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Allometric equations for four valuable tropical tree species

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Abstract

Four tree species were harvested periodically over a 13-year period from plantations in the humid lowlands of Costa Rica: *Cedrela odorata*, *Cordia alliodora*, *Hyeronima alchorneoides*, and *Euterpe oleracea*. The soil was a well-drained, volcanic alluvium, and high fertility coupled with 4 m of annual rainfall and high temperatures led to rapid growth rates; at age 13 many individual were >30 cm dbh and >30 m tall. Harvested trees were dissected into their component parts: leaves, rachises (for *Cedrela* and *Euterpe*), branches, boles, and coarse roots (i.e., >0.5 cm diameter). Roots of small trees were excavated in their entirety; those of large trees were harvested from a cylinder 1.0 m in diameter, immediately beneath the trunk. Large numbers of trees were sampled: 258–379 per species. Size classes sampled ranged from seedlings too small to have a dbh to trees of ~30 cm dbh. Two separate allometric equations (one for trees having only a basal diameter and another for trees having a dbh), with diameter-squared times height as the metrics, were developed for each component of each species. Based on breaks in linear trends of ln–ln plots and deviations of predicted from actual values, we developed separate allometric equations, by component, for trees of different sizes. The resulting 40 equations (with one exception, involving very small trees) fit the data well and enable the user to predict biomass, by component, for each of the four species. A single (non-allometric) linear equation, combining all plant parts of all three dicot species, also fit the data well, but it would not provide either the detail or the accuracy provided by the species-specific, plant-part-specific equations. Large sample sizes, a 13-year run of data collection, and the economic and ecological importance of the species studied make this data set uniquely useful for biomass estimations and for understanding the inherent heterogeneity of tree structure in dynamic tropical environments.

Keywords: Allocation; Allometry; Biomass; Boles; Branches; *Cedrela odorata*; *Cordia alliodora*; Costa Rica; *Euterpe oleracea*; *Hyeronima alchorneoides*; Regression; Roots

1. Introduction

A number of circumstances call for sound estimates of tree biomass. Tree biomass is useful, for example, in assessing forest structure and condition (e.g., Westman and Rogers, 1977); it is essential for estimates of forest productivity and carbon fluxes based on sequential changes in biomass (e.g., Chambers et al., 2001); it provides a means of assessing sequestration of carbon in wood, leaves, and roots (e.g., Cooper, 1983; Specht and West, 2003); and it can be used as an indicator of site productivity, both biological and economic.

Several biomass-prediction equations have been developed from mixtures of tropical species (e.g., Dawkins, 1961; Ogawa et al., 1965; Brown et al., 1989; Overman et al., 1994; Brown, 1997; Araújo et al., 1999; Chambers et al., 2001; Ketterings et al., 2001; Chave et al., 2005). Inevitably, however, species – especially dicotyledonous trees – differ in allometry, wood density, and architecture, all of which can affect the relationship between the measurements taken during forest inventories and the biomass of individual trees. Equations developed from mixtures of species yield useful estimates for large-scale global and regional comparisons, but they are of limited utility for application to particular species on specific sites. Furthermore, the inventory data to which mixed-species equations are often applied typically include only diameter at breast height (dbh ≡ 1.3 or 1.4 m, or above buttresses) and exclude small trees, non-commercial species, and measurements of total height. Thus, the pooled-species approach (and its extrapolation to other size classes and species; see Gillespie et al., 1992) is a reasonable tool if the database to which it is to be applied includes a very large number of species or lacks important information.

Where species-specific information is available, including measurements of all size classes and total height, then equations

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tailored to estimate biomass of the particular species can provide more accurate estimates of biomass. This situation typically obtains in the case of plantations of high-value tree species, or when precise estimates are needed for research. Much of the early work on tree allometry and development of biomass equations involved conifers (e.g., Ovington, 1957; Ovington and Madgwick, 1959; Baskerville, 1965). As they typically have monopodial growth, strong apical dominance, and consistently tapered boles, most conifers yield allometric equations that accurately predict biomass. Angiosperms, with their less consistent architecture and complicated branching patterns, are more problematic, but they do demonstrate predictable allometric relationships. Examples of single-species biomass equations from the tropics include Whitesell et al. (1988), Stewart et al. (1992; 16 species), Dudley and Fownes (1992; eight species), Fuwape et al. (2001; two species), Ong et al. (2004), Padrón and Navarro (2004), Swamy et al. (2004), and Saint-André et al. (2005).

Taking advantage of measurements made during an intensive study of tree growth in experimental plantations, we developed allometric equations for four valuable tropical tree species: *Cedrela odorata*, *Cordia alliodora*, *Hyeronima alchorneoides*, and *Euterpe oleracea* (a palm). Growth rates were fast at the site, located in Costa Rica's humid Atlantic lowlands. The research design lent itself to harvesting large numbers of trees, 1190 individuals, over the 13 year study period. Those trees spanned a wide range of sizes, seedlings to individuals >30 cm in diameter. Although the trees sampled did not reach the largest sizes attainable by the species, they are typical of today's plantation-grown trees grown on short-rotations or for carbon sequestration. Each harvested tree was dissected into various components (leaves, bole, stems, roots), enabling us to develop allometric equations for each component. The economic and ecological value of the four species studied, the uniquely large sample sizes, and the breakdown of each species into morphological components make this an unusually rich data set, one that can provide insights into the architecture and biomass allocation in architecturally divergent tropical trees.

2. Methods

2.1. Study site

The research was conducted at La Selva Biological Station, a facility of the Organization for Tropical Studies Inc., located at 10°26′N, 83°59′W. Mean annual temperature and rainfall at La Selva are about 26 °C and 4 m, respectively. The 8 ha site is 41 m.a.s.l. on well drained, deep, fertile, recent alluvium derived from volcanic material: a Eutric Hapludand (Weitz et al., 1997).

The experimental design comprised three blocks. In each block, there were four plantations of each of three dicotyledonous tree species. The initial tree spacing in all plantations was 2 m between trees (2887 trees/ha). One of the four plantations of each species in each block was cut and replanted annually (with the same species); another was cut and replanted every 4 years; and the other two were uncut. One of the uncut plantations was a monoculture, and the other was a polyculture containing a palm (*Euterpe*; described below) and a large, perennial herb, *Heliconia imbricata* (Kuntze) Baker. Palms were planted additively (to the dicotyledonous tree species) in the polycultures. They were planted in alternate rows of trees, 2.0 m apart, at the midpoint of the space between trees. As root systems and crowns closed in older monocultures (4-year rotation or uncut) the stands were periodically thinned lightly to maintain full use of resources while avoiding stagnation. For the biomass determinations reported here, dicotyledonous trees were harvested only from monocultures; the palm was harvested from the polycultures.

2.2. Species

For the research project of which this study was a part, four tree species were chosen because they comprised a broad range of phenological, architectural, and physiological traits, and were species known to grow well in the climate and soil at the study site. All of them are fast-growing species that reach the canopy, and all are species of economic importance. Three of the species are dicotyledonous trees, and the fourth is palm. Subsequent to the first use of the specific epithet in the descriptions that follow, each species is referred to by its genus: *Cedrela*, *Cordia*, *Hyeronima*, or *Euterpe*; use of the generic name implies the particular species we studied.

Cedrela odorata L. (Meliaceae) is perhaps the species of the four that is best known in international timber markets, where its fragrant wood is commonly traded as Cedar, or Spanish Cedar. Its range extends from northern Mexico to Brazil, Bolivia, and Peru, and extends into the West Indies. *Cedrela* is highly desired for almost any purpose for which wood can be used, as it works well and is strong, attractive, and rot resistant. The specific gravity of *Cedrela* ranges from about 0.43–0.45 (Brown, 1997). Repeated attacks by the mahogany shoot borer, *Hypsipyla grandella* (Zeller), from the seedling stage to a height of 5–8 m result in a highly branched habit in this otherwise monopodial tree. Its pinnately compound leaves are up to 0.6 m long, and each contains 5–11 pairs of leaflets, 6–17 cm long by 3–5.5 cm wide (Croat, 1978). The leaf phenology of *Cedrela* is extremely variable. Small saplings tend to be evergreen, larger saplings are semi-deciduous, and larger trees tend to be dry-season deciduous, but in our plantations some trees can be found in almost any state of foliation in any month. At maturity *Cedrela* attains heights >30 m and diameters >100 cm. The oldest trees we planted (in 1991) were from seed obtained from the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba, Costa Rica: Lot 4472, stock 10685; provenance Jiménez, Pococi, Costa Rica (10°12′N, 83°45′W). Subsequent plantings were from CATIE seed collected from the same provenance.

Cordia alliodora (R&P) Oken (Boraginaceae) is also a large tree, up to 45 m tall and 90 cm in diameter (Somarriba and Beer, 1987). This widespread species is found throughout tropical America where it commonly invades abandoned agricultural lands. Near La Selva it is very common in the surrounding agricultural landscape, but it is rare in primary forest. It may be a relatively short-lived species as evidenced by the observation that trees planted at La Selva in the 1950s are beginning to die. The wood of *Cordia* works well and, like that of *Cedrela*, is put to many uses. Its specific gravity ranges from 0.42 to 0.57 (Brown, 1997). The branches of *Cordia* are tiered, forming a layered crown that is quite open, permitting substantial light penetration. Branch nodes are swollen, and the resulting domatia are used by a number of ant species (Tillberg, 2004). Its simple leaves are 7–18 cm long by 3–8 cm wide and are covered with stellate pubescence (Croat, 1978). *Cordia* demonstrates a strong ability to acquire nitrogen; at our site foliar concentrations commonly exceed 4%. As a seedling and sapling, *Cordia* is evergreen, but as an adult (from age 5–7 years at our site) it is deciduous for about 2 months at the onset of the rainy season. The oldest trees we planted (in 1991) were from seed obtained from CATIE: Lot 4486, stock 18750; provenance Talamanca, Limón, Costa Rica (9°33′N, 83°55′W). Subsequent plantings were from CATIE seed collected from the same provenance.

Hyeronima alchorneoides Allemão (Euphorbiaceae) is a massive canopy tree, attaining diameters >1.2 m and heights >45 m. Its range includes lowland rainforests of much of Central America, northern South America, and the West Indies (Flores, 2002). The specific gravity of *Hyeronima* is 0.60–0.67 (Chudnoff, 1984), and its heartwood is durable, hard, and heavy. *Hyeronima* forms a dense crown that captures most incident radiation and, unlike *Cedrela* and *Cordia*, it is evergreen. Its simple leaves markedly decline in size with tree age, from 1200 cm^2 in meter-tall seedlings to 80 cm^2 in mature trees, a phenomenon having physiological and hydraulic implications (Reich et al., 2004). Seeds for our plantations were collected from trees in the immediate vicinity, outside the boundaries of La Selva Biological Station.

Euterpe oleracea Mart. (Arecaceae) is a multi-stemmed, clump-forming palm native to floodplains of South American rivers, particularly the lower Amazon Basin. It attains a height of 25 m, even though its diameter tends to be <20 cm. The pinnately compound leaves of Euterpe are up to 5 m long. The purple fruits of Euterpe are highly prized for refreshments, and the palm is harvested for its edible bud (heart of palm). The only non-native species used in the experiments, our *Euterpe* seeds were obtained from a plantation at CATIE.

2.3. Samples

In each of the 36 plots from which trees were harvested, a 5 m band containing three rows of trees was designated along either side of the plot for biomass harvests. Plants to be harvested were chosen at random from the harvest zones, and those in the outermost row (outside the plot) were excluded from the selection process. We attempted to harvest trees of deciduous species when they were in full leaf. When the plants were very small (typically too small to have a dbh), harvests were conducted at 3–6 month intervals, and a harvest typically included three trees of each species from each of three blocks. Older trees were harvested at 5–20 month intervals, and a harvest typically involved one to three trees from each of three blocks (minimum two blocks). During the 13-year research project, 1190 trees were harvested for biomass determination: 258 *Cedrela*, 271 *Cordia*, 282 *Hyeronima*, and 379 *Euterpe* (Table 1).

Table 1
Sample size and range of heights of trees harvested to determine stature–biomass relationships

Species	Diameter measure	*N*	Height range (m)
Cedrela	bd	133	0.1–2.3
	dbh	125	1.4–26.1
Cordia	bd	111	0.1–3.6
	dbh	160	1.4–28.7
Hyeronima	bd	94	0.4–2.8
	dbh	188	0.7–27.0
Euterpe	bd	182	0.1–1.6
	dbh	197	1.3–20.0

Diameter measurement bd refers to basal diameter (0.5 m above ground); dbh refers to diameter at breast height (1.3 m). The largest diameter (cm) trees of each species that were harvested were *Cedrela*, 29.4; *Cordia*, 32.1; *Hyeronima*, 29.6; and *Euterpe*, 18.3.

Diameters of trees <5 cm dbh were recorded to 0.1 cm using calipers, and diameters of larger trees were recorded to 0.1 cm using diameter tapes. The basal diameters (bd ≡ diameter at height of 0.5 m) of harvested trees too small to have achieved a dbh were recorded. Heights of trees <5 cm dbh were recorded to 0.01 m, and the heights of larger trees were recorded to 0.1 m. The heights of harvested trees taller than ~2 m were measured after felling.

Harvested trees were dissected into their component parts. At a minimum this comprised leaves, stems, and roots. Once trees achieved a dbh, branches were considered separately from the main stem, or bole. The long, thick petioles of *Hyeronima* were included with branch material, and the short petioles of *Cordia* were included with leaf tissue. Rachises of *Cedrela* and *Euterpe* were treated as a separate component, but in the Results section that follows they are pooled with branches (*Cedrela*) or leaves (*Euterpe*) where they are not identified separately. Because much of the research involved tissue chemistry, we do have separate biomass values for petioles of *Hyeronima* and *Cordia*, and although those data are not presented here, they are available from JJE.

Root systems of small trees (i.e., $\lesssim$5 cm dbh) were harvested manually in their entirety and separated into diameter size classes. Because each palm, *Euterpe*, had multiple shoots in each clump, and the allometric data refer to individual shoots, root data for that species are not reported here. Only data from the largest diameter class of roots (coarse roots, >0.5 cm), are included here. Root harvests of larger trees were restricted to those >0.5 cm in diameter. From mid-1998 onwards, the trees were so large that excavation of roots began to disturb the soil far from the harvested tree. At that point we switched to excavation of a soil cylinder, 1.0 m in diameter, immediately beneath the center of the bole. All coarse roots, including the tap root, were removed from this cylinder, which extended in depth until no more coarse roots were encountered.

(Total coarse and fine root mass in plots containing large trees were routinely determined by taking cores and excavating pits, and adding them to the roots sampled from the below-tree cylinders, but because the roots in cores and pits could not be traced to the individual trees that produced them, those data are not included here.)

The total fresh weight of each component was obtained in the field using electronic balances and recorded to 1 g for material weighing <5 kg or to 10 g for heavier material. Material having a fresh weight <1 kg was oven-dried (to constant weight at 70 °C) in its entirety, and subsamples of 0.1–1.0 kg were taken for dry-weight determination of larger material. Dry weights were recorded to 0.1 g.

2.4. Data analysis

Data analyses for this paper were generated using SAS software (SAS Institute Inc., Cary, NC, USA). In analyzing the data, we first examined scatter plots. In the case of values suspected of being erroneous, we checked field and laboratory data and all calculations. If we could be confident that data had been taken and recorded properly, those data remained in the data set at least temporarily.

We opted for use of a standard form for allometric equations: $y_i = a(X)^b$, where y_i = biomass of tree component i, X is the product of one or more dimensions, and a and b are scaling factors. Dimensions used were diameter (squared, d^2), height (h), and, in the case of *Euterpe* leaf biomass, the number of fronds (f). The single exception to use of this equation was the fit of a non-logarithmic linear model [$y = a + b\ (d^2h)$] for whole-tree biomass that combined all three dicotyledonous tree species. We then examined the fit of the data to the equation and reviewed for possible data-recording errors any data point whose studentized residual (i.e., the ratio of the residual to its standard error; SAS, 2000–2004) exceeded ±3 (Cook's D). In almost all cases those data points (only 1.3% of the total) were declared to be outliers and excluded from further analysis. After eliminating outliers, we again calculated the equation's parameters.

We first calculated the scaling factors for two sets of equations for each component of each species, one for trees having only a bd and another for trees large enough to have a dbh. We found that many of the resulting equations tended to underestimate the biomass of larger trees. Unsatisfied with the fit, but reluctant to abandon the allometric approach, we then attempted to use the variable-allometric-ratio approach of Ruark et al. (1987). This most often led to the opposite result: the variable allometry equations tended to over-estimate biomass of larger trees.

In the end we developed multiple allometric equations for each component of each tree species, fitting separate equations to subsets of the data that were defined by points(s) where the slope of ln–ln scatterplots changed: basal diameter, plus combinations of 0–5, >5–10, or >10 cm dbh. The break points were chosen visually from scatterplots and by graphing predicted over actual biomass; if the two did not conform, the break point was moved to the size class where actual and predicted values diverged consistently, and a new equation was calculated.

Because the erroneous assumption that transformed Y values on a ln–ln plot are normally distributed can lead to errors of 10–20%, we applied the Baskerville (1972) correction to the intercept (i.e., scaling factor a) of the ln–ln plot. That correction assumes a log-normal distribution and is calculated as $\exp((\text{rmse}^2)/2)$, where rmse is the root mean square error in ln form. Variables were log-transformed to stabilize variances. Slopes and intercepts of all relationships were determined, as were the significance (or not) of differences among them, using PROC MIXED (SAS, 2000–2004). This procedure accounts for the fact that the species had different variances, an important consideration for species of extremely different architectures. Model assumptions met in the experimental design and sampling, or tested for, included independence of observations, representative sample and inclusion of relevant variables in the model, normality of the residuals or errors, equality of variance of the errors, and no distortion due to outliers.

3. Results

The equations generally fit the data well, and in most cases (35 of 40 equations) more than 50% of the observed variation in biomass was explained by diameter and height (plus leaf count in the case of *Euterpe* leaves; Table 2). All but one equation (for leaves of *Cordia*, trees ≤ 5 cm dbh) were highly significant ($p < 0.0001$) for both scaling parameters, a and b.

The species differ in allometric relationships, though moreso with leaves than boles (Fig. 1). The regression lines for leaves reflect a substantial amount of inherent variation in leaf biomass especially among small trees, resulting in few significant ($p < 0.05$) differences in slope among regression lines: *Euterpe* has a steeper slope than the other species. Among larger trees, where leaf biomass is more predictable, *Cedrela* has a steeper slope than *Cordia* and *Euterpe*, but slopes did not differ significantly among *Cordia*, *Hyeronima*, and *Euterpe*. The allometry of boles is similar among the four species (Fig. 1a), despite differences in wood density. Nevertheless, several of the slopes are different. Among small trees, *Hyeronima* has a significantly steeper slope than the other species, while the slope of *Euterpe* is significantly lower, and for larger diameter trees the slope for *Euterpe* is significantly lower than those of the other species, as might be expected of a palm. In every case in which we developed more than one regression equation for a component of a species (Table 2), the slopes of those regressions differed significantly.

The residuals for the individual components of any particular species might be correlated, so it would have been necessary to employ a procedure such as seemingly unrelated regression (SUR) if we had wished to report an estimate of the error associated with calculation of whole-tree biomass determined by summing the values derived from equations for individual components (Parresol, 1999). Because we developed equations based on different size classes for different components within a species, however, an approach such as SUR was not feasible. Nevertheless, we did perform the

Table 2
Biomass equations for four tropical tree species

Species	Component	Diameter measure	*N*	r^2	rmse	*a*	*b*
Cedrela	Leaf	bd	132	0.70	0.651	0.0214	0.4516
		≤10	84	0.29	0.811	0.1265	0.2787
		>10	40	0.58	0.619	0.0013	0.9218
	Bole	bd	132	0.83	0.506	0.0448	0.4879
		≤10	84	0.84	0.461	0.2002	0.5615
		>10	38	0.97	0.149	0.0072	1.0451
	Branch	≤10	68	0.57	1.003	0.0120	0.8265
		>10	39	0.67	0.565	0.0029	1.0172
	Rachis	≤10	76	0.28	0.634	0.0727	0.2089
		>10	36	0.59	0.536	0.0010	0.8038
	Root	bd	133	0.59	0.772	0.0460	0.4022
		≤10	84	0.62	0.532	0.2548	0.3707
		>10	37	0.62	0.327	0.0893	0.5326
Cordia	Leaf	bd	101	0.89	0.404	0.0185	0.7803
		≤5	68	0.02	1.003	0.3041	0.1082 (ns)
		>5	91	0.51	0.713	0.0391	0.5151
	Bole	bd	101	0.93	0.368	0.0212	0.8796
		≤5	68	0.78	0.359	0.1232	0.5542
		>5–≤10	46	0.90	0.217	0.0266	0.8994
		>10	42	0.91	0.229	0.0085	1.0450
	Branch	All	146	0.83	0.588	0.0853	0.5345
	Root	bd	101	0.77	0.559	0.0122	0.6866
		All	155	0.94	0.393	0.0427	0.6437
Hyeronima	Leaf	bd	93	0.94	0.315	0.0210	0.7775
		≤10	114	0.34	0.606	0.2144	0.2852
		>10	71	0.54	0.516	0.0094	0.6910
	Bole	bd	92	0.96	0.333	0.0190	0.9298
		≤10	114	0.90	0.359	0.0662	0.7186
		>10	72	0.96	0.191	0.0046	1.1159
	Branch	≤10	116	0.64	0.734	0.0435	0.6518
		>10	72	0.71	0.513	0.0031	0.9902
	Root	bd	93	0.95	0.325	0.0078	0.9008
		All	185	0.96	0.366	0.0288	0.6924
Euterpe	Leaf	bd	158	0.86	0.591	0.0028	0.8227
		All	182	0.94	0.267	0.0237	0.5121
	Bole	bd	178	0.76	0.661	0.0486	0.6194
		≤5	39	0.26	0.339	0.3764	0.3463
		>5	156	0.95	0.279	0.0314	0.9174
	Rachis	bd	158	0.77	0.711	0.0047	0.7960
		All	187	0.90	0.263	0.0458	0.3880

Most equations are in the form $y_i = a(d^2h)^b$, where y_i = biomass (kg) of tree component i, d = diameter (cm), h = height (m), and a and b are constants. *Euterpe* leaf and rachis equation forms are $y_i = a(d^2hf)^b$, where f = frond count. Scaling factors a and b differ significantly from 0 ($p < 0.01$) unless noted as (ns). rmse is root mean square error. Diameter measure 'all' refers to all trees having a dbh, not separated into diameter classes.

following analysis: we summed the biomass components (i.e., the actual data) for each of 188 *Hyeronima*, 160 *Cordia*, and 123 *Cedrela*. We then compared those results with the values calculated using our equations to predict the mass of the individual components (leaves, trunks, branches, etc.), which were then summed to yield the predicted totals. Individual tree totals (both actual and predicted) were then summed to get grand totals for hypothetical stands of 188 *Hyeronima*, 160 *Cordia*, or 123 *Cedrela*. The differences were extremely small: *Hyeronima*, 7.26 t actual, 7.36 t predicted (1.4% difference); *Cordia*, 4.22 t actual, 4.22 t predicted (0.04% difference); and *Cedrela*, 3.13 t actual, 3.25 t predicted (3.8% difference).

Height–diameter relationships (Fig. 2) are quite similar among the three dicotyledonous tree species, each of which has a slope very close to unity. They differ most among larger trees. The largest trees sampled were about 30 cm in diameter and 30 m tall. Among the dicotyledonous species, only *Cordia* has a linear height–diameter relationship over the entire range of tree sizes measured (Fig. 2b). The height–diameter relationship of *Cedrela* is linear up to a tree that is about 20 cm in diameter and 21.4 m tall (the terminus of the solid line in Fig. 2a), after which height begins to level off as a function of diameter. Likewise, the relationship for *Hyeronima* is linear up to a diameter of 24 cm and a height of 24.5 m, after which its height–diameter relationship also begins to flatten (Fig. 2c). The palm, *Euterpe*, has a curvilinear height–diameter relationship (Fig. 2d), as one would expect of a life form with limited capability of diameter increment and an apical meristem.

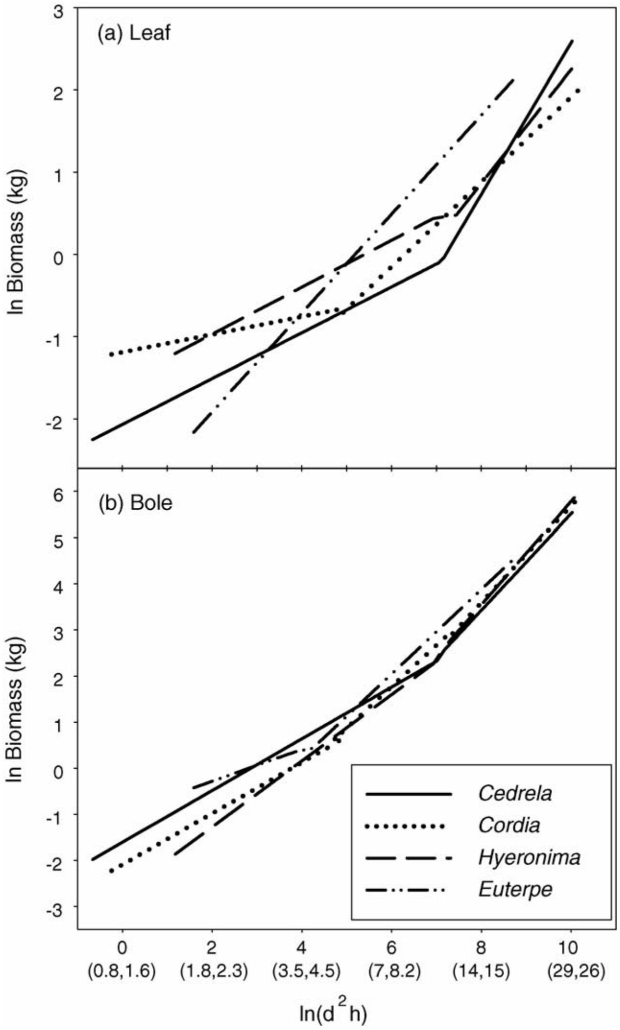

Fig. 1. Allometry of (a) leaves and (b) boles of four species of fast-growing tropical trees. Changes in slope indicate a change in scaling factors. $X = \ln(d^2h)$ or, in the case of *Euterpe* leaves, $\ln(d^2hf)$. Parenthetical numbers along the X axis (d, h) are typical tree sizes for an individual of the $\ln(d^2h)$ value indicated, where d = dbh (cm), h = height (m), and f = *Euterpe* frond count. Trees having only a basal diameter are not included.

The partitioning of biomass differed among the three dicotyledonous species and reflects their contrasting architectures and ecological attributes (Fig. 3). Seedlings of *Cedrela*, for example, invest heavily in roots (thus have a low aboveground–aboveground biomass ratio). Until they are large enough to have a dbh, their shoot–root ratios (off scale to the left of Fig. 3) are nearly constant at about 1.6, after which the ratio increases until it eventually surpasses that of *Cordia* and *Hyeronima* at a dbh of 10–12 cm. Small trees of *Cordia* and *Hyeronima*, in contrast, make a substantial initial investment in foliage, such that seedlings have a shoot–root ratio of 3–5, gradually increasing to ~12–14 when the trees are about 30 cm dbh (Fig. 3).

For some applications of allometric equations, the interspecific differences we dealt with represent an unwarranted degree of fine-tuning. This is often the case, for example, when forest inventory data, involving dozens or even hundreds of species, need to be extrapolated to estimates of biome- or region-wide carbon storage. To help address the needs of such users, we also developed all-species equations. Equations for the combined data of all three dicotyledonous tree species, by component, are available from the authors; here we present only whole tree equations that combine all components: bole, leaves, branches, coarse roots (in the 1-m diameter beneath-trunk cylinder), rachises or petioles, and reproductive parts (Fig. 4). Because this approach combines species having different physiognomies, we deviated from our use of the standard allometric equation parameterized in Table 2 and developed simple linear relationships ($n = 457$): $Y_{\sum} = 1.631 + 0.017\,(d^2h)$, where $Y_{\sum}$ = total biomass, including roots, (kg); $r^2 = 0.98$, and $Y_{\mathrm{A}} = 0.525 + 0.015\,(d^2h)$, where Y_{A} = aboveground biomass (kg); $r^2 = 0.98$.

4. Discussion

Hundreds of equations have been published relating tree biomass to diameter or diameter coupled with height. Almost all of these relationships, whether intended for application to particular species, mixed-composition forests, specific sites, biogeographical regions, or climate-related biomes, are based the allometric equation. Use of the allometric equation is appealing because of its grounding in theory (Pearsall, 1927; Causton, 1985; Niklas, 1994; West et al., 1997), but its application to dicotyledonous trees is problematic for two reasons: first, woody dicots have complicated branching patterns, and second, much of what is considered biomass consists of non-living xylem; both of these factors obfuscate form-function relationships, and both factors change with tree age and stature, as is clear from our data.

In one instance, involving leaves of very small (0–5 cm dbh) *Cordia* trees, the allometric equation was not a satisfactory predictor of biomass ($r^2 = 0.02$; Table 2). The relationship is much stronger for larger trees (i.e., those having a dbh > 5 cm: r^2 of 0.51). What is there about saplings in the 0–5 cm dbh range that might make their leaf mass so unpredictable? *Cordia* is vulnerable to dry-season outbreaks of a hemipteran, *Dictyla monotropidia* (Stål), which leads to leaf necrosis and sometimes complete defoliation. Furthermore, the leaf phenology of *Cordia* is extremely variable, especially in the small-sapling stage and during the 4-month drier season at La Selva.

Not surprisingly, the ability to predict the biomass of large woody components such as boles and coarse roots tends to be stronger than that of smaller, shorter-lived components such as leaves. Foliage biomass, in particular, is susceptible to weather, herbivores, and inter-plant competition. In our densely spaced plantations, it is likely that intraspecific competition influenced crown geometry and therefore the heterogeneity of leaf biomass from tree to tree. Because of the unusually large number of trees sampled, the equations are indicative of the degree of variation to be anticipated among conspecific trees: breakage, reiteration, herbivory, competition, and a number of other factors lead to the irregularity that is typical of species such as these.

The single metric most commonly used for tree allometry is diameter, as is evident in the review (65 species) of Ter-Mikaelian and Korzukhin (1997) and the synthesis (279 equations) compiled by Zianis and Mencuccini (2004).

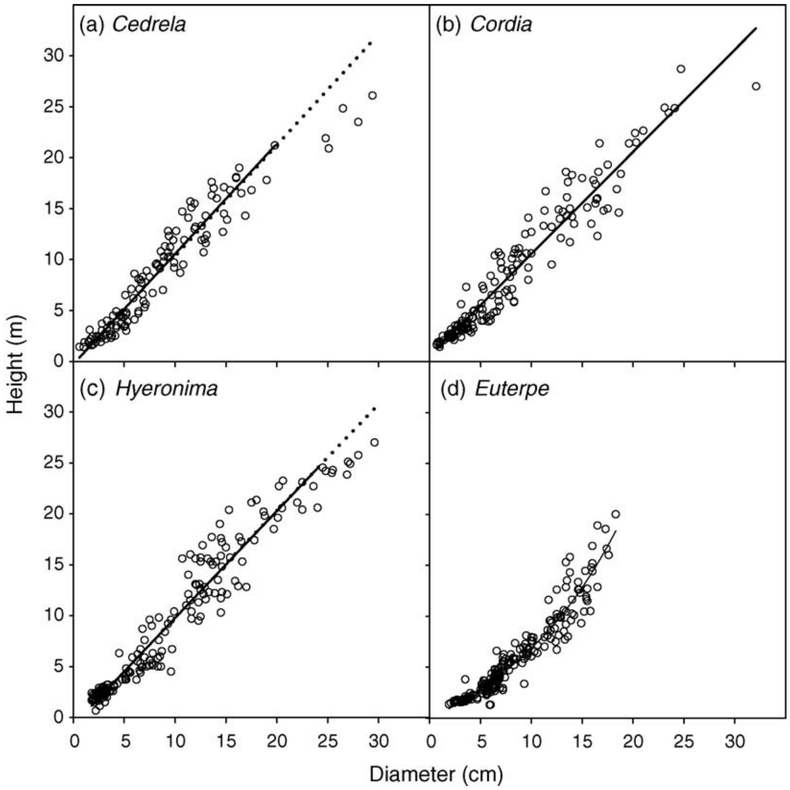

Fig. 2. Height–diameter relationships of four tropical tree species. Dotted line extension indicates the portion of a relationship that departs from linearity. Slopes are very close to unity for all three dicotyledonous tree species: *Cedrela*, 0.97; *Cordia*, 1.00; *Hyeronima*, 1.01. Trees having only a basal diameter are not included.

Statistical fits are generally good, enabling one to use locally developed equations with confidence for the stands from which they were derived. Tree height is more tedious to measure and may not explain more of the variance at the site where the data originated, but its incorporation has the advantage of increasing the equation's potential applicability to different sites (Ketterings et al., 2001). The height (m)–diameter (cm) relationships of our three dicotyledonous tree species (Fig. 2) are similar and unusually steep, having slopes of ~1. This is a significantly steeper height increment per unit increment in diameter than was observed, for example, by Somarriba and Beer (1987) for *Cordia* and probably reflects the excellent quality of our site: fertile soil, abundant rainfall, high temperature, and controal of weed competition.

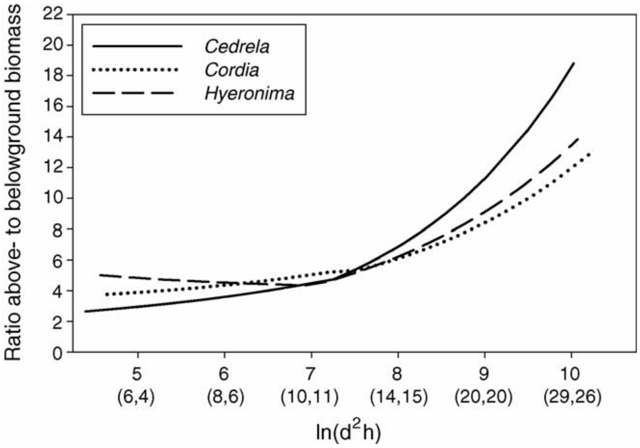

Fig. 3. Change in allocation to aboveground plant parts and coarse roots as a function of tree size for three tropical tree species. Parenthetical numbers along the *X* axis (d, h) are typical tree sizes for an individual of the ln (d^2h) value indicated, where d = dbh (cm) and h = height (m). Coarse roots include only those in a cylinder of 1.0 m diameter immediately beneath the trunk. Ratios for trees having only a basal diameter are not shown.

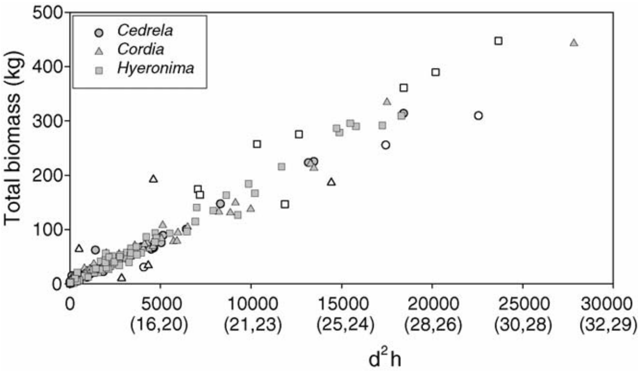

Fig. 4. Total biomass (including coarse roots), three species combined, as a linear function of tree size. Open symbols are values treated as outliers because they deviated by > ± 3 studentized residuals. Parenthetical numbers along the *X* axis (d, h) are typical tree sizes for an individual of the value (d^2h) indicated, where d = dbh (cm) and h = height (m). Coarse roots include only those in a cylinder of 1.0 m diameter immediately beneath the trunk.

Even when height is incorporated into the equation, however, our trees have lower biomass than that predicted by more general equations. For example, for a tree of 25 cm dbh, 22 m tall, and having a specific gravity of 0.52 (the mean of our three dicot species), the most recent mixed-species, mixed-region equation for wet tropical forests developed by Chave et al. (2005) predicts an aboveground biomass of 326 kg, significantly more than the mean of 224 kg predicted by our equations. This difference may be due to the fact that our equations were fitted to relatively small trees (maximum diameter ∼30 cm), whereas the species-diverse data sets used by Chave et al. (2005) included much larger trees, >150 cm dbh. We have confidence in our data, in part because of the huge sample size, and we suspect that the presence of much larger trees in the data assembled by Chave et al. (2005) may lead to overestimation of biomass of smaller trees such as those we sampled. Furthermore, we found that the allometric ratio changed with tree stature, and if such change extends well beyond the upper size of the trees we measured, it is likely that predictions based on constant allometry would fail to predict biomass as accurately as equations based on a narrow range of size classes. Finally, the Chave et al. (2005) datasets specifically exclude plantation-grown trees such as ours. Branches are likely to be shed more readily in dense, monospecific plantations than in diverse natural forests, and this would result in much lower biomass in sympodial species.

Given that all three of the tree species we worked with are fast-growing and have medium-density wood, does it make sense to develop separate equations for each, rather than combining all data into development of a single equation? The answer depends upon the intended use of the estimates. Consider, for example, four trees, one of each species, each of which is 15 cm in diameter. A *Cedrela* of that diameter would be predicted to be 16.0 m tall (Fig. 2) and have an aboveground biomass of 52.7 kg; a *Cordia* of that size would be 15.5 m tall and weigh 52.1 kg; a *Hyeronima* would be 13.1 m tall and weigh 45.0 kg; and a *Euterpe* would be only 12.8 m tall but weigh 47.6 kg. For some purposes, such as regional estimates of biomass, these differences might be well within tolerable limits of error, as might the linear all-species equation, which yielded an aboveground biomass (±95% confidence limits) for a tree of that size of 52.1 ± 13.1 kg. For our research, however, in which we needed to accurately estimate nutrient stocks across treatments of cutting frequency, species richness, and soil fertility in stands of controlled density (e.g., Hiremath and Ewel, 2001, 2002; Bigelow et al., 2003), having separate equations for each component of each species was essential. An approach that might have led to biomass estimates differing by as much as 17% per tree would have been too coarse for our purposes.

Roots sampled by digging soil pits or coring in the interstices between trees are commonly used to estimate root mass, but this approach misses the mass of roots immediately beneath the trunk, and these need to be sampled separately (e.g., Ford and Deans, 1977; Young et al., 1980; Ruark and Bockheim, 1987; Resh et al., 2003). The applicability of the root equations we developed (Table 2) is restricted to the cylinder (1.0 m diameter) immediately beneath the trunk, making our estimates

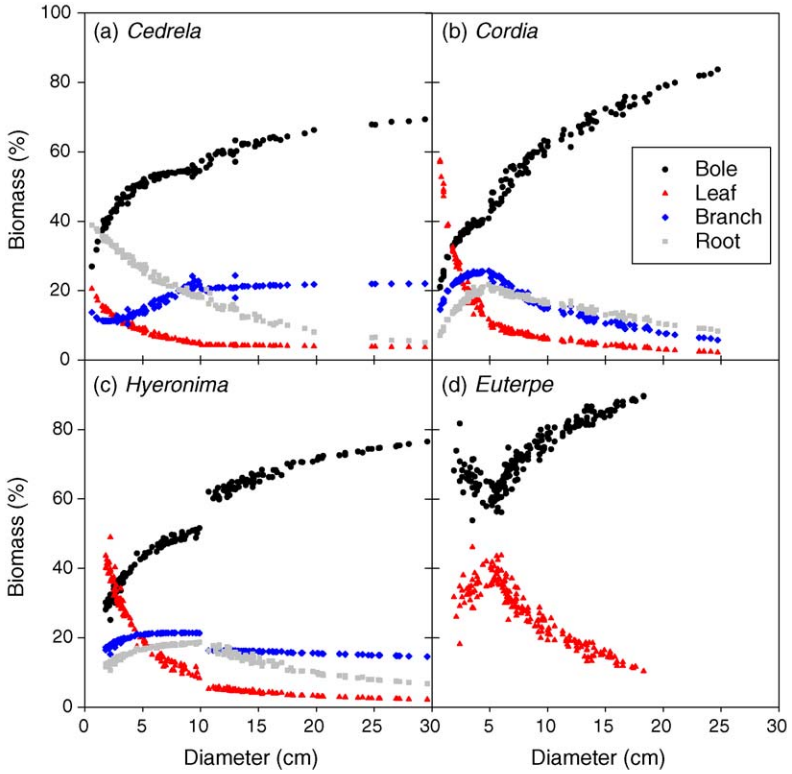

Fig. 5. Distribution of biomass among tree components as a function of tree size for four tropical species. Discontinuities in the lines reflect changes in the scaling constants of the allometric equations used to calculate biomass.

of aboveground-to-belowground biomass ratios high (higher than those reported by Specht and West (2003) and Xiao and Ceulemans (2004), for example) but useful for interspecific comparisons. Ratios of aboveground to belowground biomass for the three dicotyledonous tree species tended to increase with tree size, ranging from just over 2 to about 5 for very small trees (<10 cm dbh) and about 12–20 for trees of ∼30 cm dbh (Fig. 3). *Cordia* and *Hyeronima* behave similarly, but *Cedrela* is different; when very small, it invests heavily in roots (above:below ≈2), which are rich in starch and fuel recovery following *Hypsipyla* attack (Rodgers et al., 1995). As it ages and increases in stature, however, *Cedrela* escapes further attack by *Hypsipyla* and develops heavy branches, resulting in aboveground:belowground ratios of ∼20, which are about 50% higher than those of the other two species.

The proportional distribution of mass among plant parts changes with tree stature and differs among species in interesting ways (Fig. 5). *Cedrela* is the only one of the four species that invests more heavily in roots than in other plant part when very young. The biomass of very young *Hyeronima* and *Cordia* is dominated by foliage, but woody parts soon begin to dominate such by the time these species are 30 cm dbh leaves account for only 1.8–3.4% of their biomass. Bole wood accounts for most biomass in larger individuals of all four species. The fraction of *Cordia* biomass accounted by the bole is still increasing steeply at 25 cm dbh, whereas the contribution of bole mass to total *Cedrela* mass begins level at that size. Total wood of *Cedrela* continues to increase, however, as much of it is allocated to the large branches that result from the highly branched architecture induced by *Hypsipyla* attack. The palm, *Euterpe*, which lacks branches and whose roots-per-shoot were not measured, is dominated by bole tissue throughout, although the ratio between stem and leaf tissue mass approaches constancy as it reaches its maximum diameter of about 20 cm.

Our large sample size, coupled with the sampling of very small (pre-dbh) trees, provide unusually precise estimates of biomass as well as a degree of insight on the dynamics of tree allometry that would not have been forthcoming had we sampled fewer individuals of larger trees. Where biomass estimates are needed for accurate determination of linked factors such as carbon and nutrient storage, or for evaluation of the performance of high-value species such as the four we studied, species-specific equations are very useful. Biomass allocation among plant parts is particularly dynamic in the early phases of growth, and it is then that the resource manager probably has the greatest opportunity to influence a plant's future deployment of carbon.

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