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REVIEW ARTICLE

Revisiting the hypothesis for increasing liana abundance in seasonal forests: a theoretical review

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Abstract
Background A decade ago, to address the question, "Why are lianas most abundant in seasonal tropical forests across the globe?", the Mechanistic Explanation of Liana Global Abundance (MELGA) relied on the assumption that lianas have deeper roots than trees and are able to tap water from relatively deeper soil layers, giving them a competitive advantage during drought.

Scope We assess whether the assumption that lianas have deep roots is corroborated by the literature. We accessed the initial MELGA paper and evaluated all papers citing it. To date, we found that two papers tested the MELGA, and only one corroborated it.

Conclusions Deeper roots in lianas are not the single mechanism explaining liana success, due to limited empirical support. Instead, we propose that while liana success in seasonal forests may relate to deep roots for some species, it should not be viewed as the exclusive result of a single trait but as the possible result of multiple traits such as hydraulic redistribution, multifocal growing, drought resilience, higher water storage capacity, and acquisitive resource syndrome. Additional hypotheses should be evaluated along with predicted changes in plant community structure. These hypotheses should stimulate research on the mechanisms driving liana success in tropical forests.

Keywords Drought · Hydraulic redistribution · Maximum-root-depth · Multifocal-growth · Tropical forest · Woody-vine

Introduction

Investigating mechanisms predicting shifts in community assembly due to environmental change is a main focus in ecology (Fauset et al. 2012). The use of functional traits as proxies for mechanisms offers insight into how species respond to environmental drivers (Fauset et al. 2012; Rosado et al. 2016). Despite the advantages of a trait-based approach (Shipley et al. 2016), proper selection of functional traits is complex and important for describing how species cope in a given environmental filtering (Pivovaroff et al. 2016; Shipley et al. 2016). Across studies/scales, the same trait may respond

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differently to a given factor (Wright and Sutton-Grier 2012; Rosado et al. 2016), suggesting that the best approach to identify how species respond to environmental factors incorporates multiple traits (Pivovaroff et al. 2016; Shipley et al. 2016; Rosado and de Mattos 2017).

According to widespread hypothesis, deep roots are the mechanism underpinning increased liana abundance in seasonal forests (Schnitzer 2005). Because lianas use other plants as support, they do not need to invest in mechanical tissue and can develop deep roots to access water (Schnitzer 2005). This hypothesis, however, does not preclude alternative mechanisms explaining this pattern. While some studies indicate that deep roots in lianas are an important coping trait for water deficits, others indicate that deep root evidence is lacking (Powers 2014; Santiago et al. 2014).

We argue that the main problem arises when deep roots in lianas are assumed to explain increased liana abundance alone. We advocate that the main gap in liana ecology is in determining the relative importance of mechanisms responsible for their success in drought environments. We revisit this "paradigm" by showing that root depth is an important, but not unitary, hypothesis for liana abundance, because other traits and strategies may reliably and plausibly explain the observed patterns. Although some studies have shown that the deep roots assumption in lianas is not a general rule (Ewers et al. 2015; Carvalho et al. 2016), we aim to strengthen this reasoning by focusing on evidence from studies challenging this assumption by indicating alternative mechanisms. It is possible that lianas have deep roots, but we do not have enough knowledge to generalize that. We intend to show the paucity of evidence for universally deep roots in lianas (Schnitzer 2005), inviting the contribution of other concurrent causes, which may vary among species, to the relative success of lianas in seasonal tropical forests.

Lack of evidence of deep roots in lianas

To investigate how the deep roots hypothesis in lianas has been evaluated in the literature, we first accessed the original paper proposing it (Schnitzer 2005), here after the Mechanistic Explanation for Liana Global Abundance (MELGA), and reviewed references citing the paper. To date, September 2017, the paper was cited in 183 studies (Online Resource 1). We identified mentions of the MELGA in each paper. We then identified, among those that mentioned the MELGA, how many aimed to test the hypothesis, and among those that tested it, how many corroborated it. Fifty-eight studies mentioned MELGA, two tested the hypothesis, and only one corroborated it (Fig. 1). Our findings show that despite considerable acceptance of the MELGA, to date, there is a lack of empirical evidence indicating that deep roots alone explain liana advantages over trees in seasonal tropical forests. Amongst the studies supporting the MELGA proposition (Schnitzer 2005), only one measured root length in a single liana species, and did not compare it with tree species (Restom and Nepstad 2004). Similarly, Moreira et al. (2000) found that trees tapped deeper water in comparison with lianas. Additionally, the findings of Andrade et al. (2005) "do not support the common assumptions that lianas rely primarily on deep soil water".

We also found that "deep roots" are poorly defined (Pierret et al. 2016). The lack of appropriate methodologies measuring deep roots limits our ability to further understand the factors affecting them and their role in plant performance and ecological processes (Pierret et al. 2016). Defining deep roots is complicated by difficulties associated with measuring maximum root depth, which may be technically impaired depending on the environment/study site (Pierret et al. 2016). Conversely, soil properties such as soil penetrometer resistance and pore network presence are significant factors affecting deep root development, irrespective of plant species (Gao et al. 2016). These constraints in measuring and defining deep roots may underlie the evidence that lianas and tree saplings compete intensely for belowground resources, affecting aboveground biomass allocation in trees (Schnitzer et al. 2005; Martínez-Izquierdo et al. 2016).

A recent model predicting root penetration in soil showed that for a given soil bulk, a penetrometer resistance >2.5 MPa limits root growth (Gao et al. 2016). Consequently, root growth under increasing soil resistance is restricted to existing pores (Gao et al. 2016). Thus, deep roots may be a trait associated with the responses of individual plants in different climates rather than a "typical" trait representing a functional group, for example, lianas (Gao et al. 2016; Pierret et al. 2016). Chen et al. (2015) compared tree and liana water use in three tropical forests differing in drought season length and water availability. They assumed that lower predawn water potential of trees compared with that of

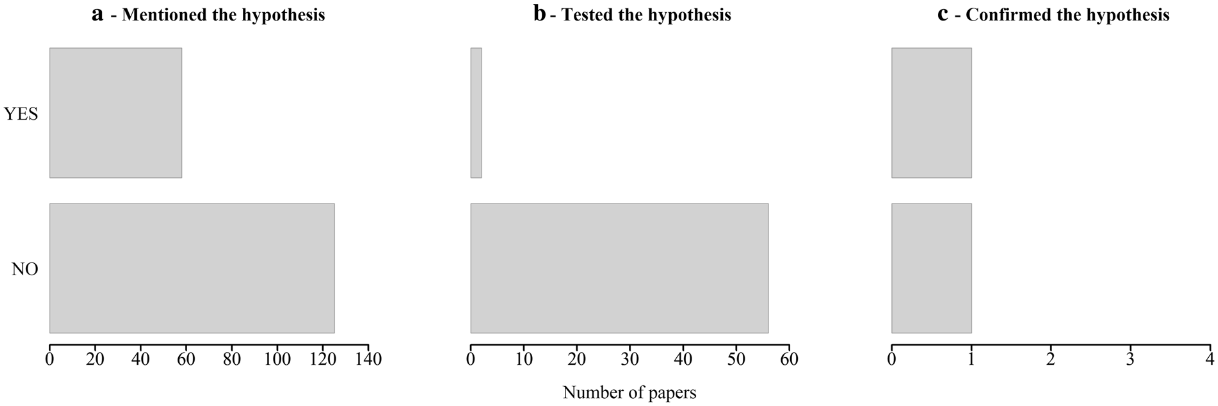

Fig. 1 Results of the investigation of the 183 papers citing the Mechanistic Explanation for Liana Global Abundance (MELGA). **a**: Papers that mentioned the hypothesis of higher maximum root depth in lianas than in trees. **b**: Number of papers that tested the hypothesis. **c**: Number of papers that corroborated the hypothesis

lianas indicates lower moisture in the soil surrounding tree roots. Yet, pre-dawn water potential cannot be used to infer root depth (i.e., based on the equilibrium between leaf and soil water potential) due to nighttime transpiration that may decrease leaf pre-dawn water potential because of water loss, leading to potential plant-soil water disequilibrium (Donovan et al. 2001). Comparing the deuterium of water tapped by roots in three soil intervals with the proportion of deuterium in the xylem of trees and lianas, Chen et al. (2015) concluded that lianas tend to show proportionally more water uptake from deeper soil layers only during the dry season and in the driest forest types. However, also using a stable water isotopic approach, De Deurwaerder et al. (2018) recently reported liana root activity in the upper soil layer. Although this paper was excluded from the 183 evaluated studies due to its publication after September 2017, its fundamental recommendation that "Root excavation or the examination of deeper soil samples in future investigations should resolve this uncertainty" is useful, highlighting that their isotopic approach does not definitively evaluated the MELGA

In a large in situ drought-induction experiment, Nepstad et al. (2007) showed a further lack of empirical evidence supporting MELGA by demonstrating that lianas in a tropical rainforest had higher mortality than trees and palms. Similarly, Carvalho et al. (2016) showed that lianas were more drought-prone and had low abundance in a semiarid climate due to a lower resistance to cavitation, shallow roots, and leaf deciduousness. Therefore, access to deep water may be one of multiple reasons accounting for high liana abundance in seasonal forests. MELGA also considered that due to CO_2 increases, lianas may have increased growth rates, favoring their competitiveness (Schnitzer 2005). However, comparing liana and tree growths under elevated atmospheric CO_2 showed that lianas had no advantage (Marvin et al. 2015). Moreover, if the CO_2 enrichment hypothesis for liana growth is applied, one may expect it to occur in other ecosystems beyond seasonal forests.

Looking ahead: additional functional hypotheses

Based on the above, we propose alternative hypotheses to explain liana success in seasonal tropical forests. Importantly, each presented hypothesis should not be viewed as a universal mechanism for all liana species, but as additional hypotheses that may work for different liana species. Assuming that all lianas have similar traits is the same as assuming that liana abundance is associated with deep roots. Secondly, we argue that MELGA and any additional hypotheses should be tested based on the foundational steps of functional plant ecology (Shipley et al. 2016): identifying (i) if deep roots and additional traits are proxies for increases in fitness/abundance by evaluating the relationship between trait values of co-occurring liana species and their relative abundance to validate trait functionality (e.g., deep roots; Shipley et al. 2016); and (ii) whether such traits vary predictably along an environmental gradient (Shipley et al. 2016). Based on the relationship between environment and trait, from wetter to drier sites, community-weighted mean (CWM) values of root depth should increase if they are functional (Shipley et al. 2016).

Asner and Martin (2012) showed that, due to a greater acquisitive strategy and nutrient use efficiency, compared with trees, lianas increased along a gradient of increasing irradiance and disturbance. Moreover, average water-use efficiency did not differ between lianas and trees; differences between life-forms were site precipitation- and temperature-dependent, leading to lianas and trees showing trait convergence (Asner and Martin 2012). Van Der Heijden and Phillips (2008) asserted that disturbance degree was the main factor leading to higher liana density, not climate or soil variables. Explaining the mechanisms of increased liana abundance in seasonal sites is evidently not straightforward; thus, testing environment-traits and trait-abundance relationships is essential to validate trait functionality. Additionally, comparisons between life-forms must account for phenology because lianas and deciduous trees may have similar water-use strategies compared with lianas and evergreens (Chen et al. 2017).

Hydraulic redistribution and multifocal growth

Lianas show horizontal and vertical growth (Putz 1984), reaching lengths of up to 310 m (Sakai et al. 2002), frequently reaching the canopy from the ground (Putz 1984) and allowing the same individual to be rooted at many points in an environment (Schnitzer et al. 2008). We hypothesize that this multifocal growing strategy (MFS) may provide drought coping, by enabling water uptake over a broader area (Tang et al. 2012). MFS allowing access to different soil water availability and creating a soil water potential gradient driving water flow may promote water movement from wet to dry soil through roots (hydraulic redistribution; HR) (Neumann and Cardon 2012). HR is widespread and may provide several advantages for plants, such as increasing root life span (Bauerle et al. 2008) and nutrient uptake (Neumann and Cardon 2012). To our knowledge, although not measured in lianas, HR is documented in other life-forms and may potentially occur across species and rooting patterns (Neumann and Cardon 2012). Thus, HR should be an important factor in liana research (Powers 2014). We predict that an MFS may allow lianas to explore soil resources at multiple locations. HR should be described based on sap-flow sensors capable of capturing bi-directional fluxes (Burgess et al. 1998), combined with mapping their spatial distribution to detect MFS. We expect that lianas with more rooting points will have a greater HR magnitude in response to rainy events after drought. Another prediction may utilize MFS as an HR proxy: along a gradient of water availability, there will be an increase in rooting points from wetter to drier sites.

Combining trade-offs to describe water use

Although the functional significance of deep roots may be lower water capacitance in lianas than in trees (Chen et al. 2015, 2017; De Guzman et al. 2016), the opposite is also possible: liana species may be better able to transport and store water (Ewers et al. 2015), indicating that multiple traits affect liana responses to drought. Consequently, higher water storage in stems could be associated with lower investment in deep roots; this trade-off between deep roots and water storage capacity has been observed in trees (Paz et al. 2015). By comparing trait differences among tree species from three successional stages, Paz et al. (2015) demonstrated that early- and mid-successional tree species invested more in root depth elongation, while old-growth species were shallow-rooted but had higher water storage capacity. This trade-off provides important insights into lianas' investment in root depth because different life-forms may share similar trait relationships (Wright et al. 2004). Some lianas have a high proportion of parenchyma in the secondary xylem (Morris et al. 2016), suggesting susceptibility to cavitation/embolism (Ewers et al. 2015; De Guzman et al. 2016; Chen et al. 2017). Therefore, deep roots in lianas may not be mandatory; rather, they may be a trait dependent on water storage trade-offs. Importantly, although Morris et al. (2016) indicated that lianas have one of the highest proportions of parenchyma in the secondary xylem of all life-forms, we should not assume that all lianas have similar functioning.

A secondary potential trade-off is related to resistance/resilience to cavitation, which is mediated by wood density. Although lower wood density plants may be more susceptible to cavitation, they have a greater ability for xylem refilling (Ogasa et al. 2013). Although this negative correlation between recovery performance in xylem hydraulic conductivity and cavitation resistance has been observed in trees, a physiological mechanism of xylem refilling could also be observed in life-forms with low wood density, like lianas (Ewers et al. 2015). Based on these trade-offs, we hypothesize that the higher abundance of some lianas may be due to the combination of shallow roots, lower wood density, and higher capacitance conferring high resilience to embolism.

Alternative functional designs

Hypotheses explaining liana abundance are not mutually exclusive due to the concept of alternative functional designs (Marks and Lechowicz 2006; Marks 2007). Based on the hierarchy of traits, different trait arrays, indicating different routes for plant success (Marks and Lechowicz 2006; Marks 2007), may lead to plant dominance (Rosado and de Mattos 2017). We propose that although liana success in seasonal forests may be related to deep roots for some species, it may be the result of different combinations of traits, such as deep roots, HR, multifocal growing strategies, drought resilience, and higher water storage capacity, for other species. For instance, recent findings indicated that foliar water uptake (FWU), an additional water source maintaining physiological processes and growth (Eller et al. 2013), was greater in lianas than in trees in a tropical seasonal forest (Fu et al. 2016). As the authors identified, fog was the most important water source for lianas, contrary to their hypothesis that lianas would use more soil water.

This theoretical background of alternative functional designs may indicate the co-occurrence of liana species with multiple phenotypes. Thus, examining environment-traits and trait-abundance relationships should focus on not only organ-level traits but also traits at the whole-plant level, which may more accurately describe species' responses to the environment (Marks 2007).

Conclusions

The common hypothesis explaining global patterns of liana abundance is a valid and important mechanism (Schnitzer 2005) but should not be considered alone, as research indicates alternative strategies for drought coping without deep root systems. Sufficient evidence reveals that species from the same life-form (e.g., trees or lianas) do not have the same drought-resistance strategies. This has important implications because it may improve our interpretation of community structures and processes involving liana species, and predictions related to climate change. The proposed hypotheses may guide future research on the mechanisms driving the success of lianas in tropical forests.

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