American Journal of Botany 95(4): 516–519. 2008.

BRIEF COMMUNICATION

The relationship between stem and branch wood specific gravity and the ability of each measure to predict leaf area[1]

Nathan G. Swenson[2] and Brian J. Enquist

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA

A few trait axes that represent differential biomass allocation may summarize plant life-history strategies. Here we examine one of these axes described by wood specific gravity. Wood specific gravity represents the location of a species on a continuum of the rate of growth vs. the likelihood of mechanical failure, ranging from rapid volumetric growth/increased probability of mechanical failure to slow volumetric growth/decreased probability of mechanical failure. Wood specific gravity has been quantified primarily using three separate methods: a section from terminal branch, a section from the main stem or from a trunk wood core. What is unclear is how comparable these methods are and whether one or the other is a better predictor of other important plant traits such as leaf area. Here we measured stem and branch wood specific gravities from individual trees and shrubs in a tropical rain forest, quantified their relationship and determined their ability to predict leaf area. Stem and branch measures were highly correlated with each measure having a weak correlation with leaf area in trees and strong correlation with leaf area in shrubs. These results indicate that various methodologies for measuring wood specific gravity are comparable, and thus less destructive methods than are currently used are available to determine values for this important trait.

Key words: functional trait; life-history trait; Puerto Rico; trait correlations; trait measurement; tropical rain forest.

Over the past decade botanists have focused on identifying a few key plant traits that capture most of the overall variation in plant function (Baker, 1972; Grime, 1974, 1977; Weiher et al., 1998; Westoby, 1998; Westoby et al., 2002; McGill et al., 2006; Westoby and Wright, 2006)). This work has highlighted a small number of key functional traits that represent differential plant biomass allocation. It is believed that these traits may provide novel insights into the ecology of plants (Reich et al., 1997; Hacke et al., 2001; Westoby et al., 2002; Wright et al., 2004; Westoby and Wright, 2006; Swenson and Enquist, 2007). Traits of interest include asymptotic plant height, seed mass, leaf area, foliar stoichiometry, specific leaf area (SLA: leaf area/leaf dry mass) and wood specific gravity.

Here we discuss just two of these traits, wood specific gravity and leaf area. Wood specific gravity has been identified as a key trait because it represents biomass allocation to stem tissue and it is correlated with growth and mortality (Putz et al., 1983; Enquist et al., 1999; Muller-Landau, 2004). Specifically, species with lighter wood tend to have rapid volumetric growth rates with shorter life-spans, while heavier wooded species tend to grow more slowly and have lower mortality rates. Variation in wood specific gravity also appears to be linked to stem hydraulic function (Hacke et al., 2001). In particular, light wooded species tend to have higher hydraulic efficiency at the cost of higher vulnerability to embolism (Hacke et al., 2001). Further, a growing number of studies have begun to report a negative relationship between wood specific gravity and leaf area (Ackerly, 2004; Cavender-Bares et al., 2004; Wright et al., 2006, 2007). Although this relationship is often reported, the mechanism underlying the correlation has been less well studied (Wright et al., 2006). One possibility is that lower wood specific gravity is linked to higher stem conductance, which can therefore support larger leaves, but this hypothesis still needs to be broadly tested (Wright et al., 2006). For these and other reasons, interest in intraspecific and interspecific variation in wood specific gravity continues to grow. As such, an increasing number of plant functional ecologists are now including this trait in their analyses, and large data sets are being compiled (Chave et al., 2006; Swenson and Enquist, 2007).

Foresters have traditionally determined wood specific gravity by using large sections of trunks from harvested trees, but plant functional ecologists have used alternative methods. Specifically, plant functional ecologists have determined wood specific gravity from trunk cores and sections of twigs from large individuals and from sections of the basal stem from smaller individuals. This variability in methodology is a consequence of variability in plant life forms and the degree to which the researcher is willing to destructively sample the plant.

Although there are preexisting studies that examine the range of wood specific gravities in branches and stems within a single species (e.g., Okai et al., 2003, 2004), it is still unclear how correlated these measures are across many species. Thus we raise three unanswered questions. (1) How comparable are the values derived from alternative methods using different parts of a plant across multiple species? (2) Does one method provide values that correlate better with other functional traits that may covary with wood specific gravity such as leaf area? (3) Is it possible to estimate stem wood specific gravity by using a less destructive sampling methodology? The purpose of the current study was

[1] Manuscript received 30 September 2007; revision accepted 24 January 2008.

The authors acknowledge Ian Wright in particular and the NESCent—ARC-NZ Vegetation Function Wood Anatomy and Density Working Group in general for conversations that helped inspire this project. N.G.S. thanks J. Thompson, M. Aponte, and the staff at the El Verde Field Station for helping to make the study possible. N.G.S. was supported by the Galileo Circle Scholars Program and the Institute for the Study of Planet Earth at the University of Arizona. B.J.E. and N.G.S. were supported by an NSF CAREER Award to B.J.E.

[2] Author for correspondence (e-mail: swenson@email.arizona.edu)

to address these questions by measuring wood specific gravity using multiple methodologies on the same individuals in a neotropical rain forest.

MATERIALS AND METHODS

The current study was designed to test for the relationships between different measurements of wood specific gravity and how different measurements relate to mean leaf area. We examined 33 individual trees and 14 individual shrubs representing 27 species (Table 1) occurring in and around the El Verde Field Station located in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (18.32°N, 65.82°W). The area of forest studied is a premontane moist forest with 3500 mm of annual precipitation with no distinct dry season.

We located 33 individual trees in the LEF that were between 10 cm and 20 cm in diameter at breast height (d.b.h.; 1.30 m off the ground). For these trees, we used an increment borer to extract a stem wood core ranging from 5 cm to 10 cm deep into the trunk. Upon returning from the field, the wet volume of the core (cm^3) was determined by water displacement using a graduated cylinder (Archimedes method; Cornelissen et al., 2003). Next, using a pole clipper, we cut down a branch with radius approximately 1–2 cm in diameter on this same individual. Care was taken to sample branches that had sun-exposed leaves. A basal wood section from the branch was collected as well as all of the leaves subtended by it. All bark was removed from the branch wood section in the field, and its wet volume was determined by water displacement in the laboratory. The water displacement method allowed for better estimates of wood volume for species with hollow branch sections by filling in large air spaces with water, while smaller air spaces were likely not filled causing a slight overestimation of wood volume (Cornelissen et al., 2003). The wood cores and wood sections were then placed in a 60°C drying oven at the El Verde Field Station in the LEF. They were dried until a consistent mass (g) was achieved (Cornelissen et al., 2003). This dry mass was then used to calculate the wood specific gravity (g/cm^3) for the core or section. The fresh leaf area (cm^2) for the subtended leaves was measured using a CI-202 portable leaf area meter (CID, Camas, Washington, USA), and an average leaf area for the branch was calculated.

The 14 individual shrubs used in this study all had a d.b.h. of 1–2 cm and were collected from private lands just outside the LEF. For each individual, we cut a basal wood section from the main stem and a wood section from a primary branch (generally 0.4–0.6 cm diameter). Last, all leaves subtended by the branch were collected. Upon returning to the laboratory, we calculated the wood specific gravity and leaf area using the same methods described. All samples were collected and measured by the first author.

TABLE 1. A list of the species and the number of individuals (No. inds.) included in the study.

Species	Family	No. inds.	Life form
Alchornea latifolia Klotzsch	Euphorbiaceae	2	Tree
Byrsonima wadsworthii Little	Malpighiaceae	1	Tree
Casearia sylvestris Sw.	Salicaceae	2	Tree
Dendropanax arboreus (L.) Decne. & Planch	Araliaceae	2	Tree
Eugenia stahlii Krug & Urb.	Myrtaceae	1	Tree
Guatteria caribaea Urb.	Annonaceae	2	Tree
Guettarda valenzuelana A.Rich.	Rubiaceae	2	Tree
Henriettea fascicularis M.Gómez	Melastomataceae	2	Tree
Manilkara bidentata (A.DC.) A.Chev.	Sapotaceae	2	Tree
Maytenus elongata Britton	Celastraceae	2	Tree
Miconia laevigata Griseb.	Melastomataceae	2	Tree
Ocotea leucoxylon Benth. & Hook.f.	Lauraceae	2	Tree
Pterocarpus officinalis Jacq.	Fabaceae	1	Tree
Quararibea turbinate Poir.	Malvaceae	1	Tree
Samyda spinulosa Vent.	Samydaceae	2	Tree
Sloanea berteriana Choisy ex DC.	Elaeocarpaceae	2	Tree
Symplocos martinicensis Griseb.	Symplocaceae	1	Tree
Syzygium jambos (L.) Alston	Myrtaceae	2	Tree
Tetragastris balsamifera Kuntze	Burseraceae	2	Tree
Coccoloba swartzii Meisn.	Polygonaceae	1	Shrub
Hibiscus spp.	Malvaceae	2	Shrub
Miconia prasina (Sw.) DC.	Melastomataceae	2	Shrub
Myrcia leptoclada DC.	Myrtaceae	2	Shrub
Piper blattarum Spreng.	Piperaceae	2	Shrub
Piper umbellatum Vahl.	Piperaceae	2	Shrub
Psychotria berteriana DC.	Rubiaceae	2	Shrub
Psychotria grandis Sw.	Rubiaceae	1	Shrub

RESULTS

We measured stem and branch wood specific gravity for 33 individual trees and 14 individual shrubs in a Puerto Rican rain forest. In both cases, we found branch wood specific gravity to be a good predictor of stem wood specific gravity using a reduced major axis (RMA) regression (trees: $r^2 = 0.89$; shrubs: $r^2 = 0.89$; Fig. 1). This suggests that stem wood specific gravity could be estimated for the species in this study using branch sections without having to core the main stem of the tree or

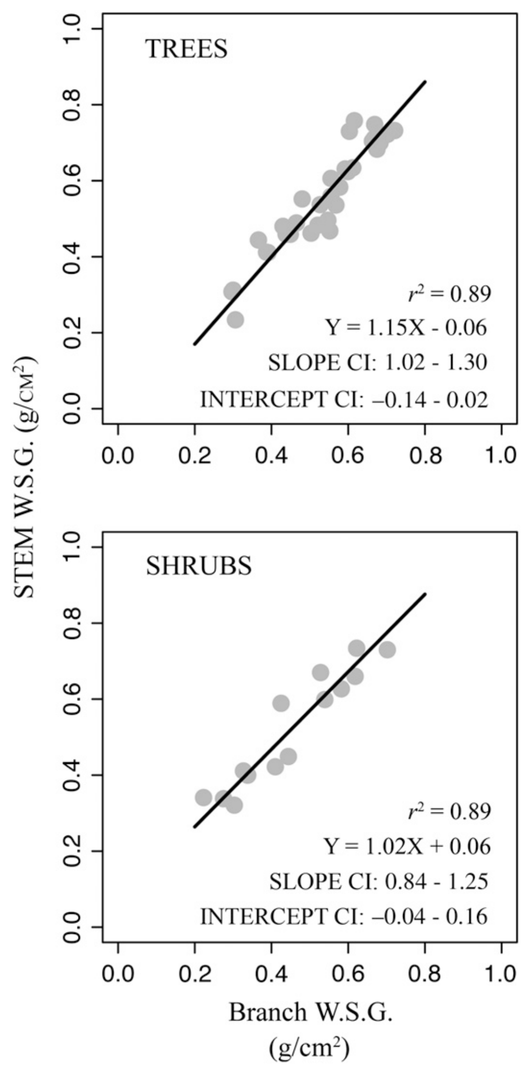

Fig. 1. The relationship between stem and branch wood specific gravity for individual trees (top) and shrubs (bottom). All statistical results reported are from reduced major axis (type II) regressions. CI = 95% confidence interval.

shrub. Using an ordinary least squares (OLS) regression forced through the origin, we wanted to determine whether branch sections tended to have higher or lower wood specific gravity and the degree to which this was predictable. We found the following regression equations that both suggest branch wood specific gravity was lower than stem wood specific gravity in the same individual and that this relationship was fairly consistent across species in this study. The tree equation was $S_{wsg} = 1.411 \cdot B_{wsg}$, and the shrub equation was $S_{wsg} = 1.134 \cdot B_{wsg}$. In each equation, S_{wsg} represents stem wood specific gravity (wsg), and B_{wsg} represents branch wood specific gravity. Both regression equations explained large proportions of the variance (trees: $r^2 = 0.89$; shrubs: $r^2 = 0.87$).

Stem and branch wood specific gravities in trees were not good predictors of leaf area, but the wood specific gravities of branches and stems in shrubs were good predictors of leaf area (Fig. 2). The exclusion of compound leaves from the tree data set improved the strength of the relationship mildly, but it was still much weaker than that found for shrubs. The RMA regression slopes for the leaf area–wood specific gravity relationships were indistinguishable between methodologies and life forms (Fig. 2). The slopes of the OLS and RMA regressions of leaf area on stem and branch wood specific gravity were dissimilar for trees and similar for shrubs (Fig. 2). In particular, the OLS slopes were shallower for the tree species studied.

DISCUSSION

A central goal in plant functional ecology has been to identify traits that represent plant functional strategies. The quantification of plant functional strategies may be used to provide information pertaining to species diversity, coexistence, and responses to abiotic gradients (Schimper, 1898; Raunkier, 1934; Grime 1974, 1977; Weiher et al., 1998; Westoby, 1998; Westoby et al., 2002; McGill et al., 2006; Westoby and Wright, 2006; Enquist et al., 2007; Swenson et al., 2007). Thus, many recent studies have focused on identifying important plant functional traits. Wood specific gravity represents one such trait. Because wood specific gravity is measured using a variety of methodologies, our goal in this article is to compare values derived from separate methodologies on the same individual. Further, we determined whether the strength of the correlation between wood specific gravity and another functional trait, leaf area, varied when using different methods for measuring wood specific gravity.

We have found that stem wood specific gravity can be adequately estimated from branch wood specific gravity in both shrubs and trees in the tropical rain forest species we studied. It is important to note that we did not sample all species of shrubs and trees in this forest, other life forms in this forest (i.e., lianas, hemiepiphytes), or species from other forests, and caution should be taken in extrapolating our results to other life forms or forests. Future studies will be needed to assess the generality of our findings. We have also found that stem and branch wood specific gravity have similarly poor abilities to predict leaf area in tree species. The relationship between leaf area and wood specific gravity was stronger for shrubs. Although the slopes of the RMA regressions plotting mean branch leaf area against stem and branch wood specific gravity were indistinguishable, the relationship was consistently weak across trees, thereby increasing the size of our confidence intervals.

The identification of a few central functional traits that are indicative of plant life-history strategies has spurred an increasing number of studies quantifying these traits. As the collection of traits continues, it will be important to determine how comparable are trait values generated from alternative

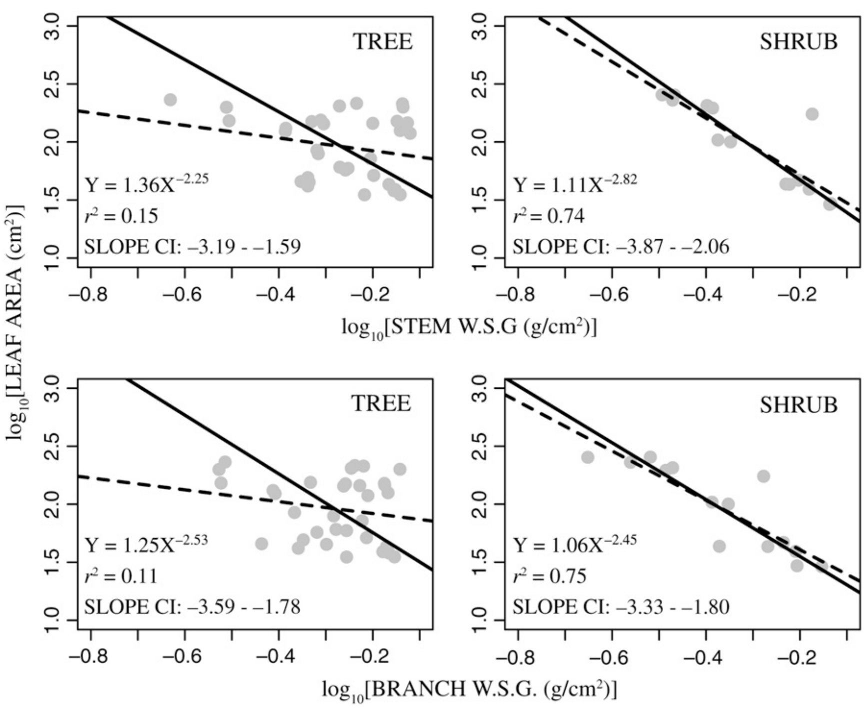

Fig. 2. The relationship between stem or branch wood specific gravity and the mean fresh leaf area of the subtended leaves. The dashed lines represent the ordinary least squares regression slopes, and the solid lines represent the reduced major axis (type II) regressions. All statistical results reported are from reduced major axis (type II) regressions. CI = 95% confidence interval. Note that this figure contains both species with simple and compound leaves.

methodologies and whether less destructive routes can be taken to the same end. Here we have presented one such analysis that suggests various methodologies for measuring wood specific gravity are indeed comparable in the species studied presently and less destructive methods may potentially be used to determine values for this important trait. Future work focusing on other life forms, forest types, and regions will help further elucidate whether less destructive sampling methodologies can be broadly used to estimate stem wood specific gravity.

LITERATURE CITED

Ackerly, D. D. 2004. Functional strategies of chaparral shrubs in relation to seasonal water stress and disturbance. *Ecological Monographs* 74: 25–44.

Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53: 997–1010.

Cavender-Bares, J., K. Kitajima, and F. A. Bazzaz. 2004. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs* 74: 635–662.

Chave, J., H. C. Muller-Landau, T. R. Baker, T. A. Easedale, H. ter Steege, and C. O. Webb. 2006. Regional and phylogenetic variation of wood density across 2,456 neotropical tree species. *Ecological Applications* 16: 2356–2367.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardisation and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Enquist, B. J., A. J. Kerkhoff, S. C. Stark, N. G. Swenson, M. C. McCarthy, and C. A. Price. 2007. A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature* 449: 218–222.

Enquist, B. J., G. B. West, E. L. Charnov, and J. H. Brown. 1999. Allometric scaling of production and life history variation in vascular plants. *Nature* 401: 907–911.

Grime, J. P. 1974. Vegetation classification by references to strategies. *Nature* 250: 26–31.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.

Hacke, U. G., J. S. Sperry, W. T. Pockman, S. D. Davis, and K. McCulloh. 2001. Trends in wood density and structure are linked to xylem implosion by negative pressure. *Oecologia* 126: 457–461.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21: 178–185.

Muller-Landau, H. C. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36: 20–32.

Okai, R., K. Frimpong-Mensah, and D. Yeboah. 2003. Characterization of moisture content and specific gravity of branchwood and stemwood of *Aningeria robusta* and *Terminalia ivorensis. Holz Als Roh-und Werkstoff* 61: 155–158.

Okai, R., K. Frimpong-Mensah, and D. Yeboah. 2004. Characterization of strength properties of branchwood and stemwood of some tropical hardwood species. *Wood Science and Technology* 38: 163–171.

Putz, F. E., P. D. Coley, K. Lu, A. Montalvo, and A. Aiello. 1983. Uprooting and snapping of trees: Structural determinants and ecological consequences. *Canadian Journal of Forest Research* 13: 1011–1020.

Raunkier, C. 1934. The life forms of plants and statistical plant geography. Claredon Press, Oxford, UK.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* 94: 13730–13734.

Schimper, A. F. W. 1898. Pflanzengeographie auf Physiologischer Grundlage. G. Fischer, Jena, Germany.

Swenson, N. G., and B. J. Enquist. 2007. Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* 94: 451–459.

Swenson, N. G., B. J. Enquist, J. Thompson, and J. K. Zimmerman. 2007. The influence of spatial and size scales on phylogenetic relatedness in tropical forest communities. *Ecology* 88: 1770–1780.

Weiher, E., G. D. P. Clarke, and P. A. Keddy. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81: 309–322.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199: 213–227.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.

Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution* 21: 261–268.

Wright, I. J, D. D. Ackerly, F. Bongers, K. E. Harms, G. Ibarra-Manriquez, M. Martinez-Ramos, S. J. Mazer, H. C. Muller-Landau, H. Paz, N. C. A. Pitman, L. Poorter, M. R. Silman, C. F. Vriesendorp, C. L. Webb, M. Westoby, and S. J. Wright. 2007. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99: 1003–1015.

Wright, I. J., D. S. Falster, M. Pickup, and M. Westoby. 2006. Cross-species patterns in the coordination between leaf and stem traits, and their implications for plant hydraulics. *Physiologia Plantarum* 127: 445–456.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, F. S. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, N. L. Nava, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. Veneklaas, and R. Villar. 2004. The world-wide leaf economics spectrum. *Nature* 428: 821–827.