BIOTROPICA 38(5): 581–591 2006 10.1111/j.1744-7429.2006.00187.x

Censusing and Measuring Lianas: A Quantitative Comparison of the Common Methods[1]

Stefan A. Schnitzer[2]

Department of Biological Sciences, University of Wisconsin–Milwaukee, Milwaukee, Wisconsin, 53211, U.S.A.

Saara J. DeWalt

Department of Biological Sciences, Clemson University, Clemson, South Carolina, 29634, U.S.A.

and

Jérôme Chave

Laboratoire Evolution et Diversité Biologique, CNRS/UPS 118 route de Narbonne, 31062 Toulouse, France

ABSTRACT

Lianas contribute to many aspects of tropical forest diversity and dynamics, and interest in liana ecology has grown substantially in recent years. Methods to census lianas and estimate biomass, however, differ among studies, possibly hindering attempts to compare liana communities. At Nouragues Research Station (French Guiana), we tested the extent to which liana abundance, basal area, and estimated biomass differed depending on stem diameter measurement location, inclusion of ramets, inclusion of lianas rooted within versus passing through the plot, and plot shape. We found that the mean per plot abundance and basal area of lianas were significantly greater when lianas were measured low on the stem, when ramets were included, and when lianas were sampled in transects (2×50 m) than in square plots (10×10 m). Mean per plot liana abundance and basal area were 21 percent and 58 percent greater, when stems were measured at the largest spot on the stem compared to 130 cm from the ground, respectively. Including liana ramets increased average per plot liana abundance, basal area, and estimated biomass by 19, 17, and 16 percent, respectively. To facilitate cross-study comparisons, we developed conversion equations that equate liana abundance, diameter, and basal area based on the measurements taken at four different stem locations. We tested these equations at Lambir Hills National Park, Malaysia and found that they did not differ significantly between the two sites, suggesting that the equations may be broadly applicable. Finally, we present a new allometric equation relating diameter and biomass developed from 424 lianas from five independent data sets collected in four countries.

RÉSUMÉ

Les lianes contribuent de diverse manière à la diversité et à la dynamique des forêts tropicales, et l'intérêt pour l'écologie des lianes s'est beaucoup accru ces dernières années. Cependant, les méthodes pour recenser les lianes et estimer leur biomasse varient d'une étude à l'autre, et peuvent entraver les tentatives de comparaison des communautés de lianes. A la Station de Recherche des Nouragues (Guyane Française), nous avons évalué la variation de l'abondance, de la surface terrière et de la biomasse des lianes, en fonction de la position de mesure du diamètre sur le tronc, de l'inclusion des rameaux, de l'inclusion des lianes enracinées dans la parcelle plutôt que passant dans la parcelle, et de la forme de la parcelle. Nous avons trouvé que l'abondance et la surface terrière moyennes des lianes par parcelle étaient significativement plus importantes lorsque les lianes étaient mesurées en bas de la tige, lorsque les rameaux étaient inclus, et lorsque les lianes étaient échantillonnées dans des transects (2x50m) plutôt que dans des parcelles carrées (10x10m). L'inclusion des rameaux dans l'échantillonnage augmentait l'abondance moyenne des lianes par parcelle de 19 pour cent, leur surface terrière de 17 pour cent et leur biomasse de 16 pour cent. Afin de faciliter les comparaisons entre études, nous avons développé des équations de conversion qui relient l'abondance, le diamètre et la surface terrière des lianes à partir de mesures prises à quatre endroits sur la tige. Nous avons testé la validité de ces équations au Parc National de Lambir Hills (Malaisie): les équations ne variaient pas de manière significative entre les deux sites, suggérant qu'elles pourraient être largement applicables. Finalement, nous présentons une nouvelle équation allométrique reliant diamètre et biomasse des lianes, construite à partir de 424 lianes de cinq ensembles de données échantillonnées dans quatre pays.

Key words: biomass; census methods; climbers; forest plots; French Guiana; Lambir Hills; lianas; Malaysia; Nouragues; tropical forest; vines.

LIANAS (WOODY VINES) ARE AN IMPORTANT COMPONENT OF TROPICAL FORESTS, contributing to many aspects of forest ecology and ecosystem function (Schnitzer & Bongers 2002). Lianas compose between 10 and 45 percent of the woody individuals and species in lowland tropical forests (Gentry 1991, Schnitzer 2005), and they can equal or even surpass the abundance of canopy trees in particularly liana-dense forests, such as those in southern margin of the Amazon basin in Bolivia, the western margin of the Amazon basin in Ecuador, and in Southern India (Pérez-Salicrup *et al.* 2001, Burnham 2002, Parthasarathy *et al.* 2004). Lianas compete aggressively with trees for both above and belowground resources (Schnitzer & Bongers 2002) and can reduce canopy tree growth (Clark & Clark 1990, Pérez-Salicrup & Barker 2000), as well as seedling recruitment and growth in the understory (Pérez-Salicrup 2001, Grauel & Putz 2004) and in treefall gaps and secondary forests (Schnitzer & Carson 2000, 2001, Schnitzer *et al.* 2000, 2005, Tábanez & Viana 2000). Commonly, lianas contribute around 4–5 percent of the total biomass in lowland moist forests (Putz 1983, Hegarty & Caballé 1991, DeWalt & Chave 2004); however, when abundant, they can displace trees, potentially lowering overall forest biomass and thereby reducing the ability of forests to sequester carbon (Laurance *et al.* 1997, 2001, Phillips *et al.* 2002). Furthermore, large lianas may be increasing in abundance and basal area in Neotropical lowland

[1] Received 12 May 2005; revision accepted 16 November 2005.
[2] Corresponding author; e-mail: Schnitze@uwm.edu

forests (Phillips *et al*. 2002, Wright *et al*. 2004), which may increase the impact of lianas on these forests.

Despite their importance, lianas historically have been overlooked in studies of forest dynamics (Schnitzer & Bongers 2002), primarily because of perceived difficulties in measuring and identifying them. Unlike trees, which tend to grow straight up into the canopy, lianas grow more erratically and often are found looping around the understory, where they can produce numerous vegetative stem sprouts. Consequently, a variety of different methods and techniques have been used to census lianas, with little agreement as to which is the most appropriate (Parren *et al*. 2005, Gerwing *et al*. 2006, Kurzel *et al*. 2006). For example, while the diameter of trees is commonly and consistently measured 130 cm from the roots (or above the buttress for some tropical trees), liana diameter has been measured at a variety of stem locations. The most common measurement locations for lianas include: (1) the largest point along the stem (*e.g.*, Gentry 1982, 1991; DeWalt *et al*. 2000; Burnham 2002); (2) 20 or 30 cm from the roots or close to the ground (Burnham 2004, Gehring *et al.* 2004); (3) 130 cm from the roots (Eilu 2000, Gerwing & Farias 2000, Mascaro *et al*. 2004, Schnitzer *et al*. 2004); and (4) 130 cm from the ground, regardless of the actual distance from the roots (Putz 1983, Condit 1998, Schnitzer *et al*. 2000, Ibarra-Manríquez & Martínez-Ramos 2002, Gerwing 2004, Grauel & Putz 2004, Rice *et al*. 2004). If stem diameter varies substantially with stem measurement location, then the liana abundance (given minimum cut-off diameters), basal area, and estimated biomass will also vary with stem measurement location, confounding comparisons of lianas among different studies.

Another methodological difference among studies on lianas is whether only independently rooted individuals (apparent genets) or both apparent genets and vegetatively produced ramets are included in censuses (Parren *et al*. 2005, Gerwing *et al*. 2006). Because of their pliable stems and anomalous stem anatomy (Fisher & Ewers 1991), lianas often survive falling from the canopy, upon which they can produce copious numbers of ramets along the length of the fallen stem (Putz 1984, Gerwing & Vidal 2002, Schnitzer *et al*. 2004). Including ramets may substantially increase estimates of liana abundance, basal area, and estimated biomass.

Additional factors that may potentially confound comparisons among liana studies include the following: (1) different criteria for the inclusion of lianas with respect to the rooting location (*e.g.*, including only lianas rooted within a plot vs. including all lianas growing in and into the plot); (2) different shapes and dimensions of sampling units (*e.g.*, square plots vs. long thin transects); and (3) the interaction between rooting location and plot's shape or size. For example, some researchers have included only lianas that are rooted within the plot (*e.g.*, DeWalt *et al*. 2000, Mascaro *et al*. 2004, Parthasarathy *et al*. 2004), while others have included all lianas that were crossing through the plot at 130 cm from the ground, regardless of where they were rooted (Burnham 2002, 2004, Grauel & Putz 2004, Rice *et al*. 2004). Plot size and shape also differs greatly among studies, with plots varying from long, thin transects (Gentry 1991, DeWalt *et al*. 2000) to rectangular plots (Burnham 2002, Ibarra-Manríquez & Martínez-Ramos 2002, DeWalt & Chave 2004, Mascaro *et al*. 2004) to square plots (Parren & Bongers 2001, Pérez-Salicrup *et al*. 2001) to circular plots (Putz 1984). We might expect that equally sized sampling units, regardless of plot shape, would yield the same number of lianas rooted in the plot, provided that replication at the plot level was adequate. Plot shape, however, may affect estimates of liana abundance, basal area, and biomass when all lianas growing in and into the plot are included because liana stems often loop around the understory on their way up to the canopy, and the increased edge-to-volume ratio of long thin transects, such as those used by Gentry (1982, 1991), may include more lianas than would square plots of the same area (DeWalt & Chave 2004).

The choice of allometric equation to estimate liana aboveground biomass (AGB) from stem diameter may confound comparisons of AGB among studies and prevent accurate comparisons of liana communities among forests. Existing allometric equations specific to lianas may yield distinctly different estimates of biomass because of the limited number of individuals used to calculate these equations. 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). Yet, researchers commonly compare estimates of liana abundance, basal area, and biomass among forests, while ignoring the methodological differences mentioned above (*e.g.*, DeWalt & Chave 2004, Mascaro *et al*. 2004). The assumption that sampling effects are nominal has never been tested and, if wrong, may result in substantial errors in comparisons of liana abundance, basal area, and biomass among studies.

In this study, we determine how different measurement locations on the stem, inclusion criteria, and plot shape affect estimates of liana abundance, basal area, and biomass. Specifically, we quantify the change in liana abundance and stem basal area when lianas are measured at the largest point on the stem, followed by the common measurement points of 20 cm from the roots, 130 cm from the roots measured along the stem, and finally 130 cm perpendicular to the ground. We quantify the increase in liana abundance, basal area, and biomass when we include both apparent genets and ramets in the census. We compare long, thin transects with compact square plots of the same area to test whether estimations of liana abundance, basal area, and biomass change with plot shape. We also test whether such inclusion criteria as being rooted in the plot versus passing through the plot at 130 cm above the ground affect estimates of liana abundance, basal area, and estimated biomass, and how these inclusion criteria interact with plot shape. We examined these different census methods at Nouragues Research Station in French Guiana and at Lambir Hills National Park in Malaysian Borneo. We then use the stem measurement location data to develop equations that facilitate the conversion of liana abundance and basal area from one stem measurement location to another. We also present a novel allometric equation to estimate liana AGB from stem diameter that represents 424 liana individuals $\geq$1 cm diameter compiled from five independent data sets collected in Brazil (2), Venezuela, French Guiana, and Cambodia.

METHODS

STUDY SITES.—The Nouragues Research Station was established in 1986 and is located within a 1000 km^2 wilderness reserve 120 km south of Cayenne in French Guiana (Bongers *et al*. 2001). The forest in this region is classified as a wet tropical lowland forest, which receives *ca* 3000 mm of precipitation on average per year. Rainfall is distributed relatively evenly throughout the year (*ca* 300 mm per month), except for a 2-mo dry season in September and October, during which average rainfall is less than 90 mm per month (Bongers *et al*. 2001). See Bongers *et al*. (2001) for a detailed description of Nouragues.

We conducted this study in October 2002 in two upland forested areas near the Nouragues field station: the Grand Plateau (GP) and the Petit Plateau (PP), where permanent sampling plots have been established for studying tree dynamics (Chave *et al*. 2001). The GP plot is 70 ha in size and the PP plot is 12 ha, both of which have been subdivided into a grid of 1-ha plots. The GP and PP have different parent material and are separated by a small valley, but are located within *ca* 500 m of each other. The GP is composed of metamorphic bedrock of the Paramaca series covered with clayey soil. The PP is slightly smaller and is composed of granitic and crystalline bedrock covered with sandy clayey soil (Bongers *et al*. 2001).

To test the generality of our findings at Nouragues, in March 2004 we collected similar data on the lianas in the 52-ha forest dynamics plot at Lambir Hills National Park in Malaysian Borneo, which is part of the Center for Tropical Forest Science's global network of demographic tree plots (Lee *et al*. 2004). Lambir Hills is a 6800-ha National Park, composed mostly of wet tropical lowland, mixed dipterocarp forest, which receives on average around 3000 mm of precipitation per year with no marked seasonality (Lee *et al*. 2002, Palmiotto *et al*. 2004). Lee *et al*. (2004) provide a detailed description of Lambir Hills.

PLOT SHAPE, LIANA INCLUSION CRITERIA, AND RAMETS VERSUS GENETS AT NOURAGUES.—We established twenty 10 × 10 m plots uniformly (one plot every other ha) over a 40-ha area on the GP and five 10 × 10 m plots uniformly over a 10-ha area on the PP (0.25 ha in total). The corner of each of the 10 × 10 m plots was located approximately 15 m into the northwest corner of the larger 1-ha plot and was oriented in the same direction as the edge of the 1-ha plot in order to remain at least 10 m from any trail. We did not alter our plot placement to avoid treefall gaps or swampy areas. To compare square plots versus transects, we established ten 2 × 50 m transect plots (0.1 ha total) within a 20-ha area on the GP, in the same areas of the hectare in which our square plots were located. In each of the 10 transect and 25 square plots, we enumerated and measured the diameter of all lianas ≥0.5 cm in diameter.

Within the square plots and transects, we compared two different criteria for inclusion: lianas that were rooted within the plot or crossing the plane of the plot at 130 cm. We considered a liana to be rooted in the plot if any part of its stem was rooted within it, regardless of the location of the original root system or where the stem ascended into the canopy. For lianas crossing the plane at 130 cm, we included any liana that broke the plane of the plot at 130 cm from the ground, regardless of its rooting location or where the stem ascended into the canopy.

For all plot shapes and inclusion criteria, we censused all apparent genets and vegetatively produced ramets that were ≥0.5 cm in diameter at the largest point on the stem. We considered an apparent genet to be an independently rooted individual with no aboveground or obvious belowground connections to any stem included in the study. We considered a ramet to be a stem that had its own root system but had sprouted from and was still attached to a larger "main" stem already included in the study. When a liana had multiple root or stem sprouts, we counted and measured only the largest stem fitting our inclusion criteria as the apparent genet and included each of the remaining rooted stems as ramets. In all cases, we were careful to follow the stems back to their origin of rooting at the soil surface so that we could distinguish vegetative ramets from independently rooted apparent genets (Putz 1984, Schnitzer & Carson 2001).

STEM MEASUREMENTS.—We used dial calipers to measure each apparent liana genet and ramet with a diameter between 0.5 and 4 cm and a cloth diameter tape for stems >4 cm. For each apparent genet, we measured the diameter at four locations on the stem: (1) the largest point on the stem, devoid of such stem abnormalities as large growths, knots, fissures, or wounds; (2) 20 cm along the stem from the last substantial root; (3) 130 cm from the last substantial root; and (4) 130 cm perpendicular to the ground (breast height), regardless of the distance from the roots. If the liana branched before the site of measurement, we measured the liana along the larger of the stems (*i.e.*, the main stem). For stems that were flattened or elliptical rather than cylindrical, we measured the diameter at the widest and narrowest points and calculated the geometric mean, which is the best estimate of diameter for the purposes of calculating basal area of elliptic stems. We estimated liana biomass from stem diameter using a novel allometric regression equation that we present in this manuscript (see below). We present equations for differences in apparent liana genet diameter, basal area, and biomass among the four stem measurement locations. For stem diameter, these equations are calculated and presented at the level of the liana apparent genet. For basal area and biomass, these equations are calculated and presented at the 0.01-ha plot level and integrate the change in each of these variables combined with the change in liana abundance among the measurement locations.

For each ramet rooted within the plots, we measured the stem diameter only at 130 cm from the ground. Because measuring 130 cm from the ground commonly resulted in the smallest diameter compared to the other locations (see below), our estimates of liana ramet basal area and biomass are conservative. To calculate the increase in the abundance, basal area, and estimated biomass of lianas when ramets were included, we used the 130 cm from the roots measurement for genets and the 130 cm from the ground measurement for ramets; these two measurement locations did not yield significantly different estimates of liana abundance or basal area (see below). For the transects, we also counted both genets and

ramets, but we measured only the diameter of the main stem and not the ramets.

TESTING THE GENERALITY OF THE LIANA STEM ALLOMETRIC RELATIONSHIPS AT LAMBIR HILLS.—We assessed whether differences in apparent liana genet diameter, basal area, and abundance among the four stem measurement locations from Nouragues could be generalized to lianas of other forests by conducting a similar study at Lambir Hills National Park. Specifically, at Lambir Hills we measured the same four stem locations of all liana apparent genets $\geq$0.5 cm in diameter rooted within 25 10 $\times$ 10 m plots that were spread uniformly across a 52-ha area. In total, we measured 338 lianas ranging in stem diameter from 0.5 to 31.0 cm at Lambir Hills (S. Schnitzer, pers. obs.); however, we did not examine the effect of plot shape, rooting location, or inclusion of ramets on liana abundance, basal area, or biomass at Lambir Hills.

DATA ANALYSIS.—We compared the effect of stem measurement location on the number, basal area, and estimated biomass of lianas rooted within the 10 $\times$ 10 m plots at Nouragues using analysis of variance (ANOVA; SAS version 8, SAS Institute 2000). The level of replication was the plot, which was treated as a random effect. We compared the means among the four stem measurement locations using Tukey's HSD test. For the effect of plot shape on the number of lianas, we compared the areas in which we placed both 10 $\times$ 10 m plots and 2 $\times$ 50 m transects (N = 10 areas). One of the transects, but not its paired square plot, crossed a large gap and was a clear outlier with many more lianas encountered than in any other plot, which caused the residuals of the ANOVA model to be nonnormally distributed. We omitted this transect and its paired plot for analysis, although the results were similar whether it was included or excluded. Our results did not change when we compared all 25 10 $\times$ 10 m plots to the nine 2 $\times$ 50 m transects; thus, we present only the results for the more conservative test that used the nine paired plots and transects.

We conducted analysis of covariance (ANCOVA) to test whether the slopes and intercepts of liana diameter and abundance for each of the pairwise relationships of the four stem measurement locations differed between the Nouragues and Lambir Hills lianas (SAS version 8, SAS Institute 2000). We used an alpha value of 0.10 to control for Type-II error to determine whether the data could be pooled. The interaction term for site $\times$ predictor diameter measure was not statistically significant in any of the pairwise tests ($P > 0.1$ for all diameter, basal area, and abundance pairwise tests; see Results). We therefore combined the data from the two sites and used reduced major axis (RMA) regression to calculate slopes and intercepts for each pairwise relationship (Bohonak 2002). RMA is appropriate when x-axis measurements are measured with error and is commonly used for examining relationships between two morphological or physiological measurements. The pairwise equations generated from the RMA regression can be used to estimate liana abundance, basal area, and diameter at one stem measurement location based on another measurement location.

CALCULATING A NEW ALLOMETRIC BIOMASS EQUATION FOR LIANAS.—We constructed a new allometric biomass regression equation by using data on the diameter and biomass of 424 liana individuals from five studies for which lianas between 1.0 and 23 cm in diameter were measured, harvested, oven-dried, and weighed. The five studies comprised three studies with published allometric biomass regression equations (Putz 1983, Gerwing & Farias 2000, Gehring *et al.* 2004) and two that contained the diameter and biomass data, but not the equations (Hozumi *et al.* 1969, Beekman 1981). See Table 2 for details. Because different studies used different conventions for measuring stem diameter, we first standardized all data sets by converting them to a measurement location of 130 cm from the roots. Gerwing and Farias (2000) included 18 lianas measured at 130 cm from the roots in eastern Brazilian Amazon. Putz (1983) included 17 lianas measured at 130 cm above the ground in San Carlos de Rio Negro, Venezuela. Hozumi *et al.* (1969) reported data for 77 lianas measured in Western Cambodia, but did not publish a regression equation based on these data. The combined data sets of Beekman (1981) and J. P. Lescure and H. Puig (pers. comm.) included 85 lianas harvested in French Guiana (for a description of these studies, see Lescure *et al.* 1983, Chave *et al.*, in press). The stem locations of the diameter measurements for the Cambodia and French Guiana studies were not recorded, but were apparently taken 130 cm from the ground (J. P. Lescure and H. Puig, pers. comm., and T. Kira, pers. comm.).

Gehring *et al.* (2004) provided dry weight for 336 lianas $\geq$1 cm in diameter when measured at 30 cm from the roots in forests of central Amazonia. We converted the diameter at 30 cm to predicted diameters at 130 cm from the roots using the equation in Gehring *et al.* (2004) and included only those lianas with predicted diameters $\geq$1.0 cm at 130 cm from the roots (N = 227). This conversion increased the comparability of Gehring's data to those of Putz (1983) and Gerwing and Farias (2000). From the Gehring *et al.* data set, we excluded flat-stemmed species of the genus *Bauhinia* (N = 6) because their diameter cannot be accurately measured with a single measurement (Gehring *et al.* 2004), allowing us to remove this controllable source of error from our equation. For the most accurate use of our allometric biomass equation for irregular-shaped species, one should estimate the diameter of the individual using the geometric mean of diameter measurements at the widest and narrowest points of the stem. If only one basal area measurement is available, one should first convert this measurement into a diameter using the formula D = sqrt (4 $\times$ BA /PI) before using our equation.

We natural log-transformed both liana diameter (D) and dry AGB and examined linear regressions between these two variables. We also tested whether there were significant site effects using a linear regression of ln(AGB) against ln(D). The quality of this regression model is measured by the correlation coefficient (R^2) and by the residuals mean standard error (RMSE). From this regression,

we constructed a predictive model by back-log-transforming estimated AGB and accounting for the change in the structure of residuals due to this transformation by multiplying by the appropriate correction factor $CF = \exp(RMSE^2/2)$, (Baskerville 1972, Beauchamp & Olson 1973). Most studies have ignored this correction factor and therefore tend to underestimate individual AGB (see review by Parresol 1999).

RESULTS

THE LIANAS OF NOURAGUES.—We quantified the lianas of Nouragues by including only apparent genets that were ≥0.5 cm in diameter, measured 130 cm from the roots, and were rooted within plots. The largest liana recorded was a *Bauhinia* sp. with an approximate diameter of 22.6 cm. For all lianas, the average diameter was 1.71 cm (± 1.8 SD), and the median was 1.15 cm. Across the 25 plots, average liana abundance, basal area, and estimated biomass per hectare were 1788 (± 234 SE), 0.81 m^2 (± 0.19), and 11.15 mg (± 4.11), respectively. Including ramets measured at 130 cm from the ground increased average liana abundance, basal area, and estimated biomass per hectare to 2128 (±297 SE), 0.95 m^2 (±0.22), and 12.18 mg (±4.31), respectively. Lianas were most abundant in the smallest size classes and declined sharply in number up to 5 cm in diameter, after which their abundance remained relatively low (Fig. 1). Large lianas (≥10 cm diameter; *sensu* Phillips *et al.* 2002) were fairly common at Nouragues (24/ha). In a separate study of all woody stems ≥10 cm diameter, J. Chave *et al.* (pers. comm.) found a lower mean abundance of large lianas (15.3/ha), with 208 lianas in a 10-ha subplot of the GP and 128 lianas in the 12-ha PP plot (see also Chave *et al.* 2001).

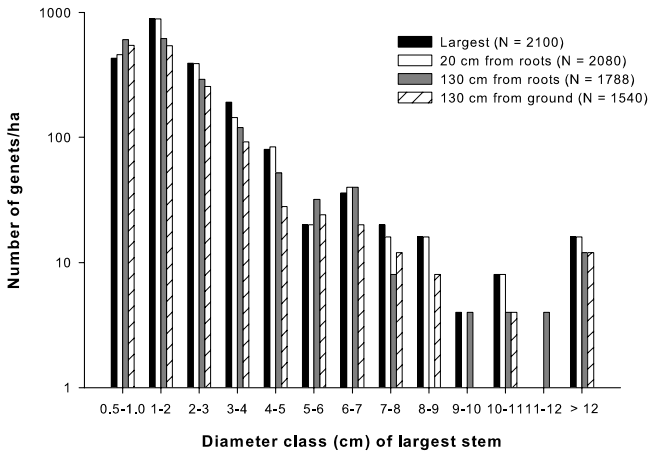

FIGURE 1. Size-class distribution on a log scale of lianas at Nouragues for each of the four stem measurement locations. Although it appears that liana abundance initially increased, the smallest size class is from 0.5 to 1 cm, half the range of the subsequent size classes.

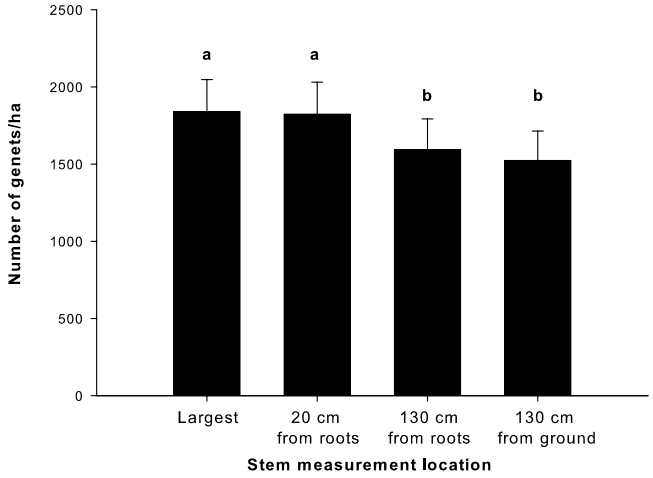

FIGURE 2. Mean number of liana genets ≥0.5 cm diameter per hectare at Nouragues for lianas rooted in the plots as measured at four stem locations. Each bar represents the mean + 1 SE calculated and scaled up from the number of lianas measured in $N = 25$ square 0.01-ha plots. The number of lianas differed significantly depending on the point along the stem where the diameter was measured ($F_{3,72} = 20.1$, $P < 0.001$). Different letters above bars indicate significant differences among the measurement locations (Tukey's HSD, $P < 0.05$).

STEM MEASUREMENT LOCATION INFLUENCES ESTIMATES OF PLOT-LEVEL LIANA ABUNDANCE AND BASAL AREA.—In nearly every size class, lianas were significantly more abundant when we measured stems at the largest point or 20 cm from the roots compared to 130 cm from the roots or 130 cm above the ground (Fig. 1). This finding was particularly evident for the smallest size classes (<5 cm diameter). For all sizes combined, mean liana abundance and basal area per 100 m^2 plot were significantly higher when we measured liana diameter lower on the stem (20 cm from the roots or at the largest point) compared to measurements higher on the stem (130 cm from the roots or 130 cm from the ground; Figs. 2 and 3). The largest point of the stem was typically close to the root system and thus, in many cases, yielded the same diameter measurement as that at 20 cm, differing only if the stem bifurcated within 20 cm of the roots. Diameters measured at 130 cm from the roots were slightly, but not significantly, larger than diameters measured at 130 cm from the ground.

CALCULATING CONVERSION EQUATIONS FOR CROSS-STUDY COMPARISONS.—Liana apparent genet stem allometric relationships at Nouragues did not differ statistically from those at Lambir Hills, suggesting that our findings from Nouragues may be broadly applicable to other forests. None of the interaction effects of site by predictor diameter differed significantly between Nouragues and Lambir Hills in any of the ANCOVA analyses of mean liana abundance, diameter, and basal area for the pairwise comparisons among stem measurement locations (18 tests, $P > 0.1$ in all cases, data not shown). At Nouragues, stem diameters measured at 20

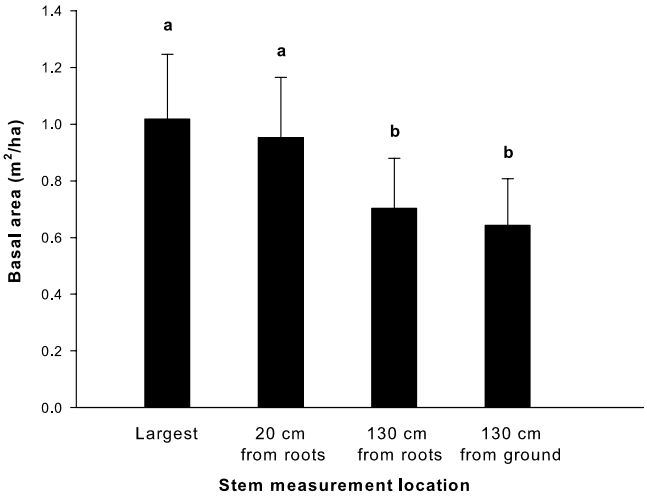

FIGURE 3. Mean basal area of lianas ≥0.5 cm diameter per hectare for the four stem measurement locations at Nouragues. Each bar represents the mean + 1 SE calculated and scaled up from the number of lianas measured in $N =$ 25 square 0.01-ha plots. Stem measurement location significantly affected basal area ($F_{3,72} = 91.4$, $P < 0.001$). Different letters above bars indicate significant differences among measurement locations for the two variables (Tukey's HSD, $P < 0.05$).

cm from the roots, 130 cm from the roots, and 130 from the ground were on average 94, 71, and 66 percent, respectively, of the diameters measured at the largest point. At Lambir Hills, these percentages for the three measurement locations were nearly identical: 94, 73 and 68 percent, respectively. The linear relationships between the pairwise stem measurement comparisons were very strong for the combined RMA regressions, with coefficients of determination (R^2) above 0.88 (Table 1), suggesting a strong ability to predict stem diameter measured at one location on the stem based on that measured at one of the other three locations. These conversion equations (Table 1) can be used to convert estimates of mean liana abundance, diameter, and basal area from any of the four stem measurement locations to another, which will facilitate comparisons among data sets that differ in stem measurement location. Note that the conversion equations for liana abundance and basal area were based on 0.01-ha plots and thus data must first be scaled to the 0.01-ha plot size prior to conversion. In contrast, the equation for converting stem diameter among the four measurement locations is based on liana apparent genets and should therefore be used at the individual level.

INCLUDING RAMETS SUBSTANTIALLY INCREASES ESTIMATES OF MEAN LIANA ABUNDANCE, BASAL AREA, AND BIOMASS.—For the 25 square plots with lianas, including both ramets and apparent genets increased mean liana abundance by 19 percent, basal area by 17 percent, and estimated biomass by 16 percent compared to including apparent genets alone. For the transects, including ramets increased the total abundance of lianas by approximately 9 percent, substantially less than in the square plots. We calculated the contribution of ramets to total liana stem density as a percentage, which is independent of plot size. We did not measure ramet basal area for the transects.

PLOT SHAPE INFLUENCES ESTIMATES OF MEAN LIANA ABUNDANCE.—We found a significantly greater number of apparent liana genets in the transects than in the square plots of the same area, regardless of whether they were rooted in the plot or broke the plane of the plot at 130 cm (Fig. 4). These patterns were consistent whether we compared the per plot mean number of lianas for the nine square plots and transects in the same overlapping 100 m^2 area or expanded our analysis to compare all 25 square plots to the nine transects.

CALCULATING A NEW ALLOMETRIC EQUATION FOR LIANAS BASED ON MULTIPLE DATA SETS.—We pooled the data from the five different geographic locations to produce a unique allometric biomass equation for lianas (Fig. 5a). We calculated the following model:

$$\mathrm{AGB} = \exp[-1.484 + 2.657 \ln(D)],$$

which had an $R^2 = 0.694$ and RSE = 1.02, based on $N = 424$ lianas (Table 2). In this model, D is the diameter at 130 cm from the roots expressed in centimeters, while AGB is the predicted aboveground oven-dry weight of the liana in kilograms. The correction factor CF is included in this model. Qualitatively, for lianas up to 6 cm in diameter, the equation from Pará state, Brazil (Gerwing & Farias 2000) estimates the most AGB while the equation based on lianas harvested in Cambodia (Hozumi *et al.* 1969) estimates the least (Fig. 5b). For lianas between 6 and 14 cm diameter, the French Guiana equation (Beekman 1981 and J. P. Lescure & H. Puig, pers. comm.) estimated the most AGB per stem, while the Venezuela liana equation (Putz 1983) estimated the least (Fig. 5c). For lianas >14 cm, the equation from French Guiana (Beekman 1981 and J. P. Lescure & H. Puig, pers. comm.) and for all sites combined estimated the highest amount of AGB per stem, which was considerably more than the other three equations.

We compared our new allometric equation to the equations constructed from the five single-site studies reported in Table 2. None of the pairwise comparisons was significantly different at the 5 percent confidence level (comparison of slope and intercept), except for the Venezuela site (Putz 1983). Therefore, we also provide a consensus allometric equation excluding this site (Table 2). Note that in order to most accurately estimate liana biomass from basal area using either of these new regression models, data must be taken at 130 cm from the roots or converted to this measurement location using the appropriate conversion equation (Table 1; see also Discussion).

DISCUSSION

Our findings demonstrate that several of the common methods used to census lianas provide substantially different estimates of mean per plot liana abundance and basal area, thereby resulting in differing

TABLE 1. *Reduced major axis regression equations relating individual diameter (D (cm)), plot abundance (A (0.01/ha)), and plot basal area (BA (cm^2/0.01 ha)) of apparent liana genets ≥0.5 cm in diameter in 0.01-ha plots as measured at 20 cm from the roots, 130 cm from the roots, 130 cm above the ground (passing 130), and at the largest point devoid of stem abnormalities. Standard errors (SE) are also provided for the intercepts and slopes. The diameter equations are based on 460 apparent genets measured at Nouragues, French Guiana and 338 genets measured at Lambir Hills, Malaysia. The abundance and basal area equations are based on plot-level sums of liana apparent genets for the 24, 100 m^2 plots at Nouragues and 25, 100 m^2 plots at Lambir Hills. Because the equations for abundance and basal area are based a plot size of 0.01 ha, data must first be scaled to this plot size prior to conversion. The equation for stem diameter conversion is based on apparent liana genets and thus conversions should be conducted at the genet level.*

RMA equation	SE of intercept	SE of slope	R^2
$D\_20 = -0.064 + 0.988$ (D_largest)	0.013	0.005	0.98
$D\_20 = 0.346 + 1.069$ (D_passing 130)	0.025	0.011	0.92
$D\_130 = -0.322 + 0.944$ (D_largest)	0.021	0.008	0.95
$D\_130 = -0.261 + 0.956$ (D_20)	0.019	0.007	0.96
$D\_130 = 0.070 + 1.02$ (D_passing 130)	0.015	0.006	0.97
D_passing $130 = -0.384 + 0.924$ (D_largest)	0.026	0.009	0.92
D_largest $= 0.415 + 1.08$ (D_passing 130)	0.025	0.011	0.92
D_largest $= 0.341 + 1.06$ (D_130)	0.021	0.008	0.95
D_passing $130 = -0.068 + 0.978$ (D_130)	0.015	0.006	0.97
D_passing $130 = -0.324 + 0.935$ (D_20)	0.025	0.009	0.92
D_largest $= 0.065 + 1.01$ (D_20)	0.013	0.005	0.98
$D\_20 = -0.261 + 0.956$ (D_130)	0.019	0.007	0.96
$A\_20 = -0.339 + 1.01$ (A_largest)	0.172	0.009	0.996
$A\_20 = 2.07 + 1.09$ (A_passing 130)	0.744	0.049	0.91
$A\_130 = -2.78 + 0.989$ (A_largest)	0.806	0.043	0.91
$A\_130 = -2.67 + 0.991$ (A_20)	0.713	0.039	0.93
$A\_130 = -0.285 + 1.07$ (A_passing 130)	0.297	0.020	0.98
A_passing $130 = -2.49 + 0.93$ (A_largest)	0.876	0.047	0.88
A_largest $= 2.40 + 1.088$ (A_passing130)	0.813	0.054	0.89
A_largest $= 3.04 + 1.003$ (A_130)	0.697	0.044	0.91
A_passing $130 = 0.466 + 0.931$ (A_130)	0.342	0.022	0.98
A_passing $130 = -1.98 + 0.919$ (A_20)	0.772	0.042	0.90
A_largest $= 0.035 + 1.01$ (A_20)	0.327	0.018	0.99
$A\_20 = 2.47 + 1.02$ (A_130)	0.634	0.040	0.93
$BA\_20 = -1.67 + 0.961$ (BA_largest)	1.134	0.007	0.998
$BA\_20 = 18.4 + 1.10$ (BA_passing 130)	3.705	0.027	0.97
$BA\_130 = -14.5 + 0.893$ (BA_largest)	3.204	0.018	0.98
$BA\_130 = -13.0 + 0.917$ (BA_20)	2.799	0.017	0.98
$BA\_130 = 4.49 + 1.02$ (BA_passing 130)	1.487	0.011	0.995
BA_passing $130 = -18.7 + 0.871$ (BA_largest)	4.165	0.024	0.97
BA_largest $= 20.9 + 1.15$ (BA_passing 130)	4.414	0.032	0.96
BA_largest $= 16.5 + 1.13$ (BA_130)	3.506	0.024	0.98
BA_passing $130 = -4.42 + 0.997$ (BA_130)	2.274	0.016	0.99
BA_passing $130 = -17.1 + 0.91$ (BA_20)	3.643	0.022	0.97
BA_largest $= 1.42 + 1.03$ (BA_20)	2.069	0.012	0.99
$BA\_20 = 13.9 + 1.08$ (BA_130)	2.619	0.018	0.99

estimates of aboveground biomass. We estimated significantly fewer apparent liana genets in the forest of Nouragues as we increased the height of the stem measurement location. The most likely explanation for this finding is that more individuals made the minimum diameter cutoff when we measured closer to the roots, presumably because liana stems taper substantially between 20 and 130 cm from the roots. This explanation is supported by the size-class distribution, which showed that lianas in the smallest size classes (<5 cm diameter) were more abundant when we measured stems at the largest point or 20 cm from the roots compared to 130 cm from the roots or 130 cm above the ground. These differences disappeared for the larger size classes (≥5cm diameter), perhaps because of the

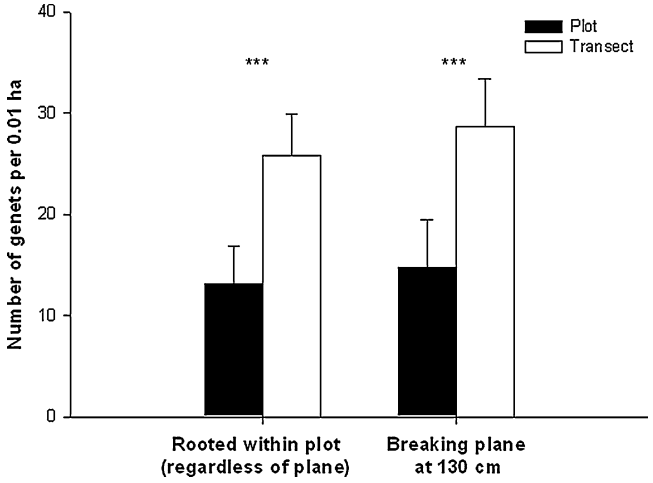

FIGURE 4. Mean number of apparent liana genets rooted in and breaking the plane at 130 cm above the ground in paired square plots and transects. Each bar represents the mean + 1 SE for nine paired square plots and transects (one pair was excluded because of a large treefall gap). Plot shape significantly affected the number of lianas observed ($F_{1,24} = 54.3$, $P < 0.001$), but method of measurement (rooted vs. breaking the plane) did not ($F_{1,24} = 1.51$, $P > 0.05$).

paucity of these larger stems or decreasing stem taper with larger sizes. Nevertheless, because most studies have a minimum size limit of 1 cm diameter (Parren *et al.* 2005), the stem measurement location will almost certainly affect the number of lianas included in the census.

Measurements taken low on the stem (≤20 cm from the roots) also resulted in significantly higher estimates of mean per plot liana basal area than measurements taken higher on the stem (≥130 cm from roots). These higher estimates were not merely the result of including more lianas in the census, but also reflected the substantial amount of stem taper. At both Nouragues and Lambir Hills, the diameter of a liana stem measured at 130 cm from the ground was, on average, 66 percent and 68 percent of that measured at the largest point on the stem.

The liana conversion equations (Table 1) may substantially increase the comparability of liana data sets compiled using different stem measurement locations. For example, at La Selva Biological Station in Costa Rica, Mascaro *et al.* (2004) measured lianas 130 cm from the roots in nine 864 m^2 plots and found an average of 1493 apparent genets (≥0.2 cm)/ha (excluding ramets) and a mean basal area of 9027 cm^2/ha. Using our conversion equations, we estimated that liana apparent genet abundance would have increased to 1801 individuals/ha and basal area to 11,850 cm^2/ha had the stems been measured at the largest point. Note that abundance was first scaled to 0.01 ha, converted using the equations in Table 1, and then scaled back to 1 ha. In this example, the predicted increases in liana abundance and basal area were *ca* 17 and 24 percent, respectively. Had Mascaro and colleagues also included ramets, liana abundance may have increased an additional 19 percent to 2143 lianas/ha, *ca* 30 percent more than the original estimate. The 19 percent increase in liana stem abundance due to the inclusion of ramets, however, has not been tested outside of Nouragues, and may differ from other forests.

RAMETS VERSUS APPARENT GENETS: TO INCLUDE OR NOT TO INCLUDE.—Including ramets can lead to substantially higher estimates of liana abundance (19%), basal area (17%), and biomass

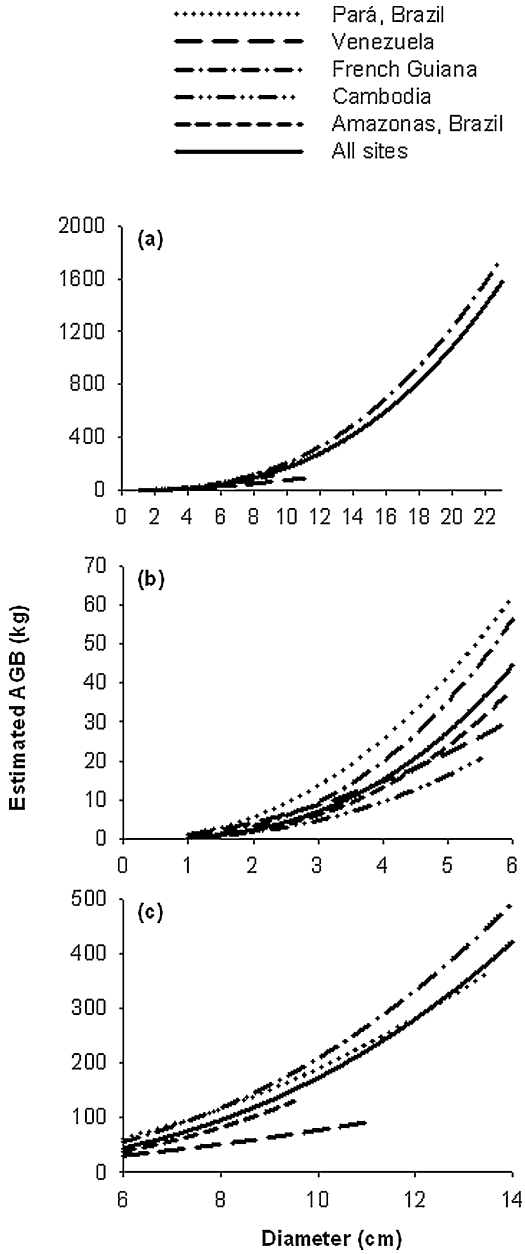

FIGURE 5. Relationship between diameter and estimated aboveground biomass (AGB) for allometric equations calculated from individuals harvested in two sites in Brazil and in Venezuela, French Guiana, and Western Cambodia, and all these sites combined. Equations are not extrapolated beyond the stem diameter of the individuals used to calculate each equation, and they are presented from 1 to 23 cm diameter (a), 1–6 cm diameter (b), and 6–14 cm diameter (c). Refer to Table 2 for more details on allometric equations.

TABLE 2. *The five individual liana biomass data sets and allometric regressions and all five sites combined. Because the parameter estimates for the Venezuela site differed significantly from the other sites, we provided the consensus equation both with and without this dataset.*

	Amazonas Brazil	Cambodia	French Guiana	Pará Brazil	Venezuela	All sites	Excluding Venezuela
Intercept	−1.547	−1.347	−1.459	0.147	0.036	−1.484	−1.519
Intercept (includes Baskerville correction)	**−1.082**	**−1.056**	**−0.570**	**0.218**	**0.185**	**−0.968**	**−0.999**
SE of intercept	*0.109*	*0.176*	*0.212*	*0.649*	*0.491*	*0.079*	*0.081*
Slope	**2.640**	**2.391**	**2.566**	**2.184**	**1.806**	**2.657**	**2.682**
SE of slope	*0.161*	*0.239*	*0.174*	*0.389*	*0.335*	*0.086*	*0.091*
RMSE	0.965	0.763	1.333	0.378	0.548	1.016	1.020
R^2	0.559	0.693	0.593	0.931	0.864	0.694	0.682
F	284.9	169.6	120.8	217.3	95.3	956.1	868.1
Sample size	227	77	85	18	17	424	407
Minimum diameter	1.04	1.00	1.10	1.76	1.18	1.00	1.00
Maximum diameter	9.66	5.70	23.00	13.65	11.28	23.00	23.00
Reference	Gerhing *et al.* 2004	Hozumi *et al.* 1969	Beekman 1981*	Gerwing & Farias 2000	Putz 1983	This study	This study

*also, J.P. Lescure and H. Puig, pers. comm.

(16%). The decision to include or exclude ramets, however, depends on the main question of the study. For example, when estimating liana biomass or the impact of lianas on tree regeneration, all ramets are usually included in the census, even ramets originating from fallen stems resting on the soil surface (*e.g.*, Schnitzer *et al.* 2000). The exception to this example is the liana ramets that are more analogous to branches of a tree than independently rooting lianas (Mascaro *et al.* 2004), and measuring the thickest part of the stem between the roots and the branches may account for the biomass of the branch. In contrast, if the purpose is to study liana diversity or demography, liana ramets that are clearly attached to and that may be getting resources from a larger stem are commonly excluded, or at least distinguished from apparent genets. By our definition, a ramet becomes an apparent genet once it is an independently rooted individual that is physically disconnected from the parent stem.

Estimates of liana abundance based on apparent genets are still probably an overestimate of the number of true genetically distinct individuals. We refer to independently rooted lianas as apparent genets because it is difficult to discern whether the individual is truly a genet, arising directly from seed, or is an independently growing ramet that originated as an offshoot of another stem. In many cases, the distinction between true genets and ramets can be determined only by genetic analyses. For the majority of studies on liana ecology, however, the number and basal area of apparent genets may be the best measures of the liana community (*e.g.*, Putz 1984, DeWalt *et al.* 2000, Pérez-Salicrup *et al.* 2001, Schnitzer & Carson 2001, Burnham 2002, Mascaro *et al.* 2004), and thus distinguishing true genets from apparent genets may be less important than determining whether a liana is an independently growing individual. Optimally, any study on lianas would include both apparent genets and ramets, with both types of stems presented separately (*e.g.*, Ibarra-Manriquez & Martinez-Ramos 2002), even if only one type of stem is used to address the main question of the study (see also Parren *et al.* 2005, Gerwing *et al.* 2006).

THE SHAPE OF STUDY PLOTS.—For lianas that were growing into the plot (breaking the plane of the plot at 1.3 m above the ground), our expectation was that long, thin transects would include more apparent liana genets and thus have higher apparent liana genet basal area and estimated biomass because the greater edge-to-volume ratio would capture more lianas looping through the understory than would compact, square plots. Another expectation, however, was that equally sized sampling units, regardless of plot shape, would yield the same number of apparent liana genets that are rooted in the plot because abundance typically scales linearly with area. Regarding the first prediction, we did find that apparent liana genets that broke the plane of the plot at 1.3 m above the ground were more than 50 percent more abundant in long, thin transects than in square plots. However, we found that rooted apparent liana genets were also more than 50 percent more abundant in long, thin transects than in square plots, in contrast with our initial expectation. One possible explanation for this latter finding is that lianas are able to root at multiple locations (*e.g.*, Peñalosa 1984, Parren *et al.* 2005), which may increase the effective area of long, thin plots more than that of compact, square plots. Essentially, both plot shapes should encounter the same number of liana rooting locations, but long, thin transects may encounter more liana individuals. Another possibility is that long, thin transects provide a greater chance of hitting a patch of forest with high liana density, such as a gap, where lianas are commonly in high abundance (*e.g.*, Schnitzer *et al.* 2000, 2004, Schnitzer & Carson 2000, 2001). Using our data, however, we cannot test either of these hypotheses. Furthermore, we cannot determine whether one plot shape will provide a better estimate of liana abundance or basal area over another. This question could be tested by comparing estimated liana abundance and basal area in plots and transects nested within a much larger plot, where liana

abundance and basal area is known. Nevertheless, our data suggest that reliable comparisons of liana abundance and diversity among plots of different shapes may be problematic due to the uncertain and potentially nonlinear relationship between plot shape and liana abundance.

ON THE ACCURACY OF LIANA ALLOMETRIC EQUATIONS.—Currently, allometric equations used to estimate liana biomass from stem diameter are relatively inaccurate due to sparse replication across species and size classes. Stem diameter does not appear to be as good of a predictor for aboveground stem biomass for lianas ($R^2 = 0.69$) as it is for trees ($R^2 > 0.95$; J. Chave *et al.*, pers. comm.). The error in liana allometric equations may be because the allometry of lianas is weakly constrained evolutionarily and mechanically through ontogeny. Too few lianas, however, have been harvested to adequately test this hypothesis or to address such questions as how liana allometric relationships vary with forest type and age, annual rainfall, seasonality, or edaphic characteristics. Furthermore, our data suggest that AGB predictions for lianas >12 cm are particularly spurious for all equations because of the paucity of data for large lianas. The lack of predictability of AGB for large lianas is an intrinsic limitation of current liana biomass allometric equations and only more direct harvest experiments are likely to resolve this limitation.

Our allometric equation may be the best general equation available for lianas because it uses many individuals and species across a range of diameter size-classes and from a variety of different forests. It is also based on far more large lianas than previous studies. Nevertheless, allometric relationships between liana stem diameter and biomass may vary across specific forest types, as has been found in trees (Brown 1997), and may vary taxonomically, with taxa differing in wood density and branching patterns. Consequently, we cannot confirm whether a general equation composed of many individuals and species from disparate locations is more accurate than a site-specific equation composed of far fewer individuals. To further complicate matters, the published studies on liana allometric relationships measured lianas at different stem locations. As shown in this study, different measurement locations can significantly affect plot abundance, basal area, and estimates of liana biomass, which may, in part, explain some of the differences among the different studies presented in Figure 5 and Table 2. To accurately use our allometric equation, stem diameter must be measured at 130 cm from the roots or converted to this measurement location using the conversion equations (Table 1).

CONCLUSIONS.—The criteria used to census and measure lianas can have a considerable effect on estimates of liana abundance, basal area, and biomass. Estimates of mean per 100 m^2 plot liana abundance and basal area both increase significantly with decreasing height of stem measurement. Likewise, including ramets can increase the estimate of liana abundance, basal area, and estimated biomass substantially, by up to 19 percent. Even plot shape can have a significant impact on liana abundance, with long, thin transects including about 50 percent more lianas than square plots. Estimates of biomass are complicated by the choice of allometric equation, with different equations resulting in very different estimates of biomass. The empirically derived and across-site tested conversion equations presented in this study may help standardize some data sets and facilitate cross-study comparisons. Furthermore, the allometric equation to estimate the biomass of a liana from its stem diameter presented here may be the best general equation available, primarily because it is based on a large number of individuals from five different sites. Identifying the differences among the various methods commonly used to census lianas and the use of empirically derived conversion equations will help standardize data sets and result in more accurate comparisons of liana abundance, basal area, and biomass among studies.

ACKNOWLEDGMENTS

S. Tonkin provided invaluable help with data collection at Lambir Hills National Park. We are grateful to D.A. Clark, C. Gehring, and an anonymous reviewer for providing valuable comments on this manuscript. We thank C. Gehring and J. Gerwing for generously providing their raw data, and F. Bongers for providing us with a copy of Beekman (1981). We especially thank Pierre Charles-Dominique and Pierre-Michel Forget for their support at the Nouragues field station. This study was made possible by generous funding from CNRS and the Organization for Tropical Studies for fieldwork in French Guiana, and the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute for fieldwork in Malaysia. All three authors contributed equally to this work.

LITERATURE CITED

BASKERVILLE, G. 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res. 2: 49–53.

BEAUCHAMP, J. J., AND J. S. OLSON. 1973. Correction for bias in regression estimates after logarithmic transformation. Ecology 54: 1403–1407.

BEEKMAN, F. 1981. Structural and dynamic aspects of the occurrence and development of lianes in the tropical rain forest. Department of Forestry, Agricultural University, Wageningen, The Netherlands.

BOHONAK, A. J. 2002. RMA: Software for reduced major axis regression. http://www.bio.sdsu.edu/pub/andy/RMA.html.

BONGERS, F., P. CHARLES-DOMINIQUE, P. M. FORGET, AND M. THÉRY. 2001. Nouragues: Dynamics and plant animal interactions in a Neotropical rain forest. Kluwer, Boston, Massachusetts.

BROWN, S. 1997. Estimating biomass and biomass change of tropical forests: A primer. Forestry Paper 134. Food and Agriculture Organization, Rome.

BURNHAM, R. J. 2002. Dominance, diversity and distribution of lianas in Yasuní, Ecuador: Who is on top? J. Trop. Ecol. 18: 845–864.

———. 2004. Alpha and beta diversity of lianas in Yasuní, Ecuador. For. Ecol. Manage. 190: 43–55.

CHAVE, J., C. ANDALO, S. BROWN, M. A. CAIRNS, J. Q. CHAMBERS, D. EAMUS, H. FÖLSTER, F. FROMARD, N. HIGUCHI, T. KIRA, J. P. LESCURE, B. W. NELSON, H. OGAWA, H. PUIG, B. RIÉRA, AND T. YAMAKURA. In press. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Nat. Life Southeast Asia.

———, B. RIÉRA, AND M. A. DUBOIS. 2001. Estimation of biomass in a Neotropical forest of French Guiana: Spatial and temporal variability. J. Trop. Ecol. 17: 79–96.

CLARK, D. B., AND D. A. CLARK. 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. J. Trop. Ecol. 6: 321–331.

CONDIT, R. 1998. Tropical forest census plots: Methods and results from Barro Colorado Island, Panama and a comparison with other plots. Springer, Berlin.

DeWalt, S. J., and J. Chave. 2004. Structure and biomass of four lowland Neotropical forests. Biotropica 36: 7–19.

———, S. A. Schnitzer, and J. S. Denslow. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. J. Trop. Ecol. 16: 1–19.

Eilu, G. 2000. Liana abundance in three tropical rain forests of Western Uganda. Selbyana 21: 30–37.

Fisher, J. B., and F. W. Ewers. 1991. Structural responses to stem injury in vines. *In* F. E. Putz and H. A. Mooney (Eds.). The biology of vines, pp. 99–124. Cambridge University Press, Cambridge.

Gehring, C., S. Park, and M. Denich. 2004. Liana allometric biomass equations for Amazonian primary and secondary forest. For. Ecol. Manage. 195: 69–83.

Gentry, A. H. 1982. Patterns of Neotropical plant species diversity. *In* M. K. Hecht, B. Wallace, and G. T. Prance (Eds.). Evolutionary biology, Volume 15, pp 1–84. Plenum Press, New York, New York.

———. 1991. The distribution and evolution of climbing plants. *In* F. E. Putz and H. A. Mooney (Eds.). The biology of vines, pp. 3–49. Cambridge University Press, Cambridge.

Gerwing, J. J. 2004. Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon. For. Ecol. Manage. 190: 57–72.

———, and D. L. Farias. 2000. Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. J. Trop. Ecol. 16: 327–335.

———, and E. Vidal. 2002. Changes in liana abundance and species diversity eight years after liana cutting and logging in an eastern Amazonian forest. Conserv. Biol. 16: 544–548.

———, S. A. Schnitzer, R. J. Burnham, F. Bongers, J. Chave, S. J. DeWalt, C. E. N. Ewango, R. Foster, M. Martinez-Ramos, M. Parren, N. Parthasarathy, D. R. Pérez-Salicrup, F. E. Putz, and D. W. Thomas. 2006. A standard protocol for liana censuses. Biotropica 38: 256–261.

Grauel, W. T., and F. E. Putz. 2004. Effects on lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. For. Ecol. Manage. 190: 99–108.

Hegarty, E. E., and G. Caballé. 1991. Distribution and abundance in forest communities. *In* F. E. Putz and H. A. Mooney (Eds.). The biology of vines, pp. 313–335. Cambridge University Press, Cambridge.

Hozumi, K., K. Yoda, S. Kokawa, and T. Kira. 1969. Production ecology of tropical rain forests in south-western Cambodia. I. Plant biomass. Oecologia 145: 87–99.

Ibarra-Manríquez, G., and M. Martínez-Ramos. 2002. Landscape variation of liana communities in a Neotropical rain forest. Plant Ecol. 160: 91–112.

Kurzel, B. P., S. A. Schnitzer, and W. P. Carson. 2006. Predicting liana crown location from stem diameter in three Panamanian lowland forests. Biotropica 38: 262–266.

Laurance, W. F., S. G. Laurance, L. V. Ferreira, J. M. Rankin-de Merona, C. Gascon, and T. E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. Science 278: 1117–1118.

———, D. Pérez-Salicrup, P. Delamônica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82: 105–116.

Lee, H. S., S. J. Davies, J. V. LaFrankie, S. Tan, A. Itoh, T. Yamakura, T. Ohkhubo, and P. S. Ashton. 2002. Floristic and structural diversity of 52 hectares of mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia. J. Trop. For. Sci. 14: 379–400.

———, S. Tan, S. J. Davies, J. V. LaFrankie, P. S. Ashton, T. Yamakura, A. Itoh, T. Ohkhubo, and R. Harrison. 2004. Lambir forest dynamics plot, Sarawak, Malaysia. *In* L. C. Losos and E. G. Leigh (Eds.). Tropical forest diversity and dynamism, pp. 527–539. Chicago University Press, Chicago.

Lescure, J. P., H. Puig, B. Riéra, D. Leclerc, A. Beekman, and A. Bénéteau. 1983. La phytomasse épigée d'une forêt dense en Guyane française. Acta Oecol. 4: 237–251.

Mascaro, J., S. A. Schnitzer, and W. P. Carson. 2004. Liana diversity, abundance and mortality in a tropical wet forest in Costa Rica. For. Ecol. Manage. 190: 3–14.

Palmiotto, P. A., S. J. Davies, K. A. Vogt, M. S. Ashton, D. J. Vogt, and P. S. Ashton. 2004. Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. J. Ecol. 92: 609–623

Parren, M. P. E., and F. Bongers. 2001. Does climber cutting reduce felling damage in southern Cameroon? For. Ecol. Manage. 141: 175–188.

———, F. Bongers, G. Caballé, J. Nabe-Nielsen, and S. A. Schnitzer. 2005. On censusing lianas: A review of the common methodologies. *In* F. Bongers and D. Traore (Eds.). Lianas of West Africa, pp. 41–58. Cabi Publishing, Wallingford.

Parresol, B. R. 1999. Assessing tree and stand biomass: A review with examples and critical comparisons. For. Sci. 45: 573–593.

Parthasarathy, N., S. Muthuramkumar, and M. S. Reddy. 2004. Patterns of liana diversity in tropical evergreen forests of peninsular India. For. Ecol. Manage. 190: 15–31.

Peñulosa, J. 1984. Basal branching and vegetative spread in two tropical rain forest lianas. Biotropica 16: 1–9.

Pérez-Salicrup, D. R. 2001. Effects of liana cutting on tree regeneration in a liana forest in Amazonian Bolivia. Ecology 82: 389–396.

———, and M. G. Barker. 2000. Effect of liana cutting on water potential and growth of *Senna multijuga* (Caesalpiniodae) trees in a Bolivian tropical forest. Oecologia 124: 369–475.

———, S. A. Schnitzer, and F. E. Putz (Eds.). 2004. The community ecology and management of lianas. For. Ecol. Manage. Special Issue 190: 1–118.

———, V. L. Sork, and F. E. Putz. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. Biotropica 33: 34–47.

Phillips, O. L., R. Vásquez M., L. Arroyo, T. R. Baker, T. Killeen, S. L. Lewis, Y. Malhi, A. Monteagudo M., D. Neill, P. Nuñez V., M. Alexiades, C. Ceron, A. Di Fiore, T. Erwin, A. Jardim, W. Palacios, M. Saldias, and B. Vinceti. 2002. Increasing dominance of large lianas in Amazonian forests. Nature 418: 770–774.

Putz, F. E. 1983. Liana biomass and leaf area of "tierra firme" forest in the Rio Negro basin, Venezuela. Biotropica 15: 185–189.

———. 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65: 1713–1724.

Rice, K., N. Brokaw, and J. Thompson. 2004. Liana abundance in a Puerto Rican forest. For. Ecol. Manage. 190: 33–41.

SAS Institute. 2000. SAS/STAT user's guide, Version 8, Volumes 1, 2, and 3. Cary, North Carolina.

Schnitzer, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. Am. Nat. 166: 262–276.

———, and F. Bongers. 2002. The ecology of lianas and their role in forests. Trends Ecol. Evol. 17: 223–230.

———, and W. P. Carson. 2000. Have we missed the forest because of the trees? Trends Ecol. Evol. 15: 376–377.

———, and ———. 2001. Treefall gaps and the maintenance of diversity in a tropical forest. Ecology 82: 913–919.

———, J. W. Dalling, and W. P. Carson. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. J. Ecol. 88: 655–666.

———, M. E. Kuzee, and F. Bongers. 2005. Disentangling above-and below-ground competition in a tropical forest. J. Ecol. 93: 1115–1125.

———, M. P. E. Parren, and F. Bongers. 2004. Recruitment of lianas into logging gaps and the effects of pre-harvest liana cutting. For. Ecol. Manage. 190: 87–98.

Tábanez, A. A. J., and V. M. Viana. 2000. Patch structure within Brazilian Atlantic forest fragments and implications for conservation. Biotropica, Special Issue 32: 925–933.

Wright, S. J., O. Calderón, A. Hernandéz, and S. Paton. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Barro Colorado Island, Panama. Ecology 85: 484–489.