WOOD SPECIFIC GRAVITY OF TREES AND FOREST TYPES IN THE SOUTHERN PERUVIAN AMAZON

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ABSTRACT — Estimates of terrestrial biomass depend critically on reliable information about the specific gravity of the wood of forest trees. The study reported on here was carried out in the southern Peruvian Amazon and involved collection of wood samples from trees (70 spp.) in intact forest stands. Results demonstrate the high degree of variability in specific gravity (oven-dry weight/green volume) in trees at single locations. Three forest types (swamp, high terrace forest with alluvial soil, and sandy-soil forest) had values close to the average reported for tropical forest woods (.69). Two early successional forest types, which make up as much as 12% of the total vegetated area in this part of the Amazon, had values significantly lower (.40). An increase in specific gravity with increasing age of the tree, which has been reported in some species of tropical-forest woods, is seen in a positive relationship between specific gravity and diameter for a species prevalent in one plot. Increases in specific gravity with tree and forest age may be significant in estimating changes in carbon stores over time.

Key-words: wood specific gravity, tropical forest biomass, Southern Peruvian Amazon

Densidade Específica da Madeira de Árvores e Tipos de Floresta no Sul da Amazônia Peruana

RESUMO — Estimativas de biomassa em ecossistemas terrestres dependem de informações confiáveis sobre a densidade da madeira das árvores. Neste estudo, realizado no sul da Amazônia peruana, foram coletadas amostras de madeira de árvores (70 spp.) em florestas intactas. Os resultados demonstram a grande variabilidade na densidade espec'fica (peso seco / volume fresco) entre as árvores de um único sítio. Três tipos de floresta (baixio de terraço alto, floresta sobre terraço aluvial alto argiloso, e floresta de terra firme sobre solo arenoso) tiveram valores de densidade específica próximos à média reportada para madeiras de floresta tropical (0,69). Duas florestas em fase sucessional, que constituem até 12% da área vegetada nesta parte da Amazônia, tiveram valores significativamente menores (média de 0,40). Um incremento da densidade específica com a idade da árvore, reportada anteriormente para algumas espécies de árvores de floresta tropical, foi também encontrado para uma espécie avaliada neste estudo, com uma relação positiva entre sua densidade específica e seu diâmetro. Os aumentos de densidade específica com a idade, tanto das espécies como das florestas, podem ser importantes para estimativas de mudanças temporais nos estoques de carbono.

Palavras-chave: Densidade específica de madeira, biomassa de floresta tropical, Amazônia peruana

INTRODUCTION

Information on the wood specific gravity of forest trees, an important factor influencing the amount of forest biomass, is available in various databases around the world (Detienne & Chanson, 1996). Such sources, however, are not complete and include only a portion of the diversity of tree species that occur in the tropics (Fearnside, 1997). Field-based research is an additional source of information about this important quantity.

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This study reports values for wood specific gravity for a variety of forest types in the southern Peruvian Amazon.

METHODS

The field sites were located in the Tambopata-Candamo Reserve in the southern Peruvian Amazon. This area of the Amazon has very high biodiversity (574 bird species within walking distance of the lodge where I was based), some portion of which is undoubtedly attributable to the diversity of forest types present. The vegetation types sampled are as follows (Fig. 1)

1) An area of low, early-successional vegetation growing alongside the Rio La Torre on a sandbar deposit. Dominant taxa are *Cecropia* and *Salix* spp. and other taxa typical of disturbed riverine habitats. [n = 32 (8 spp.), mean dbh = 10 cm]

2) Mature floodplain forest growing along the La Torre on alluvial soils within a meander bend. The smooth-barked *Capirona* is a distinctive element of these gallery forests. There is standing water at some times of the year and severe flooding occurs at a recurrence interval estimated at 10-12 years. A plot for long-term ecological monitoring is near the transect (Phillips & Gentry, 1994; Phillips, 1999). [n = 34 (22 spp.), mean dbh = 22 cm]

3) Clay-soil forest on an "upper terrace." This surface is actually an ancient floodplain of the Tambopata with an age estimated at 40,000 or more years (Salo & Kalliola, 1990). *Pseudolmedia laevis* and *P. macrophylla* are dominant species at the site. [n = 36 (21 spp.), mean dbh = 23 cm]

4) Sandy-soil forest. Away from the main river system, blackwater rivers drain substrates distinctly sandy in nature. The sandy-soil forest sampled here was growing alongside the Aguasnegras River approximately 6 km from the confluence of the Tambopata and the La Torre. [n = 29 (20 spp.), mean dbh = 24 cm]

5) Swamp forest on an upper terrace. This floodplain feature may be a meander lake or an ancient channel. The palm *Mauritia flexuosa* is common in these swampy areas. The trees sampled are adjacent to a permanent monitoring plot (Phillips & Gentry, 1994; Phillips, 1999). [8 spp. sampled, mean dbh = 29 cm]

Stand surveys were carried out by sampling on either side of a 60-m line transect. For the low vegetation along the riverbank, the transect was laid out parallel to the river's edge where all the trees present were small in diameter (<10 cm). In the higher-statured forests, sampling was limited to trees with diameters >10 cm.

Wood samples were obtained by harvesting a section of the trunk, in the case of the small-diameter riverine trees, or by means of a 12-mm increment borer, in the case of the larger trees. In all cases, the material collected was at breast height and represents one sample per tree. Cores were sealed and stored frozen until measurements could be made so that the wood remained hydrated and above the fiber saturation point. Leaves were

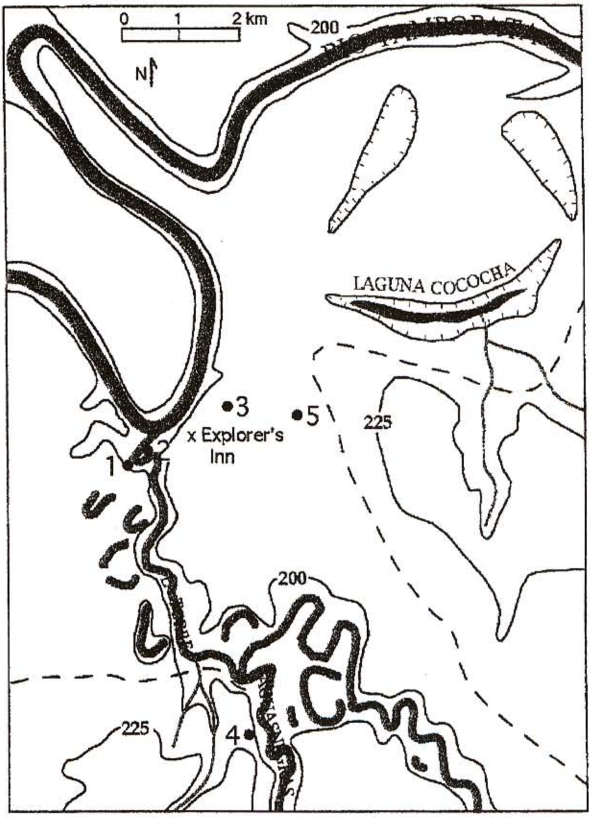

Figura 1. Location of plots: 1) low vegetation growing along a river bank; 2) mature floodplain forets; 3) high-terrace forest growing on rich alluvial soil; 4) sandy-soil forest; and 5) swamp forest.

also obtained and identifications are available for the majority of the trees sampled; voucher specimens are in the herbarium in the Department of Forest Sciences, National Agrarian University-La Molina in Lima (MOL).

Specific gravity is determined here as oven-dry weight/green volume (with specimens oven-dried at 103° C for 24 hr). This measure represents density relative to water(density of 1 g.cm^{-3}) and thus is dimensionless. Values are for the outer sapwood and were determined on pieces approximately 2 cm long.

Altogether, 130 trees were surveyed and values of specific gravity were obtained for 70 species. Wood specific gravity for the various forest types is presented by species. Differences between forest types were tested for by analysis of variance (Tukey-Kramer HSD test with the significance level set at .05). Values for specific gravity averaged by individual were also determined and represent either the average of all individuals present or a value that is weighted by number of individuals of each species present in the plot. Specific gravity for the species studied are presented in the appendix.

RESULTS

Range of variation in specific gravity. Specific gravity is known to be a variable quantity (Detienne & Chanson, 1996), especially in tropical forests (Fearnside, 1997). Wood specific gravity of the Peru woods (Fig. 2) varies by an order of magnitude, and variation of almost this degree is present at single locations.

An example of the degree of variation present is seen in plot 2, where the least dense wood is that of *Erythrina ulei* with value of .10 (close to that of *Ochroma*) and the most dense that of *Minquartia guianensis* with specific gravity of .70. The difference between these woods is quite apparent under the microscope since the extent of stained (i.e., cell wall) material correlates well with specific gravity. The degree of variation exhibited is rather remarkable considering that both species reach the forest canopy and compete with one another for light and water. Clearly, different adaptive types are represented. The light-wooded *Erythrina* stores large amounts of water in its wood and during the short dry season, drops its leaves and is able to stay hydrated due to decreased evaporative demand. *Minquartia*, on the other hand, is evergreen and continues to photosynthesize during the dry season, aided by thick leaves resistant to desiccation. Other researchers have also related the range in specific gravity in tropical forests to niche partitioning (Williamson, 1984; Borchert, 1994), with Borchert (1994) recognizing a variety of functional types in dry tropical forest based on differences in specific gravity and other aspects of tree biology.

Differences between vegetation types. The sample plots included two early successional associations growing on low riverside terraces subject to frequent to occasional flooding. Trees in these plots have values of specific gravity (average of .40) significantly lower than those in mature clay-soil forest, swamp forest, or sandy soil forest (Fig. 2). All of the latter have values of specific gravity much closer to averages for tropical forest woods (.65-.69; Brown & Lugo, 1992; Fearnside, 1997). In this part of the Amazon, as much as 12% of the forests may be actively disturbed by river processes (Salo & Kalliola, 1991) and thus in early stages of forest succession characterized by trees with lower-specific-gravity wood.

Many pioneer species have light woods. Cottonwood and aspen (*Populus* spp.) are temperate-latitude examples, although these woods, with specific gravity about .30, are not as light as the lightest tropical woods. It also appears to be generally the case that early successional forests, even in areas of high diversity like the study area, are characterized by trees with low specific gravity wood. Saldarriaga (1989) has reported similar results for areas recovering from clearing in the northern (Venezuelan) Amazon. That study showed that specific gravity averaged .54 in the 20 years after clear-

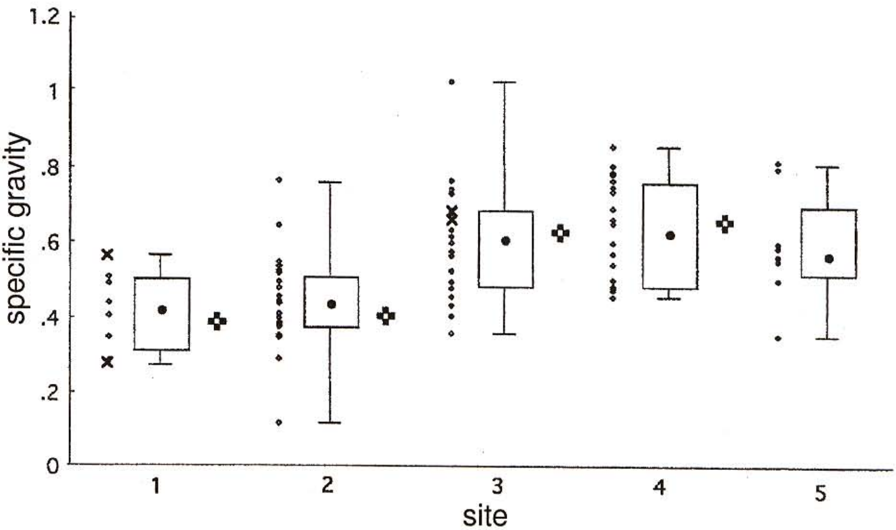

Figura 2. Specific gravity by species for different vegetation types in Tambopata. 1) low riverside vegetation (8 spp., n= 32); 2) floodplain forest growing on a low terrace (22 spp., n= 34); 3) clay-soil forest on upper terrace (21 spp., n= 36); 4) sandy-soil forest (20 spp., n= 29); 5) swamp forest on upper terace (8 spp.). For each site, plots are as follows: (left) specific gravity by species with species representing >20% of the stand indicated by x's; (middle) box plots showing the median, the boundary between the middle and outer quartiles (ends of box), and range (bars); (right) averages by individual - either for all individuals or weighted by number of individuals of each species (stand data not available for plot 5).

ing, ~.60 for years 30-80, and between .66 and .68 for mature forest.

A few caveats are in order in considering the significance of these results with respect to biomass estimates. First, the data presented here are for outer sapwood and may not be representative of average values. (Note, on the other hand, that published values for specific gravity are generally for heartwood.) Second, even though specific gravity averaged by individual (Fig. 2) also shows a difference between early and later-successional forests, it is not certain that these differences would show up in volumetric representations of forest biomass.

Variation within trees. The prevalence of one species (*Pseudolmedia laevis*) in plot 3 provided an opportunity to see how specific gravity varied with diameter in this species (Fig. 3). The positive relationship found (correlation of .84) is understandable in terms of biomechanical principles since structural reinforcement in the outer part of the trunk is an economical way of achieving strength and rigidity (Mosbrugger, 1990). In its early life, the tree puts its energy into growing up toward the light, only gradually producing wood of greater density at the periphery where it is more effective in support. The intensely competitive environment of the forest may serve to intensify this growth pattern. Although

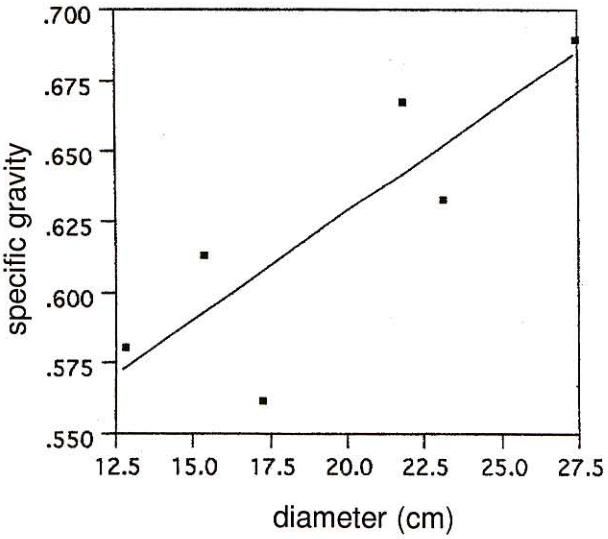

Figura 3. Specific gravity vs. tree radius for Pseudolmedia laevis. r= .84 (p <.05)

Wiemann & Williamson (1989a) report that pioneer species with low-density wood are most likely to display such increases, P. laevis has specific gravity near the average for tropical forest woods.

Information on the directional trends most typical of tropical forest trees is incomplete. Increases were found in ≥50% of species in a variety of forest types in Costa Rica (Wiemann & Williamson, 1989a;b). Generally the degree of increase in specific gravity is on the order of .1-.4 (radial increase from inside to outside of tree; Wiemann & Williamson 1988; 1989a; Omolodun *et al.*, 1991; Butterfield *et al.* 1993; de Castro *et al.*, 1993; Woodcock *et al.*, 2000). The considerations pertaining to support noted above also suggest that increases in specific gravity are common if not prevalent.

Significance for biomass estimates. Of the various techniques used to estimate forest biomass, only one involves direct weighing of trees, litter, and soil in forest plots (Fearnside 1985; 1987). But because the sample plots are by necessity limited in size, the high degree of heterogeneity in species composition and structure of the world's tropical forests means that it is difficult to obtain representative samples using this method. Another technique is to base analysis on values of specific gravity that are averaged by forest type or region and forest characteristics such as tree height and diameter that are either 1) known from forest inventory data or 2) can be determined in the field. Specific gravity is clearly a source of uncertainty for these determinations (Fearnside, 1997).

Yet another approach to biomass estimation relies on studies in which trees of various sizes and representing different species have been assessed by direct weighing. Generalized relationships between biomass and tree characteristics included in forest inventories (primarily diameter) are then derived and applied to inventory statistics to to arrive at biomass estimates. Since the forest inventory data collected and maintained by governments around the world have broad spatial coverage, it has been possible to estimate forest biomass of large areas such as the Brazilian Amazon and the eastern US in this way (Brown & Lugo, 1992; S. Brown *et al.*, 1997; Schroeder *et al.*, 1997). But although variation in specific gravity with age/size of trees may be incorporated into the derived relationships, one equation is used to represent large biotic regions (Amazon forest, Eastern Deciduous Forest). If, as suggested here, there can exist significant differences in specific gravity within regions, these differences could quite likely affect biomass estimates.

There exists considerable evidence of specific gravity increases with age/diameter in individual tropical forest trees, although how widespread this pattern is, and the extent to which this variability is a source of error in biomass estimates, remains a question. It is notable that the trend is the same as that for forests — that is, specific gravity appears to increase both with increasing age of trees and increasing age/successional status of forests. The implication is that older forests are proportionately more important biomass sinks than younger forests for reasons additional to the presence of large trees and the increased carbon present in woody debris, leaf litter, and soils.

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Appendix. Specific gravity of Tambopata Woods. Asterisks indicates taxa constituting >20% of stand diversity.

Site	Species	Family	Specific gravity ($g.cm^3$)
*1	*Cecropia ficifolia* Warburg ex Snethlage	Cecropiaceae	.266
1	*Enterolobium schomburgkii* (Bentham) Bentham [1,2]	Leguminosae	.399-.501
1	*Ficus insipida* Willdenow ssp. *insipida* [1,2]	Moraceae	.281-.397
*1	*Margaritaria nobilis* L. f.	Euphorbiaceae	.557
1	*Miconia calvescens* DC.	Melastomaceae	.4
1	*Salix humboldtiana* Willdenow	Salicaceae	.343
1	*Sapium glandulosum* (L.) Morong	Euphorbiaceae	.432
1	*Visma angusta* Miquel	Guttiferae	.488
2	*Erythrina ulei* Harms	Leguminosae	.111
2	*Eugenia florida* DC.	Myrtaceae	.634
2	*Ficus mathewsii* (Miquel) Miquel	Moraceae	.379
2	*Guatteria olivacea* R. E. Fries cf.	Annonaceae	.387
2	*Inga semialata* (Vell. Conc.) C. Martius [2,4]	Leguminosae	.446-.449
2	*Inga* sp.	Leguminosae	.471
2	*Minquartia guianensis* Aublet	Olacaceae	.754
2	*Ocotea* sp.	Lauraceae	.282
2	*Perebea angustifolia* (Poeppig & Endicher) C. C. Berg	Moraceae	.517
2	*Pourouma cecropiifolia* C. Martius [2,3]	Cecropiaceae	.373-.561
2	*Pourouma guianensis* Aublet spp. *guianensis*	Cecropiaceae	.370
2	*Sylogene cauliflora* (Miguel & C. Martius) Mez	Myrsinaceae	.535
2	*Symphonia globulifera* L. f.	Guttiferae	.527
2	*Tabernaemontana flavicans* Willdenow ex Roemer & Shultes	Apocynaceae	.487
2	? *Tetragastris*	Burseraceae	.469
2	*Theobroma cacao* spp. *sphaerocarpum* (A. Chevalier) Cuatrecasas	Sterculiaceae	.430

2	*Trichilia quadrijuga* H. & B. spp. *quadrijuga*	Meliaceae	.338
2	*Unonopsis veneficiorum* (C. Martius) R. E. Fries	Annonaceae	.436
2	*Virola calophyllum* Warburg	Myristicaceae	.342-.449
2	*Xylopia cuspidata* Diels	Annonaceae	.510
3	*Casearia javitensis* H. B. K.	Flacourtiaceae	.736
3	*Cecropia sciadophylla* C. Martius	Cecropiaceae	.474
3	*Ceiba pentandra* (L.) Gaertner cf.	Bombacaceae	.489
3	*Endlicheria bracteata* Mez	Luraceaea	.573
3	*Guarea glabra* M. Vahl	Meliaceae	.592
3	*Hevea guianensis* Aublet [3,4]	Moraceae	.595-.609
3	*Jacaranda copaia* (Aublet) D. Don	Bignoniaceae	.402
3	*Licania britteniana* Fitsch [3,4]	Chrysobalanaceae	.675-.779
3	*Naucleopsis ternstroemiiflora* (Mildbraed) C. C. Berg	Moraceae	.612
3	*Nectandra lucida* Nees	Lauraceae	.682
3	*Pourouma minor* Benoist [3,4]	Cecropiaceae	.428-.481
3	*Pouteria hispida* Eyma	Sapotaceae	.758
3	*Pouteria torta* (C. Martius) Radlkofer	Sapotaceae	.629
*3	*Pseudolmedia laevis* (R & P.) J. F. Macbride	Moraceae	.563-.691
*3	*Pseudolmedia macrophylla* Trecul	Moraceae	.635-.686
3	*Quiina florida* Tulasne	Quiinaceae	.728
3	*Quiina* sp.?	Quiinaceae?	.489
3	*Simarouba amara* Aublet cf.	Simaroubaceae	.352
3	indet.	Moraceae?	.450
3	indet.	Lauraceae?	1.022
4	*Abarema jupunba* (Willdenow) Britton & Killip	Legiminosae	.660
4	*Calycophyllum spruceanum* (Bentham) Hooker f. ex Schumann	Rubiaceae	.645
4	*Casearia* cf. *decandra* Jacquin	Flacourtiaceae	.563

4	*Conceveiba guianensis* Aublet	Euphorbiaceae	.538
4	*Cordia scabrifolia* D.C.	Boraginaceae	.474
4	*Dialium guianensis* (Aublet) Sandwith	Leguminosae	.481
4	*Inga* cf. *chartacea* Poeppig	Leguminosae	.481
4	*Iryanthera juruensis* Warburg [4,5]	Myristicaceae	.553-.685
4	*Micropholis guyanensis* (A. DC.) Pierre	Sapotaceae	.783
4	*Nectandra cuspidata* Nees	Lauraceae	.482
4	*Sloanea fragrans* Rusby	Elaeocarpaceae	.470
4	*Tachigali peruviana* (Dwyer) Zarucchi & Herendeen	Leguminosae	.763
4	*Virola sebifera* Aublet	Myristicaceae	.500
4	indet. [pink wood - Aspidosperma?]	Apocynaceae?	.849
5	*Brosimum lactescens* (S. Moore) C. C. Berg	Moraceae	.804
5	*Licaria armeniaca* (Nees) Kostermans	Lauraceae	.553
5	*Maquira coreacea* (Karsten) C. C. Berg	Moraceae	.541
5	*Nectandra* sp.	Lauraceae	.342
5	*Pseudolmedia* sp	Moraceae	.787
5	indet.	Myristicaceae?	.804
5	indet.	Leguminosae	.787