



Wanted: new allometric equations for large lianas and African lianas

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ABSTRACT

Liana abundance appears to be increasing, possibly to the detriment of trees, but methods for measuring liana biomass are undependable. We show that five commonly used allometric equations produce disparate results and discuss two large information gaps—Central African lianas and large lianas—that currently preclude accurate liana biomass estimation.

Abstract in French is available with online material.

Key words: aboveground biomass; Afrotropics; carbon sequestration; Gabon; tropical forest; tropics.

LIANAS (WOODY VINES) HAVE LARGE INDIRECT NEGATIVE EFFECTS ON GLOBAL CARBON STORAGE DUE TO INTENSE COMPETITION WITH TREES (Schnitzer & Bongers 2011, Tobin *et al.* 2012). Although lianas have historically accounted for just 4–5 percent of the total aboveground biomass (AGB) in moist tropical forests (Putz 1983, DeWalt & Chave 2004), lianas are increasing in abundance (Phillips *et al.* 2002, Wright *et al.* 2004) in response to various global change factors. Phillips *et al.* (2002) documented a doubling of liana abundance over a 20-yr period in Amazonia, Northwest South America, and Central America, with increases occurring in both small and large lianas. Numerous studies from the Neotropics (*e.g.*, Ingwell *et al.* (2010), Laurance *et al.* (2014)) now support this increasing liana hypothesis (ILH), with forest fragmentation, logging, changes in temperature and seasonality, and increased atmospheric CO₂ often invoked as causal factors (Phillips *et al.* 2002, Schnitzer 2015). Since most of the tropics are severely threatened by at least one, if not all, of these factors (Malhi *et al.* 2013), the liana contribution to total AGB is likely to grow over the coming decades.

Lianas substantially decrease tree diversity, recruitment, growth, and survival (van der Heijden & Phillips 2009, Ingwell *et al.* 2010, Schnitzer & Carson 2010), and thus increasing liana abundance may not only restructure tropical forests but also drastically modify carbon dynamics (Duran & Gianoli 2013, Schnitzer *et al.* 2014). Dependable methods for quantifying liana AGB are needed to accurately estimate both their direct and indirect effects on total AGB in tropical forests (Schnitzer *et al.* 2006), yet these methods are largely lacking. Current approaches rely on allometric equations to predict liana AGB from liana diameter. While similar equations are used extensively in forestry to measure trees, the same allometric relations are not applicable to lianas (Schnitzer *et al.* 2006).

Lianas have a much greater canopy biomass relative to stem biomass than trees because their stems are non-structural (Putz 1983, Kazda *et al.* 2009). In addition, liana growth is more erratic, often looping around the understory, unlike the relatively linear growth of trees (Schnitzer *et al.* 2006). Yet, although allometric measurements for lianas may be more complicated than trees, the only alternative is destructive sampling and weighing of the liana. As a result of the paucity of destructive sampling studies, most studies of liana biomass rely on allometric equations developed at the regional or global level (Addo-Fordjour & Rahmad 2013a). Numerous allometric equations have been put forward, yet rarely are they compared (but see Addo-Fordjour & Rahmad 2013a).

Here, we compared the performance of five previously published liana allometric equations (Table 1) in estimating large liana (≥ 10 cm diameter at breast height [dbh]) AGB in Gabon, Africa. If a given region, like Central Africa, does not have a local allometric equation for lianas, will pantropical and other regional allometric equations produce significantly different estimates? In 2012, Gabon initiated the establishment of a national resource inventory (NRI), a network of 104 permanent plots (100 × 100 m) each located randomly within a cell created by a 50 × 50 km grid laid out across the country. The locations span a wide precipitation gradient and are located in old growth, secondary, and logged forest. Across the 104 plots, we recorded 1354 large lianas for which we measured the diameter at 130 cm from the roots (D_{130}). These measurements were used to calculate plot-level liana AGB using five different allometric equations (Table 1).

While we used our specific dataset, liana measurements from any site or study could be used to examine the variability in liana AGB estimates produced by various allometric equations. The most commonly used pantropical equation (PT1) for liana AGB was developed by Schnitzer *et al.* (2006) using data from five independent data sets in four countries (Brazil [x2], French Guiana, Cambodia, and Venezuela). The equation, which estimates liana AGB from stem diameter at 130 cm from the roots,

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TABLE 1. *Liana aboveground biomass (AGB) allometric equations used for comparison. D_{130} is the diameter of a liana at 130 cm from the roots.*

Eq. name	Equations	Data Location
PT1*	$AGB = e^{[-1.484+2.657 \ln(D_{130})]}$	Pantropical
PT2*	$AGB = e^{[-1.519+2.682 \ln(D_{130})]}$	PT1 excluding Venezuela
CH†	$AGB = e^{[0.1498+1.7895 \ln(D_{130})]}$	South China
MY‡	$\text{Log}_{10}(AGB) = 0.490 + 1.09 \text{Log}_{10}(D_{130})$	Malaysia
GH§	Primary: $\text{Log}_{10}(AGB) = 1.077 + 0.85 \text{Log}_{10}(D_{130})$ & Secondary: $\text{Log}_{10}(AGB) = 0.236 + 1.128 \text{Log}_{10}(D_{130})$	Ghana

*Schnitzer *et al.* (2006).

†Lü *et al.* (2009).

‡Addo-Fordjour and Rahmad (2013a).

§Addo-Fordjour and Rahmad (2013b).

represents 424 liana individuals ≥ 1 cm diam. from both primary and secondary forests ($R^2 = 0.694$). Pantropical equation PT2 ($R^2 = 0.682$) is based on the same data as PT1, but excludes Venezuela ($N = 17$), which had a significantly different site-specific allometric equation (Schnitzer *et al.* 2006). We excluded allometric equations developed by Beekman (1981), Putz (1983), Gerwing and Farias (2000), and Gehring *et al.* (2004) for the Neotropics and Hozumi *et al.* (1969) for Cambodia, since Schnitzer *et al.* (2006) used the same data to develop PT1 and PT2. Addo-Fordjour and Rahmad (2013a) also evaluated those five excluded equations as well as PT1. In addition, because the pantropical equations consist mostly of data from the Neotropics and no data from Africa, we also estimated liana AGB using several regional allometric equations based on data from South Asia (Southern China: CH; Lü *et al.* 2009) and Malaysia (MY; Addo-Fordjour & Rahmad 2013a) and West African tropical forest (Ghana: GH; Addo-Fordjour & Rahmad 2013b) for comparison.

CH represents 25 liana individuals ≥ 2 cm diameter that were harvested from undisturbed old growth forest in south central China ($R^2 = 0.870$). MY represents 60 liana individuals ≥ 1 cm which were harvested in primary and secondary forest in Malaysia ($R^2 = 0.986$). GH represents 100 liana individuals ≥ 1 cm, that were harvested in primary and secondary forest in Ghana. For this equation, separate models were applied to primary ($R^2 = 0.996$) and secondary ($R^2 = 0.994$) forest plots based on findings from Addo-Fordjour and Rahmad (2013b).

We found that the mean liana AGB of Gabon differed widely depending on the equation that was employed ($F_{4,490} = 52.59$, $P < 0.001$; Fig. 1A). PT1, the most commonly used Pantropical equation, yielded a mean liana AGB of 2.5 ± 2.0 Mg/ha (mean ± 1 S.D.). Other equations estimated mean liana AGB to be as low as 0.5 Mg/ha (MY) and as high as 2.6 Mg/ha (PT2) – a fivefold variation in biomass depending on the equation used. Regional allometric equations CH, MY, and GH yielded significantly lower estimates of AGB than PT1, with mean AGBs 52 percent, 80 percent, and 72 percent lower, respectively. Interestingly, we found that secondary forests had significantly lower liana AGB than primary forests across all equations (Equation: $F_{4,490} = 56.42$, $P < 0.001$; Forest type: $F_{1,493} = 33.03$, $P < 0.001$; EqxF: $F_{4,485} = 1.91$, $P = 0.107$; Fig. 1B), suggesting that while overall values may not yet be reliable, using any of the equations presented here for comparisons between treatments within a site may be appropriate.

The allometric equation used to calculate liana AGB from stem diameter clearly affects the resulting estimate of liana AGB. Currently lianas in this study only make up 1 percent of total AGB across Gabon using PT1; however, depending on the equation used this number could drop as low as 0.2 percent—a fivefold variation. While this number is small, the variation is quite large and lianas are increasing in abundance throughout most of the tropics due to various global change factors (Schnitzer 2015). Therefore, the accuracy of this estimate will become more

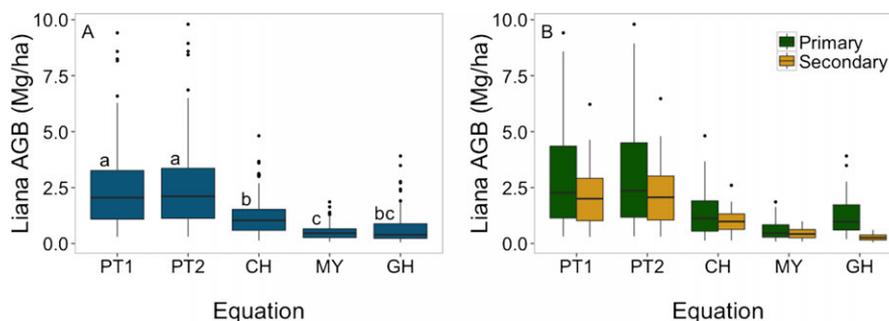


FIGURE 1. Uncertainty in liana AGB estimated by various liana allometric equations shown in Table 1. PT1 is a Pantropical equation created using data from five independent data sets in four countries (Brazil (x2), French Guiana, Cambodia, and Venezuela). PT2 used the same data minus the Venezuela site. CH used data from Southern China, and MY used data from Malaysia. GH used data from Ghana and is the only known allometric equation based on data from Africa. (A) Mean plot-level liana AGBs across Gabon estimated by each of the five different allometric equations. Lowercase letters denote significant differences among liana AGB estimates ($P < 0.005$). (B) Mean plot-level liana AGB by forest type across Gabon estimated by each of the five different allometric equations. Note the estimate produced by GH was developed using two separate equations for primary and secondary forests, as Addo-Fordjour and Rahmad (2013b) found forest type to have a significant influence on allometric models. All other estimates use a single equation regardless of forest type.

important for calculation of total forest AGB in the future. Moreover, the application of different allometric equations may confound comparisons of AGB among studies and complicate comparisons of liana communities among forests (Schnitzer *et al.* 2006). Existing liana allometric equations may yield distinctly different estimates of biomass because of the limited number of individuals used to calculate these equations. Prior to Schnitzer *et al.* (2006) only one of the three published allometric equations for lianas in mesic and wet tropical forests used more than 20 individuals for all species and size classes combined (Putz 1983, Gerwing & Farias 2000, Gehring *et al.* 2004). And while PT1 (Schnitzer *et al.* 2006) drastically decreased this shortcoming, the authors noted that additional harvest experiments were needed to improve their equation. Ten years later, PT1 is still the pantropical equation built from the most individual lianas and is perhaps the most relevant for use in central Africa, as no regional equation is available and liana allometric equations are scarce for the continent as a whole. We add our voices to the Schnitzer *et al.*'s (2006) call for more direct harvest experiments.

We acknowledge that direct harvest experiments are costly in terms of time, money, and energy. While other methods of estimating liana abundance such as the Crown Occupancy Index (van der Heijden *et al.* 2010) can be less time-consuming and less costly they do not produce biomass estimates and lack the ability to be compared across sites and experiments. In addition to creating allometric equations for biomass, there are other benefits of destructive harvesting. For example, many types of complementary allometries can be examined when destructive harvesting occurs with minimal additional fieldwork like comparing DBH to leaf area or sapwood area. While tedious, these destructive sampling are necessary to accurately estimate liana AGB, and here we call attention to two important deficits in current allometric equations on which to focus efforts.

First, little information exists on central African lianas. While pantropical equations are useful, evidence suggests that allometric relations of lianas may differ among regions (Addo-Fordjour & Rahmad 2013a) and forest types, as has been shown for trees (Brown 1997). As the lianoid growth form is prevalent throughout vascular plants with polyphyletic and diverse origins (Gentry 1991, Lahaye *et al.* 2005), the allometry of lianas may be weakly constrained evolutionarily. Too few lianas, however, have been harvested to adequately test how liana allometric relationships vary across regions or taxonomic groups (Schnitzer *et al.* 2006). The Congo basin is the second largest continuous tropical forest in the world, yet its lianas are completely lacking from pantropical equations (Schnitzer *et al.* 2006). We urge that scientists working in central Africa fill this gap, and encourage the creation of a central African regional model as has been done for Malaysia, south-east China, and Ghana.

The second large knowledge gap in liana AGB allometric equations comes from the fact that the majority of liana measurements used to develop these equations are from small lianas (<10 cm D_{130}) (Schnitzer *et al.* 2006, Lü *et al.* 2009, Addo-Fordjour & Rahmad 2013a). Although large lianas (>10 cm D_{130}) are less numerous than small lianas, large lianas contribute a

disproportionately large amount of liana biomass (estimated to be 41% of total liana AGB (Phillips *et al.* 2005, Laurance *et al.* 2014)). In an ideal world, lianas of all size classes would be measured at all sites in every AGB study. Logistically, however, measuring all lianas (both large and small) at a study site is time consuming and difficult. Measuring only large lianas decreases the time investment and increases accuracy in repeat measurements (Phillips *et al.* 2005). Using 24 sites around the world, DeWalt *et al.* (2010) found approximately 10 large liana stems/ha. In contrast, they found 376 (± 330) stems of lianas greater than 2.5 cm per ha with a maximum of 1414 stems/ha in Brazil and a minimum of 94 in India. For large-scale projects with multiple sites, measuring every liana may not be practical, but measuring large lianas can usually be accommodated by any sampling scheme. Given the role of forests in climate mitigation through REDD+ and carbon markets (Cerbu *et al.* 2011, Alemagi *et al.* 2014) a unique equation for large lianas could facilitate the estimation of AGB from national forest inventories.

As efforts increase to mitigate climate change via increased carbon storage in AGB (Malmsheimer *et al.* 2008), understanding and accurately estimating total forest AGB is a necessity. To avoid underestimating forest carbon stocks, incorporating liana AGB into total forest AGB is essential as liana numbers and biomass increase in response to global change drivers. In addition, allometries like dbh to AGB or dbh to leaf area are important variables for forest ecosystem and hydrology modeling (Turner *et al.* 2000). We recommend that efforts to increase the accuracy of liana biomass estimates be focused on large lianas in underrepresented areas like Central Africa. Regional models may prove to more accurately predict site level liana AGB than pantropical models (Addo-Fordjour & Rahmad 2013a); however, until data from all tropical regions are collected and incorporated into a truly pantropical equation, this theory is difficult to test.

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