

Commentary

Digging deeper? Biomass allocation patterns in trees and lianas in tropical seasonal forests

How do plants grow? It seems like a simple question. Most of us believe that we know the answer, but our observations of the natural world indicate that it might not be so simple after all. A long-standing discussion in ecology aims to understand how plants allocate their biomass among roots, stems and leaves to acquire limiting resources aboveground and belowground, and how environmental factors and ontogeny can influence such patterns. Two theories are usually tested to explain plant allocation strategies: the allometric partitioning theory (APT) and the optimal partitioning theory (OPT). On the one hand, APT proposes a universal allocation pattern for all plants, following allometric rules that constrain biomass partitioning to plant organs (Enquist & Niklas, 2002; Niklas & Enquist, 2002). OPT, on the other hand, proposes that biomass allocation is flexible, allowing plants to optimize resource acquisition, depending on which resource is most limiting at a given point in time (Bloom *et al.*, 1985; Chave *et al.*, 2014). Due to the increasing dominance of lianas growing in tropical forests and their potential role in decreasing carbon accumulation in forests by intensifying tree mortality (van der Heijden *et al.*, 2015), understanding how co-occurring trees and lianas share the same space and allocate carbon aboveground and belowground becomes crucial. In this issue of *New Phytologist*, Smith-Martin *et al.* (2020; pp. 714–726) dug deep into these questions by bringing together results from fieldwork, a common-garden experiment, and also by incorporating their results in an individual-based terrestrial biosphere model to test the effects of changing biomass allocation and the rules behind such patterns. While Smith-Martin *et al.* confirm some of the expectations regarding biomass allocation of lianas and trees in tropical dry forests, they also find surprising and important trends that contradict prevailing wisdom.

Much of our understanding of biomass allocation patterns comes from ecosystems that are far less diverse than tropical forests, or from controlled experiments with young plants. Owing to the high species diversity, sometimes not so welcoming environmental conditions, and remote access, working in tropical forests is a major challenge that becomes even harder when harvesting whole mature trees and lianas *in situ*. Nonetheless, by using shovels and picks, Smith-Martin *et al.* shone a needed spotlight on ecological concepts that have been studied since the 19th century (Kny, 1894), proving that we may need to revisit some theories before

generalizing them across biomes and life forms. It was hypothesized that because lianas use trees as support to grow, they would allocate less biomass to stems and potentially invest their resources in leaves to reach the canopy and also in roots to provide anchorage and to explore deeper soils in search for water and nutrients, especially during dry periods (Selaya *et al.*, 2007; van der Heijden *et al.*, 2013). Contrary to the general belief, Smith-Martin *et al.* found that mature lianas do not invest less in stem biomass and do not display deeper root systems when compared to deciduous and evergreen mature trees in a tropical dry forest. Their model simulations indicate coordination between belowground allocation and aboveground phenology, mainly related to water supply, where evergreen trees invest in deeper roots to sustain leaves for longer periods than deciduous trees and lianas, since the latter display shallower root systems. However, that lianas have root systems shallower than deciduous co-occurring trees could be attributed to the fact that lianas use other trees' stems for support, not necessarily relying on roots for anchorage.

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The similar allocation rules that apply for mature individuals of different life forms, however, do not apply for juveniles. Young plants may need to be more flexible regarding their patterns of biomass allocation when compared to mature plants, responding strongly to changes in their environment and therefore allocating their biomass according to aboveground and belowground resource availability (Poorter *et al.*, 2015). When young, lianas studied here seem to invest more in leaves and stems, perhaps aiming to compete with trees for light and establish themselves in the canopy, whereas with age, lianas tend to invest consistently aboveground and belowground, following the same allocation rules as mature evergreen and deciduous trees. Juvenile and mature plants experience different environmental conditions and therefore it is not so surprising to find out that they exhibit different allocation patterns. The problem, however, is that since confirming such differences means digging mature trees in the forest, ecologists usually rely on young plants as models to infer about biomass allocation in adult plants. Such ontogenetic differences could lead to incorrect conclusions about the functioning of tropical forests, which are in turn replicated in model simulations that do not separate plant individuals by age.

This article is a Commentary on Smith-Martin *et al.* 226: 714–726.

The implications of the results in Smith-Martin *et al.* are numerous. Observed increases in liana dominance to date have been attributed to the assumption that lianas outcompete neighbouring trees due to a deeper root system that allows access to water deep in the soil profile during drought events. By finding that the opposite is true, Smith-Martin *et al.* make us look for new answers to the question of how lianas perform better than co-occurring trees, at least in this tropical seasonal forest. For example, aboveground competition may play a large role in determining liana success in this forest, perhaps due to the direct effect of light suppression in the tree crown (van der Heijden *et al.*, 2013) or by differences in leaf physiology between lianas and trees (Cai *et al.*, 2009). By adding a new piece to the puzzle of tropical forest functioning, these findings will also help us understand forest dynamics in scenarios of future climate, where lianas are expected to play a big role and even reduce carbon sequestration by winning the competition with trees (Schnitzer & Bongers, 2011).

In a changing world where the increase in carbon dioxide (CO₂) emissions could promote a fertilization effect on our forests (Phillips & Brienen, 2017), understanding where and how this potential extra carbon could be allocated is crucial. Moreover, the interaction between increasing CO₂ and water and nutrient limitation is key to comprehending the actual extent to which forests, and especially tropical forests, could work as a sink or source of carbon (Fleischer *et al.*, 2019). By showing how tropical trees and lianas in different life stages allocate biomass and how these patterns impact their maximum rooting depth, Smith-Martin *et al.* invite us to think outside the box in terms of how plants occupy their space aboveground and belowground. The work presented by Smith-Martin *et al.* leaves us with many more questions than answers, which I hope will inspire future studies, but most importantly, inspire ecologists to not only use new approaches to answer new questions, but to come back to the root of some concepts and if needed, dig deeper and tackle old theories from different perspectives.

Acknowledgements

The author would like to acknowledge the AmazonFACE programme for financial support in cooperation with CAPES (Coordination for the Improvement of Higher Education Personnel) and the National Institute of Amazonian Research as part of the grant 88887.154643/2017-00

ORCID

Laynara F. Lugli  <https://orcid.org/0000-0001-8404-4841>

Laynara F. Lugli 

National Institute of Amazonian Research (INPA), Manaus, Brazil
(tel +55 92 993330094; email laynaralugli@gmail.com)

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Key words: biomass allocation, lianas, rooting depth, trees, tropical seasonal forests.