<i>Serjania grandis</i> Seem.	Sapindaceae	179	1.53 $\pm$ 0.63
<i>Paullinia spicata</i> Benth.	Sapindaceae	115	2.02 $\pm$ 0.81
<i>Tetracera</i> sp.	Dilleniaceae	111	2.78 $\pm$ 1.20
<i>Paragonia pyramidata</i> (Rich.) Bureau	Bignoniaceae	104	1.78 $\pm$ 0.76
<i>Bauhinia guianensis</i> Aubl.	Fabaceae	98	2.33 $\pm$ 1.14
<i>Serjania mexicana</i> (L.) Willd.	Sapindaceae	69	1.72 $\pm$ 0.74
<i>Anemopaegma chrysanthum</i> Dugand	Bignoniaceae	32	1.75 $\pm$ 0.74
<i>Pristimera verrucosa</i> (Kunth) Miers	Celastraceae	30	1.54 $\pm$ 0.53
<i>Senegalia riparia</i> (Kunth) Britton & Killip	Fabaceae	26	3.63 $\pm$ 1.88
<i>Arrabidaea candicans</i> (Rich.) DC.	Bignoniaceae	21	1.93 $\pm$ 0.66
<i>Tetracera</i> aff. <i>volubilis</i> L.	Dilleniaceae	17	2.85 $\pm$ 1.30
Sp. 1	Unknown	12	1.87 $\pm$ 0.50
<i>Aristolochia maxima</i> Jacq.	Aristolochiaceae	11	1.90 $\pm$ 0.80
<i>Gouania</i> sp.	Rhamnaceae	10	2.25 $\pm$ 0.95
<i>Mucuna mutisiana</i> (Kunth) DC.	Fabaceae	10	1.87 $\pm$ 0.38
<i>Dalechampia canescens</i> Kunth	Euphorbiaceae	9	2.48 $\pm$ 1.35
<i>Aristolochia</i> sp.	Aristolochiaceae	5	1.86 $\pm$ 0.73
<i>Lycoseris mexicana</i> (L.f.) Cass.	Asteraceae	2	3.37 $\pm$ 2.52
Total		861	

associated with soil water availability (Ibarra-Manríquez & Martínez-Ramos 2002, DeWalt et al. 2006, Addo-Fordjour et al. 2013), and vines in a desert scrub community were more abundant in habitats close to streams compared to plains and hill slopes (Molina-Freaner & Tinoco-Ojanguren 1997). An-

drade et al. (2005), using water isotope composition, found in a moist tropical forest that lianas tap shallow sources of soil water at the beginning of the dry season, which does not support the assumption that lianas rely primarily on deep soil water (Schnitzer 2005). Nepstad et al. (2007) reported that lianas were as prone as large trees to experimentally-induced drought mortality in the Brazilian Amazon. In a seasonal forest in Panama, van der Sande et al. (2013) found that liana saplings had lower cavitation resistance than tree saplings, which implies lower drought tolerance. Thus, both field patterns of liana abundance and mechanistic approaches to compared water economy question the general assumption that lianas should outcompete trees in reduced soil moisture scenarios across spatial scales (Schnitzer 2005). Liana competition with trees should be particularly important in tropical dry forests, where water availability may be a limiting factor for both life forms during the dry season (Murphy & Lugo 1986). However, our results, obtained during the dry season, indicate that lianas outnumber trees in the moister sites and not in the drier sites. This pattern could suggest that lianas in this tropical dry forest have a greater ability to capitalize on water availability compared to trees, but the fact that liana density was not affected by soil moisture indicates that another, unmeasured local factor should account for the decrease in tree abundance with water availability.



**Figure 1** – Change in the relative abundance of lianas with soil moisture in a tropical dry forest in Northern South America.

In the study forest, soil moisture had no effect on liana species richness or Fisher's  $\alpha$ . Likewise, Malizia et al. (2010) reported that liana composition in a subtropical montane forest was not affected by soil moisture. In contrast, liana diversity has been associated positively with soil moisture both across a number of Neotropical forests (van der Heijden & Phillips 2009) and in single forest studies (Burnham 2002, Ibarra-Manríquez & Martínez-Ramos 2002, DeWalt et al. 2006, Addo-Fordjour et al. 2013) as well as in a desert plant community (Molina-Freaner et al. 2004). A global analysis recently showed that liana species diversity (Fisher's  $\alpha$ ) seemingly has a hump-shaped relationship with mean annual precipitation (DeWalt et al. 2015). In sum, it is currently not clear under which conditions, forest type or spatial scale that liana diversity would reflect water availability.

Liana species richness in the study area (eighteen species) lies within the range of values found in comparable surveys (in terms of sampled area) made in tropical dry forests worldwide (Phillips & Miller 2002). The study forest shares with those tropical dry forests the dominant plant families: Sapindaceae, Bignoniaceae, and Fabaceae. The dominant species was *Serjania grandis* (Sapindaceae), with 179 individuals, accounting for 20.8% of all liana individuals recorded. This is one of the highest values of single liana dominance reported for any tropical forest (DeWalt et al. 2000, Nabe-Nielsen 2001, Burnham 2002, Nabe-Nielsen & Hall 2002, Mascaro et al. 2004, Addo-Fordjour et al. 2008, de Oliveira et al. 2014). Nonetheless, it must be kept in mind that these forests are wetter than the study forest, and it is known that Neotropical dry forests tend to show higher values of abundance for any particular liana species as compared to rain or moist forests (similar liana density across forests but fewer liana species in dry forests, Gentry 1991).

Dry forests are the most threatened of lowland tropical ecosystems (Janzen 1988, Miles et al. 2006). Despite the structural and physiological diversity in life forms in tropical dry forests (Mooney et al. 1995, Kalácska et al. 2004), relatively few studies addressing liana ecology have been carried out there (Castellanos et al. 1989, 1999, Andrade et al. 2005, Avalos et al. 2007, Madeira et al. 2009). In this tropical dry forest, we found that soil moisture is positively associated with liana relative abundance at the local scale, but no relationship was observed between water availability and liana diversity. The latter could suggest that there is no competitive displacement of the rare species by the dominant species throughout the water gradient; but this has to be tested experimentally. Our results show at a local scale that lianas – relative to trees – are not favoured by water shortage, which does not support Schnitzer's hypothesis (2005), originally set at a geographical scale but also explicitly claimed to hold at the local scale. Results suggest that different mechanisms may prevail in the liana-tree interaction across water availability gradients. In any case, the evolution of greater performance of lianas compared to trees would occur at the local scale, which is where selective processes take place (see Gianoli & Saldaña 2013). Further research at both geographical and local scales should show whether lianas actually take advantage of reduced water availability. This is particularly important because one of the potential causes of the global pattern

of increased dominance of lianas relative to trees is climate change (Schnitzer & Bongers 2011).

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