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Stronger seasonal adjustment in leaf turgor loss point in lianas than trees in an Amazonian forest

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Pan-tropically, liana density increases with decreasing rainfall and increasing seasonality. This pattern has led to the hypothesis that lianas display a growth advantage over trees under dry conditions. However, the physiological mechanisms underpinning this hypothesis remain elusive. A key trait influencing leaf and plant drought tolerance is the leaf water potential at turgor loss point (π_{tlp}). π_{tlp} adjusts under drier conditions and this contributes to improved leaf drought tolerance. For co-occurring Amazonian tree ($n = 247$) and liana ($n = 57$) individuals measured during the dry and the wet seasons, lianas showed a stronger osmotic adjustment than trees. Liana leaves were less drought-tolerant than trees in the wet season, but reached similar drought tolerances during the dry season. Stronger osmotic adjustment in lianas would contribute to turgor maintenance, a critical prerequisite for carbon uptake and growth, and to the success of lianas relative to trees in growth under drier conditions.

1. Introduction

Over the past decades, lianas have been increasing in abundance in tropical forests [1]. Across the tropics, liana density and biomass tend to increase with decreasing rainfall and increasing seasonality [2]. Locally, lianas tend to proliferate in gaps or forest edges where evaporative demand is high [3]. These patterns have led to the hypothesis that lianas display a growth advantage over trees under dry conditions. In support of this hypothesis, Schnitzer [3] found that lianas grow significantly more than trees during the dry season relative to the wet season in a tropical forest of Panama. However, the physiological mechanisms underpinning this dry season advantage remain elusive.

One explanation is that lianas have a deeper root system than co-occurring trees, enabling them to access soil water when the upper soil layer dries out. Indeed, lianas would seem capable of investing more into root development, as they need to allocate fewer resources than trees to stem support. However, the few empirical comparisons of root depth have thus far provided mixed or contradictory results [4,5]. Another possibility is that lianas may benefit from higher light intensity in the dry season, as their leaves are on average higher in nutrient concentrations and photosynthetic capacities than trees at some sites, though not at others [4]. Additionally, stronger stomatal control in lianas [5] may result in stronger reduction in carbon assimilation during dry periods. Other aspects of the water transport system do not show a clear advantage for lianas. Even though lianas tend to show wider vessels than trees (but see [6]) and higher stem-specific hydraulic conductivities, their larger leaf area and longer stem may lead to lower leaf-specific conductivity [4].

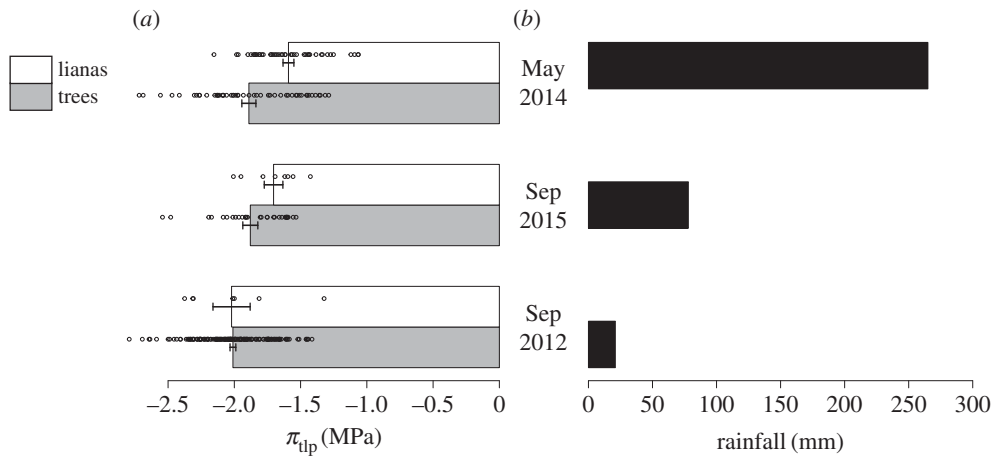


Figure 1. (a) Leaf water potential at wilting point (points: all values; bars: means \pm s.e.; π_{tlp} , in megapascal) across growth form and water availability, illustrated in (b) by the cumulative rainfall one month prior to the ending date of each sampling session (in millimetres).

Additionally, lianas have been found to be more vulnerable than trees to drought-induced embolism [4]. Overall, evidence for a physiological advantage of lianas under a seasonally dry environment has been elusive.

Here, we explore another hypothesis. When plants are water-stressed, the first response is the reduction of turgor-driven cell expansion and division, and hence growth [7]. Leaf cell turgor also controls stomatal dynamics and thus plant water regulation [8]. A well-recognized leaf drought tolerance trait is the negative water potential at which leaves wilt, or turgor loss point (henceforth π_{tlp}). Leaves with a more negative π_{tlp} are able to maintain leaf hydraulic conductance under drier conditions, contributing to greater plant drought tolerance. This functional trait is a good predictor of tree species distribution relative to water supply [9]. Another mechanism of leaf drought tolerance is seasonal adjustment of π_{tlp} by osmotic regulation. Evidence exists for this process in general [10], and in tropical rainforest trees to a limited extent [11,12]. We hypothesized that liana leaves are less drought-tolerant than those of trees, i.e. they have a less negative π_{tlp} , but they are better able to osmotically adjust and to achieve sustained growth under dry conditions. This would be consistent with the greater plasticity of lianas [13]. Another implication would be that in more water-stressed environments, such as canopy gaps, lianas would display more drought-tolerant leaves [3]. To test this hypothesis, we conducted measurements of π_{tlp} for co-occurring tree ($n = 247$) and liana ($n = 57$) individuals in an Amazonian forest, during both the dry and the wet season.

2. Material and methods

Field measurements were conducted at the Nouragues Ecological Research Station in French Guiana, within an undisturbed forest (4°05' N, 52°40' W). This forest receives approximately 3000 mm yr⁻¹ rainfall, with a long wet season from December to July, often interrupted by a short dry period in March. The long dry season (less than 100 mm month⁻¹) lasts two to three months, from the end of August to the end of November. Lianas have been reported to increase in abundance and productivity at this site [14], and a liana-infested forest formation has encroached [15].

Data were collected in September 2012, May 2014 and September 2015. The cumulative rainfall one month prior to the

ending date of each sampling session was calculated from half-hourly data (Campbell Scientific SBS500, Shepshed, Leicestershire, UK). In 2012, cumulative rainfall was 21 mm; in 2014, 265 mm; and in 2015, 78 mm (figure 1b). The 2012 and 2015 sampling periods were considered as dry and the 2014 as wet, with the 2012 sampling the driest.

In 2012, we sampled 165 trees of 71 species spanning a wide gradient of ecological strategies. In 2014 and 2015, we sampled 32 and 50 individuals, respectively. During the three sessions, we sampled 7, 42 and 8 individual lianas, respectively. Liana taxonomy was resolved using DNA barcoding of leaf samples based on *rbcL* and *matK* plastid DNA gene regions amplified using classic protocols [16]. Our liana sampling included more than 11 families, the two most represented being Fabaceae and Bignoniaceae ($n = 10$ each). In 2012 and 2015, sampling was restricted to canopy lianas. In 2014, lianas climbing on canopy trees ($n = 14$) and growing in open gaps ($n = 28$) were both sampled. Small branches were collected by climbing the trees using the single-rope technique. π_{tlp} was measured using a previously published field protocol [17]. Briefly, a vapour pressure osmometer (Vapro 5520, Wescor, Logan, UT, USA) is used to measure the osmotic potential at full hydration, which is converted into π_{tlp} using a physical calibration relationship, which was validated at our site [11].

First, we tested the difference in mean π_{tlp} between canopy and gap lianas in the 2014 sampling using a *t*-test. We then tested for the effect of water availability and growth form on log-transformed π_{tlp} using a two-way ANOVA, with sampling session and form as fixed factors. Effect sizes were computed as the proportion of variance explained by each effect (η^2 , ratio of the effect sum of squares and the total sum of squares in the type II ANOVA). Post hoc comparisons were further explored using the *t*-test or Mann–Whitney–Wilcoxon test, as appropriate. All statistical analyses were conducted using the R software [18]. Test prerequisites of normality and homoscedasticity were thoroughly checked using the Shapiro–Wilk and Bartlett tests, respectively.

3. Results

Canopy and gap lianas did not significantly differ in their π_{tlp} ($p = 0.07$; table 1); they were thus grouped for subsequent analyses. Both season and growth form significantly influenced π_{tlp} ($p < 0.001$), and the interaction term was also significant ($p = 0.05$). These effects explained, respectively, 5%, 6% and 2% of the total variance. Lianas had a less negative π_{tlp} than trees during the 2014 wet season ($p < 0.001$; table 1,

Table 1. Mean and standard error, and range, of π_{tip} values for trees and lianas, at the three sampling dates. For the May 2014 sampling, values are provided for all lianas, and for lianas collected in gaps or on canopy trees separately. ind., individuals.

	trees				lianas			
	<i>N</i> (ind.)	mean \pm s.e.	minimum	maximum	<i>N</i> (ind.)	mean \pm s.e.	minimum	maximum
Sep 2012	165	-2.01 \pm 0.02	-3.14	-1.41	7	-2.02 \pm 0.14	-2.38	-1.32
Sep 2015	32	-1.88 \pm 0.06	-2.93	-1.53	8	-1.70 \pm 0.07	-2.01	-1.43
May 2014	50	-1.89 \pm 0.05	-2.72	-1.29	42	-1.59 \pm 0.04	-2.15	-1.06
					lianas in gaps			
				28	-1.54 \pm 0.05	-2.15	-1.06	
					lianas on canopy trees			
				14	-1.69 \pm 0.08	-1.98	-1.33	

figure 1), but the difference was not significant during either the 2015 mild dry sampling session ($p = 0.16$) or the 2012 drier sampling session ($p = 0.61$).

4. Discussion

Lianas sampled in a tropical rainforest showed a stronger osmotic adjustment than trees during the dry season. Liana leaves were less drought-tolerant than trees in the wet season, but had similar drought tolerances during the dry season. Plasticity in π_{tip} could allow lianas to avoid costly investment into drought-tolerant tissues, while adjusting their tolerance to stressful conditions.

In the absence of osmotic adjustment, turgor in developing cells declines with water potential. The water potential may be sustained by access to deep water or strong stomatal control under drying conditions, and osmotic adjustment also contributes to turgor maintenance, a critical prerequisite for growth [19]. All these mechanisms would contribute to a liana growth advantage. Previous studies have mainly concentrated on growth limitation due to limited carbon, whereas evidence is mounting that dry season tree growth is not carbon-limited but constrained by turgor-mediated sink activity [20,21]. Anatomically, lianas are exceptionally plastic and resilient. They have more stem parenchyma tissue, especially in contact with vessels [13,22], which constitutes a major storage compartment for non-structural carbohydrates (NSC) [23]. NSCs are critical in maintaining the leaf osmotic regulation, turgor and long-distance vascular integrity in xylem and phloem [21].

Focusing on trees exclusively, Binks *et al.* [12] did not find an osmotic adjustment in π_{tip} during the dry season in an eastern Amazonian site. However, they did detect an adjustment under stronger water stress induced by artificially excluding throughfall. Based on the finding of stronger osmotic adjustment by lianas shown here during a seasonal drought, we hypothesize that under more intense water stress, the contrast between tree and liana responses could be stronger and lianas would be enabled to equal or outperform trees in drought tolerance. In contrast with our findings, Zhu & Cao [24] found a stronger osmotic adjustment in trees than in lianas in a seasonal tropical rainforest in China. If our results are confirmed at other sites, we predict a lower increase in NSC storage in lianas than observed in co-occurring trees during the dry season because of sink activity limitation [25].

We did not find clear differences between lianas growing in gaps or on canopy trees in the wet season, which would explain a greater abundance of lianas in gaps. An alternative hypothesis is that the proliferation of lianas in gaps is explained by their clonal reproduction [26]. Further tests during the dry season would be needed to test these alternatives.

Our study suggests a stronger osmotic adjustment in lianas than in co-occurring trees during the dry season. This provides a mechanism to explain the ability of lianas to maintain growth alongside or exceeding that of trees in the dry season. Future studies should compare π_{tip} adjustment within given species and seek to simultaneously measure NSC concentration, water balance, C assimilation and growth on co-occurring trees and lianas. Integrated understanding of the responses of hydraulic and plant-level

carbon dynamics for lianas and trees is critical for improved prediction of tropical forest responses to climate change.

Data accessibility. Data are available as the electronic supplementary material.

Authors' contributions. I.M. and J.C. designed the study. I.M., M.K.B, L.S. and J.C. collected field data. A.I. extracted, amplified and sequenced markers for DNA-based identification. I.M. performed the analyses

and drafted the manuscript. All authors commented on the manuscript, gave final approval for publication and agreed to be held accountable for the content of this work.

Competing interests. We have no competing interests.

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