BRIEF COMMUNICATION

STILL RETHINKING THE VALUE OF HIGH WOOD DENSITY[1]

MARKKU LARJAVAARA[2–4] AND HELENE C. MULLER-LANDAU[2]

[2]Smithsonian Tropical Research Institute, Unit 9100 Box 0948, DPO AA 34002-9998 USA; and [3]University of Helsinki, Department of Forest Sciences, P. O. Box 27, FI-00014 University of Helsinki, Finland

- *Premise of the study:* In a previous paper, we questioned the traditional interpretation of the advantages and disadvantages of high wood density (*Functional Ecology* 24: 701–705). Niklas and Spatz (*American Journal of Botany* 97: 1587–1594) challenged the biomechanical relevance of studying properties of dry wood, including dry wood density, and stated that we erred in our claims regarding scaling.
- *Methods:* We first present the full derivation of our previous claims regarding scaling. We then examine how the fresh modulus of rupture and the elastic modulus scale with dry wood density and compare these scaling relationships with those for dry mechanical properties, using almost exactly the same data set analyzed by Niklas and Spatz.
- *Key results:* The derivation shows that given our assumptions that the modulus of rupture and elastic modulus are both proportional to wood density, the resistance to bending is inversely proportional to wood density and strength is inversely proportional with the square root of wood density, exactly as we previously claimed. The analyses show that the elastic modulus of fresh wood scales proportionally with wood density (exponent 1.05, 95% CI 0.90–1.11) but that the modulus of rupture of fresh wood does not, scaling instead with the 1.25 power of wood density (CI 1.18–1.31).
- *Conclusions:* The deviation from proportional scaling for modulus of rupture is so small that our central conclusion remains correct: for a given construction cost, trees with lower wood density have higher strength and higher resistance to bending.

Key words: allometric relationship; breaking stress; elastic modulus; flexural stiffness; mechanical properties; specific gravity; trunk strength; tree stem; wood density; Young's modulus.

Last year, we challenged the traditional thinking on the costs and benefits of high wood density, specifically high dry wood density, ρ_d (Larjavaara and Muller-Landau, 2010) (Terms are defined in Table 1.). We claimed that comparisons of trunks of identical diameter and the consequent conclusion that a high ρ_d trunk provides greater strength at greater expense are misleading, because a given strength can be achieved at lower cost (less biomass invested) with low ρ_d. Our claim rested on the assumption that the fresh modulus of rupture, MOR_f, is proportional to ρ_d, an assumption we made based on a previous analysis of the dry modulus of rupture, MOR_d, vs. ρ_d (Chave et al., 2009). MOR is a measure of maximal bending strength measured in a laboratory; this measurement is analogous to the natural bending of tree trunks due to wind drag and other forces and reflects properties important for the survival of trees. Niklas and Spatz (2010) criticized our arguments, presenting equations that suggested that we had erred in our claims regarding scaling of strength with ρ_d for constant construction cost, and argued that all such analyses should be based on fresh wood properties and that these scale differently with ρ_d—a point they supported with analyses of the scaling of fresh wood properties with density at 50% moisture content.

Here we show first in the remainder of the introduction that our original theses were correct and that Niklas and Spatz (2010) erred in their criticism of our verbal equations. Thereafter, we assess the validity of the assumption that MOR_f is proportional to ρ_d using data from Lavers (1983) and discuss the importance of a potential deviation from proportionality for our conclusions. In addition, we examine the relevance of MOR_d for the mechanics of living trees.

In the last paragraph of the section "Engineering physics—how diameter and wood density affect stem breakage" in our original article (Larjavaara and Muller-Landau, 2010), we presented six theses. We claimed that for constant construction cost (cross-section dry mass) and varying ρ_d and stem radius, r:

(1) Relative resistance to bending, RRB (Niklas and Spatz, 2010) or flexural stiffness for a given construction cost, is proportional to r^2.

(2) Relative strength, RS (Niklas and Spatz, 2010) or critical bending moment for a given construction cost, is proportional to r.

(3) RRB is inversely proportional to ρ_d.

(4) RS is inversely proportional with the square root of ρ_d.

And that with a constant ρ_d and varying r and construction cost:

(5) Construction cost is proportional to r^2.

(6) Strength or critical bending moment, M_{crit}, is proportional to r^3.

Niklas and Spatz (2010) examined how *RRB* and *RS* vary with r and fresh wood density, ρ_f, in their eqs. 3 and 4. Their equations are technically correct, but their conclusion that these equations demonstrate a fundamentally different scaling than we reported is incorrect.

Niklas and Spatz's (2010) eqs. 3 and 4 contain both the radius, r, and wood density. Their wood density is wood density at 50% moisture content divided by fresh volume, which is by definition directly proportional to dry wood density, and thus we substitute dry wood density in our proportionality below. When comparing stems that have the same construction cost, as we did, radius and wood density do not vary independently, but are instead precisely related because $\rho_d \pi r^2 = $ constant. To examine how these quantities vary with ρ_d for stems having the same construction cost (i.e., dry mass per unit length), as we did, one needs to substitute $r \propto 1/\rho_d^{0.5}$. Niklas and Spatz's (2010) eq. 3 thus becomes

$$\text{RRB} = \frac{E_f I}{M/L} = \frac{r^2 E_f}{4 \rho_d} \propto \frac{E_f}{\rho_d^2}, \qquad \text{(Eq. 1)}$$

where E_f is elastic modulus or Young's modulus of fresh wood, I is second moment of area, M is dry mass, and L is length of the cylindrical object. Following Niklas and Spatz (2010), we take critical breaking stress, σ_{crit}, to be synonymous with MOR_f for the purposes of this study. With parallel substitutions, their eq. 4 on "relative strength" (Niklas and Spatz, 2010) becomes

$$\text{RS} = \frac{M_{crit}}{M/L} = \frac{r \sigma_{crit}}{4 \rho_d} \propto \frac{\text{MOR}_f}{\rho_d^{1.5}}. \qquad \text{(Eq. 2)}$$

We had assumed $E_f \propto \rho_d$ and $\text{MOR}_f \propto \rho_d$. Under these assumptions, Eqs. 1 and 2 become

$$\text{RRB} \propto \rho_d^{-1} \qquad \text{(Eq. 3)}$$

and

$$\text{RS} \propto \rho_d^{-0.5}, \qquad \text{(Eq. 4)}$$

exactly our theses 3 and 4 listed earlier, thus demonstrating the correctness of our original theses under our stated assumptions, namely, that both E_f and MOR_f are proportional to ρ_d.

Our assumption regarding the proportionality of E_f and MOR_f with ρ_d was based on data for properties of dry wood (Chave et al., 2009) and on a simplified model of wood structure. In this model, wood consists only of "structural fibers"; other space is cost-free to construct and does not influence the mechanical properties of the wood (Larjavaara and Muller-Landau, 2010). However, in a more realistic model, some solid matter is required not only to maintain the position of individual "fibers" relative to other fibers, especially on the compression side of a bending trunk, but also to avoid fatal deformation caused by shear or torsional stresses. This additional solid matter increases mass, mass that is not part of the structural fibers. The lower the ρ_d, the more of this additional solid matter is required as the distances between the structural fibers increase. As a result, MOR_f should increase more than proportionally with increasing ρ_d.

In the remainder of this article, we critically examine our assumptions that $E_f \propto \rho_d$ and $\text{MOR}_f \propto \rho_d$ (Larjavaara and Muller-Landau, 2010). Because mechanical properties of dry wood have been studied much more widely than those of fresh wood, we further compare E_f with E_d, and MOR_f with MOR_d in their scaling with ρ_d. We used the same data set on fresh properties that Niklas and Spatz (2010) used to examine relationships with

wood density at 50% moisture content. We calculated confidence intervals on fitted parameters via bootstrapping and evaluated whether parameters differ among regions of origin of the wood.

MATERIALS AND METHODS

The data we analyzed are all from Lavers (1983) and are in very large part exactly the same as those used by Niklas and Spatz (2010), with only the small differences described here and detailed in Appendix S1 (see Supplemental Data with online version of this article). (Note that Niklas and Spatz [2010] cited the older edition of Lavers [1969], but the data they used include points found only in the later [1983] edition.) The small differences between our data set and that used by Niklas and Spatz (2010) are that we corrected three values that they appear to have mistranscribed, we include two samples and one value that they excluded for unknown reasons, we excluded one sample for which fresh properties were not available in the original source (the data Niklas and Spatz [2010] presented for this sample appear in the neighboring row in the original), and we included only one sample of *Populus canescens*—the sample that appears in Lavers (1983). (Niklas and Spatz [2010] listed three samples of *Populus canescens*, each with some data identical to one sample in Lavers [1983] and some data that do not appear in Lavers; this is presumably the unpublished data from the laboratories of Niklas and Spatz and their colleagues to which they refer in their methods.) In total, the data we used included 176 samples from 161 species and 108 genera (Lavers, 1983). The data are available in online Appendix S1.

Comparisons of wood density among studies can be challenging because the definition of wood density varies (referring variously to dry, fresh, or other wood density), and moisture content influences not only mass but also volume. Wood density in both Lavers (1983) and Niklas and Spatz (2010) is defined as wood density at 50% moisture content—that is, the mass of wood containing water whose mass equals 50% of oven dry mass, divided by fresh volume. By definition, this wood density at 50% moisture content, which we denote with ρ_{50}, equals 1.5 times ρ_d, and we used this relationship to calculate ρ_d for each sample.

Lavers (1983) reported 10 mechanical properties for both fresh and dry wood. Fresh wood properties were quantified on wood with actual fresh moisture contents, moisture contents that were typically over 50% (see fig. 1 in Niklas and Spatz [2010]). The mechanical properties of dry wood were quantified at 12% moisture content, with few exceptions (Lavers, 1983). Niklas and Spatz (2010) analyzed four of these properties: MOR_f, E_f, maximum shear strength, and maximum compressive strength for fresh wood. We focused here on just the two properties that are relevant to testing our assumptions (Larjavaara and Muller-Landau, 2010): MOR_f and E_f. We further included MOR_d and E_d in the analysis to compare with results on MOR_f and E_f, to evaluate to what degree the relationship of ρ_d with dry properties is predictive of the relationship with fresh properties.

Since our interest is the degree to which the mechanical properties can be predicted from ρ_d, we conducted only ordinary least squares regressions of the properties on ρ_d. We first log-transformed both variables, as we expected relationships to be power functions. We computed bias-corrected, accelerated (Fox and Weisberg, 2010) 95% confidence intervals with 5000 bootstraps using the "boot" package in R (R Development Core Team, 2008). We repeated the analyses for all samples combined, for all angiosperms, for all conifers, and for geographically defined subsets of the data. We specifically examined geographic subsets to evaluate the possibility that selection bias toward species that are important in timber construction might have influenced the results. Since the data set is British, we assumed that nearly all large British tree species were included making the British species an unbiased sample, while imported species might be a mechanically biased sample of all tree species (e.g., exceptionally high MOR_d for a given ρ_d). Therefore, we classified the origin of the samples into UK, other nontropical and tropical based on the origin given by Lavers (1983). In the few cases in which the origin was not clear (e.g., "Australia"), we based the classification on information on the natural distribution of the species gleaned from an Internet search (mostly Wikipedia articles). Our 176 samples for MOR_f included 38 conifers (19 UK, 13 other nontropical, and 6 tropical) and 138 angiosperms (26 UK, 7 other nontropical, and 105 tropical).

In addition, we examined the relationship between MOR_f and MOR_d, and between E_f and E_d, to evaluate whether dry properties could be used to predict fresh properties, and if so, with what confidence. As with ρ_d, we conducted

ordinary least squares regressions of the fresh properties on the dry properties, after log-transforming both variables. We grouped the data based on the three aforementioned geographic regions and later combined both nontropical groups as no distinct patterns could be seen.

RESULTS AND DISCUSSION

We found that MOR_f scales with ρ_d to the power 1.25, consistent with Niklas and Spatz's (2010) finding of power 1.24 for the scaling of MOR_f with ρ_{50}. (Note that the small difference here reflects the slightly different data sets, not the difference in type of wood density. For variables that are directly proportional, as are ρ_d and ρ_{50}, fitted power function exponents are identical, and only coefficients differ. See Table 1.) This fitted exponent is significantly higher than 1 (Table 2), clearly inconsistent with our previous assumption of proportionality (Larjavaara and Muller-Landau, 2010). In contrast, we found that E_f scaled with ρ_d to the power 1.01 and that this exponent was not significantly different from 1 (Table 2). This finding is consistent with our previous assumption that E_f is proportional to ρ_d (Larjavaara and Muller-Landau, 2010).

The estimated scaling exponent for MOR_d, 1.09, was smaller than that for MOR_f, although the difference was not statistically significant at the 95% confidence level either for the full data set or for various subsets of the data (Table 2). This result is broadly consistent with Niklas and Spatz's (2010) arguments that scaling of dry properties does not provide information on fresh properties, albeit we cannot reject the null hypothesis that the scaling with ρ_d is the same for MOR_f and MOR_d. On the other hand, the scaling exponents for E_f and E_d are indistinguishable (Table 2). There were no significant differences in the scaling exponents for different regions (Table 3 shows these results for the most important variable, MOR_f). The exclusion of nontropical or non-UK samples from the analysis did not substantially influence the estimated exponents, suggesting that MOR_f and E_f of species imported to Britain are not mechanically exceptional for their ρ_d.

We found that across the full data set, MOR_f scaled with MOR_d to the power 1.05 (95% CI = 0.96–1.13, R^2 = 0.84), and E_f scaled with E_d to the power 1.00 (95% CI = 0.96–1.06, R^2 = 0.94). The high coefficient of determination (R^2) suggests that the traits of dry wood have considerable value in predicting the traits of fresh wood, although in the case of the modulus of rupture, dry wood density has similar predictive value (Table 2).

TABLE 1. Most important variables used.

Variable	Definition	Unit
ρ_d	Dry wood density (oven dry mass divided by fresh volume), ρ_d relative to density of water is often referred to as wood specific gravity	kg/m^3
ρ_f	Fresh wood density (fresh mass divided by fresh volume)	kg/m^3
E_d	Elastic modulus (Young's modulus) of dry (12% moisture) wood (force needed for a given elastic deformation)	N/mm^2
E_f	Elastic modulus, aka Young's modulus, of fresh wood (force needed for a given elastic deformation)	N/mm^2
MOR_d	Modulus of rupture of dry (12% moisture) wood (force needed to break)	N/mm^2
MOR_f	Modulus of rupture of fresh wood (force needed to break)	N/mm^2

TABLE 2. Results of the regression analysis of log-transformed wood properties against log-transformed ρ_d (see Table 1 for variables). The confidence intervals for the coefficient b (the scaling exponent in equation Mechanical property = $a\rho^b$, where a is another coefficient) are based on bootstrapping (see Methods). N is the number of samples and R^2 the coefficient of determination.

Mechanical property	N	b (95% CI)	a	R^2
MOR_f	176	1.25 (1.18–1.31)	0.028	0.86
MOR_d	173	1.09 (1.01–1.20)	0.110	0.87
E_f	176	1.01 (0.90–1.11)	17.12	0.70
E_d	173	0.99 (0.87–1.12)	22.95	0.72

In posthoc explorations, we found that the scaling of MOR_f with MOR_d differed significantly between tropical and nontropical species, with higher values of MOR_f relative to MOR_d for tropical species (significantly higher coefficients in the fitted power function). Tropical species also had higher coefficients for E_f vs. E_d, but the difference was much smaller.

In our previous article, we assumed MOR_f and E_f were both proportional to ρ_d. We now examine how conclusions change if we start instead from the more realistic assumption $MOR_f \propto \rho^{1.25}$. Then Eq. 2 becomes

$$RS \propto \frac{\rho_f^{1.25}}{\rho_f^{1.5}} = \rho_f^{-0.25}. \qquad (Eq. 5)$$

This means that even with the corrected scaling of MOR_f to ρ_d, the paradox that Anten and Schieving (2010) and we (Larjavaara and Muller-Landau, 2010) raised remains—increasing ρ_d decreases RS. Thus, increasing strength is not a benefit of high ρ_d as has been traditionally thought (Lüttge, 2007). Even the upper 95% confidence limit of the exponent, 1.31, is well below 1.50, which would be the limit after which RS increases with increasing ρ_d.

Because E_f scales linearly with ρ_d, Eq. 1 becomes Eq. 3, as we previously stated (Larjavaara and Muller-Landau, 2010), meaning that much more force is required to bend a lower ρ_d trunk for the same construction cost. Note that in this case, the upper confidence limit on the fitted exponent, 1.11, is far below the exponent of 2.0 required to reverse the relationship (Eq. 1). So it is very clear that for trunks of equal biomass or construction cost, more force is required to achieve a given bending as ρ_d decreases. However, if the force causing the bending is the weight of the tree itself (elastic buckling [McMahon, 1973]), what matters is the fresh mass and not dry mass. Therefore, if the fresh mass increases as ρ_d decreases at a rate that is faster than ρ_d^{-1} (i.e., exponent smaller than −1), the pattern is reversed and low ρ_d trees have more trouble supporting their own weight

TABLE 3. Regional and taxonomic variation in the scaling exponent estimated from the regression analysis of MOR_f against ρ_d (see Table 1 for variables). Estimated values and uncertainty (95% CI) of coefficient b in equation Mechanical property = $a\rho^b$ for nine combinations of taxonomic groups and regions.

Taxa included	World	Nontropical	UK
All	1.25 (1.18–1.31)	1.20 (1.10–1.30)	1.20 (1.07–1.38)
Angiosperms	1.19 (1.11–1.27)	1.23 (1.09–1.40)	1.25 (1.04–1.54)
Conifers	1.14 (0.91–1.34)	1.21 (0.94–1.42)	1.10 (0.71–1.39)

for a given trunk dry mass. However, data shows that the moisture content increases far more slowly with decreasing ρ_d (fig. 1 in Niklas and Spatz [2010]). In addition, elastic buckling seems to be of only marginal importance in most ecosystems (Mattheck and Kubler, 1995), having perhaps its greatest importance for understory rain forest trees that never reach the windy canopy (King et al., 2009).

The much higher correlation with ρ_d for MOR_f than for E_f (Table 2) can be understood in terms of the life history strategies and biomechanics of trees. High MOR_f has clear advantages, and it is difficult to think of any disadvantages. Thus, we would expect taxa with relatively lower MOR_f for a given ρ_d to have been selected against over the course of the evolutionary history of trees. In contrast, increasing E_f for a given ρ_d has both advantages and disadvantages (Larjavaara and Muller-Landau, 2010) and optimal E_f depends on the life history strategy of the tree species. For example, high E_f for a given ρ_d could be favored by rain forest understory species to avoid elastic buckling, while trees in windier conditions could favor the higher flexibility and therefore reduced sail area conferred by low E_f.

The fact that E_f increases proportionally with ρ_d while MOR_f increases more than proportionally suggests that our original structural model of wood (Larjavaara and Muller-Landau, 2010) is useful for understanding the former but misleading for the latter. Modeling studies based on a realistic modular structure of wood composed of connected tubes could potentially provide insight into the mechanisms underlying these differences.

In the entire discussion so far, we have assumed that trunks are slender and that wood has evolved to avoid bending leading to fatal trunk breakage or elastic buckling. The structure and anisotropy of wood supports our perspective. However, other modes of failure could become relevant at lower ρ_d than are currently observed. For example, simple vertical collapse (without bending) might become an issue at very low ρ_d if moisture content increases or breaking strength decreases disproportionately with decreasing ρ_d, but we believe this is unlikely to influence wood evolution within the range of currently observed ρ_d.

Wood density, ρ_d, is a central variable for both wood technology (Bowyer et al., 2007) and ecology (Chave et al., 2009). Yet most of the wood density research in the past decades has been conducted from the wood technological or timber use perspective and has accordingly focused on properties of dry wood. Thus, we still have only a limited understanding of wood characteristics from an ecological or evolutionary perspective, and we are still debating basic questions. In this short paper, we have shown that our earlier assumption of proportionality of MOR_f with ρ_d was inaccurate but not misleading. Our qualitative conclusions on the fundamental problem with the traditional explanation for the benefit of high ρ_d (Larjavaara and Muller-Landau, 2010) continue to hold when this assumption is

corrected and the 1.25-power scaling relationship observed in the analyses in this article is used.

As we discussed in our original article, this conclusion begs the question of the true advantage of high wood density. Why invest in high wood density if it entails higher construction costs for the same strength? We reviewed a number of possible explanations, including flexibility, lower implosion risk under drought stress, and resistance to decay. We argued that neither lower implosion risk nor higher resistance to decay need inevitably accompany higher ρ_d, and that their general correlation with wood density instead reflects correlated selection. We suggested that the decreased maintenance cost of trunks of smaller surface area could be the main benefit of high ρ_d (Larjavaara and Muller-Landau, 2010), as maintenance respiration can be modeled as proportional to the surface area or to the sum of surface area and sapwood volume (Larjavaara, 2010). We look forward to future critical tests of these ideas.

LITERATURE CITED

ANTEN, N. P. R., AND F. SCHIEVING. 2010. The role of wood mass density and mechanical constraints in the economy of tree architecture. *American Naturalist* 175: 250–260.

BOWYER, J. L., R. SHMULSKY, AND J. G. HAYGREEN. 2007. Forest products & wood science: An introduction. Blackwell, Oxford, UK.

CHAVE, J., D. COOMES, S. JANSEN, S. L. LEWIS, N. G. SWENSON, AND A. E. ZANNE. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.

FOX, J., AND S. WEISBERG. 2010. An R companion to applied regression, 2nd ed. Sage Publications, Thousand Oaks, California, USA.

KING, D. A., S. J. DAVIES, S. TAN, AND N. S. M. NOOR. 2009. Trees approach gravitational limits to height in tall lowland forests of Malaysia. *Functional Ecology* 23: 284–291.

LARJAVAARA, M. 2010. Maintenance cost, toppling risk and size of trees in a self-thinning stand. *Journal of Theoretical Biology* 265: 63–67.

LARJAVAARA, M., AND H. C. MULLER-LANDAU. 2010. Rethinking the value of wood density. *Functional Ecology* 24: 701–705.

LAVERS, G. 1969. The strength properties of timbers, 2nd ed. Her Majesty's Stationery Office, London, UK.

LAVERS, G. 1983. The strength properties of timber, 3rd ed., revised by G. L .Moore. Her Majesty's Stationary Office, London, UK.

LÜTTGE, U. 2007. Physiological ecology of tropical plants. Springer, Berlin, Germany.

MATTHECK, C., AND H. KUBLER. 1995. Wood—The internal optimization of trees. Springer, Berlin, Germany.

MCMAHON, T. 1973. Size and shape in biology. *Science* 179: 1201–1204.

NIKLAS, K. J., AND H. C. SPATZ. 2010. Worldwide correlations of mechanical properties and green wood density. *American Journal of Botany* 97: 1–8.

R DEVELOPMENT CORE TEAM. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.