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Integrative biomechanics for tree ecology: beyond wood density and strength

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Abstract

Functional ecology has long considered the support function as important, but its biomechanical complexity is only just being elucidated. We show here that it can be described on the basis of four biomechanical traits, two safety traits against winds (SW) and self-buckling (SB), and two motricity traits involved in sustaining an upright position, tropic motion velocity (MV) and posture control (PC). All these traits are integrated at the tree scale, combining tree size and shape together with wood properties. The assumption of trait constancy has been used to derive allometric scaling laws, but it was more recently found that observing their variations among environments and functional groups, or during ontogeny, provides more insights into adaptive syndromes of tree shape and wood properties. However, over-simplified expressions have often been used, possibly concealing key adaptive drivers. An extreme case of over-simplification is the use of wood basic density as a proxy for safety. Actually, since wood density is involved in stiffness, loads and construction costs, the impact of its variations on safety is non-trivial. Moreover, other wood features, especially the microfibril angle (MFA), are also involved. Furthermore, wood is not only stiff and strong, but it also acts as a motor for MV and PC. The relevant wood trait for that is maturation strain asymmetry. Maturation strains vary with cell wall characteristics such as MFA, rather than with wood density. Finally, the need for further studies about the ecological relevance of branching patterns, motricity traits and growth responses to mechanical loads is discussed.

Keywords

Biomechanics, Ecological strategy, Gravitropism, Shape, Size, Trees, Wood

Introduction

The mechanical design of trees as achieved by Nature, in particular, the perennial self-supporting habit of extremely slender stems, is both fascinating and complex (Rowe and Speck, 2005), and understanding how tree and wood traits involved in this design are or are not adapted to the environment is a major challenge in functional ecology. Many physical models have been developed in the past to increase our understanding of why tree design works so efficiently (Niklas, 1992; Moulia and Fournier-Djimbi, 1997; Niklas *et al.*, 2006b). These models are still used to address some questions that exist in plant ecology today such as the maximum height that trees can reach (Niklas, 2007; Banin *et al.*, 2012), self-thinning rules (Larjavaara, 2010), biomass partitioning within tree organs (Taneda and Tateno, 2004), and developmental, phylogenetic and environmental wood variations (Watt *et al.*, 2006; Lachenbruch *et al.*, 2011; Zhang *et al.*, 2011). Indeed, in all of these questions, an understanding of how a given design leads to tree mechanical performance first requires an integrative mechanical framework that lays the groundwork for a dedicated mechanical model (Niklas, 1992). In such a modelling approach, the mechanical design of a tree is specified by wood mechanical properties and morphological characteristics that make it possible to resist forces and control strains, as well as by their interaction with loads from external factors (wind flows and gravity) and internal factors (supported fresh biomass, crown area, lever arms, etc.). Mathematical expressions can then be derived to explicitly link the tree mechanical performance in terms of strains, stresses and safety margins, to the design variables such as tissue properties and tree size and shape. However, this modelling phase is only a very preliminary step towards understanding how tree and wood traits are or are not ecologically adapted to the environment. From this point of view, most ecologists who speak of biomechanics have actually been focusing on design safety associated with survival (Read and Stokes, 2006). The two most frequently discussed design features are wood mechanical properties (Chave *et al.*, 2009) and optimal allometries between height and diameter that maintain a given safety margin against mechanical failure (see Niklas (1994) and Moulia and Fournier-Djimbi (1997) for a review of related studies, and Niklas *et al*. (2006a) for a recent case study).

Moreover, as developed by Moulia and co-workers (Moulia *et al.*, 2006), plant biomechanical performance must continually adapt during growth, implying that a developmental plasticity rather than a genetically-fixed design was probably selected in most environments. Generally speaking, phenotypic plasticity and more accurately ontogenetic plasticity (*i.e*. variation in the ontogenetic trajectory induced by environment) are nowadays widely debated by plant ecologists (Sultan 2002, Wright and McConnaughay 2002, Herault *et al*. 2012). Biomechanical ontogenetic plasticity has been widely observed, especially on woody climbers (*e.g*. Menard et al. 2009, Rowe and Speck 2006).It is based on mechanosensing that triggers specific growth responses to mechanical signals (Moulia *et al.*, 2011) . Analysing these responses has led to the identification of two different components of the support function: (i) a skeletal design based on stem thickness and taper together with the strength and stiffness of wood (Niklas, 1992); and (ii) a motricity design involving active movements generated by mechanical auto-stresses. It has been shown that motricity is required to control the posture of the tree (Moulia *et al.*, 2006) and to explore its aerial environment (Martone *et al.*, 2010). So far, advances in plant biomechanics dealing with the involvement of motricity in tree habit and its consequences in terms of mechanical design have been poorly studied in ecology. It is still assumed that plants support mechanical stresses but do not actively generate them (see, for example, how tree biomechanics and reaction wood are presented in Turner, 2001). In their review about biomechanics and plant ecology, Read and Stokes (2006) mentioned ontogenetic variations of mechanical traits due to development constraints as well as stem-righting movements, but biomechanical traits have not integrated such sensing or moving processes up until now (see Chave *et al*. (2009) about wood traits, and King *et al*. (2006; 2009) about tree mechanical performance). By the same token, plant signalling is an active field of research in ecology (Givnish, 2002), but mechanical signals have been much less considered than chemical signals, for example.

In this paper, we propose concepts and methods that make it possible to better integrate, from an ecological point of view, the way trees mechanically explore their aerial environment “without muscle” (Martone *et al.*, 2010). Since we emphasize developmental biomechanics during growth, we show that safety against wind damages or against self-buckling is a necessary but not a sufficient condition for the adaptive success of tree habits. We propose a new view of biomechanical performance, describing the biomechanical framework for studying “motricity”, i.e., the ability to slowly but actively control the orientation of stems (Moulia *et al.*, 2006) by monitoring stem lean and curvature (Bastien *et al.*, 2013) and generating bending forces that actively compensate for the effect of increasing self-loads (Almeras and Fournier, 2009). The way this biomechanical framework has been and could be used in tree ecology at species and community levels is reviewed and discussed.

Before beginning this review, we would like to justify why we focused uniquely on trees. Obviously, the previous arguments concern not only trees but all land plants as well (see, for example, Moulia *et al.*, 2006). However, the long-term adaptation of mechanical design is particularly emblematic in tall and long-living trees. Indeed, during their ontogeny, trees always experiment with a wide range of changing mechanical loads: they increase their mass by up to 10^5 or more during their lifetime. Moreover, cambial growth, although it is not a feature specific to trees (Lens *et al.*, 2012), has specific implications regarding biomechanics. Contrary to herbaceous plants in which living cells have a significant share in mechanical functions, the bulk of the tree body consists of dead cells that are almost unmodified after their death. Only the very thin living cambiumenables through the secondary growth the continuous adaptation of stem mechanical design parameters such as flexural stiffness or orientation over the years. Although the biomechanical comparative analysis of different plant forms is a promising domain (see Rowe and Speck, 2005), we have limited our discussion to woody trees. Moreover, we have primarily focused on forest trees and limited development to the biomechanical performance of aerial support systems mainly focusing on trunks. It is suggested that the reader consults Tobin *et al*. (2007), Stokes (2000) and Ennos (2000) for some insights into root biomechanics. In this review, trees are defined as self-supporting plants where cambial indeterminate growth enables a large and reactive increase of thickness.

This review is organized as follows. After introducing briefly the concepts of functional biomechanical traits, we will develop usual mechanical models of strength and safety, and less usual models of motricity, in order to define integrative traits of biomechanical performance at the tree level that combine load characteristics, stem morphology and wood properties. Figure 1 summarizes the mechanical constraints and processes covered. We will discuss how these integrative traits can be estimated by sets of measured traits (obtained by usual or unusual metrologies). Then we will emphasize the interests and limits of scaling laws that link together measured traits under hypotheses of constant biomechanical performance. A specific section will deal with this question of scaling laws along ontogenetic trajectories. Subsequently, we will put stress on wood properties in order to disentangle the different meanings of wood density, a soft trait widely used in ecology, and provide biomechanical interpretations of how wood structure at different level (from tissue to cell wall) could be evolutionarily or physiologically driven. The conclusion will return to general issues, suggesting future research challenges.

Symbols are not systematically defined in the text, but can be found in the list of abbreviations at the end. For a better understanding of formulas, readers unfamiliar with biomechanical terms are invited to report to this glossary. General definitions of stresses, strains or auto-stresses are not restated, readers are referred to general reviews (Niklas 1992, or Boudaoud 2010), to the general glossary of Moulia (2013), or to definitions (Box 1) of Baskin and Jensen (2013).

Functional biomechanical traits at the tree level

Ecological strategies specify the different ways in which organisms and species secure carbon profit during vegetative growth and ensure gene transmission in the environment where they grow in order to maintain their fitness (Westoby *et al.*, 2002). To characterise the different strategies, plant ecologists measure functional traits, i.e., "any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, and that impacts fitness indirectly, without explicit reference to environment" (Violle *et al.*, 2007). Strategies are inferred from the analysis of the relationships between these traits. A major challenge for plant ecology is then: (i) to define consistent sets of measurable traits; and (ii) to develop extensive databases from the recording of these sets of traits in order to quantify ecological strategies of species along environmental gradients (Violle *et al.*, 2007). These databases are then analysed through multidimensional analysis, revealing syndromes of traits that separate different functional strategies, i.e., clustering of plants among the huge diversity of species and traits, and among the wide range of environments. By doing so, plant ecologists have found only a few basic contrasted strategies (Westoby *et al.*, 2002; Grime, 2001). Interest has focused on tropical forests since they provide a tremendous diversity of tree species to study strategies. Although a greater number of tree strategies have been discussed for a long time (Turner, 2001; Delcamp *et al*., 2008; Fortunel *et al.*, 2012), tropical species have often been opposed along one single predominant axis that expresses growth vs. survival. This axis can be equally interpreted as opposing shade-avoidant or pioneer species vs. shade-tolerant species or dryads (Turner, 2001). Generally speaking, the question is how traits associated with particular functions such as carbon storage, sap ascent, etc., or mechanical support, are more or less closely linked to this axis. As pointed out by Wright *et al*. (2004), a further question concerns the direct or indirect causality of correlations observed between traits. On the basis of the leaf economics spectrum of Wright *et al*. (2004), Chave *et al*. (2009) reviewed variations of wood properties across large biogeographic gradients and showed that (i) wood basic density ρ is a good proxy for the predominant growth-survival axis, and that (ii) since wood mechanical properties are positively correlated to ρ, a high degree of wood stiffness and strength is also associated with survival. However, the biomechanical causality behind these relationships requires a cautious analysis, bringing us to the issue of mechanical design and the biomechanical modelling of the support function of trees in their environment. Actually, the causality between high wood density and high biomechanical performance is not self-evident and will be widely discussed in further sections.

In the following sections, we (i) propose four tree-level integrative traits that characterise the support function and that synthesize the literature on the topic, and (ii) develop a set of biomechanical models that clarifies how wood properties and tree morphology interact with loads to define these integrated traits at the tree level. Indeed, mechanics leads to quite complex geometrical effects compared, for example, to gas exchanges or sap conduction. Whereas the latter are mainly based on fluxes through surfaces, the former involve the transmission of forces through lever arms and second moments of area, leading to geometry-dependent amplifications (Gordon 1978). We show that using integrative models could rebut some intuitive assumptions often made by ecologists such as, for example, “the greater the wood strength is, the greater the safety will be” Indeed, ecologists need to develop a better understanding of integrative biomechanical models that underlie the definition of wood and tree traits: if biomechanical models are designed by physicists alone, there is a risk that they may build only general “first order” models, not adapted to the diversity of life nor to adaptations or responses to specific environments. We show, for example, that shape factors (such as taper or biomass distribution along the stem) have been neglected in the past, despite the fact that their effects on mechanical safety could be important.

Common traits of strength and safety

Risk of wind damage and tree strength

In trees, wind loading may lead to the most commonly experienced mechanical abiotic risk (Read and Stokes, 2006). Safety factors against risk are the ratio of the load capability to the actual load (Niklas, 2000). The higher they are, the higher the margin of safety against the risk will be.

Obviously, both wind velocity and air density are environmental factors. In order to define a tree-level trait for wind firmness without any reference to environment, we propose estimating tree safety (SW) as a critical wind drag pressure $\rho_{air}\ U_w{}^2$ that makes the trunk break. The usual dimensionless safety factor (Fig. 2 ,Niklas 2000), can then be obtained as the ratio of our SW trait to the current wind drag pressure, according to specific wind climates. This dimensionless safety factor remains the relevant parameter for discussing the ecological significance of an observed tree design, since the same design could be highly risky in windy conditions and very safe in other ones. Several different mechanistic models have been developed to calculate SW (Gardiner *et al.*, 2008; Schindler *et al.*, 2012), all based on the following steps: i) estimating the drag force from interactions between wind and crown properties, ii) converting this drag force into bending moments adding the lever arm to any cross-section of the trunk, iii) distributing bending moments in local forces per area unit, namely bending stresses, across the woody cross-section, iv) comparing these stresses due to wind to the maximal stress wood can support, namely wood strength. The stem breaks down if bending stresses exceed wood strength, if not the tree is safe. Then, the critical wind pressure is the one that causes bending stresses just at the limit of wood strength.

Quite simple engineering models based on both empirical measurements and physical laws are commonly used by forest managers (see synthesis of Gardiner *et al*. (2008)) for wind risk assessment. These models overlook the dynamic effects of turbulent flows (de Langre, 2008) and tree vibrations (James *et al*., 2006), including them through a corrective “gust factor” by which the meteorological U_w is multiplied (Gardiner *et al.*, 2008).

Concerning the steps (i) and (ii), wind is assumed to act as a static bending moment calculated at the height *X* as:

$$M_w(X) = 0.5\ c_d\ \rho_{air}\ A_w U_w{}^2\ (H_w - X)\ \ F_w \qquad (1)$$

This frequently used formulation is more relevant for isolated trees but has also been validated in forestry and included in wind risk management tools (Gardiner *et al.*, 2008).

In such tools, parameters that cannot be directly measured in managed forests are calibrated. A_w, which is the streamlined projected area of the stem and crown against which the wind acts, is estimated from basic tree dimensions (*H*, *D*, crown dimensions).

The shape factor F_w in (1) represents both the interaction between the wind and crown profiles, and the relationship between the wind around the tree (that is usually not assessed) and the meteorological data that are available.

Then, according to step (iii), the bending moment in (1) is distributed across the cross-section of the trunk into bending stress $\sigma_w(X)$. Bending stress is locally perceived as forces per area unit along the trunk axis. The maximum tensile stress is developed on the windward side whereas maximum compressive stress is located on the opposite leeward side. Then (step iv), $\sigma_w(X)$ is compared to the wood critical limit for plastic behaviour or for rupture, $\sigma_c(X)$, measured by bending tests in the laboratory (see general concepts in Niklas 1992 and example of available data in Chave *et al.*, 2009).

To calculate the tree safety, the location X_w of the weakest cross-section (i.e. the height X_w where damage should occur first) must be estimated. X_w minimises the safety factor $\sigma_c(X)/\sigma_w(X)$ along the height X. The function $\sigma_c(X)/\sigma_w(X)$ varies along stems with complex patterns (Niklas, 2000, Fig.2). Actually, a constant stress $\sigma_w(X)$ along the stem is a quite old and frequently used assumption (e.g. Dean and Long 1986, see Moulia and Fournier-Djimbi, 1997, for a review). Such a constant stress design should constrain the variations of diameter and wood properties along the stem. However, as claimed by Niklas and Spatz (2000), such a design agrees neither with empirical observation nor biomechanical theory.

Then, as in Niklas (2000), we suggest carefully checking where the minimum safety factor, $\sigma_c(X)/\sigma_w(X)$ is located. Actually, Figure 2 illustrates a case of complex patterns of variations of safety with height. Nevertheless, in usual forest trees made of a single and well-differentiated trunk, safety is usually minimal near the stem base (Gardiner *et al.*, 2008; Sterck and Bongers, 1998). The critical wind pressure SW is then calculated at the stem base as:

$$SW = \frac{\pi \sigma_c D^3}{16\, c_d\, A_w\, H\, k_w\, F_w}$$

SW (Safety against Wind) increases with wood strength σ_c and stem thickness *D*. It decreases with the drag coefficient c_d, the wind-exposed surface area A_w, and the height of the centre of pressure Hk_w. In the case of a non-circular cross section, the criterion can be easily modified by adding a cross-section shape factor.

Are there theoretical limits to the self-supporting habit?

Self-buckling is the mechanical situation where an erect and slender tree is no longer self-supporting, since supported weights exceed a critical limit and make it bend dramatically. This has been identified as another major mechanical constraint on tree stability (Greenhill 1881, Niklas, 1992). Safety against self-buckling is independent of the actual environment since it relies only on the biomass and stiffness characteristics of the tree, without any external factor except gravity acceleration g, whose variations are negligible. Safety against self-buckling is based on the calculation of critical dimensions that the tree mechanical design cannot exceed. According to our previous definition of safety, self-buckling load capability is thus defined as the maximum height a tree can reach before buckling, when other parameters involved in the self-bending loads are kept constant. Then, safety against buckling is the ratio of this maximum height to the actual one.

Models of self-buckling safety, calculated as the ratio of the real dimension to the theoretical limit

Such a theoretical concept has led to many different models (see the synthesis in Holbrook and Putz, 1989, and Jaouen *et al.*, 2007), all based on the use of two independent dimensions among the thickness *D*, the height *H* or the volume *V*. The simplest one assumes a cylindrical pole loaded with wood weight alone. More complex ones add a power-law taper (Greenhill, 1881), an additional weight at the top of the pole to take leaves and branches into account (King and Loucks, 1978), or a distributed mass along the pole (Holbrook and Putz, 1989). The ratio between the real dimension and the theoretical critical one then gives a dimensionless safety factor against self-buckling (SB), which usually exceeds 1 for normally self-supporting trees. Choosing a parsimonious but accurate model for SB calculation requires experimental validations. Whereas Holbrook and Putz (1989) and Jaouen *et al.* (2007) showed wide discrepancies between different models and discussed their reliability on the basis of observations of trees at the self-supporting limit, most authors trusted the simplest cylindrical pole formula without any discussion (see Sterck and Bongers, 1998; Osunkoya *et al.*, 2007 and Read *et al.*, 2011, among others). Both Jaouen *et* *al*. (2007) and Holbrook and Putz (1989) showed that in the tree sapling samples they studied, the simplest cylinder formula fits well with more realistic models that account for trunk shape and load distribution. Figure 3 illustrates this result since the safety factor of the crowned stem (iv) is better approximated by the cylinder (ii) than by the tapered stem (iii). Actually, the additional weight gained by considering a cylinder roughly compensates for the weight of branches and leaves, disregarded in the tapered stem model. However, in many works that focused on self-buckling through the cylindrical pole model, crown morphology was considered as an important tree functional trait (Sterck and Bongers, 1998; Osunkoya *et al*., 2007). Since results pointed out that branches and leaves should have different weights from one species to another, it was unfortunate that the crown morphology could not have been integrated into calculations of self-buckling safety. Indeed, Jaouen *et al*. (2007) demonstrated that both the stem taper and the height of the tree centre of mass explain a larger part of the variation of the critical self-buckling height than, for example, the wood modulus of elasticity. Thus, the soundness of a general cylinder pole model, which is the least physically relevant, is questionable.

More generally, should other additional weights (such as ice, rainfalls or snow, epiphytes, animals, etc.) be included in the calculation of the critical self-buckling height? Obviously, as it is generally implicitly assumed since Greenhill (1881), they can be considered as random events, associated with an oversized design to face uncertainties. That is why a safety factor SB that is too close to 1 is not viable, whereas an optimal SB would be probably a bit larger than 1 (King et al. 2009). For additional accuracy, an estimation of these additional weights could be included in critical height calculations (Holbrook and Putz 1989, King and Loucks 1978). When comparing ecological situations of different regimes of rainfalls or of variable abundance of epiphytes or lianas, such detailed approaches would make it possible to quantify how much more safety is required in the most constrained environments. Actually, the height of the centre of mass - m parameter – may have been substantially underestimated, as well as the load factor, when abusively neglecting epiphytes, ice or snow. In Fig. 3, models of increasing complexity have been used to calculate SB on a tree of a given diameter and height, assuming less and less uncertainty concerning loads (practical formulas are given above, inputs are developed in the legend). Figure 3 demonstrates that additional weights (case (v)) could have an impact on SB on the same order of magnitude as taper or crown load.

In any case, the magnitude of the safety factor bears important ecological information in itself: a low safety factor (close to 1) indicates a real risk, whereas a high safety factor instead suggests that the constraint is not ecologically relevant or improperly calculated since important drivers have been neglected. Then, as reported by Niklas and Spatz (2004), it is really problematic to assume that the tree biomechanical design is driven by a constant and high safety factor. Therefore, each time a high safety factor (higher than 5 to 10, for example) is observed, both the relevancy of the biomechanical constraint (is buckling a real risk?) and the method used for calculation (are loads, shape or wood properties properly assessed?) must be questioned.

The critical self-buckling height refers to different dimensional limits, depending on environmental drivers

As effectively pointed out by Holbrook and Putz (1989), calculating critical dimensions addresses a last but sensitive question: should we calculate the critical minimum diameter with a fixed height of the tree? Alternately, should the basal diameter be maintained constant to calculate the critical maximum height? This choice must be discussed from an ecological perspective. Buckling is a great limiting mechanical constraint when the intense competition for light foraging is the main environmental force at play, suggesting that investment capability in the support function is limiting. Maximum height for a given support tissue volume (or biomass) would then be meaningful, as assumed by Jaouen *et al*. (2007) and Holbrook and Putz (1989) when dealing with understorey trees, where trees are sheltered from winds but allocate comparatively more biomass to height growth than to diameter increment. On the other hand, when comparing canopy trees of similar height, minimising the diameter or the volume of support tissue for a given height, as done by King *et al*. (2009), is also relevant.

Whereas the above-mentioned authors carefully rewrote Greenhill’s criterion to argue their choice of critical self-buckling dimensions, most authors use the formula based on a constant diameter without any ecological justification (e.g., Sterck and Bongers, 1998, among others). Maximising height at a forced constant diameter can be the relevant criterion to compare plants from a wide variety of biological types or plants, including species that lack perennial secondary growth (Niklas, 1992). However, among trees characterised by indefinite growth in thickness, using a fixed diameter seems difficult to justify.

Practical criteria to estimate the safety margin against self-buckling

The following section gives practical equations (provided as supplementary material in a .xlsx file) to compute safety against self-buckling, adapted to populations of varying heights based on the maximum height achievable with a constant support tissue volume. By reformulating Greenhill's model (1881) and revisiting Jaouen's formula (2007), the critical self-buckling height is:

$$H_c = 0.88\ V^{1/4}\, E^{1/4}\, (\rho_T g)^{-1/4} F_b^{\ 1/2}$$

The density of the carried load ρ_T is significantly higher than the fresh density of wood alone ρ_{green} , or than the wood basic density ρ, sometimes improperly extended to SB calculations (Sterck and Bongers, 1998). The shape factor F_b is 1 when the tree is represented by a cylindrical pole loaded by its own mass alone, as recently assumed by most authors. In other situations, it is a function of biomass and diameter profiles along the stem:

$$F_b\ = 0.1785(|m - 4n + 2|).(2n + 1)\, J^{-1}_{\frac{4n-1}{m-4n+2}}(0)$$

The parameters *n* and *m* are defined by $D(X) = D\left(\frac{H-X}{H}\right)^n$, and $M(X) = \rho_T V\left(\frac{H-X}{H}\right)^m$, where *D*(*X*) is the diameter at height *X* and *M*(*X*) is the biomass supported above height *X*. The higher *n* is, the higher the taper will be (*n*=0 is a cylinder). The higher the value of *m* is, the nearer to the base of the tree the biomass is concentrated. *m*+1 is the ratio of the total height to the height of the centre of mass H_g (Fig. 1). The Bessel function first root $J^{-1}_{\frac{4n-1}{m-4n+2}}(0)$ can be practically solved with an adapted computing software programme or by using the linear regressions fitted by Jaouen *et al*. (2007). The safety factor SB is then defined as the ratio H_c/H. Since the volume *V* is $\pi H D^2/(4(2n+1))$ (Jaouen *et al.*, 2007), SB is given by the following equation:

$$SB\ = 0.836\, H^{-3/4}\, D^{1/2}\, E^{1/4}\, (\rho_T g)^{-1/4} (2n+1)^{-1/4} F_b^{\ 1/2}$$

Safety against self-buckling increases with wood stiffness *E*, the amount of support tissue *V* or the diameter *D*, and decreases with height *H* and specific mass ρ_T.

It can be observed that for a cylinder (*n*=0, $F_b\ = 1$), this SB based on constant volume is a power of ¾ of the widely used safety factor $0.792\, H^{-1}\, D^{2/3}\, E^{1/3}\, (\rho_T g)^{-1/3}$, based on a constant diameter (which is then higher, as shown in Fig. 3). Actually, the three safety factors calculated from (i) a minimum diameter at constant height, (ii) a maximum height at constant diameter, or (iii) a maximum height at constant volume, are closely related. Due to the multiplicative relationships linking H_c, H, D and V, they are powers of each other. Therefore, they can be used indifferently for comparing safety between trees, regardless of the ecological conditions. Moreover, the limit for the self-supporting habit is always 1, and the optimal allometry between H and D that leads to constant safety during growth (assuming that the other parameters are constant) is also $H \sim D^{2/3}$, regardless of the criterion.

Including motricity in functional biomechanical traits

Motricity of lignified stems: what enables trunks to actively curve?

Although trees have been idealised as perfectly vertical structures when calculating SW or SB traits, real trees always lean, at least slightly. Without any gravitropism, trees could not maintain a vertical orientation because their increasing weight would always bend them towards the ground. As highlighted by Darwin and Darwin (1880), gravitropism is a major growth process that takes part in light foraging strategies and is achieved through local curving along stems and auto-stressing systems (Archer and Wilson, 1973; Hejnowicz, 1997). Curving stiff, thick and lignified tree stems requires a specific source of energy, supplied by an internal straining process, leading to asymmetric auto-stresses (Martone *et al.*, 2010). In radially growing stems and differentiating wood, this process, namely the maturation strain induction, occurs at the end of cell formation, and the asymmetry is achieved through the differentiation of reaction wood (Scurfield, 1973). After reviewing traits of the skeletal design, we now formalise which tree features characterise the motricity design.

Following the work of Fournier *et al*. (1994a), Almeras and Fournier (2009) modelled the bending curvature of a growing stem due to auto-stresses as:

$$\frac{dC_m}{dD}(X) = -4\frac{F_m(X)\,\Delta\alpha(X)}{D(X)^2}$$

This minimal model expressed the basic limits and drivers of the movement: tropisms require growth, so the model represents a rate of curvature per unit of radial growth in diameter (dC/dD). The thinner the stem is, the easier the bending will be and, moreover, the rate of curvature is proportional to D^{-2}. Motricity is then less constrained in thin axes, as noticed by Collet et al. (2011) or Jaouen (2007) studying saplings, and then carefully discussed by Dassot et al. (2012) on beech stands of different tree density or by Almeras et al. (2004) on branches. The difference in maturation strain $\Delta\alpha$ from one side to the other is the main driving force that generates an asymmetry of pre-stresses. Radial growth asymmetry is an additional way to generate such an asymmetry from the mean value $\bar{\alpha}$: stems curve by making more straining wood and/or more wood of the same quality on one side. The shape factor F_m represents the radial growth asymmetry motor as $F_m = 1 + 2k_m\bar{\alpha}/\Delta\alpha$, where k_m is the asymmetry of radial growth, $k_m = (R_+ - R_-)/(R_+ + R_-)$. Actually, Almeras et al. (2005) showed that except in extreme eccentric growth, the second motor is less efficient, so F_m can be taken as 1 in many cases. At a second order, this basic motor process is also catalysed by radial variations of the modulus of elasticity *E*.

Moving as fast as possible: the curvature rate as a first trait of motricity

Curvature velocity $\frac{dC_m}{dt}(X)$ could therefore be a good candidate for describing stem motricity. As reported by Moulia and Fournier (2009), curvature, which is the relevant variable to describe stem movement, follows complex spatial patterns along the stem. Although these spatial patterns by themselves contain information (Bastien *et al*., 2013), a first approach, focused on time variations, retained curvature velocity near the base (for example, at breast height, which is the usual height of forest measurements) to describe tree motricity, since the bending of the base is essential to move the whole stem *(*Dassot *et al*., 2012).

When the lean has been disturbed, trees have to react as fast as possible to recover an adapted posture to avoid loosing competition for height growth and light foraging (Fournier *et al.*, 2006). A first motricity trait is therefore defined as tropic Motion Velocity (MV), i.e., the curvature rate near the base due to radial growth and maturation strains:

$$MV = \frac{dC_m}{dt}(0) = -4\frac{F_m\,\Delta\alpha}{D^2}\frac{dD}{dt}$$

MV is the way the trunk is able to react to disturbances of the trunk lean from its set-point angle by generating asymmetric pre-stresses at the stem periphery. The trunk set-point angle is driven by the environment. It is generally vertical, leading to negative orthogravitropism, but becomes oblique on slopes (Matsuzaki *et al.*, 2006; Lang *et al.*, 2010), or during regeneration stages in shade conditions (Collet *et al.*, 2011), due to interactions with phototropism.

Competition for light, slenderness and long-term stability

As a founder of biomechanics, Gordon (1978) stated that Nature seems to have accepted stiffness quite reluctantly, except in trees that must be both light and rigid. However the incredibly low stiffness of a slender young sapling tree competing for light would puzzle any civil engineer responsible for design of such a tall, heavy and durable structure exposed to winds and other loads, as a tree should be. Then, since trees are very common elements of our landscapes, a question of more ecological relevance is how such a design can grow and remain upright for such a long time (Moulia *et al.*, 2006). Actually, wood produced at the tree stem periphery is not only a rigid and strong perennial material, as it is in wood houses built by humans, but the tissue of a smart thickening process as well. This process enables the physiological acclimation of the support system to changing mechanical constraints and increasing supported masses, but requires a tremendous coordination between growth in diameter and height (or biomass), on the one hand, and growth and wood properties, especially maturation strains, on the other. According to Grime's strategies (Grime, 2001), in environments with low wind stress and disturbance (low chronic winds, no storms, no sudden changes of wind sheltering such as forest understories not disturbed by large gaps), trees should develop a high efficiency to compete for the light resource, at a low cost to support tissue. Since stems become very slender and close to the non-self-supporting habit in such conditions, a first above-mentioned criterion of biomechanical performance is safety against self-buckling. It is a necessary condition but not a sufficient one. As soon as a tree is slightly disturbed from perfect verticality and symmetry, further growth in biomass makes it bend downwards so that motricity must be activated to control a safe posture over time.

Maintaining an erect habit: moving to compensate gravitational bending

The biomechanical performance of erect trees is thus based on the way trunks are able to maintain the trunk set-point angle by the above-mentioned active curving. Almeras and Fournier (2009) suggested defining such a biomechanical performance as follows:

i) Growth in biomass induces a curvature rate due to the continuous change of biomass in a growing tree (near the stem base, *X*=0). It can be calculated as:

$$\frac{dC_g}{dD} = 16(1+b)F_g\, sin\varphi \frac{\rho_T g}{E}\frac{H^2}{D^3}$$

The higher the load ρ_T, the lever arm *H* and the lean φ are, and the lower the stem thickness *D* and the wood stiffness *E* are, the higher the flexibility $\frac{dC_g}{dD}$ will be. The form factor F_g is 1 in a cylindrical pole (*n*=0 and *m*=1), and in other situations, for a given total biomass (fixed by ρ_T, *H* and *D*), the higher the centre of mass is, the higher F_g will be. Through the allometric exponent *b*, the bending under self-weight also increases when relative growth in height compared to relative growth in diameter is more rapid.

ii) Therefore, the performance of posture control (also called gravitropic performance by Almeras and Fournier, 2009) is the ratio of the value of the reaction, i.e., the tropic motion rate per unit of radial growth $\frac{dC_m}{dD}$, to the gravitational curvature rate $\frac{dC_g}{dD}$:

$$PC = \frac{-dC_m}{dC_g} = \frac{E\,\Delta\alpha}{4(1+b)\,\rho_T g\, sin\varphi}\frac{F_m}{F_g}\frac{D}{H^2}$$

Like previous biomechanical integrative traits, PC is the balance between a load action independent of environmental factors, in this case, $F_g\, \rho_T g\, sin\varphi$, and a tree reaction, in this case, $F_m E\Delta\alpha$. Size and shape interacts with these latter actions and reactions, with an immediate effect of size through *D* and *H*. PC=0 means that the tree is not able to react any longer. Therefore, it will bend more and more under its self-weight. PC=1 is the situation where a given posture is maintained when no more bending, upward by reaction or downward by gravity, occurs. When PC>1, the tree is righting itself, whereas when PC<1, it is sagging down.

Functional diversity and variations of motricity traits

When dealing with the diversity of tree functional traits, ecologists have exclusively considered stem biomechanical properties as a way to understand how the tree design either avoids or tolerates failure risk. Data collected concerning tree morphology and wood properties are therefore analysed from this standpoint. With this in mind, the assumptions tested were the following: (i) Are high wood strength and stiffness associated with a survival strategy against mechanical constraints and, as a result, with high SB and SW (Read *et al*., 2011); (ii) Is tree design based on low but optimised stem safety SB or SW that maximises survival and minimises the stem construction costs (Kooyman and Westoby, 2009; King *et al*., 2006); (iii) How can the association between wood density and the growth-survival axis be explained (van Gelder *et al*., 2006) or disturbed (Read *et al*., 2011) by biomechanical requirements? We argue that such a view is restrictive and that motricity could also be an important component of tree strategy. Surprisingly, although tropisms are widely investigated via their physiology, their ecological significance has received less attention (Iino, 2006). The two previous motricity traits have been designed to quantify these movements with their different components. PC has been specifically designed as an efficiency trait that should be linked to high survival at low construction costs. Using data from Jaouen (2007), Duchateau (2008) and Delcamp *et al*. (2008), Figure 4 illustrates the use of PC among functional groups in tropical tree communities to investigate relationships between the motricity traits and the demographic ones. PC is variable among species and functional groups, and negatively associated with mortality rate. Actually, the functional response groups defined from species demography, independently of any biomechanical considerations (Favrichon, 1994; Delcamp *et al*., 2008), appear here to be more discriminated by PC than by SB, which is the usual biomechanical trait of ecologists in such conditions.

In addition to PC associated with competition, MV is proposed as an adaptive trait to disturbance. Disturbances such as windstorms, avalanches and landslides immediately refer to the previous biomechanical traits of safety against the abiotic mechanical constraints. However, a general biomechanical view of disturbance should include not only mechanical strength but resilience as well. Thus, a better understanding of how plants explore and colonise space and compete over time in a changing environment is required (Read and Stokes, 2006). Hamilton *et al.* (1985) described the switching from a shade-tolerant to a sun-adapted design after gap opening, which is a very common situation of forest community dynamics. Although they were not focused on tropisms and biomechanics, they mentioned righting movements as important morphological adaptations to such a disturbance. Actually, in such situations, the question is no longer how to maintain a given angle to offset the increase of weight (this performance is associated to PC), but mainly to make large and fast movements, described by MV. For instance, in their work on natural regeneration of mixed hardwood forests, Collet *et al.* (2011) used MV to discuss how the immediate radial growth after gap opening, that speeds up MV, contributed to explain the success of pre-existing advanced regeneration. Actually, an immediate allocation of carbon to cambial growth (which increases motricity and stiffness) with delayed primary growth and crown development (which increase weight) is a strong necessity to avoid long-term mechanical instability.

Four integrative traits of tree stem biomechanical performance obtained by combining size, wood and shape traits

Four integrative biomechanical traits, SW, SB, MV and PC, directly interpretable as properties of the organism, were defined in the previous section. They are linked to the performance or safety of the tree support functions in these two components, the skeleton and the motricity design. We will therefore concentrate on how to use them in ecological studies. First, they must be measurable on great numbers of individuals among the tree diversity and along environmental gradients

Measuring integrative biomechanical traits directly at the whole tree level

The direct measurements of SW and SB traits at the tree level are usually cumbersome. SW can be assessed from wind tunnel experiments (Cao *et al.*, 2012) or by mimicking wind by pulling tests (Achim *et al.*, 2005). To enable direct estimation of SB,one needs to define SB as the ratio of the critical load weight to the current one as an increase of tree dimensions up to the critical height or diameter is not feasible. Then, SB may be estimated from artificial loading, adding weights to the tree until it buckles (Tateno, 1991).

The tropic motion velocity MV has been directly assessed through curvature measurements, assuming that the observed changes of curvature are mainly due to the active reaction, neglecting bending under self-weight (Collet *et al*., 2011). However, observed changes of curvatures always superimpose motricity and bending under increasing weights. On the basis of theoretical models, the two processes can be distinguished from each other through additional measurements, as proposed by Almeras *et al*. (2009) and Huang *et al*. (2010) to analyse gravitropic movements in leaning stems, where the bending under self-weight could no longer be ignored.

Assessing integrative biomechanical traits from independent measurements of size, shape and wood properties as components of load and resistance

Practically speaking, the four biomechanical traits defined are simple products of wood, size and shape traits (adding a crown property, the drag coefficient c_d, in SW) that could be measured independently. Indeed, some of these dissociated traits are already available in extensive/broad databases: height, diameter and growth rate of H and D are measured in permanent forest plots (Pretzsch, 2009); wood properties such as the modulus of elasticity E or the critical stress σ_c are available in technological databases (Chave *et al.*, 2009). The different dissociated traits are of two types: resistance (compared to motricity) traits describe how the tree resists (compared to reacts) to mechanical constraints, whereas load factors (k, c_d, A_w in SW; ρ_T in SB; or φ in PC) describe how the external environment, i.e., gravity or wind, interacts with the tree structure to transmit forces. In a particular environment, trees can in fact increase their performances by adapting resistance or motricity traits, or can limit the constraint by adapting load factors. Table 1 classifies these components according to their meaning in each integrative trait.

The particular case of maturation strains

Maturation strain α is not commonly measured in tree ecology. It can be assessed experimentally (i) by measurements of curvature repeated over time, reversing the model to measure $F_m\Delta\alpha$ (Almeras *et al*., 2009; Sierra-De-Grado *et al*., 2008; Coutand *et al*., 2007, in seedlings and greenhouse experiments; Huang *et al*., 2010, in relation to branches; and Collet *et al*., 2011, concerning natural forest regeneration), (ii) by indicators of maturation strains at the stem periphery (Almeras *et al*., 2005), developed by wood technologists and measured by different stress-releasing techniques (Fournier *et al.*, 1994b; Yoshida and Okuyama, 2002), and (iii) by going back in time from spatial mapping of reaction wood occurrence, using calibrated relationships between reaction wood and maturation strain indicators (Dassot *et al*., 2012). This last method allows retrospective growth analysis using wood as a marker of past events, as is currently done in dendrochronological approaches.

Scaling or not scaling: how trees follow or evade simple rules derived from constant biomechanical performance

One major theoretical interest of integrative traits is the possibility of using them to discuss scaling laws at constant biomechanical performance. The four integrative traits presented above are based on products of dissociated traits, as size parameters – height, diameter, volume, growth rate and wind surface area -, that interact with wood, load, and shape features. Then, a constant performance (i.e. a constant integrative trait) results in allometric laws that link dissociated traits.

Allometric laws between H and D as null hypotheses to test the effect of other variables

Implicitly assuming that size parameters are more variable, theoretical works investigated how height H and diameter D should be coordinated to maintain a constant biomechanical performance, if all the other properties were kept constant. Slenderness laws that maintain a constant safety (SB or SW) have been widely discussed (e.g. King and Loucks (1978), Mac Mahon 1973, Dean and Long 1986, see Chapter 3 of Niklas (1994) and Moulia and Fournier-Djimbi (1997) for a review). Almeras and Fournier (2009) have derived a similar law for the long-term stability, i.e. a constant posture control (PC). The associated allometric relationships are summarized in Table 1. These scaling laws between size variables provide null hypotheses to investigate how other components of shape, load factor or wood properties could vary with size in order to limit or enhance the size constraints on biomechanical performance.

Null hypotheses to be rejected

We would then like to emphasize that the use of integrative biomechanical traits to study how trees adapt to specific environments should not be limited to the "automatic checking of predetermined allometric law between H and D". Actually, more exciting results occur when such allometries fail. Dean and Long (1986) emphasized that to maintain a constant SW among trees, a constant $\underline{D}^3 H^{-1} A_w^{-1}$, rather than a simple constant D^3/H, is required.

More recently, the possibility that wood variations could compensate for the effect of size variables become a quite active field of research for tree biomechanics (Niklas, 1997; Waghorn and Watt, 2013; van Gelder *et al*., 2006). The reader can also refer to the section below on ontogenetic changes. Moreover, a constant biomechanical performance agrees with neither biomechanical nor ecological theories. Indeed, environmental conditions orient the value of biomechanical performance and, subsequently, its variation as well as its ecological relevance. For example, SW in an environment sheltered from the wind is probably very high (except if this safe environment has been recently changed at the time scale of evolution or tree development so that trees remain adapted or acclimated to a high risk). Thus, under such condition, SW is likely to be of little interest. On the contrary, in an environment where wind is the main constraint SW is meaningful and should be carefully determined. Actually, in such condition, SW should not rely only on H, D and A_w adaptations, but also on less studied traits such as drag coefficient or wind pressure area and the crown reconfiguration with increasing wind velocity (see the theoretical work of Lopez *et al*., 2011; and the comprehensive experimental study of Butler *et al*., 2012). Then, a “wind avoidance” strategy based on optimised values of SW should be much more complex than simple relationships between H, D and A_w. With regard to self-buckling safety, mature isolated trees are usually very safe, making allometries derived from optimised SB factors meaningless (Niklas and Spatz, 2004). However, self-buckling is adjusted at a minimal level in understories where several saplings are no longer self-supporting (Jaouen *et al.*, 2007).

Weak wood can make strong trees

Many previous works assumed that the higher the wood strength σ_c (or stiffness E) is, the higher the tree biomechanical performance SW (or SB) will be (e.g. Chave *et al*., 2009; Swenson and Enquist, 2007). However, since biomechanical performances are related to combinations of traits, it is very easy to make a strong trunk with weak wood by just increasing the diameter. Indeed, as developed by Larjavaara an Muller Landau (2010), due to the scaling of SW (expressed as $\sigma_c\ D^3$), decreasing the wood strength by 30% could be easily offset by increasing the diameter by 10% ($\sqrt[3]{1.3}$=1.09). Therefore, to address the question of how increasing wood mechanical properties changes the biomechanical performance, we must take account of how other components of the integrative trait, especially those such as diameter that considerably vary among trees, scale with wood properties. For example, some authors observed a significant increase in E with slenderness H^3/D^2 (Waghorn and Watt, 2013, in *Pinus radiata*). Waghorn and Watt (2013) discussed the way trees regulated E to maintain a viable level of safety SB at high slenderness, probably using mechanoperception of sways. However, they also concluded that slenderness remains the first driver of SB, so that a higher wood performance E is associated with a lower performance SB. Therefore, only if wood properties are independent of other traits, and if other traits do not vary too much, will the tree biomechanical safety increase significantly with wood strength or stiffness.

Scaling laws are based on the assumption of constant integrative traits, that involves ecology rather than biomechanics

Biomechanical scaling laws proved to be very popular (e.g. McMahon, 1973), although they are based on complex and cumbersome mechanical models which are not easily understandable by biologists. Therefore, ecologists may think that mechanical theories are the convincing basis of scaling laws. Indeed, when analysing the contribution of size, wood or shape to biomechanical performance, the preliminary mechanical analysis provides answers about the way all the parameters involved interact to generate, transmit or resist forces. However, mechanics cannot say which parameters are constant. First, as above-mentioned, the principle of a constant performance is relative to a tree population in a given environment. Secondly, modelling always uses over-simplifications and neglects parameters. When mechanical integrative modelling is used to derive scaling laws, neglected parameters are implicitly kept constant. Ecology studies which load, morphological and wood traits are variable in tree populations, according to environmental, phylogenetic or physiological limits and drivers. Mechanics can provide help to check by integrative modelling and sensitivity analysis whether these variations impact biomechanical performance. Then, to discuss adaptations of tree biomechanical performance to environment, it would be valid to use comprehensive expressions of integrative biomechanical traits, as proposed in Table 1. For example, in addition to how wood strength σ_c, D and H scale with each other, SW addresses the question of how the load parameters – crown area A_w, lever arm $H\,k_w$ - could also vary with D, H and σ_c. Similarly, on the basis of a more detailed representation of SB, it follows that taper n and biomass distribution m along the stem should also scale with other traits. Indeed, in tropical forests, weak vs. strong wood, cylindrical vs. tapered stem form, poorly vs. highly developed branching, and a single layer of leaves in the highest parts vs. multi-layered crowns, are associated traits that oppose growth to survival (synthesis in Turner, 2001; Jaouen, 2007). As reported by (Niklas and Spatz, 2010), the challenge for biologists is to explore the whole complexity of environmental contexts and tree adaptations of shape and wood properties.

That little tree will grow big!

Are ontogenetic changes of wood properties and shape functionally significant?

In long-lived organisms such as trees, understanding how observed strong ontogenetic changes in demographic rates could be explained by functional traits is a major issue for ecology (Herault *et al.*, 2011). From a biomechanical point of view, the increase in size is a major constraint during ontogeny. Therefore, now that we have assessed how functional traits vary with size as well as the above-mentioned null hypotheses on optimal allometries between basic size components, we would like to address the following questions: (i) What are the general variations of wood, shape and load during tree development? (ii) Can these variations and relationships be interpreted by their functional biomechanical role?

The variations in mechanical safety as forest trees grow are intriguing since some stages of growth are especially critical, particularly sapling stages exposed to self-buckling in dense understories (Jaouen *et al.*, 2007), and the oldest stages of canopy trees exposed to wind throws (Turner, 2001). Some authors have attempted to study how safety factors change with size and ontogeny (see Sterck and Bongers, 1998; Osunkoya *et al*., 2007; van Gelder *et al*., 2006). They used expressions of SB based on a constant D, underestimating the load factor ρ_T (taken as ρ) and ignoring shape factors, i.e., the taper and the height of the center of mass, although they did observe variations in crown characteristics. Indeed, their results concerning safety must be considered with caution.

Could ontogenetic trajectories of wood properties and shape compensate for size effects?

Using the comprehensive expression of integrative traits as a product of separated traits T at power ν_T, the functional significance of simultaneous ontogenetic variations of wood and shape could be analysed using the following general method. For the purpose of clarity, we have illustrated the method by re-analysing some data from Jaouen *et al*. (2007) concerning SB.

The population of 23 individuals of *Oxandra asbeckii* (Pulle) R.E. Fries (Annonaceae) measured by Jaouen *et al*. (2007) are assumed to represent an ontogenetic trajectory (i.e. the different sizes are supposed to represent the same individual at different stages of growth). We have fitted an allometric relationship to estimate the relationship between any trait *T* (i.e., the size *V*, the modulus of elasticity *E*, the shape factor F_b and the load factor $\rho_{T,}$ and the integrative SB; data from Jaouen *et al*., 2007) and the height *H* as $T \sim H^{\tau_T}$. Since *H* is assumed to follow the ontogenetic trajectory, τ_T is the ontogenetic trend of the variation of *T*. The ontogenetic trend of SB is therefore the sum of the ontogenetic trends τ_T of all the isolated traits *T* multiplied by their power exponent ν_T. Table 2 gives the results for the particular sample of *Oxandra asbeckii*: (i) safety against self-buckling decreases with height at a power of -0.23; (ii) if we had studied safety only on the basis of the two size factors *H* and *V*, as was done by other authors in the past, we would have concluded that safety decreases with a higher power of -0.32; (iii) additional shape and load factors slightly compensate for size, with a power of +0.02 and +0.06, respectively; (iv) no ontogenetic change was found for the modulus of elasticity. In this particular case, size (i.e., the variations of *H*, and *D* or *V*) remains a constraint, not strongly offset by variations in other features. This general method can apply every time that an integrative trait is a product of dissociated traits.

The biomechanical significance of wood properties variations

The way wood properties variations can compensate for size effects during growth is undoubtedly a challenging research question. Analysing black locust trees (*Robinia pseudoacacia*), Niklas (1997) estimated that ontogenetic variation of wood properties could maintain SB at a constant level when a tree grows in size. Considering the motricity MV trait that scales with D^{-2} when other parameters are kept constant, Dassot *et al*. (2012) investigated how adjustments of reaction wood formation would compensate for the highly limiting effect of *D* during growth in beech (*Fagus sylvatica* L.). Due to the higher content of reaction wood in juvenile wood, they found a high level of stabilisation of motricity during the first young stages that is no longer maintained after ten years of growth. Thus, the relationship between MV and *D* was no longer a power law, and decreased faster than the expected D^{-2}. This study of Dassot *et al.* (2012) gave a functional meaning to typical, very frequently reported radial patterns of reaction wood (synthesis in Lachenbruch *et al*., 2011). Generally speaking, wood radial variations (of density or mechanical properties) are studied in-depth for wood quality assessment in the area of forest science. In a recent comprehensive review, Lachenbruch *et al*. (2011) suggested that adaptation to changing mechanical constraints could explain some typical observed patterns. To test these hypotheses, a first modelling approach would be to assess how the basic integrative traits SB, SW or PC vary with wood radial variations according to simultaneous changes of other dissociated traits (size, shape, load) during growth. As already stated above in relation to scaling with size, inadequate attention has been accorded to shape (such as stem taper and distribution of mass along the stem) and load factor (the total mass per unit of trunk volume or the wind force per unit of crown surface). Indeed, they are as ontogenetically plastic as wood properties. Thus, the ontogenetic change of shape, size, wood and load properties cannot be studied separately. Foresters design forest growth models coupled with wood quality models (Makela *et al*., 2010; Auclair and Nepveu, 2012). Since some of these tools simulate simultaneous changes of height, diameter, stem profile, crown expansion and wood variations, they could provide valuable support to investigate how biomechanical performance varies with growth.

A general overview of biomechanical wood traits

The previous section ended with wood variations since they are likely to have an impact on the ontogenetic trends of biomechanical traits. A general aspect of ecological strategies concerns the way the different properties of wood are related to each other, and the impact of these relationships on the whole organism performance.

Wood densities? Simple measurements for a set of distinct functions

Wood basic density is widely used as a key functional trait indicative of the tree life history and biomechanical and physiological strategies (Chave *et al*., 2009). In contrast with wood engineering studies where properties of wood with partially dried cell walls are considered, cell walls in the living tree are fully saturated. Water bound within hydrophilic cell walls causes swelling and modifies the cell wall mechanical properties (Siau, 1984). Conversely, water present in cell lumens, also called free water, does not play any mechanical role except for the special case of parenchyma cells (Niklas, 1988; Chapotin *et al.*, 2006). It is therefore essential to distinguish between fresh wood density (ρ_{green}) representative of the load (ignoring branches and leaves), and basic density (ρ) representative of the wood mechanical properties (Larjavaara and Muller-Landau, 2010). Assuming that cell lumens are fully saturated in a living tree and that the density of cell wall material is 1500 kg m^{-3} (Kellogg and Wangaard, 1969), fresh density in kg m^{-3} can be approximated by:

$$\rho_{green} = 1000 + \frac{\rho}{3} \qquad (2)$$

However, the degree of cell lumen saturation may differ between trees or species, making fresh density a less reliable predictor of interspecific variability of mechanical properties. Basic density ρ is therefore the only appropriate parameter to use as an indicator of wood tissue properties (Larjavaara and Muller-Landau, 2012). The modulus of elasticity of green wood can be predicted from ρ (Fournier *et al*. 2006) as:

$$E = 10400 \left(\frac{\rho}{530}\right)^{1.03} \qquad (3)$$

Stiff, heavy and costly high-density wood. Does it make trees more or less safe?

Larjavaara and Muller-Landau (2010) demonstrated that "the lower the wood density is, the greater SW will be". Such a result sounds surprising. In reality, wood basic density is not only an indicator of wood strength but also of stem construction costs (approximated by the dried biomass) per unit of volume. Therefore, with a given biomass, decreasing wood density will increase the stem thickness. The question is then how the biomechanical performance scales to wood density with a constant dry biomass, that involves a trade-off between wood mechanical properties and stem thickness. Assuming a constant dry biomass of the cross-section actually equals to fix ρD^2. Then, as SW is proportional to $\sigma_c D^3$, if σ_c varies linearly with ρ (as observed by wood scientists and reported by Chave *et al.*, 2009), the safety SW scales as $\rho^{-0.5}$ thus increases with decreasing density (Larjavaara and Muller Landau, 2010). The problem becomes increasingly intricate when the biomechanical performance studied is the safety against self-buckling (SB). In fact, wood basic density becomes not only a proxy for mechanical stiffness E and a component of the construction cost ρ_V, but also a large part of the load since ρ_T is the sum of (i) wood basic density, (ii) stem water content per unit of trunk volume, and (iii) fresh biomass of leaves and branches per unit of trunk volume. On the basis of a study of tropical trees of 8–25 cm in *D* (at breast height), and carefully assuming relationships between loads (components of ρ_T) and basic density ρ, King *et al*. (2006) inferred that SB varied slightly, in proportion to $\rho^{0.27}$. Actually, our own simulations presented in Fig. 3 found a similar scaling of SB, between $\rho^{0.22}$ to $\rho^{0.26}$. More recently, Anten and Schieving (2010) studied more generally how the cost to make a trunk of given height and mechanical stability varies with wood basic density. They used the two criterions SW and SB and concluded that a higher density would only result in a slight increase in the safety margin.

Theoretical wood variations due to wood structure: ρ and MFA as key structural features

As mentioned above, the stiffness *E* and strength σ_c of wood tissues are usually assumed to vary quite linearly with wood basic density (Chave et al., 2009; Fournier et al., 2006). This is a general character of honeycomb cellular materials made of elongated cells, when cell wall properties are constant (Gibson and Ashby, 1997). Since the density of cell wall material does not significantly differ among wood species, wood basic density represents the relative quantity of the cell wall in a given volume of wood made up of cells and lumens. The quantity of the cell wall material naturally affects the wood tissue properties but cannot explain all of the variability because cell wall stiffness and strength are neither constant nor isotropic. Wood anatomical elements primarily responsible for load carrying are generally aligned with the axis of elongation of the plant organ, which makes wood much stiffer along this direction. Moreover, these load-bearing elements (fibres in angiosperms and tracheids in gymnosperms) exhibit a multi-layered composite cell wall. Some 75% to 85% of the total cell wall thickness consists of a so-called S2 layer made up of a soft viscoelastic matrix that envelops stiff cellulose microfibrils. The latter are organised in spirals that form an angle of typically 10–30°, referred to as the microfibril angle (MFA), with the longitudinal fibre/tracheid axis (Fengel and Wegener, 1984), and are responsible for most of the stiffness of the cell wall. Stiffness of wood tissues may therefore be expressed as a function of basic density, MFA and cell wall stiffness as follows (Xu and Liu, 2004):

$$\frac{E}{\rho} = \frac{E_{cw}}{\rho_{cw}} \cos^4 MFA$$

where *E* is the elastic modulus or stiffness and the index *cw* stands for the cell wall material. Since ρ_{cw} is constant, the ratio E/ρ varies with the stiffness of the cell wall along the cell axis, which is primarily determined by the MFA and secondarily by the E_{cw} variations (Salmen and Burgert, 2009).

Concerning other wood properties, strength σ_c is similarly linked to the basic density and MFA (Evans and Ilic, 2001; Lachenbruch *et al.*, 2010; Read *et al.*, 2011), whereas the amount of strain generated during cell maturation α is quite independent of wood density but related to the MFA (Clair *et al.*, 2011). Recalling that stem motricity relies on the asymmetry $\Delta\alpha$, the asymmetry $\Delta\alpha$ in hardwoods is the result of the differentiation of tension wood on the upper side, whereas in softwoods, compression wood on the lower side causes the asymmetry. Tension wood is more cellulosic with a low MFA, whereas compression wood is more lignified with a high MFA.

Adapting stiffness in the 3D space of basic density, MFA and cell wall stiffness

When observed along wide biogeographic gradients, the correlation between basic density ρ and the modulus of elasticity *E* (Chave *et al.*, 2009) has a strong physical determinism, usually interpreted as a trade-off between construction cost and wood performance. In fact, along a wide range of variations of wood density, neither the MFA nor the cell wall stiffness E_{cw} can offset the fact that “the more the better”. The MFA is generally considered in wood science to be intrinsically independent of basic density (Yang and Evans, 2003; Boiffin, 2008; Donaldson, 2008). Theoretically, a tree can therefore “choose” to vary one or both properties to adapt its tissues for different loading scenarios, using dense tissues with a low MFA to maximise stiffness *E* and strength σ_c, low-density tissues with a high MFA to enhance the tissue flexibility (low *E*), and high-density tissues with a high MFA to enhance the energy absorbed before fracture (called toughness) (Burgert *et al.*, 2004; Burgert, 2006; Jungnikl *et al.*, 2009).

Typical patterns of association between the three determinants of wood stiffness emerge from the motor function: in softwoods, the high MFA and highly lignified cell walls of compression wood are associated with lower *E*, with a trade-off between stem safety SB and stem motricity MV (Almeras *et al.*, 2005). Moreover, since the product $E\Delta\alpha$ is involved in postural control, this lower E could weaken the ability of a stem to maintain a given angle. In hardwoods, motricity is associated with a higher *E* and there is no trade-off but, instead, a positive association between the performances of both skeletal and motricity function.

Some co-variations of ρ and MFA among species are ecologically driven

Studies on interspecific variations of the MFA in ecological contexts are rare since the MFA has mainly been investigated in view of understanding variations in mechanical properties of commercial species in terms of growth conditions (Saren *et al.*, 2004; Medhurst *et al.*, 2012) and possible wood quality improvement (Baltunis *et al.*, 2007). In their pioneer studies, Read *et al*. (2011) and Boiffin (2008) observed the diversity of the MFA, E and ρ among some rainforest species. While Read *et al*. (2011) aimed at understanding how high winds in New Caledonia constrained wood properties among 15 species of different sizes and habits, Boiffin (2008) observed 22 species in French Guiana with a very low wind constraint in understorey saplings from different functional groups of species along a light demand gradient. In both samples, E is closely correlated to ρ (Table 3). In contrast to Boiffin's observations, Read and co-workers (2011) reported that this relationship was not related to the usual growth-survival trade-off in their sample. Indeed, relationships between E and ρ have a strong physical determinism, regardless of the reason why species with low and high wood densities coexist. Moreover, as shown in Table 3, whereas $\cos^4$(MFA) and ρ are independent among Boiffin's species (2008), they are closely linked in Read *et al*. (2011), suggesting a strong differentiation of species along a stiffness axis in these high wind conditions. The mean value of the cell wall stiffness, estimated as the average of $E/(\rho\cos^4(\mathrm{MFA}))$, is higher in Read *et al*. (2011) (with a value of 23.9 GPa) than in Boiffin (2008) (with a value of 21.2 GPa), also suggesting a greater stiffness of the cell wall. Read *et al*. (2011) raised the question as to why such an opposition between stiff and not stiff wood have been filtered in cyclone-prone environments. Indeed, French Guianese species structured along the light demand gradient make it possible to explore wider possibilities of associations between the MFA and ρ. Read *et al*. (2011) suggested further studies of the ecological significance of the MFA. Actually, since the MFA is a key feature of motricity, the low mean MFA of some angiosperm species (or high ones of some gymnosperms) could indicate a higher occurrence of reaction wood and, therefore, a higher motricity or postural control. We think that including motricity traits in such investigations will bring new insights into the question of trade-offs or associations between ρ and the MFA.

Beyond the skeleton: including maturation asymmetry $\Delta\alpha$ in wood databases

Studies of the evolutionary significance of PC or MV are in their infancy since they require measurements of $\Delta\alpha$, which are not the usually collected data in ecological studies. $\Delta\alpha$ is related to reaction wood formation, which has been widely studied in wood anatomy. Wood anatomy is strongly linked to evolutionary ecology (Carlquist, 2001). Would it be possible to use wood anatomical traits as a proxy for $\Delta\alpha$? Indeed, using wood anatomy databases to infer functional traits is becoming a common practice in ecology (Martínez-Cabrera *et al*., 2011). However, translating these anatomical observations into $\Delta\alpha$ is an unsolved problem, since $\Delta\alpha$ is more closely related to cell wall properties like MFA than to cellular characteristics usually observed in wood taxonomy. Normal anatomical observations related to reaction wood, for example concerning the occurrence of the G layer among tree species, are not useful to assess variations in motricity (Clair *et al*., 2006) because different cellular traits associated with different patterns of reaction wood have converged to the same functionality of motricity traits (Scurfield, 1973).

Measurements of α through growth strain indicators (GSI) are now a standard method for wood scientists (see the large database on European Beech in Jullien *et al.,* 2013). In order to enhance high throughput and non-destructive assessment with the sampling methods commonly used in field ecology, these standards should be used to calibrate indirect methods using the empirical correlation between GSI and the tangential diameter of an increment core (Ferrand, 1982), or, in a more reliable way, the relationship between GSI and MFA (Yang *et al*., 2006). New tools such as Silviscan have made extensive measurements of MFA easier (Read *et al*., 2011), making it possible to interpret their variations both as wood stiffness and strength variations related to SB and SW, and as $\Delta\alpha$ and PC or MV variations.

Once the appropriate metrology has been selected, the conditions in which maturation strains are characterised (i.e., the sampling methods) when comparing PC or MV among species along environmental gradients should also be carefully assessed. When $\Delta\alpha$ was measured as a righting capacity under controlled conditions of lean disturbance, it was found to be highly genetically determined (see Almeras *et al*., 2009, or Sierra-De-Grado *et al*., 2008). However, in natural conditions, $\Delta\alpha$ has a high phenotypical plasticity (Fournier *et al*., 1994b) since it rapidly acclimates to lean disturbances.

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Challenges for future research in ecological biomechanics

Definition and integration of biomechanical crown traits

In the current definition of integrative traits (SW, SB, PC, MV), branching patterns are included only through the load parameters (m, A_w, c_d, ρ_T). However, trees are complex fractal structure (Plucinski *et al.*, 2008). The question of relevant traits that capture the biomechanical parts of branching patterns must therefore be addressed. Indeed, the branching structure of the crown has been shown to play a significant role in wind failure through resonant and structural damping behaviours (James *et al.*, 2006). When studying plant adaptation to the environment, ecology deals with a large number of plants and environments, roughly described at the infra-individual level. Standard biomechanical models based on numerical simulations in which each specific situation is described through a large dataset of variables describing one single tree (e.g., Sellier and Fourcaud, 2009) are thus not appropriate. However, alternative biomechanical studies use parsimonious representations to address questions about the impact of branching patterns on mechanical safety (Plucinski *et al.*, 2008; Rodriguez *et al.*, 2008; Eloy, 2011; Lopez *et al.*, 2011). In several models, a simple characterization of branching through two parameters has been found to be sufficient: (i) the branching ratio, which is the reduction of diameter through branching, and (ii) the slenderness exponent, which is the relationship between length and diameter in branch segments (Rodriguez *et al*., 2008; Eloy, 2011;, Lopez *et al*., 2011). For example, using these two branching parameters, Lopez *et al*. (2011) investigated the brittle reconfiguration of the crown, i.e., the way some branches preferentially break under wind flows acting as mechanical "safety fuses". They proposed an elegant model based on the scaling of the fluid-loading with respect to the critical stress (a criterion similar to SW). Similarly, Eloy (2011) demonstrated that Leonardo's rule (i.e., the total cross-section of branches is conserved across branching nodes) can be a mechanical adaptation to winds. In our opinion, although such models seem very simplistic at first glance, they represent a great potential for ecological studies since they are based on very few parameters of load, size and shape, similarly to popular seminal works such as that of Greenhill (1881).

Assessing the evolutionary importance of motricity

As already mentioned above, studies of ecological significance of the variability of motricity traits PC or MV require data about $\Delta\alpha$, which are not as common and available as other wood traits. Using measurements of all other traits of PC, Jaouen (2007) demonstrated the importance of $\Delta\alpha$ variations in sapling growth strategy by *reductio ad absurdum* arguments. She simulated the successive curvatures and leans of saplings under the assumption of $\Delta\alpha$ =0 (and, therefore, PC=0) for different species competing in a tropical rainforest understorey, under the assumption that the lean has been slightly disturbed at an early stage of growth (Fig. 5). With no capacity of reaction, plants should bend more and more since gravitational curvature acts alone. Then, due to their extreme slenderness and quite high centre of mass, trees would achieve high tilt angles that are even not viable in some species (such as Vm in Fig. 5). Moreover, since stiffness and loads strongly differ between species, this theoretical tilt angle would be highly variable between species. Indeed, such leans and lean variations between species are not observed (Fig.5), demonstrating that motricity is active and that motricity traits necessarily differ between species, as already shown in Fig. 4.

However, in nature, trees experience successive disturbances, and the way an observed lean is reached at a given time depends on the whole history of growth and disturbances. In such a context, the success of the righting and straightening process relies on how MV can rapidly adapt after the disturbance. As reported by Almeras *et al*. (2002) who studied the bending of apricot tree shoots, and as shown in theoretical simulations of Fig. 5, even a small difference in stem form at oblique stages before disturbance and in growth rates in response to disturbance could lead, through the reciprocal dependencies between form and growth, to a considerable divergence in its later development. In particular, the timing, size and frequencies of the disturbances should be considered using conceptual approaches of the ecology of disturbances (Johnson and Miyanishi, 2007). Formalising these problems in changing environments along growth trajectories could deeply modify our representation of motricity in natural forests, so far focused on reaction wood formation (Dassot *et al*., 2012). Indeed, features other than the maturation strain asymmetry ($\Delta\alpha$), such as the relative timing of growth in height, thickness and leaf biomass, may be of greater importance (Almeras *et al.*, 2004). When observing buttress morphology in rainforest species, Chapman *et al*. (1998) concluded that most buttresses are opportunistic organs, the efficiency of which lies in their adaptability to respond to development crises such as gap openings. Actually, as buttresses act as mechanical guy ropes (Clair *et al.*, 2003), their formation cause an efficient posture control, without any reaction wood. By the same token, modelling MV or PC in thick and rigid stems of lianas or palm trees, which do not grow in thickness from concentric rings, remains an open question.

From a practical point of view, all these studies should use extensive measurements of lean using simple methods (Collet *et al*., 2011), or new digitising techniques such as T-LIDAR, whose uses are expanding in the areas of ecology and forestry (Dassot *et al.*, 2011).

Towards greater communication between sensory mechanobiology and tree ecology

It is now widely accepted that plants are sensitive to environmental signals, and that signal-driven responses explain a large part of the phenotypical plasticity (Givnish, 2002). Plants are, in particular, extremely sensitive to wind-induced deformations (Moulia *et al.*, 2011), as well as to leaning (Moulia and Fournier, 2009), and the thigmomorphogenetic and gravitropic responses are likely to be adaptive in many situations (Jaouen *et al.*, 2010). However, these responses have been widely ignored in tree ecology.

This may be due to the fact that thigmomorphogenesis and gravitropism have long been investigated by plant physiologists in particular, leading to very detailed descriptions at the cellular and molecular level. However, the situation has changed over the last decade. Just as for motricity, parsimonious and generic integrative models have been developed for wind mechanosensing (the S3m model of Moulia *et al*., 2011) and for postural control (the AC model of Bastien *et al*., 2013), both of which have been validated on a large set of species and plant habits. These models allow for simple but relevant traits to be defined. For example, Bastien *et al*. (2013) showed that the mechanosensitive control of posture depends on a single dimensionless parameter B, which is the ratio between the gravisensitivity to lean and the proprioceptive sensitivity of curvature. Moreover, this ratio can be accurately estimated by taking photos at two stages after a leaning disturbance. Finally, these approaches have also revealed genetic markers that may be used as traits of mechanosensitivity (Chevolot *et al.*, 2011; Moulia *et al.*, 2011). There is still a significant amount of work to be done before we can define simple sensory mechanobiological measurements for tree ecology. In particular, a major challenge will be to integrate these models over much longer periods of time such as the life span of trees or even climatic changes. Nevertheless, we think that the conditions are now favourable to promote better and more fruitful communication between sensory mechanobiology and biomechanical ecology.

Glossary of abbreviations and symbols: list (alphabetical order) and definition

A_w: wind surface area that creates an obstruction to wind flow, depending on crown dimensions (m^2).

b: ratio of relative height growth to relative diameter growth $(dH/H)/(dD/D)$, i.e., exponent of the relation $H{\sim}D^b$ (dimensionless).

c_d: drag coefficient (dimensionless).

D: diameter of the cross-section at the stem base (m).

$D(X)$: diameter of the stem cross-section at X-level (m) .

dC_g/dD: rate of gravitational curvature (downward and positive when weight increases) per unit of radial growth in diameter near the base (m^{-2}).

dC_m/dD or $dC_m/dD(X)$: rate of reaction curvature (upward and negative in the case of gravitropism) due to maturation per unit of diameter growth, at the stem base or at X-level (m^{-2}).

dD/dt: radial growth velocity, usually expressed in mm/year; dD/dt is then twice the annual tree ring width.

dR_+: tree ring width on one side + (m).

dR_-: tree ring width on the opposite side – (m).

E: modulus of elasticity (also called Young's modulus) ($N\ m^{-2}$).

E_{cw}: modulus of elasticity of cell wall material ($N\ m^{-2}$).

F_b: self-buckling form factor, $F_b = 0.1785(|m-4n+2|).(2n+1)J_{-\frac{4n-1}{m-4n+2}}(0)$ (dimensionless).

F_g: growing weight form factor, $F_g = \frac{2}{(m+1)(2n+1)}$ (dimensionless).

F_m: interaction between maturation strains and radial growth asymmetry, which enhances the motricity (dimensionless).

F_w: wind form factor that represents the interaction between crown shape and wind profiles (dimensionless).

g: gravity acceleration ($N\ kg^{-1}$).

H: total height of the tree (m).

H_c: critical self-buckling height (m).

H_g: height of the centre of mass (m).

H_w: height of the centre of wind drag pressure (m).

I: second moment of area of the cross-section (m^4).

k_m: eccentricity of radial growth, $k = (R_r - R_l)/(R_r + R_l)$ between -1 and 1 (dimensionless).

k_w: ratio H_w/H, smaller than 1 (dimensionless).

m: biomass profile distribution, defined by $M(x) = \rho_T V \left(\frac{H-X}{H}\right)^m$, dimensionless. m represents the relative height of the centre of mass as $m+1 = H/H_g$.

$M(X)$: biomass supported above X-level (kg).

MV: tropic Motion Velocity. Capability of a new peripheral wood to induce a curvature from the maturation of a new peripheral layer of wood during one unit of time. MV is a curvature rate (m^{-1} s^{-1}).

$M_w(X)$: bending moment induced by wind at X-level (N m).

n: taper, defined as $D(x) = D\left(\frac{H-X}{H}\right)^n$, dimensionless. Note that n can be estimated easily from the form factor $\frac{V}{D^2H}$ of volume equations of forestry as $\frac{\pi}{4(2n+1)} = \frac{V}{D^2H}$

PC: Posture Control. Ratio of reaction curvature to gravitational curvature (dimensionless).

SB: tree Safety factor against self-Buckling. Ratio of the maximum height the tree can reach (while remaining self-supporting with other parameters kept constant), to its actual height (dimensionless).

SW: Safety against Wind. Tree resistance to wind calculated as the critical pressure ρ_{air} g U_w^2 (N m^{-2}).

T: general symbol for a trait T.

U_w: wind velocity (m s^{-1}).

V: volume of the trunk (m^3).

$\Delta\alpha$ or $\Delta\alpha(X)$: contrast of maturation strain in the new ring of wood of a growing stem, at the stem base or X-level (dimensionless).

φ: mean lean of the stem, angle from the vertical (radian).

ν_T: general power of a dissociated T in the expression of an integrative trait.

ρ: wood basic density, which is the mass of dried wood per unit of fresh volume (kg m^{-3}).

ρ_{air}: density of air in kg m^{-3}. ρ_{air} can be calculated from temperature, air relative humidity and elevation. For 15°C, 60% of relative humidity, ρ_{air}=1.21 kg m^{-3} at sea level.

ρ_{cw}: basic density of the cell wall material, ρ_{cw}=1500 kg m^{-3}.

ρ_{green}: density of green wood in the living tree, ratio of fresh mass (dry matter and water) to fresh volume, in (kg m^{-3}).

ρ_T: total fresh biomass supported, including leaves, trunk and branches, per unit of trunk volume (kg m^{-3}).

σ_w or $\sigma_w(X)$: bending stress induced by wind forces, at the stem base or at X-level (N m^{-2}).

σ_c or $\sigma_c(X)$: wood critical stress usually measured by bending tests (as the standard MOR), at the stem base or at X-level (N m^{-2}).

τ_T: ontogenetic trend of a dissociated trait T.

Supplementary material

Supplementary file: SBcalculation.xls (in .xls format, Microsoft®). This tool makes it possible to recalculate the safety factors SB of Fig. 3. It can be applied for further assessments of SB, avoiding the use of two simple formulas (trees of constant diameter, cylindrical, with no crown and water load, no taper, etc.).

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Legends of tables

Table 1: Synthesis of the four traits: Safety against Wind (SW) as the critical wind pressure, Safety against Self-Buckling (SB) as the ratio of critical buckling height for the same trunk volume, to current height, Motricity (MV) as the active gravitropic curvature rate during radial growth, Posture Control performance (PC) as the ratio of the gravitropic curvature to the gravitational one, at a given angle φ (the limit 1 is the long-term stable regime where the tree maintains a constant lean φ). For each trait, the table summarizes the way to calculate it as a combination of dissociated variables, the types of the different variables involved (size, shape, wood, load), and the allometric scaling laws between size variables that maintain a constant value.

Table 2: General method for assessing ontogenetic trends on an integrative trait from a sampling of trees that represent an ontogenetic trajectory (case study: safety against self-buckling of a sample of *Oxandra asbeckii* at the sapling stage, re-analysing data from Jaouen *et al*. (2007)). The first two lines provide the mean values and the coefficient of variation for each component T. The third line τ_T is the power exponent (ontogenetic trend) from fitting the trait T to the developmental variable H. The fourth ν_T gives the power of T in the integrative trait SB. In the last line, the sum of products $\tau_T\,\nu_T$ gives the ontogenetic trend of the integrative trait (SB in this case), broken down into trends for each component.

Table 3: Scaling of E with ρ and $\cos^4$(MFA) using data from Read *et al*. (2011) and Boiffin (2008). Wood characteristics were measured on increment cores and silviscan (X-ray tomography and diffraction) in Read *et al*. (2011), whereas Boiffin (2008) measured E of entire stems in a universal testing machine (bending test), and MFA by X-ray diffraction.

Table 1 (erratum : ligne 2 trait SB remplacer 2+1 par 2n+1)

Trait	Expression as a function of size, wood, load and shape variables	Size variables	Resulting scaling laws between size variables to maintain a stable trait (everything else being constant)	Shape factors	Wood resistance or motor properties	Load factors
SW	$\frac{\pi \sigma_c D^3}{16 c_d A_w H k_w F_w}$	D, A_w, H	$D^3 \sim A_w H$	k_w, F_w	σ_c	c_d, k_w, F_w, A_w
SB	$0.88 H^{-1} V^{1/4} E^{1/4} (\rho_T g)^{-1/4} {F_b}^{1/2}$ or $0.83 H^{-3/4} D^{1/2} E^{1/4} (\rho_T g)^{-1/4} (2+1)^{-1/4} {F_b}^{1/2}$	$H, V \; or \; D$	$H \sim V^{1/4}$ or $H \sim D^{2/3}$	F_b	E	ρ_T
MV	$-4 \frac{F_m \Delta\alpha}{D^2} \frac{dD}{dt}$	$\frac{dD}{dt}, D$	$\frac{dD}{dt} \sim D^2$	-	$\Delta\alpha$	-
PC	$\frac{E \, \Delta\alpha}{4(1+b) \rho_T g \, sin\varphi} \frac{F_m}{F_g} \frac{D}{H^2}$	H, D	$H \sim D^{1/2}$	b, F_g	$E, \Delta\alpha$	$\rho_T, sin\varphi$

Table 2

Trait T	H (m)	V (m^3)	ρ_T (g/cm^3)	F_b	E (MPa)	SB
Mean value	7.0	7.5 10^{-3}	1.6	2.2	14200	1.41
Coefficient of variation (%)	40%	155%	22%	18%	10%	18%
Ontogenetic trends, τ_T ($T \approx H^{\tau_T}$)	1	2.726	-0.097	0.128	-0.018	-0.235
Power of T in SB formula, ν_T	-1	0.25	-0.25	0.5	0.25	-
$\nu_T \tau_T$: Contribution of T to SB	-1	0.68	0.024	0.065	-0.005	-0.235

Table 3

Wood trait T	ρ	$\cos^4$(MFA)	E
Mean value			
Boiffin	0.64	MFA=15°	12.2 GPa
Read	0.66	MFA=12°	14.3 GPa
Pearson coefficient of LogE vs. LogT			
Boiffin	0.78	0.25	1
Read	0.79	0.83	1
Pearson coefficient of Logρ vs. LogT			
Boiffin	1	0.08	0.78
Read	1	0.75	0.79

Legends of figures

Figure 1: The four different processes of biomechanical traits with graphical representations of geometrical traits.

Figure 2: Reproduced from Niklas (2000). Safety against wind inside one wild cherry tree as a function of distance from top of tree (H-X). The safety factor here is the dimensionless quotient of the critical wind pressure to the wind drag pressure experienced at the stem element level (83 segments of the same tree were used in the numerical computation). The tree safety is then characterised by a set of safety factors along the the tree height X. Three different wind speeds (10, 20 and 50 m/s) are simulated, leading to three different safety factors for the same stem element design. The single safety factor SW defined in the text can be calculated from the minimum values of Niklas's safety factor along the height, at different wind speeds, as $\rho_{air}\ U_w{}^2 \min(U_w)$. On the right side, tree silhouette and measured wind speed profiles.

Figure 3: Variations of safety factors against self-buckling SB as a function of wood basic density ρ, independently of size and slenderness. SB was calculated for a tree of constant D=20 cm and H=20 m: **(i)** Cylinder made of dry wood: safety factor calculated from the maximum height at a constant diameter (as done in Sterck and Bongers, 1998); **(ii)** Cylinder made of fresh wood: safety factor calculated from the maximum height at a constant wood volume; **(iii)** Tapered stem: everything else similar to (ii); **(iv)** Crowned stem, which is the (iii) situation with additional loads of branches; and **(v)** Crowned tree carrying epiphytes, i.e., (iv) where a quite small mass but with a high centre of mass has been added. Wood modulus of elasticity E is linked to wood basic density (equation 3). The density ρ_T is given by ρ in **(i)**, wood fresh density given by equation (2) in **(ii)** and **(iii),** a mean value of 1400 kg/m^3 in **(iv)** (mean value of Jaouen *et al*., 2007), a mean value of 1540 kg/m^3 in **(v)** assuming the biomass of epiphytes is 10% of the tree biomass**.** Except for cylinders (i) and (ii) where n=0**,** the taper n is 0.6 (mean value observed by Jaouen *et al*., 2007). The biomass profile distribution is m= 2n+1 for the tapered stem **(iii),** m=1.5 (mean value observed by Jaouen *et al*., 2007) for the crowned stem **(iv)**, and m=1.27 in **(v),** which means that the centre of mass of epiphytes is located at 80% of the total tree height. SB is constant with ρ in (i), scales as $\rho^{0.22}$ in (ii) and (iii), and as $\rho^{0.26}$ in (iv) and (v).

Figure 4: Relationships between mortality rate and biomechanical traits PC and SB at sapling stages on a set of tropical species. Spearman correlation coefficients are R=-0.55 (p=0.07) for PC and R=-0.47 (p=0.14) for SB. Observations from the experimental plots of Paracou in French Guiana (Jaouen *et al*., 2007; Delcamp *et al*., 2008). Mortality rates are those of Delcamp *et al*. (2008) for control (not harvested) plots. Functional groups are also developed in Delcamp *et al*. (2008): ST = strongly shade-tolerant species, small to medium size; T = shade-tolerant species, medium size; MT = mid shade-tolerant species,

emergent; H = long-lived heliophilous species of the canopy. The species biomechanical traits were calculated as in Jaouen *et al.* (2007), on 1370 saplings for morphological data (H, D, b and φ) and sub-sampling for other variables (m, n, ρ_T, E, $\Delta\alpha$). All data comes from Jaouen (2007) except $\Delta\alpha$ in PC. $\Delta\alpha$ data come from the Wood Diversity project (Duchateau, 2008). Since Duchateau (2008) presented results on only nine species, unpublished data on *Eperua falcata* and *Pradosia cochlearia* has been added.

Figure 5: Basal (between 0 and 2 m) leans on a community of tropical saplings. Plain lines represent leans simulated under the assumption of no motricity (PC=0), along growth trajectories, from an initial disturbance of 8 degrees at an initial diameter (at 1 m in height) of 1 cm. Simulations used the equation of the gravitational curvature rate ${}^{dC_g}/_{dD}$ and mean traits measured on each species, as developed in Jaouen (2007). Dots are observed leans for the whole set of trees and species (adapted from Jaouen, 2007).

Figure 1

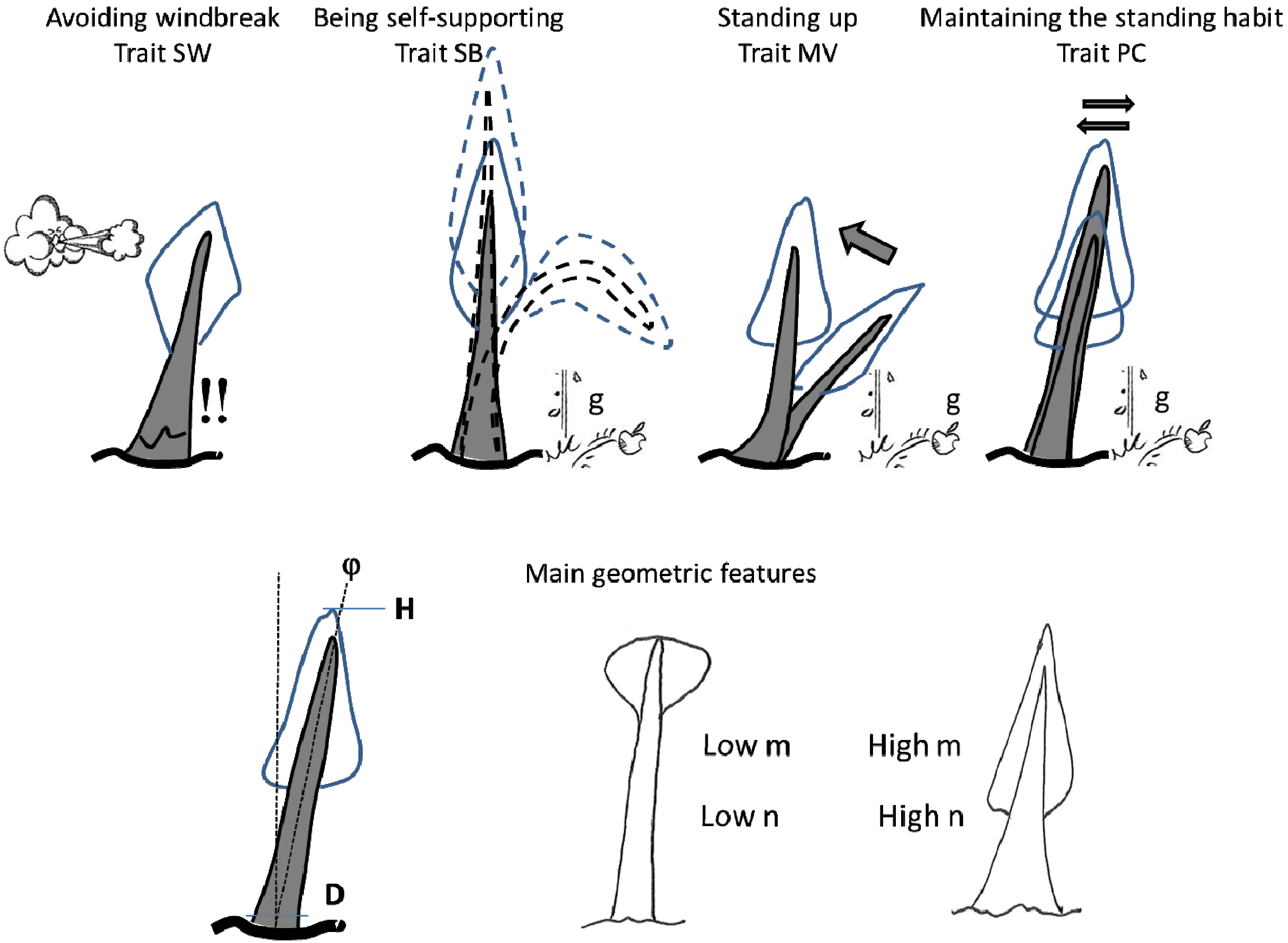

Avoiding windbreak
Trait SW
!!
Being self-supporting
Trait SB
g
Standing up
Trait MV
g
Maintaining the standing habit
Trait PC
g
φ
H
D
Main geometric features
Low m
Low n
High m
High n

Figure 2

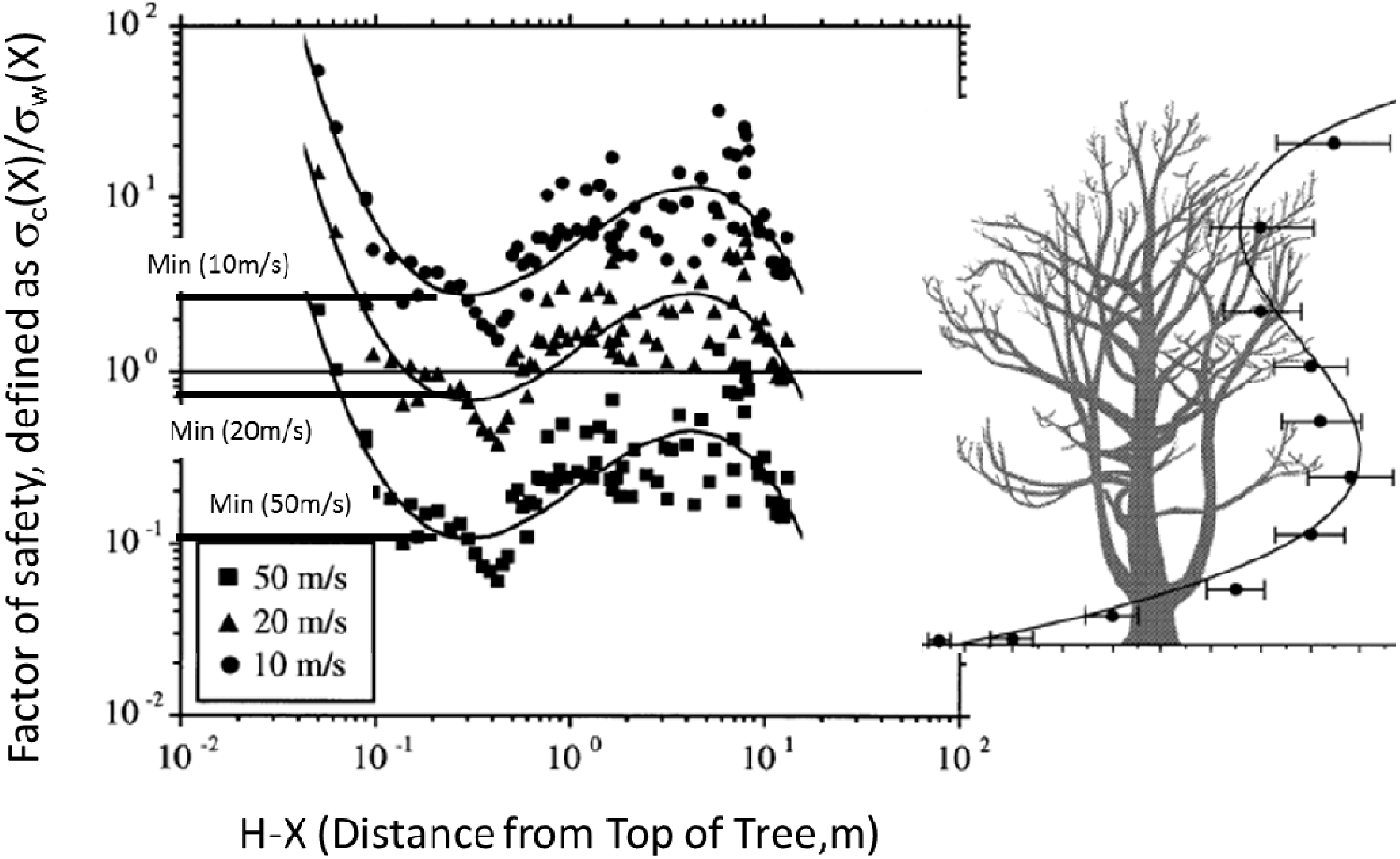

Factor of safety, defined as $\sigma_c(X)/\sigma_w(X)$
10^2
10^1
10^0
10^{-1}
10^{-2}
Min (10m/s)
Min (20m/s)
Min (50m/s)
■ 50 m/s
▲ 20 m/s
● 10 m/s
10^{-2}
10^{-1}
10^0
10^1
10^2
H-X (Distance from Top of Tree,m)

Figure3

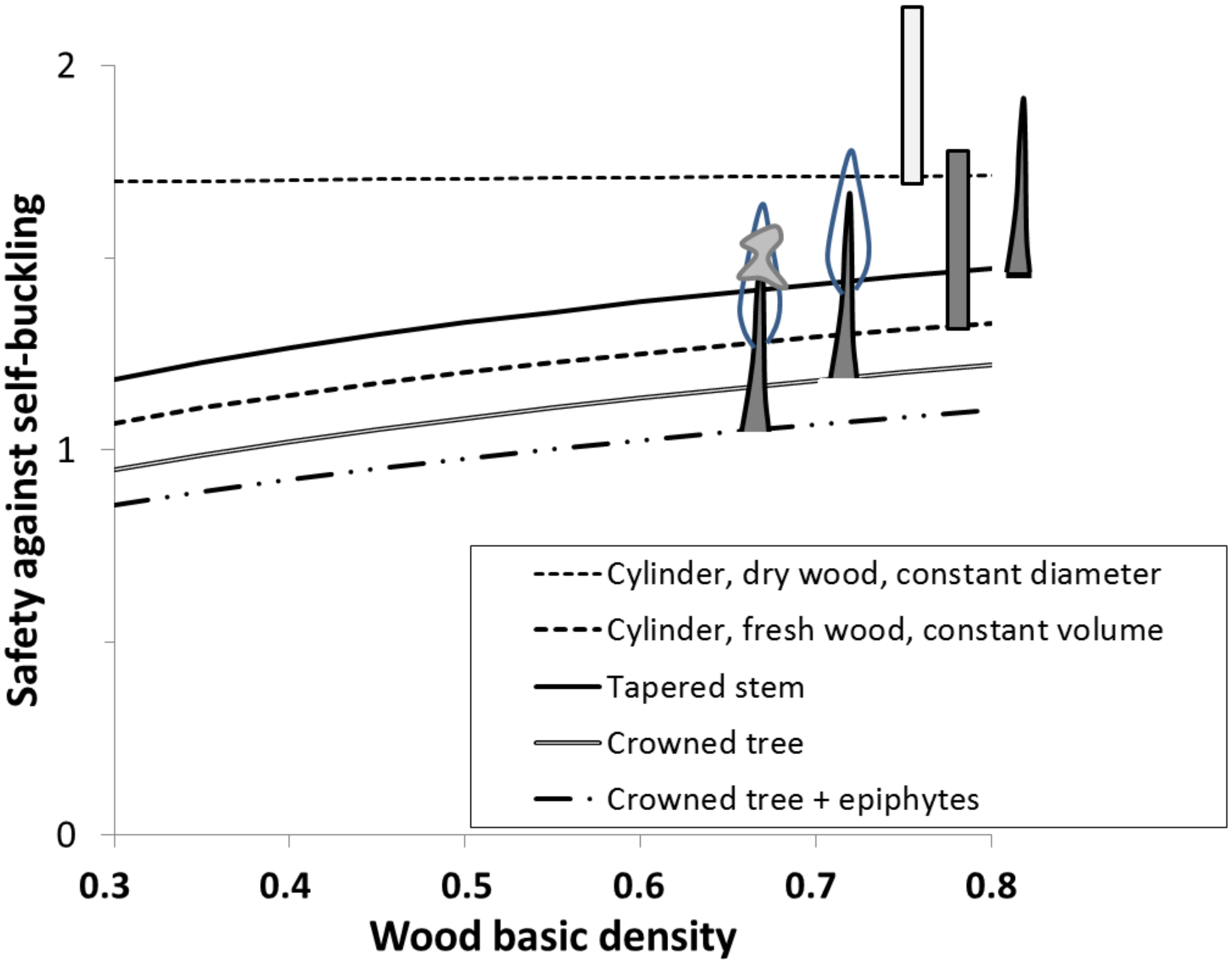
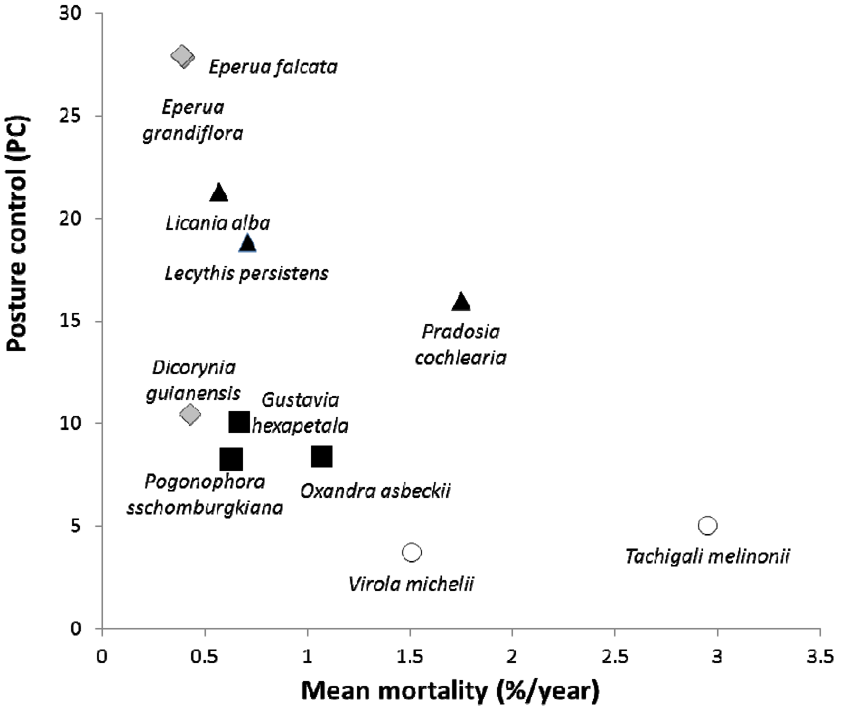

2
1
0
0.3
0.4
0.5
0.6
0.7
0.8
Wood basic density
Safety against self-buckling
Cylinder, dry wood, constant diameter
Cylinder, fresh wood, constant volume
Tapered stem
Crowned tree
Crowned tree + epiphytes

Figure 4


Posture control (PC)
30
25
20
15
10
5
0
Eperua falcata
Eperua grandiflora
Licania alba
Lecythis persistens
Pradosia cochlearia
Dicorynia guianensis
Gustavia hexapetala
Pogonophora sschomburgkiana
Oxandra asbeckii
Virola michelii
Tachigali melinonii
0
0.5
1
1.5
2
2.5
3
3.5
Mean mortality (%/year)

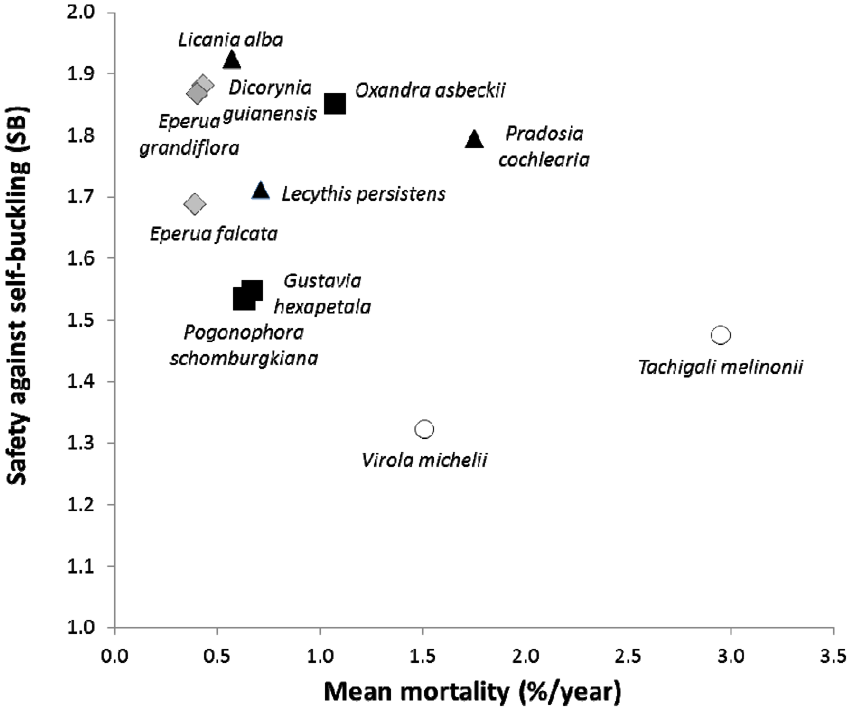
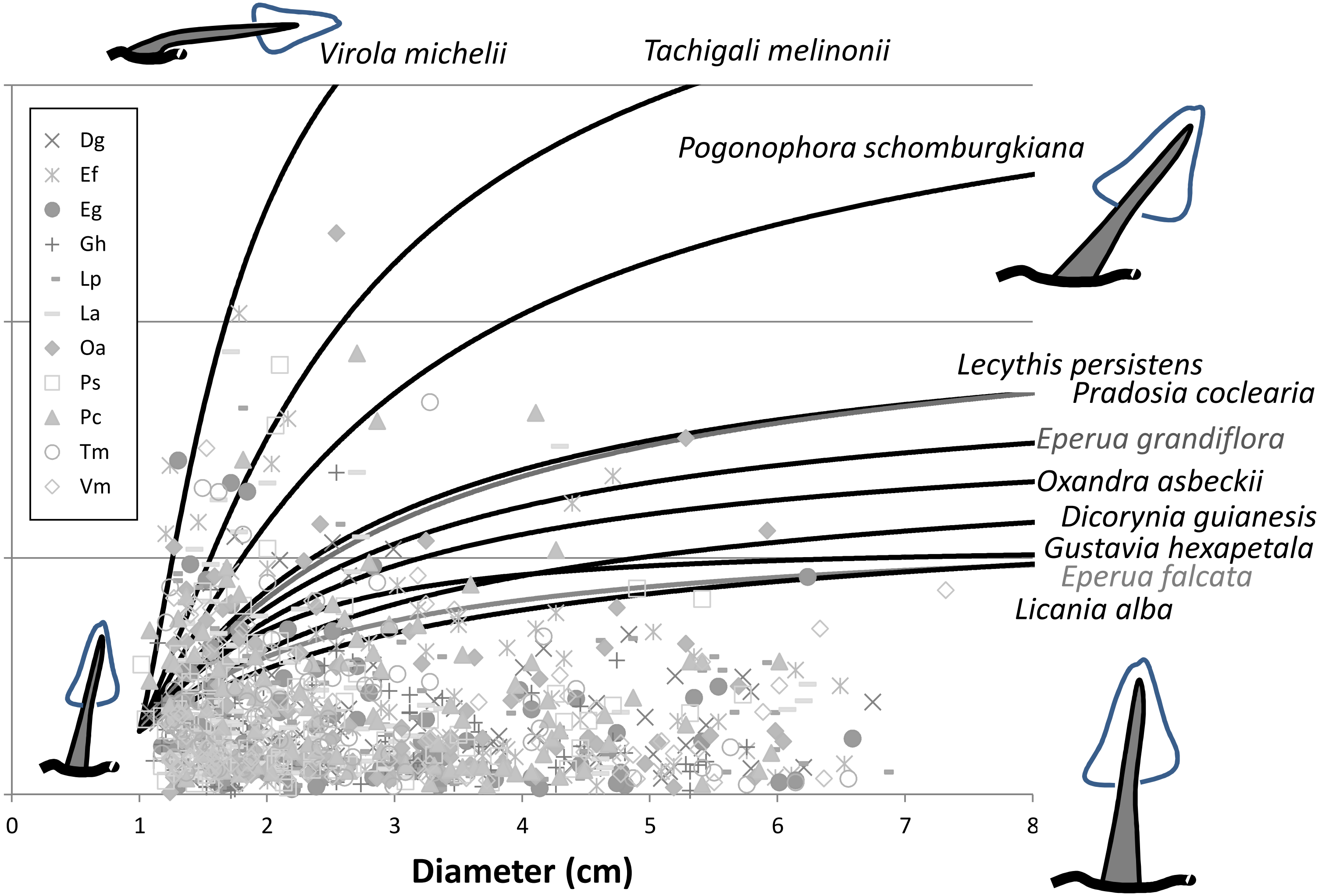

Safety against self-buckling (SB)
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
Licania alba
Dicorynia guianensis
Oxandra asbeckii
Eperua grandiflora
Pradosia cochlearia
Lecythis persistens
Eperua falcata
Gustavia hexapetala
Pogonophora schomburgkiana
Tachigali melinonii
Virola michelii
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Mean mortality (%/year)

Figure 5


Virola michelii
Tachigali melinonii
Pogonophora schomburgkiana
Lecythis persistens
Pradosia coclearia
Eperua grandiflora
Oxandra asbeckii
Dicorynia guianesis
Gustavia hexapetala
Eperua falcata
Licania alba
Dg
Ef
Eg
Gh
Lp
La
Oa
Ps
Pc
Tm
Vm
Lean (Degrees)
90
60
30
0
Diameter (cm)
0
1
2
3
4
5
6
7
8