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HOW TO DETERMINE SAPLING BUCKLING RISK WITH ONLY A FEW MEASUREMENTS

GAËLLE JAOUEN,^{2,5} TANCRÈDE ALMÉRAS,² CATHERINE COUTAND,³ AND MERIEM FOURNIER⁴

²UMR Ecologie des Forêts de Guyane, INRA, BP 709, 97379 Kourou, French Guiana; ³UMR 547 PIAF, INRA, Université Blaise Pascal, 63100 Clermont-Ferrand, France; and ⁴AgroParisTech, UMR1092 Laboratoire d'étude des Ressources Forêt-Bois (LERFoB), 54000 Nancy, France

Tree buckling risk (actual height/critical buckling height) is an important biomechanical trait of plant growth strategies, and one that contributes to species coexistence. To estimate the diversity of this trait among wide samples, a method that minimizes damage to the plants is necessary. On the basis of the rarely used, complete version of Greenhill's model (1881, *Proceedings of the Cambridge Philosophical Society* 4(2): 65–73), we precisely measured all the necessary parameters on a sample of 236 saplings of 16 species. Then, using sensitivity (variance) analysis, regressions between successive models for risk factors and species ranks and the use of these models on samples of self- and nonself-supporting saplings, we tested different degrees of simplification up to the most simple and widely used formula that assumes that the tree is a cylindrical homogeneous pole. The size factor had the greatest effect on buckling risk, followed by the form factor and the modulus of elasticity of the wood. Therefore, estimates of buckling risk must consider not only the wood properties but especially the form factor. Finally, we proposed a simple but accurate method of assessing tree buckling risk that is applicable to a wide range of samples and that requires mostly nondestructive measurements.

Key words: biomechanics; critical buckling height; French Guiana; risk factor; sapling; stem form; tropical rain forest; trunk volume.

Within the scope of forest ecology, plant functional traits must be determined to observe their diversity, to find the existing trade-offs that allow species to coexist (McGill et al., 2006), and to define species growth strategies. Biomechanical traits of plants are usually studied within different contexts, including studies of the evolution of plant forms (Esser, 1946; Larson, 1963; McMahan, 1973; Niklas, 1988; Alméras et al., 2004) and growth (Mattheck, 1990; Niklas, 1993; Henry and Aarssen, 1999; King et al., 2006). They are also studied at the practical level to develop a better understanding of the mechanical stability of cultivated plants (Brüchert et al., 2000; Coutand et al., 2000) or their potential for human use (Beismann et al., 2002; Kern et al., 2005). The interactions between mechanical constraints and tree architecture (i.e., the developmental constraint) are increasingly discussed within the context of heterogeneous forest ecology, especially in tropical rainforests characterized by a tremendous diversity of woody plant species (O'Brien et al., 1995; Sterck and Bongers, 1998; van Gelder et al., 2006). In this case, the diversity of tree traits among a wide range of samples of plants and species must be analyzed. Moreover, these traits should be assessed insofar as

possible by nondestructive measurements to enable repeated and long-term observations during growth in permanent plots.

One tree trait discussed in many works (Rich et al., 1986; King, 1987; Niklas, 1995; Sterck and Bongers, 1998; Gavin and Peart, 1999) is the risk of mechanical buckling under self-weight, usually measured by a safety factor, the ratio between critical buckling height (H_{cr}) and the actual tree height. The use of such safety factors implies the choice of a particular biophysical constraint, buckling in this case, but other constraints can be analyzed as well, such as uprooting or tree breaks under wind stress (Esser, 1946; King, 1986; Spatz and Bruechert, 2000; Karrenberg et al., 2003) or under hydraulic stress (Niklas and Spatz, 2004; Kern et al., 2005). This implicitly assumes that buckling is ecologically relevant in the studied context. However, using safety factors >1 for self-supporting trees, we highlight the safe situations where the buckling risk is obviously not ecologically significant. Actually, when a safety factor >4 , buckling is obviously not a major constraint and plant height is obviously limited by other factors. Therefore, we prefer to use the reciprocal of the safety factor, i.e., the risk factor (RF) that is the ratio between the tree's actual height and its critical buckling height. RF is strictly contained between 0 and 1 for self-supporting plants, and highlights high-risk values, i.e., situations where buckling risk is a major ecological constraint, with a transition from self-supporting to liana habit. Some authors (McMahan, 1973; Niklas, 1994) reported very low buckling risks that were fairly constant at the scale of large samples of trees or self-supporting ground plant species. In tropical rainforest understory, the very limited light (Chazdon and Fetcher, 1984; Montgomery and Chazdon, 2002) with vertical (and horizontal) light gradients induces tall and slender saplings associated with high buckling risks (Kohyama and Hotta, 1990; King, 1991, 1994). Moreover, a small percentage of nonself-supporting trees are usually observed in this case (see Fig. 1). Finally, based on the diversity of growth patterns, life histories, and architectures

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⁵ Author for correspondence (e-mail: jaouen_g@kourou.cirad.fr)



Fig. 1. A nonself-supporting *Tachigali melinonii* right after cutting (left) and a self-supporting one (right) from the same place. In the forest, the nonself-supporting sapling was supported by larger trees.

found in a tropical rainforest, we expect to find a diversity of buckling risks among species (Bongers and Sterck, 1998; Sterck and Bongers, 1998).

In this paper, we investigate a simple method for determining the buckling limit of saplings for a wide range of samples with as few measurements as possible but with sufficient accuracy and no bias. Our goal is to use this simple method to evaluate the variation of buckling limit in the population. A mechanical model of the H_{cr} of trees was proposed by Greenhill (1881). This model is based on the beam theory for a tapered, elastic pole, subjected to gravity and with restrained anchorage. Among the many models developed for buckling analysis of tapered beams under complex loadings (Garth Smith, 1988; Elishakoff and Rollot, 1999; Li, 2001), we chose this model, which is very appropriate for tree buckling risk assessment, because the parameters used to specify geometry and loads are adapted to the description of a tree. Greenhill's model considers tree size, taper, mass distribution along the trunk, and wood stiffness. Many authors (King, 1981; Niklas, 1994; Claussen and Maycock, 1995; Sterck and Bongers, 1998; van Gelder et al., 2006) have used this model to compute safety factors with more or less implicitly simplified assumptions about trunk taper, mass distribution along the trunk, and wood stiffness, but the relevance of these assumptions has seldom been assessed. Moreover, the definition of RF requires a comparison between the real height and the critical one, where all other factors remain constant. Most authors (Claussen and Maycock, 1995; Sterck and Bongers, 1998; van Gelder et al., 2006) compared trees using one diameter, the same taper, the same mass distribution and,

sometimes, the same wood stiffness. When comparing species strategies, the ecological significance of these assumptions is not always obvious. Taper or mass distribution can be easily understood as developmental architectural constraints and should therefore vary among species and with environmental conditions. Wood stiffness variations, closely linked to dry wood density, play a central role in the life-history variation of tree species (van Gelder et al., 2006). Lastly, the diameter is the usual size parameter in forest science. However, because the issue in this case is to calculate the maximal height the tree could reach with the same investment in support material, the tree should be compared to a pole of the same wood volume or same wood dry mass, rather than the same diameter.

This paper compares different methods for estimating buckling risk factors, using Greenhill's model for calculating buckling height. The H_{cr} and RF will first be computed with the complete model using a sample of 236 saplings from 16 species of the tropical rain forest of French Guiana. The sources of variation of the buckling height will be studied to determine which ones can be disregarded at the intra- and/or interspecific levels. For further applications on large samples on permanent plots where trees cannot be harvested, we will then design proxy variables using nondestructive data for the factors that greatly contribute to H_{cr} variability. Finally, we will discuss the bias and errors due to the different possible choices. This comparison is based on the consequences of simplifying the assumptions on the H_{cr} calculation and on the ranking of species according to their RF. The ability of the models to clearly discriminate between saplings known to be self-supporting or not is validated for one species.

MATERIALS AND METHODS

Greenhill's model—The risk for a tree to buckle under its self-weight is calculated by the ratio of its actual height to its critical buckling height H_{cr} , i.e., the maximal height it could reach with the same volume of material, taking its developmental constraints (mass, tree form, and wood properties) into account. Our reformulation of Greenhill's model leads to Eq. 1:

$$H_{cr} = \frac{\pi^{1/2} E^{1/2} r_0^2 c (|m - 4n + 2|)}{4(M_{tot}g)^{1/2}}, \quad (1)$$

where E is Young's modulus of elasticity of the green wood (Pa), r_0 the basal radius of the trunk (m), M_{tot} the total biomass of the tree (kg), g the gravitational acceleration ($9.81 \text{ m}\cdot\text{s}^{-2}$), n the tapering parameter defining the way the radius changes along the trunk (Eq. 2), and m the biomass distribution along the whole trunk (Eq. 3).

$$r(z) = r_0 \left(\frac{H - z}{H} \right)^n \quad (2)$$

$$M(z) = M_{tot} \left(\frac{H - z}{H} \right)^m \quad (3)$$

The variable z is the height along the trunk (m), H is the total height of the tree (m), $r(z)$ the trunk radius (m) at the z -level, and $M(z)$ the total biomass (kg; trunk, branches, and leaves together) supported above the z -level. By way of explanation, if $n = 0$, the stem is a cylinder; if $n = 1$, it is a cone. In other words, the higher the value of n , the greater the taper (i.e., the diameter variation between the basal and the upper part of the trunk). If $m = 1$, the biomass is uniformly distributed along the whole tree; the higher the value of m , the nearer to the base of the tree the biomass is concentrated. Lastly, c is a function of n and m , namely, the first root of the Bessel function J_0 with v defined by Eq. 4:

$$v = \frac{4n - 1}{m - 4n + 2} \quad (4)$$

Because the tree will be compared to a pole of the same wood volume, we modified Eq. 1 using the trunk's volume rather than its radius as the main size parameter. The section is considered as circular so that the volume of the trunk above z is given by Eq. 5:

$$V(z) = \int_z^H \pi r(z)^2 dz, \quad (5)$$

which, using Eq. 2, gives Eq. 6:

$$V(z) = \frac{\pi r_0^2 (H - z)^{2n+1}}{(2n + 1)H^{2n}}. \quad (6)$$

From Eq. 6, the total volume is given, taking $z = 0$, by Eq. 7:

$$V(0) = V = \frac{\pi r_0^2 H}{2n + 1}, \quad (7)$$

and Eq. 1 becomes Eq. 8:

$$H_{cr} = \frac{1}{2(\pi g)^{1/2}} E^{1/2} (c(|m - 4n + 2|)(2n + 1))^{1/2} V^{1/4} \left(\frac{M_{tot}}{V} \right)^{-1/4}. \quad (8)$$

Lastly, the model can be presented as in Eq. 9:

$$H_{cr} = 0.21 E^{1/4} F^{1/4} V^{1/4} L^{-1/4}. \quad (9)$$

The wood property factor E , namely, the modulus of elasticity of green wood (Pa), defines wood mechanical stiffness independently of tree form and size. The form factor F [with no unit, $F = c(|m - 4n + 2|)(2n + 1)$] depends on both m , the distribution of biomass along the whole trunk, and n , the trunk taper defining the variations of the cross section bending inertia along the pole. The load factor L ($\text{kg}\cdot\text{m}^{-3}$) is the "structural" density, i.e., the ratio of the supported mass ($=M_{tot}$, including branches and leaves) to the volume of support material (V). If branches, leaves, and bark biomass can be considered to be negligible, this factor is the green wood density. The size factor, in other words, the stem volume V (in m^3), represents the amount of support material.

If the tree is assumed to be a tapered pole of constant density (ρ) with negligible branch and leaf biomasses, $M(z) = \rho V(z)$, then according to Eq. 6, parameter m equals $2n + 1$.

A further simplified version of the model (referred to as the "classical formula" in this work) is often found in the literature (Niklas, 1995, 1999a; Sterck and Bongers, 1998; Falster, 2006; van Gelder et al., 2006). In this case, the trunk is considered as a cylinder with, in most cases, a homogeneous distribution of biomass all along the tree so that $n = 0$ and $m = 1$ and, thus, $c = 1.867$. The resolution of Greenhill's model leads to Eq. 10:

$$H_{cr} = 0.792 \left(\frac{E}{M/V} \right)^{1/3} D^{2/3}. \quad (10)$$

Obviously, the use of Bessel functions that are not as popular as other mathematical functions (such as sines, exponentials, or logarithms) deterred authors from properly taking taper and mass distribution into account in buckling height calculations; they therefore automatically used the constants explicitly given for a homogeneous cylinder. To promote the use of proper form factors (F) in further studies, we propose a polynomial regression of c vs. v obtained from our numerical calculations.

In Greenhill's initial model, the parameter used for the diameter is the basal dimension of the stem, but some authors (Sterck and Bongers, 1998; Sposito and Santos, 2001; van Gelder et al., 2006) used the diameter at breast height to define the size of the cylinder used to calculate the H_{cr} . When applying this formula to our data, we used the diameter measured 1.5 m above the ground (D_{150}), which is easier and more accurate to measure than the basal diameter because of the buttresses, stilt roots, and frequent variations of the stem's circumference near the base of the tree. In Eq. 10, the cylinder defined by the basal diameter may be significantly larger than the one defined by another diameter higher up in the tree, and the H_{cr} calculated is larger as well.

Plant material and measurements—Sixteen common species of the Guianese tropical rain forest were used (Table 1). The 236 saplings were harvested between 2002 and 2006 at the Paracou Research Station ($5^{\circ}18' \text{ N}$, $52^{\circ}55' \text{ W}$); see Gourlet-Fleury et al. (2004) for a complete description of the site. The individuals were chosen to form a representative sample of saplings with D_{150} ranging from 1 to 7 cm. The mean D_{150} was $3.9 \text{ cm} \pm 1.9 \text{ SD}$, and the mean height was $7.3 \text{ m} \pm 3.3 \text{ SD}$. The data were collected as follows: after the sapling was cut down, the total length (H) of the main axis was measured. Diameters and weights were measured along the trunk. These data were used to calculate n and m with log-log regressions. To increase the accuracy of the log-log regressions used to calculate n and m , trees were sawed into six parts of equal length, and the two distal parts were again cut into two equal parts. Each of the eight parts was weighed, including trunk, branches, and leaves, and the basal diameter of each part was measured. The determination coefficients for the individual log-log regressions were high ($R_{mean}^2 = 0.952 \pm 0.041$ for n and $R_{mean}^2 = 0.973 \pm 0.025$ for m). All the saplings for which this coefficient was under 0.85 (mostly due to broken saplings) were removed from the analysis. This excluded less than 3% of the sampled saplings. Diameters at the base of each part were also used to calculate trunk volume V , considering each stem segment as a truncated cone. Finally, a 1-cm thick segment of each part was kept and used to measure wood basic density ρ_b (oven dry mass/fresh volume). The segments were fully impregnated with water using a vacuum pump, and their volume was measured by the Archimedes principle. The segments were then dried in an oven for 3 days at 103°C and weighed. The basic density is a good proxy of Young's modulus, at least at an interspecific level, as shown for both temperate and tropical trees (Cannell and Morgan, 1987; van Gelder et al., 2006). Fournier et al. (2006) used a compilation of results to quantify the relationship between the modulus of elasticity of green wood (E) and basic density (ρ_b):

$$E = 10400 \left(\frac{\rho_b}{0.53} \right)^{1.03}. \quad (11)$$

The average coefficient of variation of basic density within saplings was low ($6.3\% \pm 3.9 \text{ SD}$), justifying the assumption of a constant Young's modulus along the stem. However, E is not a pure wood property but a composite one; near the top of the tree, the contribution of softer bark and very juvenile xylem is no longer negligible (Niklas, 1999b). Some authors (Spatz, 2000; Spatz and Speck, 2002) proposed a modified version of Greenhill's model that considers the vertical variation of E . The use of this method requires a numerical computation for each sapling and additional measurements at the individual level to accurately determine the variations in E at the highest parts of the trunk. Because the aim of this work was to determine a method to compute the

TABLE 1. The 16 species used in this study with their Latin name, botanical family, abbreviation used in the text, and the number (N) of saplings included in the analysis.

Species	Family	Abbreviations	N
<i>Dicorynia guianensis</i> Amsh.	Caesalpiniaceae	Dg	13
<i>Bocoa prouacensis</i> Aubl.	Caesalpiniaceae	Bp	5
<i>Carapa procera</i> A. DC.	Meliaceae	Cp	5
<i>Tachigali melinonii</i> (Harms) Barneby	Caesalpiniaceae	Tm	12
<i>Sextonia rubra</i> (Mez) van der Werff	Lauraceae	Sr	5
<i>Eperua falcata</i> Aubl.	Caesalpiniaceae	Ef	31
<i>Pradosia cochlearia</i> (Lecomte) Pennington	Sapotaceae	Pc	15
<i>Lecythis persistens</i> Sagot	Lecythidaceae	Lp	24
<i>Gustavia hexapetala</i> (Aubl.) J.E. Smith	Lecythidaceae	Gh	5
<i>Qualea rosea</i> (Aubl.)	Vochysiaceae	Qr	5
<i>Oxandra asbeckii</i> (Pulle) R.E. Fries	Annonaceae	Oa	23
<i>Virola michelii</i> Heckel	Myristicaceae	Vm	16
<i>Eperua grandiflora</i> (Aubl.) Benth.	Caesalpiniaceae	Eg	32
<i>Pogonophora schomburgkiana</i> Miens ex Benthham	Elaeocarpaceae	Ps	5
<i>Licania alba</i> (Bernoulli) Cuatrec.	Chrysobalanaceae	La	29
<i>Goupia glabra</i> Aubl.	Celastraceae	Gg	11

individual buckling risk for diverse samples, we preferred to use a mean E for each sapling. However, we note that use of a mean E could overestimate H_{cr} .

Data analysis—*Variance analysis of log-transformed variables*—To determine the accuracy needed for each factor, we performed a sensitivity analysis. This analysis is based on the identification of the main sources of variation of H_{cr} . The log transformation of Eq. 9 enables us to express the cumulative influence of each factor on H_{cr} :

$$\ln H_{cr} = \ln 0.21 + \frac{1}{4} \ln E + \frac{1}{2} \ln F + \frac{1}{4} \ln V - \frac{1}{4} \ln L. \quad (12)$$

The coefficient associated with each factor depends on the power to which it is elevated in the original equation and thus directly expresses the magnitude of the mechanical influence of each factor. However, the sensitivity of the buckling height to a given factor also depends on the actual variability of that factor. Assuming linear independence between the log-transformed factors, the decomposition of variance leads to:

$$\text{Var}(\ln H_{cr}) = \frac{1}{16} \text{Var}(\ln E) + \frac{1}{4} \text{Var}(\ln F) + \frac{1}{16} \text{Var}(\ln V) + \frac{1}{16} \text{Var}(\ln L). \quad (13)$$

Eq. 13 quantifies the influence of each factor on the total variability. In turn, the total variability of a factor can be decomposed into interspecific variance (Var_{spe}) and intraspecific (interindividual at a specific level) variance (Var_{ind}):

$$\begin{aligned} \text{Var}(\ln H_{cr}) = & \frac{1}{16} [\text{Var}_{\text{spe}}(\ln E) + \text{Var}_{\text{ind}}(\ln E) + 4\text{Var}_{\text{spe}}(\ln F) + 4\text{Var}_{\text{ind}}(\ln F) \\ & + \text{Var}_{\text{spe}}(\ln V) + \text{Var}_{\text{ind}}(\ln V) + \text{Var}_{\text{spe}}(\ln L) + \text{Var}_{\text{ind}}(\ln L)] \end{aligned} \quad (14)$$

Each component of the total variance is calculated, and its relative contribution to the total variance is examined to identify the factors to which H_{cr} is the most sensitive. If the intraspecific contribution of a factor to the total variance is low, then the use of a mean value at a specific level can be tested to estimate the H_{cr} of an individual. If the interspecific contribution is also low, then the use of a mean computed with all species together (an interspecific mean) is tested for this factor.

Finding proxies or mean estimations to avoid destructive measurements—According to the results of the variance analysis for the factors for which the contribution to the total variance is large enough, we tried to find the best relationship between the factor and a combination of H and D_{150} . This was done using the multiple regression tool of the Statistica software (version 7.1, Statsoft France [2006]).

Testing the simplifications of the model—To determine the acceptability of the aforementioned simplifications, we checked their influence on H_{cr} and RF

estimations. The most accurate method, which uses all the factors measured at the individual level (referred to as the “complete model” later), was taken as a reference for comparing H_{cr} and RF calculated with increasingly simplified models. A good simplified model is characterized by (1) a good correlation with the complete model; (2) no bias, i.e., a slope close to one (the intercept is set to zero); (3) an unchanged ranking of species; and (4) the ability to discriminate between self-supporting and nonself-supporting trees. This last point was then validated with a sample of *Tachigali melinonii* saplings. These saplings were sampled according to their observed state of mechanical stability (clearly self-supporting or clearly buckled as in Fig. 1) and were included in the sample used in this paper (Table 1). For each validation criterion, we compared the complete model (Eq. 9), our simplified versions, and the classical formula (Eq. 10).

RESULTS

Practical calculation of the constant c_v (root of a Bessel function)—The constant c_v , which depends on the allometric parameters through v (Eq. 4) can be computed by Eq. 15:

$$c_v = c_{v_{n=0,m=1}} + a \left(v + \frac{1}{3} \right) + b \left(v + \frac{1}{3} \right)^2 + c \left(v + \frac{1}{3} \right)^3 \quad (15)$$

The intercept is the value of c_v for the classically used assumptions of a cylindrical trunk with a homogeneous distribution of biomass, i.e., $n = 0$ and $m = 1$, thus $v = -1/3$ and $c_v = 1.867$. The coefficients are shown in Table 2. The small relative errors (the largest one is lower than 2%) confirm the validity of these equations to calculate c_v .

Analysis of variance of log-transformed factors—The main part of the total variance of H_{cr} (Table 3) was represented by the size factor V , followed by the form factor F , and then with equal weight, wood stiffness E and structural load L . Separating inter- and intraspecific contributions for each factor indicated that the main source of variance was intraspecific for V and F and interspecific for E and L .

Estimations of the four factors according to the results of the analysis of variance—Factor V has the largest inter- and intraspecific variations and thus must be accurately determined for each individual. The best relationship to estimate V was: $\ln V = a + b \ln D_{150} + c \ln H$.

Very good relationships were found to predict the volume at

TABLE 2. Coefficients necessary to calculate c_v , for any value of v in the $-1/3 \rightarrow 20$ range. c_v is the first root of the Bessel function J_v and is one of the necessary parameters to compute the critical buckling height. Columns a, b, and c give the coefficient values of the formula giving c_v as a function of v . The last two columns give the determination coefficients (R^2) of the relationship for each range of v and the maximum relative error (Max. rel. err.) between real values and the estimation of c_v .

Range of v	a	b	c	R^2	Max. rel. err. (%)
$-1/3 \leftrightarrow 0.499$	1.69086	-0.25831	0.07789	0.999	0.996
$0.5 \leftrightarrow 2.499$	1.62867	-0.13929	0.01773	0.999	0.336
$2.5 \leftrightarrow 20$	1.41260	-0.02446	0.00060	0.999	1.971

a specific level (R^2 ranging between 0.956 and 0.999) and also at the interspecific level ($R^2 = 0.982$) (Table 4). For E and L , the intraspecific variance was low so that mean specific values (Table 4) will be tested. Finally, because F has a considerable effect at both the inter- and intraspecific levels, two estimations were tested: a global regression with size parameters (the best relation found was $\ln F = 1.784 + 0.294 \times \ln H$, $R^2 = 0.319$) and mean specific values.

Are trees cylindrical with a homogeneous distribution of biomass?—The third part of Table 4 and Fig. 2 show that n was significantly different from 0 for all species. Moreover, for m , only four species (*G. hexapetala*, *Q. rosea*, *V. michelii*, and *P. schomburgkiana*) had values not significantly different from 1. Figure 2A first shows a considerable interspecific variability for the n values, which ranged from 0.3 to nearly 0.8, meaning that trunk forms were in between cylinders ($n = 0$) and cones ($n = 1$). The global mean stands for a mean form closer to a cone than to a cylinder. The m values (Fig. 2B) were also variable between species and were, for a majority of species and for the global mean, greater than 1, meaning that the center of gravity was closer to the base than to the top of the saplings. The power-law models fit well with the observed data. Examples of individual fittings are shown in Fig. 3. The species chosen are among those with the highest (*B. prouacensis*) and the lowest (*E. grandiflora*) intraspecific variability for n and m . The analysis of the n and m values also shows that the mean difference between m and $2n + 1$ was $31.3\% \pm 14.6\%$ SD.

Testing simplifications of the model—Comparisons between models—According to the previous analysis, four levels of simplification of our model (Eq. 9) were considered. All four models used a species-specific mean for E and L . F was either computed from a global regression (F_{gr} in the model name) or set to the mean species-specific value (F_m). V was computed from regression relationships (Table 4), either at the community level (V_{gr}) or at the specific level (V_{sr}). The simplified

TABLE 3. Percentages of the total variance of the critical buckling height explained by each factor: wood modulus of elasticity (E), form (F), load (L), and trunk volume (V). The interspecific and intraspecific parts are separated, and the total contribution for each factor appears in the last row.

Origin of the variance	% of the total variance			
	E	F	L	V
Interspecific part	1.6	4.8	1.1	14.1
Intraspecific part	0.2	7.6	0.7	69.8
Sum for each factor	1.7	12.5	1.8	83.9

models all led to an almost unbiased estimation of both H_{cr} and RF, with slopes close to 1 (Table 5). The determination coefficients were high for the prediction of H_{cr} but lower for RF. It clearly appears that using F_{gr} rather than F_m leads to lower determination coefficients for the RF. The classical model produced lower determination coefficients than those of models F_mV_{gr} and F_mV_{sr} , and, more importantly, it led to a substantial bias, namely an underestimation of H_{cr} and an overestimation of RF. On the basis of this analysis, models F_mV_{gr} and F_mV_{sr} were identified as the best models for predicting H_{cr} and RF. The use of V_{sr} provided the most accurate results, but V_{gr} can also be used without much decrease in accuracy. The use of global mean values of E , L , and F with V_{sr} (Table 6) also resulted in a low bias.

Ranking of species—The ranking of species obtained with models F_mV_{gr} and F_mV_{sr} were strongly correlated ($P < 0.01$) with that obtained with the complete model ($R_{Spearman} = 0.888$ and 0.921 , respectively). The ranking correlation between the classical model and the complete model was clearly lower ($R_{Spearman} = 0.456$) and not statistically significant ($P = 0.076$). Results of this test confirmed those obtained in the previous section—that model F_mV_{sr} is the most accurate.

Predicting degree of self-support—The complete model and our simplified versions, F_mV_{gr} and F_mV_{sr} , revealed significant differences between means of RF for both habits, self-supporting and nonself-supporting (Table 7). The mean values given by models F_mV_{gr} and F_mV_{sr} were close to those given by the complete model. If we used individual values and considered a margin of ± 0.1 , the RF of some saplings did not correspond (out of the margins) to their habit. Finally, for the classical model, the mean values were higher than for the three other models. The individual values were frequently higher than 1, predicting that almost all the saplings were nonself-supporting. The complete model and our simplified versions revealed an RF significantly lower than 1 for self-supporting saplings and not significantly lower than 1 for nonself-supporting saplings (Fig. 4). The classical model provided higher values with no significant distinction between mean RF of self-supporting saplings and the buckling limit 1.

DISCUSSION

This work aims at determining a way to accurately measure the buckling risk factor of saplings. Within the context of forest ecology, the study of plant functional traits and their diversity is a central issue, and the buckling risk has not been accurately studied among sapling populations. We propose a detailed

TABLE 4. Summary of the values used to estimate V (trunk volume), E (wood modulus of elasticity), F (form) and L (load, i.e., ratio of the whole biomass to V). Coefficients a , b and c are the species-specific coefficients of the relationship $\ln V = a + b \ln D_{150} + c \ln H$ (the R^2 are from the comparison between real and modeled V values). The values of E (GPa), F (no unit) and L ($\text{kg}\cdot\text{m}^{-3}$) are the species-specific means. For n (stem taper) and m (biomass distribution parameter), mean values and standard deviations are given. The last row contains values for the whole sample.

Species ^a	Volume prediction				Mean specific values of factors			Mean specific values of form parameters			
	a	b	c	R^2	E	F	L	n	SD	m	SD
Dg	-1.86	1.68	1.04	0.996	11.2	10.7	1177	0.63	0.08	1.61	0.16
Bp	-1.37	1.52	0.41	0.956	15.7	10.4	1418	0.60	0.20	1.59	0.37
Cp	-0.02	2.00	0.67	0.999	9.1	6.5	1141	0.38	0.03	0.75	0.14
Tm	-0.24	1.97	0.73	0.996	9.5	10.4	1040	0.53	0.10	1.55	0.34
Sr	-3.27	1.26	1.15	0.988	8.5	5.9	1438	0.30	0.09	0.63	0.10
Ef	-3.15	1.37	1.21	0.979	11.4	11.5	1092	0.77	0.15	1.85	0.34
Pc	1.00	2.11	0.32	0.984	11.7	11.6	1581	0.76	0.17	1.85	0.41
Lp	-0.47	1.90	0.73	0.992	12.5	11.1	1664	0.73	0.18	1.74	0.38
Gh	1.59	2.08	-0.27	0.957	10.1	8.2	1589	0.56	0.05	1.14	0.09
Qr	0.38	2.02	0.42	0.999	11.1	6.7	1595	0.45	0.07	0.79	0.23
Oa	1.27	2.18	0.31	0.991	14.2	12.6	1597	0.76	0.14	1.98	0.36
Vm	1.81	2.24	0.09	0.994	7.7	8.5	1126	0.50	0.13	1.16	0.51
Eg	-4.76	1.09	1.54	0.977	12.8	10.8	1205	0.74	0.12	1.70	0.38
Ps	7.31	3.30	-0.80	0.999	13.7	7.8	1361	0.42	0.12	1.05	0.16
La	-0.93	1.80	0.79	0.986	16.3	11.7	1458	0.67	0.27	1.65	0.47
Gg	-4.24	1.23	1.55	0.965	13.0	11.4	1157	0.54	0.17	1.76	0.40
All	-1.79	1.61	0.93	0.982	12.3	10.7	1340	0.66	0.20	1.62	0.49

^a Species abbreviations are given in Table 1.

study of this trait assessment and a method to measure it on a wide range of plant populations. The H_{cr} sensitivity analysis shows the predominance of the size factor V . This result simply expresses the fact that the maximal height that a tree can achieve mainly depends on the amount of material it is made of. It should be noted that the contribution of the volume factor to the total variance of H_{cr} is directly controlled by the range of sizes of the studied trees. If a wide size range is used, then the volume factor is the main contribution to the variance of H_{cr} . For instance, Niklas (1994) studied plants with diameters ranging from 0.003 m to 3 m. The effect of size-independent factors is of much greater biological significance in terms of biomass allocation and optimal mechanical design. The most original result of our work concerns the demonstrated preponderance of the form factor F among size-independent factors. Researchers usually assume that the form factor is constant, i.e., that trees are homogenous and cylindrical (McMahon, 1973; Claussen and Maycock, 1995; Niklas,

1995, 1997, 1999a; Sterck and Bongers, 1998; van Gelder et al., 2006). As shown in Fig. 2, this assumption does not correspond to the reality of stem form. Moreover, the form factor has large interspecific variability, showing that the distribution of biomass within the tree is an important biomechanical trait of the species. The use of the classical formula (Eq. 10) leads to an underestimation of H_{cr} and an overestimation of RF, confirmed by the analysis of the subsample of *T. melinonii* for which the habits are known. Those results are not surprising because the classical formula considers a cylinder, while the majority of the taper values are closer to a cone ($n = 1$). Obviously, with the same amount of material, a cone can be built higher than a cylinder. Indeed, a cone has both a lower load in its distal part where the lever arm is the biggest and a higher bending inertia in the basal part that is subjected to the highest bending moment. These results are consistent with those of Keller and Niordson (1966), who found optimal taper values comprised between 1/3 and 3/2 for

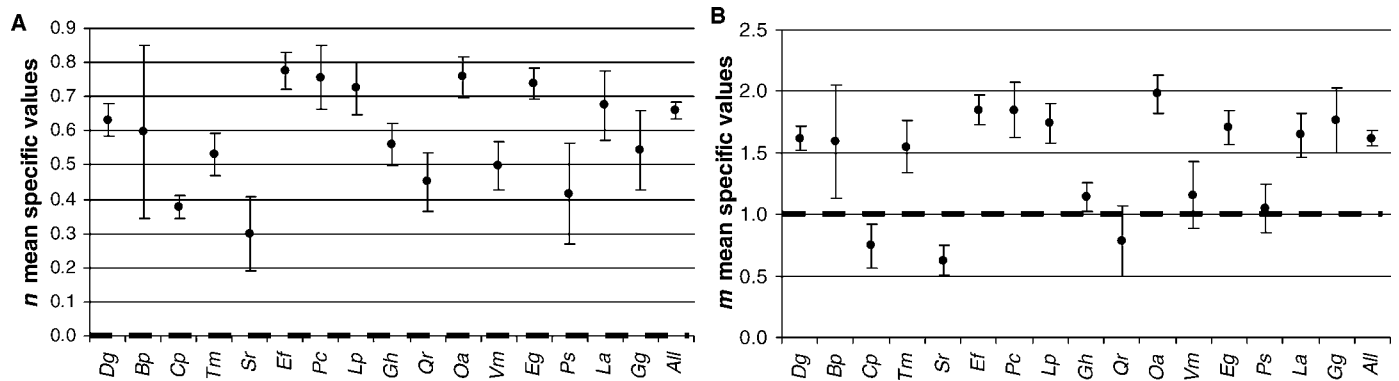


Fig. 2. Mean specific values and mean value of all species together (last point of each plot) for (A) stem taper n and (B) biomass distribution m . Vertical bars represent the confidence intervals (95%). Dotted lines highlight classical assumption values for each parameter ($n = 0$ and $m = 1$). All the mean values of n are significantly different from 0, and the majority of the mean values of m are significantly different from 1.

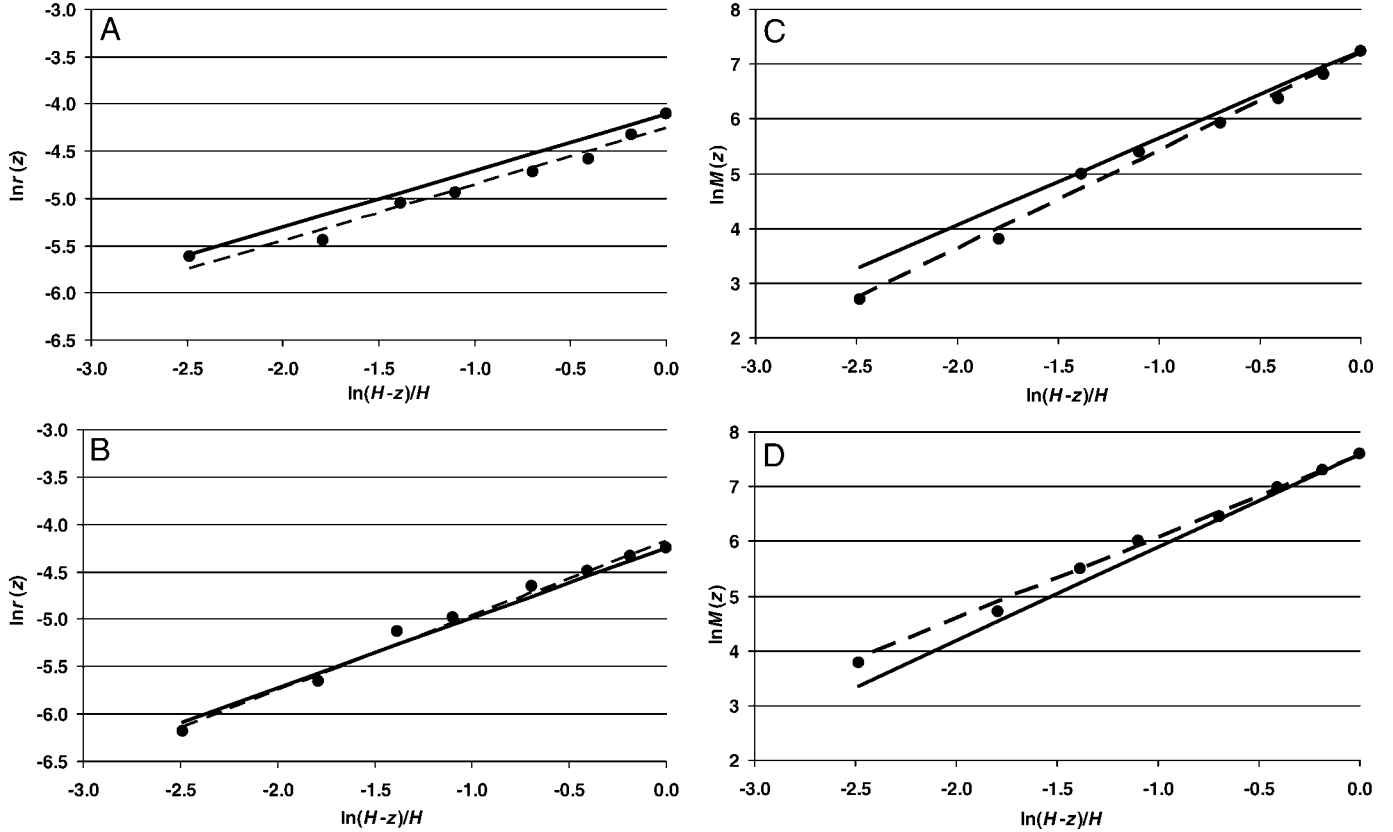


Fig. 3. Validation of the power models used to determine stem taper n and biomass distribution parameter m : $\ln r(z)$ vs. $\ln[(H - z)/H]$ for (A) *Bocoa prouacensis* and (B) *Eperua grandiflora*; and $\ln M(z)$ vs. $\ln[(H - z)/H]$ for the same (C) *B. prouacensis* and (D) *E. grandiflora* according to Eqs. 2 and 3. The points represent the measured values of $\ln r(z)$ or $\ln M(z)$; the dotted lines represent the values estimated with n (or m) determined at the individual level, i.e., the log–log regressions; the continuous lines represent the values estimated with n (or m) mean specific values. The determination coefficients for measured points are: $R^2 = 0.965$ (for n) and 0.991 (for m) for *B. prouacensis* and 0.989 (for n) and 0.997 (for m) for *E. grandiflora*.

unloaded and loaded columns (with an infinitely higher load than its own weight), respectively. Our values of n are closer to $1/3$, which corresponds to the sapling situation, i.e., loaded by noninfinite mass. Moreover, when researchers assume cylindrical trees of a given diameter (McMahon, 1973; Claussen and Maycock, 1995; Niklas, 1995, 1997, 1999a; Sterck and Bongers, 1998; van Gelder et al., 2006), the estimation of H_{cr} is very sensitive to the choice of the tree diameter (basal, at breast height, etc.), and such choices are rarely discussed. Therefore, disregarding accurate estimations of form factors leads to a bias of the RF estimate because the form factor is

both a determining factor of the RF and variable among tree species. Moreover, even if it is not strong, a significant ($P < 0.05$) relationship has been found ($R^2 = 0.319$) between form factor and the size of saplings. As a result of the small range of sizes in our sample, we were able to use a specific mean value for this factor, but the transposition of this result to a wider sample may not be advisable. Biologists and foresters have been studying stem growth and taper for a long time (Larson, 1963; Claussen and Maycock, 1995). Even if some authors (Chiba and Shinozaki, 1994; Chave et al., 2005) have reported no change in stem form of saplings over time, there is evidence

TABLE 5. Comparisons of H_{cr} and RF computations by different combinations of assumptions for E (wood modulus of elasticity), L (saplings load, i.e., ratio of the whole biomass to trunk volume), F (form), and V (trunk volume) and by the complete model. Determination coefficient (R^2) and slopes of linear regressions between both computation ways are given.

Model name	E	L	F	V	R^2		Slopes	
					H_{cr}	RF	H_{cr}	RF
$F_{gr}V_{gr}$	sp mean	sp mean	glob reg	glob reg	0.880	0.352	0.963	0.980
$F_{gr}V_{sr}$	sp mean	sp mean	glob reg	sp reg	0.886	0.394	0.971	0.979
F_mV_{gr}	sp mean	sp mean	sp mean	glob reg	0.874	0.702	0.960	0.977
F_mV_{sr}	sp mean	sp mean	sp mean	sp reg	0.889	0.733	0.967	0.975
Classical		classical formula			0.827	0.629	0.807	1.167

Note: sp mean = mean specific value (“m” in model name); glob reg = regression constructed with all of the species together (“gr” in model name); sp reg = species-specific regressions (“sr” in model name); classical formula = Eq. 10.

TABLE 6. Effects of the use of a mean interspecific value (glob mean) vs. a specific mean (sp mean) of E (wood modulus of elasticity), L (load), or F (form) in the F_mV_{sr} model for H_{cr} and RF calculations. The first part of the table explains the proxies used in each case (Table 5); the second gives the determination coefficients and slopes of comparison with the calculations done with the complete model, for both H_{cr} and RF , respectively.

Proxies used				R^2		Slopes	
E	L	F	V	H_{cr}	RF	H_{cr}	RF
glob mean	sp mean	sp mean	sp reg	0.868	0.656	0.965	0.966
sp mean	glob mean	sp mean	sp reg	0.987	0.947	0.987	1.018
sp mean	sp mean	glob mean	sp reg	0.815	0.581	0.957	0.956

that this factor is modulated by the immediate environment of the sapling: light, population density, and resource availability (Larson, 1963; Claussen and Maycock, 1995; Briand et al., 1999; Dean et al., 2002). Fewer data are available on the mass distribution parameter m along the trunk, which integrates biomasses of both the trunk and the branches (wood and leaves). Because trunk wood is quite heavy, we would expect that m could be linked to n . However, such a relationship was not found, and moreover, m is different from $2n + 1$, which means that the tree cannot be modeled as a pole of constant density. King and Loucks (1978) emphasized the importance of mass distribution and developed a model of H_{cr} based on the ratio R of crown biomass to trunk biomass. Niklas (1994) underlined and completed the results of King and Loucks (1978) using an R varying with species and size to compute the H_{cr} . A correct estimation of the form factor is the main difference between our models and the classical formula, a difference that leads to considerable discrepancies, including a different ranking of species relative to their RF. Therefore, it is essential that any biomechanical study based on buckling analysis acquire data and use existing data about form factors. To avoid the complicated problem of calculating Bessel roots that are not standard mathematical functions, we proposed a simple polynomial fitting of c_v that will provide practical help for the calculation of F and for further studies.

TABLE 7. RF calculated according to different versions of the model for saplings of *Tachigali melinonii* known to be self-supporting (S) or nonself-supporting (NS). The models used to calculate RF are complete, F_mV_{gr} , F_mV_{sr} , and the classical model. The intermediate lines contain the mean RF for each habit and each model. The last row of the table gives the P value of the Mann–Whitney test between S and NS trees for each model. A P value under 0.05 indicates a significant difference of RF between both habits. Boldface values correspond to values not in accordance with the sapling’s habit.

Habit	Complete	F_mV_{gr}	F_mV_{sr}	Classical
S1	0.80	0.67	0.70	0.87
S2	0.78	0.73	0.73	0.95
S3	0.82	0.81	0.82	1.00
S4	0.88	0.95	0.94	1.18
mean	0.82	0.79	0.79	1.00
NS1	0.95	0.79	0.85	1.09
NS2	0.93	0.86	0.92	1.10
NS3	0.98	0.90	0.94	1.14
NS4	1.19	1.02	1.06	1.38
NS5	0.87	0.96	0.98	1.18
NS6	0.98	1.04	1.07	1.38
NS7	0.99	1.05	1.07	1.17
NS8	0.94	0.99	0.98	1.22
mean	0.98	0.95	0.98	1.21
P	<0.05	<0.05	<0.05	0.06

The load factor was not very sensitive; inter- and intraspecific variabilities are comparable. Therefore, the estimation of L always leads to a slight bias of H_{cr} and RF calculations. Moreover, interspecific variations can be overlooked without much loss in the accuracy of predictions; the use of a global mean value in the F_mV_{sr} model leads to results similar to those given by the complete model. However, the stable value of L should depend on the studied situation. Finally, we chose to use a mean specific value for E . Although less sensitive than the form factor, the wood modulus of elasticity is involved in the variability of biomechanical stability, as emphasized by van Gelder et al. (2006). We found greater inter- than intraspecific differences for E . This is consistent with other works (Wiemann and Williamson, 1988; Barbosa and Fearnside, 2004; Muller-Landau, 2004). Wood density is known to depend on the ecology of the species (Wiemann and Williamson, 1989; Suzuki, 1999; Woodcock and Shier, 2003; Muller-Landau, 2004), with less dense and stiff wood on pioneer, fast-growing species. Thus, the use of a mean specific value seems acceptable and requires only a few destructive measurements because of the low intraspecific variability. However, we stress that the actual measured factor is wood basic density and not Young’s modulus of elasticity. We used a relationship between wood modulus of elasticity along the grain and basic density, as is typical in cellular materials and wood science (Kollmann and Cote, 1968), and made sure that it was very good at predicting interspecific variations of wood stiffness (Fournier et al., 2006). Wood basic density is linked to Young’s modulus, but this relationship is subject to exceptions (Guitard, 1987) because of the ultra-structure of wood cells (the microfibril angle may differ among woods of similar basic density, resulting in differences in mechanical properties as well). Wood basic density is less variable than Young’s modulus, and we may thus underestimate the participation of this factor in the total variance of H_{cr} . Nevertheless, each time we had the opportunity to directly verify the accuracy of the estimation for tropical green wood, the predicted value of E was very close to the measured value (Clair et al., 2003). However, because many studies reveal variations in the modulus of elasticity with ontogeny (Rueda and Williamson, 1992; de Castro et al., 1993; Woodcock and Shier, 2003), environment (Fearnside, 1997; Suzuki, 1999; Baker et al., 2004), or the ecology of the species (Wiemann and Williamson, 1989; Muller-Landau, 2004), it is advisable to make new measurements for each new population studied. Using a mean interspecific value of E in the F_mV_{sr} model does not reduce the precision of calculations, with the exception, once again, of the RF calculation. It is therefore acceptable to use a mean interspecific value to avoid destructive measurements. Some authors have also reported that wood properties change from pith to bark (Wiemann and Williamson, 1989;

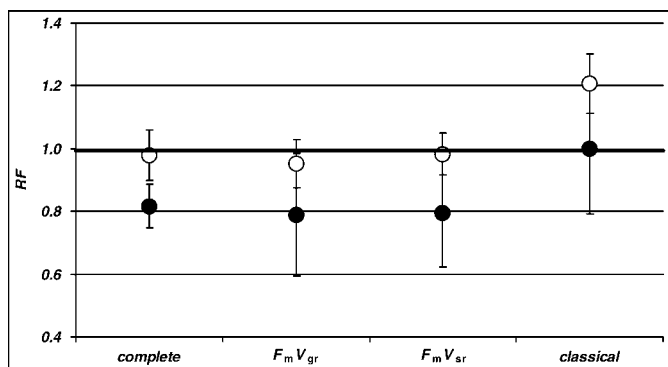


Fig. 4. Mean RF for self-supporting saplings (solid circles) and nonself-supporting saplings (open circles) calculated by different versions of the model (complete, $F_m V_{gr}$, $F_m V_{sr}$, or classical). Vertical bars represent the confidence intervals (95%). The boldface horizontal bar represents the theoretical buckling limit.

Woodcock and Shier, 2002). Changes may also occur because of reaction wood production. We measured wood properties on segments representing the whole stem section, thus giving us a “global modulus of elasticity.” The mechanically correct measurement of the equivalent modulus of elasticity would have required us to consider each different layer and its relative contribution to the flexural inertia, but because E is not the main contributing factor to H_{cr} and because of the high interspecific variations, we could use this method without inducing too large of an error.

Within the framework of this study, the analysis of *T. melinonii* saplings clearly shows that trees in a forest are not always self-supporting. Thus, RF values larger than 1 are not only due to an artifact, as suggested by Niklas (1994), but they can reveal a nonself-supporting habit as part of a growth strategy. Assumptions made in our simplified models do not considerably change the ranking of species according to their biomechanical strategy. This is not the case with the classical formula. However, the accuracy of the estimation by Greenhill’s model was not obvious because there are many underlying assumptions: consistently circular cross sections, branch weights assumed to act similarly to the trunk with no additional bending due to asymmetric development, perfectly rigid anchorage, wood variability, etc. We verified that Greenhill’s model by itself is a good estimation of the self-supporting habit. When comparing self-supporting and nonself-supporting trees, we found that the model accurately discriminated between the different habits. This type of discussion about the performance of buckling mechanical models rarely occurs in the literature (Tateno and Bae, 1990). We finally proposed a better way to estimate H_{cr} and RF ; in contrast to the widely used classical formula, our method emphasizes the importance of form factor values and variability. Concerning biomechanical ecological studies of tree species, we suggest that the height and diameter of each individual be measured nondestructively, then the mean values for E , L , and F and the relationships between V and H and D_{150} should be estimated using smaller samples of harvested trees for each population. In any case, the use of a global relationship for V does not induce a large bias. Moreover, the method developed (i.e., the analysis of variance among the

samples that justifies the choice of estimations for each factor and allows a classification of factors according to their sensitivity) is easy to reproduce in other situations, for example, in comparisons of different plant forms in phylogenetic studies. Further studies will focus on using this method to monitor and analyze the biomechanical diversity of tree species in permanent plots and to understand the relationship between biomechanical traits and species ecology.

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