

Interspecific and Inter-site Variation in Wood Specific Gravity of Tropical Trees¹

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ABSTRACT

Variation in climate and soils results in inter-site differences in the assemblages of tree life history strategies within a community, which has important implications for ecosystem structure and dynamics. I investigated interspecific and inter-site variation in wood specific gravity—an easily measured indicator of tree life history strategy—in four Neotropical forests and analyzed its correlates. Mean wood specific gravity (oven-dry weight divided by fresh volume, sometimes also referred to as wood density in the literature) differed significantly among sites, varying inversely with soil fertility and independently of rainfall, seasonality, and temperature. Mean wood specific gravity values were much higher at Kilometer 41, Manaus, Brazil, where soils are extremely poor, than at Cocha Cashu, Peru, Barro Colorado Island, Panama, or La Selva, Costa Rica, where soils are better and mortality rates of trees are higher. Within sites, wood specific gravity varied widely among species. On Barro Colorado Island, among-species variation was significantly, albeit weakly, negatively correlated with sapling and tree mortality and relative growth rates. Altogether, the results suggest that the distribution of tree life history strategies in a community varies substantially among sites, with important consequences for community and ecosystem properties such as aboveground carbon stores.

RESUMEN

La variación climática y edáfica da lugar a diferencias entre sitios con respecto a los ensambles de las estrategias de historia de vida de los árboles de una comunidad, lo cual tiene consecuencias importantes para la estructura y la dinámica del ecosistema. Investigué la variación interespecifica y espacial en la gravedad específica de la Madera—un indicador de fácil medición de la estrategia de historia de vida de los árboles—en cuatro bosques neotropicales y analizé sus factores asociados. La gravedad específica media de la madera (el peso seco dividido por el volumen fresco, frecuentemente llamado “densidad de la madera” en la literatura ecológica) fue significativamente diferente entre sitios, variando inversamente con la fertilidad del suelo, e independientemente de la precipitación, la estacionalidad, y la temperatura. La gravedad específica media de la madera fue mucho más alta en Kilómetro 41, Manaus, Brasil, donde los suelos son extremadamente pobres, en comparación con Cocha Cashu, Perú, Barro Colorado, Panamá, o La Selva, Costa Rica, donde los suelos son mejores y las tasas de mortalidad de los árboles son más altas. Dentro de los sitios, la gravedad específica de la madera varió extensamente entre especies. En Barro Colorado, la variación entre especies estuvo correlacionada negativamente, aunque sólo débilmente, con las tasas de mortalidad y de crecimiento relativo de los árboles juveniles y adultos. En conjunto, los resultados sugieren que la distribución de las estrategias de historia de vida de los árboles en una comunidad varía sustancialmente entre sitios, con consecuencias importantes para características comunitarias y del ecosistema tales como las reservas de carbono.

Key words: Barro Colorado Island; Cocha Cashu Biological Station; intermediate disturbance; landscape-level variation; La Selva Biological Station; life history strategy; lowland tropical forest; Manaus, Brazil; wood density; wood specific gravity.

ALTHOUGH ALL TREE SPECIES HAVE SIMILAR FUNDAMENTAL RESOURCE REQUIREMENTS, they vary greatly in their life history strategies. Variation in life history strategies within communities contributes to the maintenance of diversity (Pacala *et al.* 1996, Loehle 2000, Wright 2001) and determines community-level responses to disturbance, successional patterns, spatial patterns, and carbon storage and flux (Denslow 1996, Fearnside 1997, Moorcroft *et al.* 2001). The tree life history strategies represent-

ed in a forest reflect selection pressures imposed by the abiotic and biotic environment, as well as physiological and phylogenetic constraints on responses to these pressures (Condit *et al.* 1996, Condit 1998a, Chave 1999, Loehle 2000). As conditions vary across the region, selection pressures, the distribution of life history strategies, and community dynamics and structure also vary (Gentry & Emmons 1987; Gentry 1988; Condit *et al.* 1995; Burslem 1996; Wright *et al.* 1998, 2001; Loehle 2000).

Wood specific gravity is a convenient indicator of life history strategy in trees and one with direct importance for ecosystem studies. The basic spe-

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cific gravity of wood is defined as oven-dry mass divided by the mass of water displaced when green and is thus unit-less (Panshin & de Zeeuw 1980). In the literature, oven-dry mass divided by green volume in parallel SI units (*e.g.*, g and cm³; numerically identical to wood specific gravity), is often referred to as wood density (Lawton 1984, Reyes *et al.* 1992, Brown 1997, Turner 2001). Wood specific gravity is highly correlated with the density of carbon per unit volume and is thus of direct applied importance for estimating ecosystem carbon storage and fluxes (Brown 1997, Fearnside 1997, Nelson *et al.* 1999, Baker *et al.* in press). Wood specific gravity is also positively associated with successional position and thereby with species' positions along the continuum from fast-growing, short-lived pioneer species to slow-growing, long-lived climax species (Saldarriaga *et al.* 1988; Swaine & Whitmore 1988; Wiemann & Williamson 1988, 1989a). Low specific gravity woods have lower construction costs, and thus growth rates are inversely correlated with wood specific gravity among tropical tree species (Favrichon 1994, Suzuki 1999). Higher wood specific gravity is thought to confer a survival advantage, reducing the probability of physical damage (Putz *et al.* 1983, Zimmerman *et al.* 1994) and possibly fungal infection (Turner 2001).

The distribution of tree life history strategies in general and of wood specific gravities in particular within a tropical tree community is theoretically expected to vary among sites depending on disturbance regime, climate, and soil fertility. High disturbance rates and high turnover rates are expected to favor faster-growing r-selected species (Connell 1978, Huston 1979), which have relatively low density woods (ter Steege & Hammond 1996). Low soil fertility slows tree growth and lengthens the time saplings are relatively vulnerable, and thus may favor better-surviving K-selected species, which have relatively high density woods. In addition, there may be a direct morphological link; wood specific gravity is higher in individual trees that are growing more slowly than it is in conspecific individuals that grow more quickly (Koubaa *et al.* 2000). Thus, we would expect higher wood densities on less fertile soils. Drier climates select for resistance to drought stress, including the ability of xylem to withstand implosion by negative pressure, which has been shown to be positively correlated with wood specific gravity (Barajas-Morales 1985, Hacke & Sperry 2001, Hacke *et al.* 2001).

Given its basic and applied importance, the relative dearth of knowledge concerning patterns of

wood specific gravity variation among tropical tree species and sites is surprising. Overall, few studies have actually examined how wood specific gravity varies with other life history traits (Turner 2001, Wright *et al.* 2003), and the few studies of inter-site variation have come to contradictory conclusions (Wiemann & Williamson 1989a, ter Steege & Hammond 2001, Wiemann & Williamson 2002). In this study, I used two different approaches to investigate differences among four Neotropical forests in the distributions of wood specific gravity values, specifically testing hypothesized relationships of mean wood specific gravity with climate, soil fertility, and disturbance. At the site where abundant species-level data are available (Barro Colorado Island, Panama), I also examined the correlations of wood specific gravity with tree and sapling growth and mortality rates among species to establish the degree to which it can serve as an indicator trait and to what extent wood specific gravity and other life history traits form part of an integrated strategy.

METHODS

STUDY SITES.—The four sites included in this study are La Selva Biological Station in Costa Rica, Barro Colorado Island in Panama, Cocha Cashu Biological Station in Peru, and Kilometer 41 in Manaus, Brazil (Gentry 1990, Powers 2004). La Selva (LS) is essentially “everwet,” with an average annual precipitation of 4000 mm and only one month in which precipitation dips below 100 mm (McDade *et al.* 1994). The other sites are seasonally wet; Barro Colorado Island (BCI), Cocha Cashu (CC), and Kilometer 41 (KM41) have four-, three- and two-month dry seasons, respectively, with annual precipitation of 2640 (Paton 2001), 2330 (M. Silman, pers. comm.), and 2620 mm (A. de Oliveira, pers. comm.). The mean annual temperature at Cocha Cashu is 23°C (Miles Silman, pers. comm.), whereas the mean at the other three sites is 26°C (McDade *et al.* 1994, Paton 2001). Soil fertility at these sites declines in the order LS > BCI > CC >> KM41 (Powers 2004; Powers & Lerdaun, pers. comm.).

TREE DATA.—At each site, I examined the distribution of wood specific gravities among dicot species both within small samples using a design that was precisely matched across sites and within large but unmatched samples using preexisting research plots. The small, systematic samples encompassed all trees over 30 cm in diameter in six 20 × 70 m

transects censused in fall 2001 as part of a larger collaborative effort (DeWalt & Chave 2004). At each site, the six transects were distributed evenly among two soil types to provide an intra-site habitat contrast (Powers 2004) and were located within mature forest with mean canopy heights above 15 m, avoiding obvious canopy gaps, swamps, and steep slopes.

The larger, unmatched samples included all trees greater than 10 cm in diameter in larger permanent plots totaling between 3 and 50 ha per site. At La Selva, species abundances, basal area, and volume abundances were from the Carbono plots (Deborah Clark and David Clark, pers. comm.): 18 0.5 ha plots, 6 each on relatively fertile Inceptisols on flat old alluvial terraces, relatively infertile Ultisols on ridgetops, and Ultisols on steep slopes (Clark & Clark 2000). On Barro Colorado Island, species abundances, basal areas, and volumes were from the Forest Dynamics Plot, a 50 ha plot in the center of the island (Hubbell & Foster 1983, Hubbell *et al.* 1995, Condit 1998b). This plot was located on mostly well drained upland soils, and consisted mostly of gentle slopes and a high and low plateau (Harms *et al.* 2001). For Cocha Cashu, species abundances (John Terborgh, pers. comm.) were from two 2 ha upland forest plots and five floodplain forest plots, one of 2.25 ha and the others of 2 ha (Terborgh *et al.* 1996). At KM41, species abundances were from three 1 ha upland plots (Alexander de Oliveira, pers. comm.); descriptions of the plots and species lists are given in de Oliveira and Mori (1999).

WOOD SPECIFIC GRAVITY VALUES.—For analyses of wood specific gravity variation within and among sites, each tree in the transect and each species in the large plots was assigned a wood specific gravity value. For trees in the transects, I measured wood specific gravity on wood samples taken from the trees themselves whenever possible (most trees at CC and KM41) and used these values. If no tree-specific values were available (all trees at LS and BCI), I used the mean of values I measured on conspecific trees at the same site when available. In cases in which I took no wood samples from a tree or its conspecifics, I used the average species-specific wood specific gravity reported in the literature. If no tree- or species-specific values were available, the tree was omitted from the analyses. For trees in the large plots, species-specific literature values were used when available, and the averages of my measurements on conspecifics were used when no literature values were available. I tested a variety of

other methods for assigning wood specific gravity values to both transects and large plots (*e.g.*, only literature values; literature values when available, otherwise my measurements; my measurements when available, otherwise literature values), and found that all results reported here are qualitatively insensitive to the manner in which values were assigned.

For my measurements of wood specific gravity, I sampled trees with a 5.15 mm diameter increment borer to obtain cores 10–40 cm long, taken perpendicularly to the bark at between 1 and 1.3 m height. To reduce the risk of subsequent infection or infestation of the tree via the resulting holes, the holes were immediately filled with a fungicidal paste containing 3 percent TCMTB or (2-benzothiazolythio)methyl thiocyanate (Agrofixer, distributed by Indagro, S. A., Costa Rica). Cores in most cases were divided into two or more sections, with divisions perpendicular to the bark (when there were clearly visible changes in wood color or texture along the core, divisions were placed to minimize variation within each section). I cut the ends of each core section perpendicularly to the sides, measured its length, and calculated fresh volume by multiplying the length by the cross-sectional area. Samples were oven-dried at 50 to 70°C (70° in LS, 50° on BCI, 60–70° in Peru, and 65° in Brazil) in air-conditioned rooms (except at LS) to constant weight (36 hours or more), and oven-dry weights were measured to 0.001 g. I then multiplied oven-dry weights by a correction factor to account for the difference in water content at these drying temperatures and calculated humidities compared with the standard drying temperature of 105°C (Appendix A). Wood specific gravity of each core section was calculated simply as corrected oven-dry weight in grams divided by fresh volume in cubic centimeters. I calculated a single value of wood specific gravity for each sampled tree by taking a weighted average of the values measured from different parts of the core, weighting the individual wood specific gravity values by the cross-sectional area of the trunk that they represented. Where replicate cores were taken from the same tree, the values calculated from each core were averaged.

I also searched the literature for values of wood specific gravity for all tree species in the study (Ovington & Olson 1970; Sawyer & Lindsey 1971; Van der Slooten *et al.* 1971; Loureiro & Braga Lisboa 1979; Chudnoff 1980; Gazel 1983; Vink 1983; Augspurger 1984; Barajas-Morales 1987; Wiemann & Williamson 1989a, b; Chichig-

noud *et al.* 1990; INPA 1991; Lorenzi 1992; Malavassi 1992; Favrichon 1994, 1995; King 1996; Brown 1997; Fearnside 1997; Parolin & Worbes 2000; ter Steege & Hammond 2001). Literature values given as wood density at 12 percent moisture content (WD_{12}) were converted to basic wood specific gravity values (SG_{basic}) using the equation $SG_{basic} = 0.861 WD_{12}$, based on 463 values from Sallenave (1971).

ASSESSING WOOD SPECIFIC GRAVITY MEASUREMENT METHODS.—Several aspects of the measurement methods differed substantially from standard methods (Forest Products Laboratory 1999), and thus, I compared my specific gravity measurements with literature values for conspecifics and tested various aspects of my methods. With standard methods, wood samples are typically larger than what can be obtained with a 5 mm increment borer (which has the potential to compress wood); samples are most often taken as a cross-section of the whole tree rather than only outer sapwood (wood specific gravity can change with depth within the tree; Wiemann & Williamson 1989a, b); volume of cores is measured by water displacement rather than dimensional measurements; and oven-drying is usually done at 102–105°C. I chose to use nonstandard methods in order to allow for rapid, nondestructive sampling of trees in remote sites having minimal local facilities.

I used Pearson correlations and model 2 linear regressions to compare my measured specific gravity values with literature values when both were available. Model 2 regression was appropriate because there is variation within both literature values and my measurements. Because wood density varies within species among sites, among trees, and even within trees, perfect agreement was not expected. I thus conducted regressions and correlations of specific gravity values from each literature source and the average of the remaining sources to assess the typical level of agreement among different sources.

WOOD SPECIFIC GRAVITY VARIATION WITHIN AND AMONG SITES.—For each site, I calculated summary statistics (means, standard deviations, minima, and maxima) for the distribution of tree wood specific gravity values in the transects and (separately) in the large plots. Means and standard deviations were calculated by species in as many as four ways: either unweighted or weighted, with weighting by the abundance of trees, basal area, or estimated wood volume. Basal area was calculated as pi times the

radius squared, usually measured at 1.3 m height. Wood volume was estimated as basal area times estimated height, H, where height was estimated from diameter using a regression equation fitted to BCI data for 1000 trees (Chave *et al.* 2003): $H = 41.7 * [1 - \exp(-0.058 * D^{0.748})]$. I used one-way analyses of variance (ANOVAs) to test for differences in means among sites and nested ANOVAs to test for differences between soil types within sites for the small plot data set. I performed Bartlett's test for homogeneity of variances on unweighted means only.

RELATIONSHIP BETWEEN WOOD SPECIFIC GRAVITY AND DEMOGRAPHIC RATES.—For BCI, I analyzed the relationship of wood specific gravity to growth and mortality rates across dicot species. I calculated growth and mortality rates from 50 ha plot data for 1990 and 1995 censuses (Hubbell *et al.* 1995) for two size classes: "trees" from 10 to 200 cm diameter and "saplings" from 1 to 5 cm diameter (excluding shrub and treelet species that may reproduce in this size class). Growth rate here is the mean relative growth rate of individuals on the 50 ha plot between 1990 and 1995, calculated as the difference in the logarithms of the diameters of the 1990 and 1995 censuses, divided by the time interval. Mortality rate is the instantaneous mortality rate on the 50 ha plot between 1990 and 1995, calculated as the log of the number of individuals in 1995 minus the log of the number of individuals in 1990, divided by the time interval. All individuals were included in mortality rate calculations. For growth rate calculations, individuals with multiple stems, major stem breaks, irregular stems, and buttresses were excluded because they compromise the accuracy of the diameter measurements in capturing relative growth rate; individuals with large negative growth (>2 cm) were also excluded. After excluding species with small sample sizes (<20 individuals for growth or <50 for mortality), I performed linear regressions on log transformed data to assess the correlations of species' wood specific gravity with their average growth and mortality rates. I also performed regressions in which growth and mortality points were weighted by the number of individuals they represented; in this case, all species were included.

All analyses were performed using the statistical package R 1.7.1 (Venables *et al.* 2002).

RESULTS

ASSESSMENT OF THE WOOD SPECIFIC GRAVITY MEASUREMENT METHODS.—There were 90 species for

which I had both literature values of wood specific gravity and my own measurements. The correlation between the two was 0.82; the model 2 regression slope was 1.01 and the intercept was 0.0042. These values are not significantly different ($P > 0.10$) from the averages of comparisons of any given literature source with the average of all other sources. The correlations averaged 0.87, with a model 2 regression slope of 1.004 and an intercept of 0.0047. Thus, it appears that my measurements showed a trend towards higher variance than literature values, but were unbiased.

AMONG-SITE VARIATION.—The mean wood specific gravities in both the transect and large plot data sets varied significantly among sites for all weightings of species. (For the transects, $F_{3, 166} = 30.0, 43.0, 26.6,$ and 23.5 for unweighted, tree-weighted, basal area-weighted, and volume-weighted means, respectively, with $P < 0.0001$ in all cases. For the large plots, $F_{3, 458} = 27.7$ and 9.55 for unweighted and tree-weighted means, respectively; again with $P < 0.0001$ in all cases.) This variation was due mostly to the significantly higher wood specific gravities at KM41 (Table 1). Bonferroni-corrected post hoc tests consistently found that means at KM41 were significantly higher than those at every other site. In the transect data sets, CC was also significantly different (higher) than LS among all weighted means, and significantly different (higher) than BCI for basal area- and volume-weighted means. In the large plot datasets, no other differences were significant. Bartlett's test found no significant differences among sites in the variance of wood specific gravity among species in either the transect or large plot data ($K = 2.24$ and 1.19 , respectively; $P > 0.10$ in both cases). Within sites, there was no significant effect of soil fertility on mean wood specific gravities of any kind.

CORRELATES OF AMONG-SPECIES VARIATION.—Wood specific gravity was significantly correlated with sapling relative growth rate ($N = 80, r = -0.50, P < 0.001$) and sapling mortality ($N = 58, r = -0.44, P = 0.007$) on Barro Colorado Island (Fig. 2A, C), although the proportion of the among-species variance in these demographic characters explained by wood specific gravity in a log-log regression remained relatively low. Wood specific gravity was also more weakly related with adult growth ($N = 65, r = -0.34, P = 0.006$) and adult mortality ($N = 51, r = -0.28, P = 0.04$; Figure 2B, D). In the weighted regressions incorporating all species, results were generally qualitatively sim-

TABLE 1. Summary statistics of wood specific gravity values for trees over 30 cm in diameter on the transects censused in 2001 (a) and trees over 10 cm in diameter in the permanent large plots (b) at each site. SD is the standard deviation. The numbers in parentheses are the percentage of species, trees, basal area, and volume, respectively, for which wood specific gravity values were available and thus included in the calculations; in the case of species and trees, the total number found on the plots is given. The total number of species is the number of identified species plus an estimate of the number of distinct species among the remaining unidentified morphospecies.

	La Selva	Barro Colorado Island	Cocha Cashu	Kilometer 41
(a) Transects				
Minimum-Maximum	0.27–0.74	0.28–0.84	0.36–0.94	0.39–1.05
Species-level $\bar{x} \pm$ SD	0.48 \pm 0.14 (70% of 23)	0.52 \pm 0.16 (74% of 35)	0.61 \pm 0.14 (98% of 49)	0.75 \pm 0.13 (98% of 82)
Tree-level $\bar{x} \pm$ SD	0.46 \pm 0.09 (90% of 68)	0.52 \pm 0.15 (85% of 67)	0.59 \pm 0.14 (99% of 82)	0.74 \pm 0.12 (98% of 112)
BA-weighted $\bar{x} \pm$ SD	0.47 \pm 0.09 (88%)	0.51 \pm 0.16 (89%)	0.61 \pm 0.15 (99%)	0.73 \pm 0.13 (99%)
Volume-weighted $\bar{x} \pm$ SD	0.47 \pm 0.09 (87%)	0.51 \pm 0.16 (90%)	0.61 \pm 0.15 (99%)	0.72 \pm 0.14 (99%)
(b) Plots				
Minimum-Maximum	0.25–1.11	0.12–0.92	0.27–0.91	0.33–1.08
Species-level $\bar{x} \pm$ SD	0.56 \pm 0.17 (34% of 211)	0.54 \pm 0.17 (53% of 226)	0.56 \pm 0.16 (40% of 249)	0.70 \pm 0.17 (35% of 492)
Tree-level $\bar{x} \pm$ SD	0.53 \pm 0.11 (47% of 4290)	0.54 \pm 0.13 (76% of 21,455)	0.53 \pm 0.14 (44% of 6378)	0.71 \pm 0.16 (21% of 3832)
BA-weighted $\bar{x} \pm$ SD	0.54 \pm 0.11 (70%)	0.50 \pm 0.16 (85%)		
Volume-weighted $\bar{x} \pm$ SD	0.54 \pm 0.11 (72%)	0.48 \pm 0.16 (86%)		

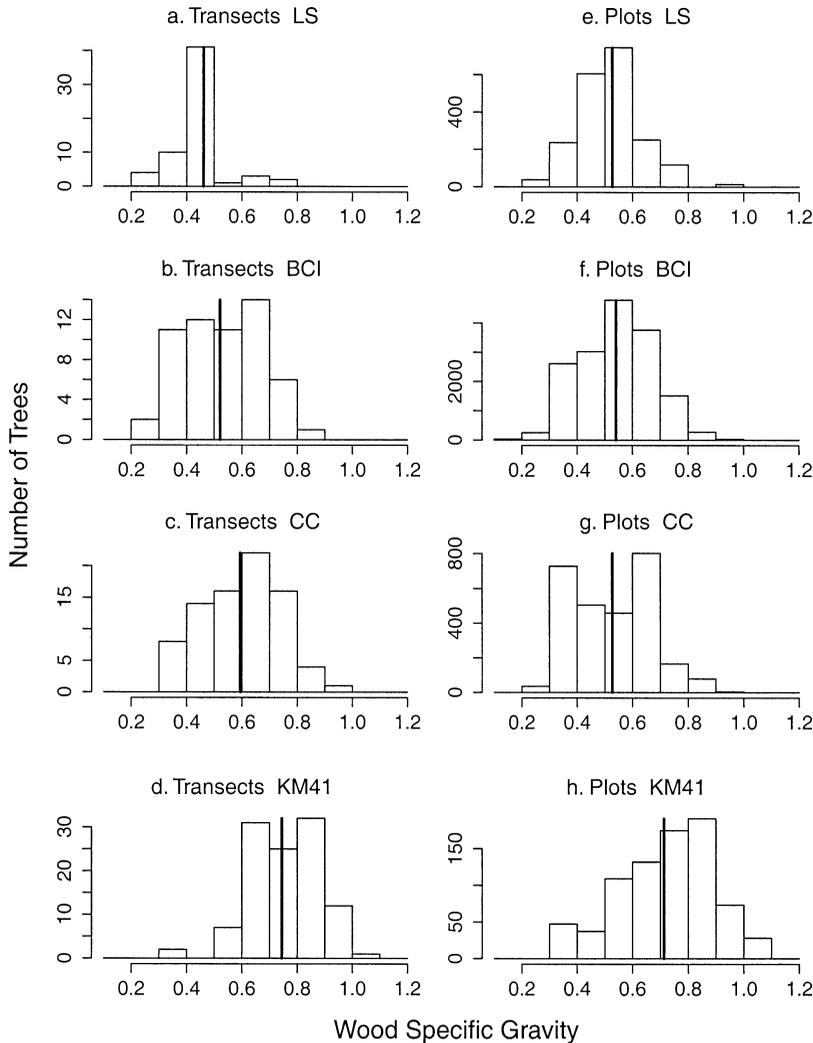


FIGURE 1. Wood specific gravity values of trees compared among sites in both the transect and large plot data sets. Heavy vertical lines indicate the means.

ilar, albeit weaker, among saplings (sapling RGR: $r = -0.15$, $P \geq 0.10$; sapling mortality: $r = -0.38$, $P = 0.003$; adult RGR: $r = -0.32$, $P = 0.008$; adult mortality: $r = -0.30$, $P = 0.03$).

DISCUSSION

WOOD SPECIFIC GRAVITY SAMPLING METHODS.—The rapid, low-impact, low-tech sampling protocol used in the transects produced estimates of wood specific gravity values that tended towards higher errors than the standard protocol, but were unbiased. None of the results reported here were sensitive to

the additional variation potentially introduced by the measured values. Thus, this protocol may prove useful in further studies in which an approximate estimate of wood specific gravity is needed and destructive sampling is not possible or when appropriate equipment (high-temperature drying ovens and high-precision balances) is not available at the field site.

The site-specific means and variances of wood specific gravity were somewhat different depending on how species were weighted (Table 1), reflecting different average abundances and tree sizes of species having different wood specific gravity. There

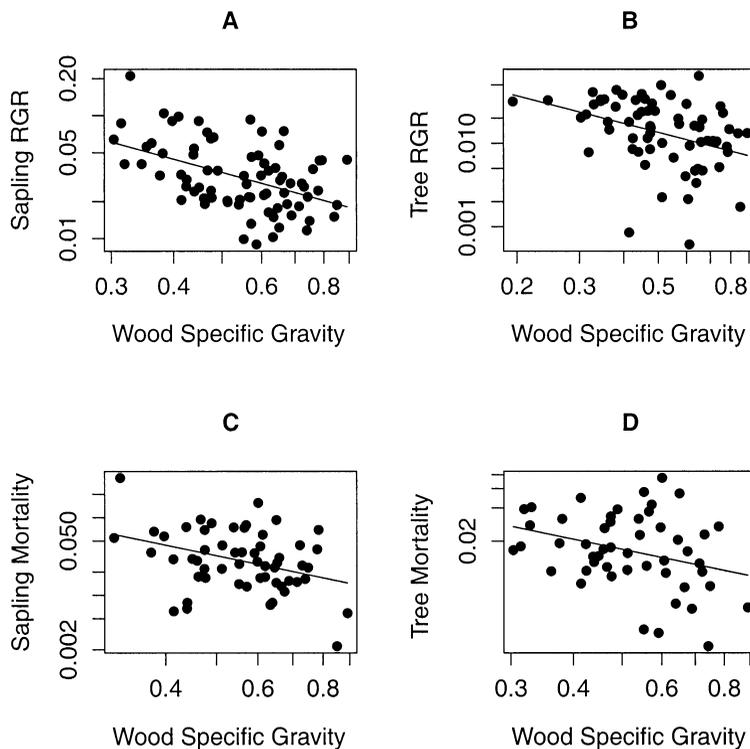


FIGURE 2. Relationship of wood specific gravity to sapling (1–10 cm DBH) and tree (>10 cm DBH) growth and mortality between 1990 and 1995 in the Forest Dynamics Plot on Barro Colorado Island. Species were included in the growth rate analyses only if 20 or more individuals could be used, and in the mortality rate analyses only if 50 or more individuals could be used. For sapling analyses, species that became reproductive below 5 cm DBH were also excluded.

was no significant relationship between wood specific gravity and abundance at any site; however, there were opposing trends, which were reflected in the differences between unweighted and tree-level means; more abundant species tended to have lower specific gravities at LS and CC, somewhat higher values at KM41, and similar values on BCI. On BCI, wood specific gravity was negatively related with total basal area among species (Table 1; results not shown). Baker *et al.* (in press) found similar differences within Amazonia; in eastern Amazonia, larger trees had relatively higher wood specific gravity than the community as a whole, while in northwestern Amazonia, they had relatively lower wood specific gravity. Different means are most appropriate for different questions; *e.g.*, for biomass calculations, site mean wood specific gravity values should ideally be weighted by wood volume. Results here suggest that for some sites, unweighted species means alone will prove a poor approximation of other means and should be used with caution.

Finally, and perhaps most importantly, mean wood specific gravity values at some sites were significantly impacted by the choice of which species to include. Comparisons of plots within sites showed that plot location appears to have a small effect (results not shown), although within-site soil fertility differences did not explain variation within the more systematically placed transects. Because sample sizes in the transects were small, our estimates of means there were also expected to show relatively high variation around the true mean, potentially contributing further to differences from large plot means. Further, the avoidance of gaps in placing the transects was expected to produce a slight upward bias in wood specific gravities there relative to the large plots, although no such difference was consistently observed. In part, the differences between the transects and large plots may also reflect biases in which species are included in literature studies of wood specific gravity (for most species in large plots, only literature values were available).

Both of the methods of obtaining site-specific means of wood specific gravity values employed in this study had problems. The transect samples were very small, and relied in many cases on crude measurements of wood specific gravity. On the other hand, wood specific gravity values were available for over 70 percent of species and over 85 percent of trees, basal area, and wood volume at each site in these samples; and the transect design was consistent at all sites. In contrast, the large plot data sets provided larger samples of trees and species; however, plot sizes and locations varied by site, and wood specific gravity values were available for as little as 36 percent of the species and 22 percent of the trees. The concordance of results obtained using these two disparate approaches having complementary faults provides stronger support for the observed among-site differences than either approach alone would provide.

VARIATION IN WOOD SPECIFIC GRAVITY AMONG SITES AND ITS CORRELATES.—Mean wood densities varied strongly among sites, due mostly to the much higher values at KM41. The ranking of mean wood specific gravity among sites was consistent with soil fertility and total adult mortality (which is directly related to gap formation rates), but not with rainfall, seasonality, or mean temperature. KM41 was the only site with geologically old, mineralized soils and thus had much lower soil fertility than the Central American and Peruvian sites, which had overlapping measurement values (Powers & Lerdau, pers. comm.). Similarly, adult tree mortality rates were much lower at KM41 (1.2%) than at the other three sites, which all had similar values: 2.03% at LS > 1.98% at BCI > 1.95% at CC > 1.2% at KM41 (Gentry 1990, Leigh 1999, J. Terborgh, pers. comm.). Thus, the results can be considered to support either or both the hypotheses that disturbance rates or soil fertility drive community-level patterns in wood specific gravity. Differences in adult tree mortality rates may be a consequence rather than a cause of differences in wood specific gravity, reflecting higher mortality rates of low specific gravity species (Fig. 2) rather than higher external disturbance forcing.

The few previous studies examining variation in mean wood specific gravity relative to soil fertility and disturbance over multiple sites have come to conflicting conclusions. In one study in the Peruvian Amazon, Woodcock (2000) found differences in mean wood specific gravity between stands of different successional stage, but not among different soil types. In perhaps the best study of land-

scape variation in wood specific gravity to date, ter Steege and Hammond (2001) found that variation in tree-weighted mean wood specific gravity among 72 plots in Guyana was unrelated to soil fertility but was related to diversity; the more diverse forests in south Guyana had lower average wood specific gravity as well as lower average seed mass. Because small seed size and low wood specific gravity are characteristics of superior colonizers, they concluded that these forests had higher disturbance rates and that the higher disturbance led to higher diversity (intermediate disturbance hypothesis) as well as lower community average wood specific gravity. As ter Steege and Hammond (1996) showed in a simulation study, higher disturbance rates disproportionately limited recruitment of slower-growing, and thus denser-wooded, species. Unfortunately, there are no independent data on disturbance rates for the study locations to verify the hypothesis that differences in disturbance explain the variation in diversity and wood specific gravity. Overall, the results of ter Steege and Hammond (2001) are exactly opposite to those found in the present study, in which wood specific gravity was higher in sites with lower soil fertility, lower disturbance rates, and higher diversity. This may reflect differences in the spatial scale of sampling. In a study of 56 plots ranging in size from 0.4 to 9 ha, Baker *et al.* (in press) found significantly higher wood densities in southern and eastern Amazonia than in northwestern Amazonia, and related this to changes in generic composition; however, they did not investigate relationships with any environmental factors. Additional work is clearly needed to determine what patterns prevail at which scales.

The accumulating evidence suggests that within the tropics, seasonality and rainfall do not explain large-scale regional variation in wood specific gravity. It had been suggested that the degree of seasonality and the magnitude of resulting drought stress may affect wood densities because of the link between wood specific gravity and xylem structure. Narrower vessels have lower conductances, but a greater number of vessels may provide insurance against catastrophic xylem dysfunction—specifically, embolism. Barajas-Morales (1985, 1987) found that trees of a deciduous forest at Chamela, Mexico, had shorter and narrower vessel elements, greater vessel wall thickness, shorter fibers and rays, greater abundance of fibers and rays, and also higher wood specific gravity than trees of the wet forest at Los Tuxtlas, Mexico. In the current study, however, the least seasonal site with highest rainfall (La

Selva) and the most seasonal site (BCI) had the lowest wood densities, whereas the highest wood densities were at a site with intermediate seasonality (KM41), where rainfall was very similar to two of the other sites (BCI and Cocha Cashu). Ter Steege and Hammond (2001) found no association between tree-level mean wood specific gravity and rainfall among 72 sites in Guyana. Ter Steege and Hammond (2001) also pointed out that there was no evidence for higher community average wood specific gravity in deciduous versus evergreen forests in Brazil (Fearnside 1997). Williamson (1984) also found no differences in the distribution of wood densities between wetter and drier sites in Costa Rica. In contrast, Wiemann and Williamson (2002) found that species-level mean wood specific gravity did vary with mean annual precipitation among eight tropical sites.

Differences in results among studies may be explained in part by differences in how mean wood specific gravity was calculated. Some studies averaged simply by species (*e.g.*, Wiemann & Williamson 2002), while others weighted by abundances, effectively averaging over trees (*e.g.*, ter Steege & Hammond 2001). Further, some studies excluded high proportions of trees or species for lack of specific gravity data.

VARIATION IN WOOD SPECIFIC GRAVITY AMONG SPECIES AND ITS CORRELATES.—Variation in wood specific gravity among species within sites was greater than variation among sites. This variation was significantly associated with demographic traits that reflect species life histories—specifically, growth and mortality—among BCI tree species (Wright *et al.* 2003). In combination, this suggests that wood specific gravity is associated with life history, and that the arrays of life history strategies selected in different sites are overlapping, but not identical.

Demographic traits such as growth and mortality are imperfect indicators of life history strategy since they are greatly influenced by resource levels, which vary stochastically among individuals and systematically among species (Wright *et al.* 2003). Saplings of pioneer species are much less likely to be located in the shaded understory than are saplings of climax species (Welden *et al.* 1991). Thus, the higher average growth of the pioneers in part reflects better conditions for growth, while the higher mortality occurs despite better conditions. Better indicators of life history strategy are the growth and mortality rates under constant conditions, which can be estimated from data on resource availability and growth for multiple individ-

uals (Pacala *et al.* 1994, Kobe *et al.* 1995). Unfortunately, few such data are available for the vast majority of tropical tree species.

Phylogenetic relationships may confound associations of wood specific gravity with other traits among species. Silvicultural studies have shown that there is genetic variation in wood specific gravity, and indeed, that most variation in wood specific gravity is genetic (*e.g.*, Yang *et al.* 2001). Wood specific gravity appears to be quite conserved (D. Ackerly, pers. comm.) and is highly consistent within genera (Baker *et al.* in press). Future studies should quantify this conservatism and take phylogenetic relationships into account using analyses of independent contrasts (Felsenstein 1985, Harvey & Pagel 1991).

CONCLUSIONS.—These results show that wood specific gravity is correlated with other aspects of tree life history strategy among species and varies significantly among wet tropical forests. Among the four Neotropical sites examined here, increases in wood specific gravity were associated with decreases in soil fertility and tree mortality rates. Overall, however, there are no clear explanations for differences in wood specific gravity among sites, and it seems likely that different factors may act at different scales. This inter-site variation will strongly affect biomass estimation at the sites (DeWalt & Chave 2004). Although wood specific gravity has attracted relatively little attention from ecologists to date, extensive data have been collected by government agencies and nongovernmental organizations in many countries for more than a century as part of applied surveys of wood properties. These data represent an untapped resource for ecological studies of among-species and among-site variation in wood specific gravity and its correlation with species' life history strategies and site characteristics.

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APPENDIX A

ADJUSTING OVEN-DRY WEIGHTS FOR OVEN TEMPERATURE AND HUMIDITY

The moisture content of wood in equilibrium varies with temperature and relative humidity. Because basic wood specific gravity values should be calculated using wood dried at temperatures of 100 to 105°C and my samples were dried at 50 to 70°C, my oven-dry weights were higher than those that would have been obtained at the standard temperature. I calculated correction factors to compensate for the difference in drying procedures.

First, I calculated the relative humidity inside the ovens at each site. I assumed that there was

some exchange of air between the oven interior and the room in which it was sitting, so that the absolute moisture content of the air was the same in both places. In air-conditioned rooms, I assumed the temperature was 22°C and the relative humidity 100 percent. At LS, where ovens are not in an air-conditioned space, I assumed the relative humidity was 93 percent and the ambient temperature 26°C (the annual mean). Given the oven temperatures of 70°C for LS, 50°C for BCI, and 65°C for CC and KM41, I calculated relative humidity values of 10, 22, and 11 percent, respectively. In contrast, the relative humidity of an oven at 105°C in a similarly air-conditioned room (22°C and 100% RH) is just 2.2 percent, and ideally the rel-

ative humidity in a drying oven should be 0 percent.

Second, I used a formula and table in the USDA Forest Service Wood Handbook to calculate the equilibrium moisture content of wood in the drying ovens used at each site and in a standard drying oven. The values of equilibrium moisture content expressed in percentages as the mass of wa-

ter divided by mass of (standard) oven-dry wood are ca 2.1 percent at LS, 3.9 percent at BCI, and 1.8 percent at CC and KM41, compared with 0 to 0.2 percent for standard conditions. Thus, to obtain standard oven-dry masses from my oven-dry masses, I multiplied my values from BCI by 0.96 and my values for other sites by 0.98.