# A SCALING LAW FOR THE EFFECTS OF ARCHITECTURE AND ALLOMETRY ON TREE VIBRATION MODES SUGGESTS A BIOLOGICAL TUNING TO MODAL COMPARTMENTALIZATION<sup>1</sup>

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Wind is a major ecological factor for plants and a major economical factor for forestry. Mechanical analyses have revealed that the multimodal dynamic behavior of trees is central to wind-tree interactions. Moreover, the trunk and branches influence dynamic modes, both in frequency and location. Because of the complexity of tree architecture, finite element models (FEMs) have been used to analyze such dynamics. However, these models require detailed geometric and architectural data and are tree-specific—two major restraints for their use in most ecological or biological studies. In this work, closed-form scaling laws for modal characteristics were derived from the dimensional analysis of idealized fractal trees that sketched the major architectural and allometrical regularities of real trees. These scaling laws were compared to three-dimensional FEM modal analyses of two completely digitized trees with maximal architectural contrast. Despite their simplifying hypotheses, the models explained most of the spatiotemporal characteristics of modes that involved the trunk and branches, especially for sympodial trees. These scaling laws reduce the tree to (1) a fundamental frequency and (2) one architectural and three biometrical parameters. They also give quantitative insights into the possible biological control of wind excitability of trees through architecture and allometries.

**Key words:** allometry; biomechanics; dimensional analysis; dynamics; frequency; model; scaling; tree architecture; vibrational properties; wind.

Wind-tree interaction is a major concern for the management of forest and urban trees because windthrow and windbreak result in substantial economical costs and potential human risks (Gardiner and Quine, 2000; James et al., 2006). Moreover, mechanosensing by trees of wind-induced strains (Coutand and Moulia, 2000) and induced thigmomorphogenetic responses are fundamental issues in understanding how trees can control their susceptibility to wind hazard (Moulia et al., 2006) and acclimate to their wind climate (Brüchert and Gardiner, 2006). Pioneer work on wind-tree interactions only considered static deformations under wind load (see review in Moulia and Fournier-Djimbi, 1997). Over the last decades, time-dependent dynamic effects have been found to play a major part in wind deformations and windbreaks (e.g., Mayer, 1987; Gardiner et al., 2000). However, the dynamic interactions between wind and trees are complex issues (Niklas, 1992). Wind velocity has a large spectrum of eddy size and frequency, as well as mean vertical profiles (de Langre, 2008). Most trees also have a branched architecture with different modes of branching (monopodial vs. sympodial) depending on species, up to 11 orders of axes, and reiterated patterns of various sizes and positions

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(Barthelemy and Caraglio, 2007). Therefore, the development of mechanical models for wind-tree interactions is necessary in addition to experiments, and the simplest relevant model is to be sought (see review in de Langre, 2008). A central question to be investigated is then obviously the influence of branched architecture and tree geometry on the dynamics of trees and the potential biological control of tree resistance to wind through the morphological development of the tree.

The mechanical response of a tree to turbulent wind results from the interaction of three components: (1) the fluctuating excitation load by wind drag, (2) the dynamic elastic behavior of the system, and (3) the damping processes (e.g., Moore and Maguire, 2008). The load is the input of mechanical energy in the system. The oscillatory elastic behavior of the structure is driven by the conservative exchange between two forms of the internal mechanical energy: (1) kinetic energy (the sum over all the material elements of the tree of the products of their masses times their square velocity) and (2) elastic-strain potential energy (Gerardin and Rixen, 1994). These internal energetic exchanges can be characterized by considering the natural free-motion dynamics of the isolated system (i.e., with suppressed energy input and negligible dissipative losses) and by studying the resonance frequencies, which characterize the exchange rate between these two forms of energy. Last, the damping processes dissipate a part of the mechanical energy out of the structure, thus resulting in the decay of the amplitude of the oscillation. This dissipation involves (1) the production of small-scale turbulence in the wake through aerodynamic drag at the level of the leaf-air and branch-air interfaces and (2) to a lesser extent in most cases, the production of heat through internal viscosity (i.e., internal friction) in the wood (Niklas, 1992).

All these components are complex spatiotemporal processes. However, a very efficient approach to tackle this complexity is to focus first on the oscillatory elastic behavior of the structure (for examples in trees, see Sellier et al., 2006; Moore and Maguire, 2008). Indeed, the oscillatory elastic

behavior of the tree represents its intrinsic mechanical excitability (Gerardin and Rixen, 1994). Moreover, this oscillatory elastic behavior can be analyzed as the superposition of distinct modes of deformation through modal analysis, a standard tool in mechanical engineering. Each mode, numbered *j*, is an eigen way of oscillatory exchange between kinetic energy and elastic-strain potential energy (Gerardin and Rixen, 1994) in the absence of any damping or external load. The mode j is defined by the modal deformation  $\Phi_i$  (the displacement vector field defining the shape of the deformed tree), modal frequency  $f_j$ , and modal mass  $m_j$  (which characterizes the inertia of the mode). Such modal analysis has two advantages. Modes can be ranked according to their contribution to the overall movement, so that simplified models casting to a limited number of modes can be defined objectively. Additionally, both the excitation load and the dissipation processes can be projected onto the set of modes (the modal basis) and thereby analyzed. For example, some modes will be more excited than others by a given load if this load applies to places where the modal deformation induces large displacements, even more if this excitation occurs at frequencies close to the corresponding natural modal frequencies. Such increased excitation is due to the phenomenon of resonance that results in a rapid uptake of the energy by the oscillating system with attendant amplification of the amplitude of the corresponding mode. By the same token, if large and fast movements of the branch tips occur in these modes, they will be more damped than others through aerodynamic damping. Modal analysis is thus a useful prerequisite to a more complete dynamic modeling of wind-tree interactions.

A few authors have used modal analysis on trees (e.g., Fournier et al., 1993; Sellier et al., 2006; Moore and Maguire, 2008). All have concluded that modes involving significant branch deformation could rank in between modes deforming mainly the trunk (Fournier et al., 1993; Sellier et al., 2006). Experiments from Moore and Maguire (2005) and Sellier and Fourcaud (2005) confirmed the excitation of several modes in conifer trees under wind load, with again some of the modes having their deformation mainly located on branches. Although not using modal analysis, James et al. (2006) also showed that the measured frequency spectra of the responses under wind excitation of four trees with different architectures, including conifers, two eucalypts and a palm tree, were also significantly dependent on the branching system. Moreover, James et al. (2006) and Spatz et al. (2007) argued that such multimodal dynamics including branch deformation could be beneficial to the tree by enhancing aerodynamic dissipation through a mechanism called multiple resonance damping or multiple mass damping. All these works contrasted clearly with previous works in which the dynamic contribution of branches and foliage was reduced to that of lumped masses fixed on a flexible beamlike trunk (e.g., Gardiner, 1992; Spatz and Zebrowski, 2001) and where only the first and eventually second modes of deformations of the trunk (i.e., first-order axis) were considered, both theoretically and experimentally. Note, however, that only monopodial architectures (Gillison, 1994; Barthelemy and Caraglio, 2007) were considered in all these studies about branch dynamics and that the only nonconifer trees were eucalypts. A comparison with sympodial trees would be interesting before generalizations are made.

In view of such complex effects, it may seem that only detailed finite element models (FEM) of the three-dimensional (3D) architecture of trees can be used for wind-tree interaction

studies of complex branched architecture and that only simulation studies can be done (Sellier et al., 2006; Moore and Maguire, 2008). Such simulation studies require a specific model for each individual tree, with intensive 3D descriptions of tree architecture (Sinoquet and Rivet, 1997; Moore and Maguire, 2008), while providing a limited perspective for generality and for the analysis of possible biological control. The geometry of trees, however, has in most cases some architectural symmetry related to the branching pattern (monopodial vs. sympodial growth) and spatial biometrical regularities-such as the allometry law for slenderness, which relates length and diameter of segments (McMahon and Kronauer, 1976; Niklas, 1994; Moulia and Fournier-Djimbi, 1997). The geometry of a tree can thus be approximately summarized using a few parameters. Moreover, the setting of some of these parameters is controlled through thigmomorphogenetic processes (Moulia et al., 2006). But the issue of whether such regularities can be reflected in general scaling laws for modal characteristics of sympodial and monopodial angiosperm and/or conifer trees has not been addressed yet. The hypothesis here is that simple scaling laws should occur. If they were to exist, these laws would make the studies of tree dynamics easier (methodological aspect) and give insights into the possible biological control of the overall tree dynamics excitability through genetic or thigmomorphogenetic changes in their parameters.

The aims of the present paper are thus (1) to explore the respective role of the architecture and allometry parameters on modal characteristics by combining FEM modeling and dimensional analysis of an angiosperm tree and a conifer tree with highly contrasting sizes and architectures and (2) to assess whether more generic scaling laws relating tree multimodal dynamics and architectural and geometrical parameters can be defined and to discuss their biological significance.

In the first section, the modal characteristics of two 3D models of extensively digitized trees with very distinct architectures—one sympodial angiosperm (walnut) and one monopodial conifer (pine)—are analyzed. Then in the second section, idealized fractal tree models are defined to explore the influence of biometrical regularities and branching patterns on the modal characteristics of a tree. Scaling laws between the successive modes of a tree based on the global parameters characterizing architecture and slenderness are then derived in these idealized trees. Finally, in the third section, we show that walnut and pine modal characteristics can be approximated using these scaling laws, so that the general multimodal behavior of trees can be reduced as a first approximation to (1) the first mode and to (2) general scaling laws for higher modes.

## MODAL ANALYSIS OF A WALNUT AND A PINE TREE

#### MATERIALS AND METHODS

**3D** descriptive data—Two real trees with highly contrasting sizes and architectures were considered (Fig. 1). The first tree, Fig. 1A, is a 20-yr-old walnut tree (*Juglans regia* L.) described in Sinoquet et al. (1997). It was 7.9 m high, 18 cm in diameter at breast height (dbh), and had a sympodial branching pattern and eight orders of branching. The second tree, Fig. 1B, is a 4-yr-old pine tree (*Pinus pinaster* Ait.) described in Sellier and Fourcaud (2005). It was 2.6 m high, 5.6 cm in diameter at 13 cm height, and had a monopodial branching pattern and three orders of branching.

The geometries of these two trees (positions, orientations, diameters of the stem segments, and the topology of branching points) are known in great detail through 3D magnetic digitizing (Sinoquet and Rivet, 1997) and are organized



Fig. 1. Geometries of (A, C) a walnut tree (from Sinoquet et al., 1997) and (B, D) a pine tree (from Sellier and Fourcaud, 2005).

in databases using the Multiscale Tree Graph MTG structure (Godin et al., 1999). Because our central concern was on the effects of branch architecture and allometry, these two trees were analyzed in this study without considering leaves or needles.

FEM modeling and computation of modal characteristics-In slender structures such as trees, the beam theory applies (Niklas, 1992), and modal deformations involve mainly bending and torsion. The mechanical model used for both trees were thus based on representing each branch segment as a beam, described by its flexural stiffness and inertia, using the Euler theory of linear elastic beams (Gerardin and Rixen, 1994). Beam sections were assumed to be circular, with a variable diameter along the beam (taper) when available. Connections between branch segments were set as rigid. The root anchorage was modeled as a perfect clamping condition at the tree basis. The green-wood material properties (density p, Young modulus E, and Poisson ratio v) were assumed to be uniform over all branches of each tree. Their values (Table 1) were taken from the measurements in Sellier et al. (2006) for the pine tree, while for the walnut tree, their values were estimated using Eq. 1 in Fournier et al. (2005). For each tree, a finite element representation was built using the CASTEM v. 3M software (Verpeaux et al., 1988). The stiffness and the mass matrices of the finite element formulation were then computed. By solving the equations for free motions using these matrices, we can fully define the modes (frequency, shapes, and mass) (see also Fournier et al., 1993; Moore and Maguire, 2005; Sellier et al., 2006). Because modes of free motion only involve exchange between kinetic energy and elastic strain energy, they can thus be studied without considering gravity effects and are defined under the assumption of linear transformation (small displacements, small strains).

#### RESULTS

In the walnut tree model (Fig. 2A), the first 25 modes were found in the range between 1.4 and 2.6 Hz. A small but clear frequency gap ( $\sim +0.4$  Hz) occurred between the first two modes and the following ones. Then modal frequencies continued to increase with mode number but at a smaller rate.

 TABLE 1.
 Geometrical and mechanical characteristics of the two analyzed trees (walnut, Juglans regia; pine, Pinus pinaster).

Species	Age (yr)	Height (m)	Diameter (m)	ρ [kg·m <sup>-3</sup> ]	E [GPa]	ν
J. regia	20	7.9	18.0 (dbh)	$\begin{array}{c} 0.805 \ 10^3 \\ 1.3 \ 10^3 \end{array}$	11.3	0.38
P. pinaster	4	2.6	5.6 (at 13 cm)		1.12	0.38

Notes: p, wood density; E, Young modulus; v, Poisson ratio



Fig. 2. (A) Mode frequencies of the walnut tree classified in terms of main localization of bending deformations: I, in the trunk; II, in second-order branches; III, in third-order branches. (B) Mode frequencies of the pine tree classified in terms of main localization of deformations: I, first bending mode of the trunk; I', second bending modes of the trunk; II, bending modes in second order branches. (C) Sketches of the mode deformations in the case of the walnut tree. (D) Sketches of the mode shapes in the case of the pine tree.

These modes can be classified according to their modal deformation  $\Phi_i$  (Fig. 2C). The first group of modes, labeled I, displayed a bending deformation mainly in the trunk basis. This resulted in a lateral displacement of the upper part of the bole mostly through rigid-body rotational effect, as sketched in Fig. 2C. In other words, deformations occurred mostly in the trunk up to the crotch, and the branches swayed like rigid bodies. Group I included two modes, corresponded to the bending in the x and y direction, respectively, with identical frequencies of ~1.4 Hz. The second group, labeled II, corresponded to deformations mainly located on first-order branches, with mostly rigid-body displacements of the branches of higher orders. Because there were six main branches bending in the x and y directions, respectively, this second group included 12 distinct modes, each one with different contributions of the deformation of these branches (modes 3–14). The third group, labeled III, corresponded to modes 15-25 with deformations mainly localized on thirdorder branches.

In the case of the pine tree (Fig. 2B), the first 25 modes were found in the range between 1 and 2.8 Hz with, here again, a clear small gap between the first two modes and the following ones. The group of the first two modes, labeled I, had frequencies at 1.08 Hz, identical to computational results from Sellier et al. (2006) on the same tree (Table 2). Bending deformations of these modes are mainly located in the trunk with displacements in the whole branching system. A second group of modes, labeled I', involved significant deformation in the trunk, but displayed higher modal frequencies around 2.41 Hz (modes 17 and 18, Fig. 2B). This group corresponded to the second bending modes of the trunk with bending deformations spread over the whole tree (Fig. 2D). As in the walnut tree, the two other groups of modes, labeled II and III, were associated with deformations located mainly on second- and third-order branches, respectively.

For both trees, modal frequencies were concentrated in a small frequency range. With frequencies of 1 Hz order of magnitude and  $\sim$ 10 modes per Hz, the frequency spacing of the modes was typically 0.1 Hz. Such a high density of modal frequencies is consistent with the conclusions of James et al. (2006) and Spatz et al. (2007).

Note, however, that the organization of modes groups differs between the two trees: the sequence is I / II / III for the walnut and I / II / I' / II for the pine tree.

# THEORETICAL CONSIDERATIONS: SCALING LAWS IN IDEALIZED TREES

Idealized fractal trees-To explore the respective effects of tree architecture and allometry on modal characteristics, we defined idealized fractal trees. Although not completely realistic (e.g., very short internodes are neglected so that several branches can be inserted at the same branching point, and no axis differentiation is considered), fractal tree construction is the simplest way of generating a reiterated architecture, with self-similar reiterations differing only by scaling coefficients (Prusinkiewicz and Lindenmayer, 1996). Two different fractal models were built, representing two extreme botanical branching patterns in the existing architectural models of plants (Barthelemy and Caraglio, 2007) The first model tree is inspired from the Leeuwenberg architectural model (e.g., cassava) and will be referred to as "the sympodial tree" in the following. At each branching point, the sympodial tree has symmetric lateral segments and no axial segment (Fig. 3). The second model tree is a highly hierarchical tree inspired from the Rauh architectural model (e.g., pine) and will be referred to as monopodial. It has an axial segment and lateral segments at each branching point (Fig. 3B). In both idealized models, lateral segments have equally spaced azimuthal directions.

Tree branches were indexed using the numbers of lateral and axial branching upstream in the direction of the tree base (Fig. 3). A branch segment in a monopodial tree is indexed [N,P] if this segment has N - 1 lateral and P - 1 axial upstream (i.e., more basal) branch segments. In the sympodial idealized tree, the same system holds, but P is constant and equal to 1. Thus a single index can be used and a branch segment of a sympodial tree is indexed N when it has N - 1 lateral upstream branch segments.

Segments sizes were defined using three parameters (Fig. 3): (1) the slenderness coefficient  $\beta$ , corresponding to an allometric law for branch segments (Fig. 3C); (2) the lateral and axial branching ratios  $\lambda$  and  $\mu$ , which define, respectively, the ratio between cross-sectional areas of segments after and before branching (Fig. 3D); and (3) the angle  $\alpha$  of divergence of lateral branches from the axial direction of the parent segment (Fig. 3E).

The mean slenderness of the population of branch segments of both trees was thus described using an allometric law that relates the length L and the diameter D of each segment (Mc-Mahon and Kronauer, 1976), in the form

$$D \sim L^{\beta},\tag{1}$$

(2B)

whereas the successive diameters at branching points were

 $D_{(N+1,P)} = \sqrt{\lambda} D_{(N,P)}$ .

$$D_{(N,P+1)} = \sqrt{\mu} D_{(N,P)}$$
 (2A)

and

Note also that the particular case where  $2\lambda + \mu = 1$  (i.e., the total section before and after branching are identical) corresponds to Da Vinci's surface conservation law (Prusinkiewicz and Lindenmayer, 1996), but this was not specially assumed hereafter.

The algorithm for generating a fractal tree as in Fig. 3 was the following: (1) the most basal diameter and the initial growth direction is given; (2) using the segment slenderness allometry (Eq. 1), the length of the first segment is computed; (3) a first "branching" occurs, and the diameter of each lateral branch is

computed using Eq. 2B for a sympodial tree or Eqs. 2A and 2B for a monopodial tree; and (4) their spatial inclination is controlled by the angle  $\alpha$  of divergence from the actual inclination angle of the parent axis and equal azimuthal spacing. For each branch, the process is iterated from step (1). In a theoretical fractal, this recursive iteration is infinite. Note however that this algorithm for tree construction is not a proper description of the real architectural development and axis growth of real trees (Barthelemy and Caraglio, 2007). For example, in real botanical trees, axes (e.g., branches) can usually be defined as a succession of segments (starting at a given branching point [*N*,*P*]) that are integrated by cambial growth (Barthelemy and Caraglio, 2007). These idealized trees are just designed as a tool to sketch some of the major symmetries and possible scalings of trees and to test them against real trees.

In the recursive process of construction of the idealized trees, the size of the successive segments depends on the segment slenderness allometric coefficient, the mode of branching (sympodial vs. monopodial), and the coefficients of area reduction at a branching point.

For the sympodial, idealized tree model (Fig. 4A), the relation between successive segments is

$$L_{N+1}/L_N = \lambda^{\frac{1}{2}\beta}$$
 and  $D_{N+1}/D_N = \lambda^{\frac{1}{2}}$ , so that  
 $L_N/L_1 = \lambda^{\frac{(N-1)}{2}\beta}$  and  $D_N/D_1 = \lambda^{\frac{(N-1)}{2}}$ . (3)

An axis length,  $l_N$ , is defined as the sum of the lengths of the segment  $L_N$  and all successive segments following a path of lateral branching, giving

$$l_N = \sum_{N'=N}^{\infty} L_{N'} = L_N \frac{1}{1 - \lambda^{1/2\sharp}}.$$
 (4)

According to Eq. 4, the slenderness coefficient,  $\beta$ , linking a segment length to its diameter, also links an axis length to its diameter:  $D_N = k_1 L_N^{\ \beta} = k_2 l_N^{\ \beta}$ . In the case of the model tree of monopodial type (Fig. 4B),

In the case of the model tree of monopodial type (Fig. 4B), the scale of a segment depends on the position of the parent segment in the central monopodial axis. If N - 1 is the number of lateral branching and P - 1 is the number of axial branching, the relation between diameters is given by

$$L_{N,P}/L_{1,1} = \lambda^{(N-1)/2\beta} \mu^{(P-1)/2\beta} \text{ and}$$
$$D_{N,P}/D_{1,1} = \lambda^{N-1/2} \mu^{P-1/2} \cdot$$
(5)

Due to the slenderness allometry, the reduction in segment length and segment diameter are thus linked by  $r_L = r_D^{/\beta}$ .

Axis length,  $l_{N,P}$ , is defined as the sum of the lengths of the segment  $L_{N,P}$  and all its "son segments" through axial branching, giving

$$l_{N,P} = \sum_{P'=P}^{\infty} L_{N,P'} = L_{N,P} \frac{1}{1 - \mu^{1/2\beta}}$$
 (6)

According to Eq. 6, the slenderness coefficient,  $\beta$ , linking a segment length to its diameter, also links the axis length to its basal diameter:  $D_{N,P} = k_1 L_{N,P}^{\ \beta} = k_2 l_{N,P}^{\ \beta}$ .

Walnut (Juglans regia L.)		Pine tree (Pinus pinaster Ait.)					
			Mode frequency (Hz)				
						Sellier et al. (2006)	
Mode number	Group	Mode frequency (Hz)	Mode number	Group	Present results	Exp.	Comp.
1	Ι	1.40	1	Ι	1.08	1.13	1.08
2	Ι	1.41	2	Ι	1.08	1.13	1.08
3	II	1.80	3	II	1.42		
4	II	1.88	4	II	1.50		
5	II	1.90	5	II	1.73		
6	II	1.94	6	II	1.73		
7	II	1.95	7	II	1.92		
8	II	1.97	8	II	1.96		
9	II	2.01	9	II	2.10		
10	II	2.02	10	II	2.12		
11	II	2.04	11	II	2.21		
12	II	2.06	12	II	2.23		
13	II	2.09	13	II	2.24		
14	II	2.12	14	II	2.27		
15	III	2.27	15	II	2.30		
16	III	2.29	16	II	2.32		
17	III	2.35	17	I'	2.41		
18	III	2.41	18	I'	2.41		
19	III	2.42	19	Π	2.58		
20	III	2.44	20	П	2.60		
21	Ш	2.47	21	П	2.66		
22	III	2.48	22	П	2.69		
23	III	2.51	23	II	2.70		
24	III	2.54	24	II	2.72		
25	III	2.56	25	II	2.72		

TABLE 2. Frequencies of walnut as described in Sinoquet et al. (1997) and of pine tree as described in Sellier et al. (2006), found via a finite element analysis.

Finally, in the idealized fractal trees, self-similar subsets of the tree starting from any branch bifurcation may be identified, as illustrated in Fig. 4. These subsets can thus follow the same index as their basal segment (i.e., N or N,P). Because of the assumption of the reiterated self-similar branching law, a given subset is identical to the whole tree, except for its main axis length scale,  $l_N$  or  $l_{N,P}$ , and its diameter scale  $d_N$  or  $d_{N,P}$ .

General scaling laws for modal characteristics—In a mechanical model of a system in which segments are represented as beams of circular sections, two length scales exist. The first one, l, fixes the scale of coordinates of these segments. A second one, d, which scales the diameters of these segments, is needed. In general, these two scales are not related because a given geometry of segments may correspond to several characteristic diameters d. Moreover, we can assume that material properties of the wood (density  $\rho$ , Young modulus E, and Poisson ratio  $\nu$ ) are constant within the tree and that their possible dependence on l and d can be neglected.

The relation between modal frequencies and these two scales may then be assessed by standard dimensional analysis. A modal frequency *f* depends on lengths, scaled by *l*, on masses per unit length, scaled by  $\rho d^2$ , and on the bending stiffness *k*, scaled by  $Ed^4$ , and is written as

$$f = F(l, \rho d^2, Ed^4)$$
<sup>(7)</sup>

But, because a physical law is by nature independent of units, this relation must be expressed in terms of dimensionless parameters (Niklas, 1994; Chakrabarti, 2002). Considering the respective dimensions of these four variables ( $f \sim \text{Time}^{-1}$ ,  $\rho d^2 \sim \text{Mass Length}^{-1}$ ,  $Ed^4 \sim \text{Mass Length}^3$  Time<sup>-2</sup>), the dimensional equation corresponding to Eq. 7 reads

$$T^{-1} = L^{a} \left( M \cdot L^{-1} \right)^{b} \left( M \cdot L^{3} \cdot T^{-2} \right)^{c} = L^{a-b+3c} \cdot M^{b+c} \cdot T^{-2c} , (8)$$

yielding c = 1/2, b = -1/2, a = -2.

All four variables may thus be combined in a dimensionless parameter:

$$fl^{2} \left(\rho d^{2}\right)^{1/2} \left(Ed^{4}\right)^{-1/2}, \qquad (9)$$

implying that the relation expressed in Eq. 7 is of the form

$$fl^2 \left(\rho d^2\right)^{1/2} \left(Ed^4\right)^{-1/2} = \text{ constant.}$$
 (10)

Or equivalently,

$$f \sim l^{-2} \left( \rho d^2 \right)^{-1/2} \left( E d^4 \right)^{1/2} \sim l^{-2} \cdot d \cdot \left( \frac{E}{\rho} \right)^{1/2} .$$
 (11)

Assuming that the modal mass *m* depends on the mass per unit length, scaled by  $\rho d^2$ , and the length, scaled by *l*, the dimensional analysis yields  $m \sim ld^2$ .

Similarly, the modal stiffness, k, defined from  $2\pi f = \sqrt{k/m}$ , scales as  $k \sim l^{-3}d^4$ .

In a given tree, where an allometric law relates length and diameter of each segment,  $d/l^{\beta}$  = constant, i.e.,  $d \sim l^{\beta}$ . Then,



Fig. 3. Examples of model fractal trees and parameters defining model trees. (A) Sympodial case,  $\alpha = 12.5^{\circ}$ , and (B) monopodial case,  $\alpha = 30^{\circ}$ ; (C) Branch slenderness coefficient,  $\beta$ ; (D) branching ratios,  $\lambda$  and  $\mu$ ; and (E) angle of branching connections,  $\alpha$ , illustrated here in the case of two lateral branches.

from Eq. 11, the frequencies of modes are expected to depend on the scale of length and of diameter as follows:

$$f \sim l^{\beta-2} \sim d^{\frac{\beta-2}{\beta}} \tag{12}$$

and similarly for the modal mass and stiffness:

$$m \sim l^{1+2\beta} \sim d^{\frac{1+2\beta}{\beta}}, k \sim l^{4\beta-3} \sim d^{\frac{4\beta-3}{\beta}}.$$
 (13)

**Relation between frequencies for a fractal tree**—Due to the symmetries of the fractal structure, groups of modes can be deduced and classified according to their modal deformation (Fig. 5). Some modes involve trunk deformation (group I in sympodial tree [Fig. 5A], group I,I in the monopodial tree [Fig. 5B]). Other modes involve mainly the bending deformation of the basal branch of all subsets of the same order (e.g., modes II for N = 2subsets, modes III for N = 3 subsets in the sympodial tree [Fig. 5A], mode II,I for [2,1] subsets and II,II for [2,2] subsets in the monopodial tree [Fig. 5B]) with negligible deformation of upstream segments. The deformation of upstream segments is strictly zero when the mode involves the symmetric deformation of two symmetric subsets as in Fig. 5. In the modes where symmetric subsets are deformed antisymmetrically, the lower part of the tree is slightly bent. But the elastic strain energy stored in this slight bending of the lower part of the tree is negligible compared to the energy stored in this same part due to modes with lower index. Consequently, scaling laws will be derived thereafter con-



Fig. 4. Identification of subsets in (A) the sympodial and (B) the monopodial model trees. Subsets are circled in black or gray.

sidering only modes of symmetric deformations of subsets. As the general biometrical laws apply to subsets, the hypothesis to be tested is that the scaling laws derived from symmetric modes will capture the dimensional behavior of the whole group of modes involving the deformation of all the subsets of a given scale.

For a sympodial, idealized tree (Fig. 5A), the modal deformations of three groups of symmetric modes (I, II, and III) can easily be deduced from one to the other. Because of the symmetry of the branching pattern, a mode of group II is associated with the deformation of a subset with a fixed part at its base. Therefore, the modal frequency of the group II of the whole tree can be considered as the frequency of a mode of group I of the subset if it is isolated. The dependence of  $f_{II}$  on  $l_{II}$  and  $d_{II}$  should therefore be identical to the dependence of  $f_{I}$  on  $l_{I}$  and  $d_{I}$ , hence yielding:

$$\frac{f_{\rm II}}{f_{\rm I}} = \frac{d_{\rm II} l_{\rm II}^{-2}}{d_{\rm I} l_{\rm I}^{-2}} = \left(\frac{d_{\rm II}}{d_{\rm I}}\right)^{\frac{\beta-2}{\beta}}.$$
 (14)

Using the relation between successive diameters in a fractal sympodial tree, Eq. 3 yields

$$\frac{f_{\rm II}}{f_{\rm I}} = \lambda^{\frac{\beta-2}{2\beta}} \,. \tag{15}$$

Similarly, the frequency of modes in the group of order N is given by

$$\frac{f_N}{f_I} = \lambda^{\frac{(N-1)(\beta-2)}{2\beta}}.$$
(16)

Therefore, all frequencies can be deduced from the first one, given the allometric parameter  $\beta$ , and the area reduction parameter at branching  $\lambda$ .

In the case of the model tree of monopodial type (Fig. 5B), the scale of a subset [N,P] depends on its central axis length and diameter,  $l_{N,P}$  and  $d_{N,P}$ . Introducing the relation between diameters and between lengths from Eq. 5 in Eq. 12, the corresponding frequency ratio can be defined as

$$\frac{f_{N,P}}{f_{I,I}} = \left[\lambda^{N-1}\mu^{P-1}\right]^{\frac{\beta-2}{2\beta}}.$$
(17)



Fig. 5. (A) Modes of groups I, II, and III of the sympodial model tree. (B) Modes [I,I], [II,I] and [II,II] of the monopodial model tree. ( $\bigoplus$ ) and ( $\bigcirc$ ) represent the centers of bending energy and kinetic energy respectively.

Through similar arguments, the modal mass of the groups of order N and [N,P] for a sympodial tree and a monopodial tree read, respectively, as

$$\frac{m_N}{m_1} = \lambda^{\frac{(N-1)(1+2\beta)}{2\beta}}, \ \frac{m_{N,P}}{m_{LI}} = \left[\lambda^{N-1}\mu^{P-1}\right]^{\frac{1+2\beta}{2\beta}}.$$
 (18)

Center of bending energy and center of kinetic energy—Comparing the spatial distributions of modal displacements  $\underline{\Phi}_j$  along the tree is not straightforward. To summarize the localization of displacement associated with a given mode, one may define two geometrical points: the center of kinetic energy of the mode and the center of elastic bending strain energy of the mode.

The modal center of kinetic energy is located at an elevation  $z_{\rm K}$  such that

$$z_{\kappa} \cdot \int_{\Omega} \rho S \underline{\Phi} \cdot \underline{\Phi} \, d\Omega = \int_{\Omega} \rho S \underline{\Phi} \cdot \underline{\Phi} \cdot z \, d\Omega \, . \tag{19}$$

Similarly, the modal center of bending strain energy,  $z_{\rm B}$ , is defined by a vertical position

$$z_{B} \cdot \int_{\Omega} EI \underline{\gamma} \cdot \underline{\gamma} d\Omega = \int_{\Omega} EI \underline{\gamma} \cdot \underline{\gamma} \cdot z \, d\Omega, \qquad (20)$$

where  $\underline{\gamma}$  is the curvature associated with the modal displacement  $\underline{\Phi}$  and where integration is performed over the whole tree ( $\Omega$ ).

These two parameters scale, respectively, as  $z_{\rm K} \sim l \sim d^{1/\beta}$  and  $z_{\rm B} \sim l \sim d^{1/\beta}$ . Exploiting again the assumption of reiterated trees, the position of the centers for a mode [N,P] reads

$$z_{N,P}^{K} = z_{N-l,P} + \mu^{(P-l)/2\beta} \left( \lambda^{1/2\beta} \cos \alpha \right)^{N-l} z_{l,l}^{K} , \qquad (21)$$

$$z_{N,P}^{\rm B} = z_{N-1,P} + \mu^{(P-1)/2\beta} \left(\lambda^{1/2\beta} \cos \alpha\right)^{N-1} z_{\rm I,I}^{\rm B} , \qquad (22)$$

where  $z_{N,P}$  is the elevation of the branching bifurcation (see Appendix 1 for the geometrical derivation).

TABLE 3. Slenderness coefficients  $\beta$ , lateral and axial branching ratios  $\mu$  and  $\lambda$ , respectively, and branching angles  $\alpha$  used to illustrate the two idealized trees. A slenderness coefficient equal to 3/2 has frequently been used in the literature (see McMahon and Kronauer, 1976; Moulia and Fournier-Djimbi, 1997), and branching ratios were chosen to follow Da Vinci's surface conservation law (Prusinkiewicz and Lindenmayer, 1996).

Idealized tree	β	λ	μ	α
Sympodial	3/2	1/2	0	20°
Monopodial	3/2	1/6	2/3	30°

Numerical illustration of scaling laws on idealized fractal trees—The scaling laws derived in the preceding section were applied to two particular occurrences of the idealized trees, one sympodial and one monopodial. The allometric and geometrical parameters defining their geometry are given in Table 3.

**Modal frequencies**—Instantiating the values of the allometric and geometrical parameters in Eqs. 16 and 17 using Table 3, the series of frequencies for the sympodial [N] and monopodial [N,P] idealized trees read, respectively, as

$$\frac{f_N}{f_1} = 2^{\frac{N-1}{6}}, \ \frac{f_{N,P}}{f_{1,1}} = 6^{\frac{N-1}{6}} \left(\frac{3}{2}\right)^{\frac{P-1}{6}}.$$
 (23)

These series of frequencies are illustrated in Fig. 6A and 6B. In the case of the sympodial [*N*] idealized tree in Fig. 6A, frequencies of group of modes are seen to increase progressively. Conversely, for the monopodial [*N*,*P*] idealized tree in Fig. 6B, sets of frequencies corresponding to the double-indexed branching pattern can be observed. For a given value of *N* (i.e., for sequential subtrees along a given monopodial axis, e.g., N = 2), frequencies increased progressively with *P*. For a given *P* (i.e., for series of lateral subtrees, e.g., P = 1), frequencies also increased with *N*. From Eq. 23, it appears that  $f_{N,P}$  values from different groups intercalate, e.g.,  $f_{2,5} < f_{3,1} < f_{2,6}$ . In the two cases, however, the organization of frequencies is clearly dependent on the architecture, through the parameters  $\lambda$  and  $\mu$  of area reduction at branching, and on the slenderness allometry, through the parameter  $\beta$ .

By the same token, the modal mass reads

$$\frac{m_N}{m_1} = 2^{-\frac{4}{3}(N-1)}, \ \frac{m_{N,P}}{m_{1,1}} = 6^{-\frac{4}{3}(N-1)} \frac{3^{-\frac{4}{3}(P-1)}}{2}.$$
 (24)

*Localization of modal mass and modal stiffness*—The localization in height of the centers of bending energy and the centers of kinetic energy for the modes in each idealized tree were determined from Eqs. 21 and 22 using the values for parameters from Table 3, then plotted as a function of the corresponding modal frequency (Fig. 6C, D). In both trees, the distance between the center of bending energy and the center of kinetic energy is a decreasing function of the modal frequency. Modes thus tended to be more local as their modal frequency increased.

In the sympodial tree in Fig. 6C, modes localized higher in the tree as the modal frequency increased. In the monopodial tree in Fig. 6D, the mixed axial and lateral branching pattern



Fig. 6. Vibration modes of the sympodial and monopodial idealized trees. Modal frequencies, relative to the first one, as a function of the index of the corresponding subsets in the case of the (A) sympodial and (C) monopodial trees, respectively. Vertical position of the centers of bending energy  $(\bullet \bullet)$  and of the centers of kinetic energy  $(\bigcirc \circ \bigcirc)$  as a function of the frequency, respectively in the (C) sympodial and (D) monopodial trees.

resulted in the centers of bending energy and the centers of kinetic energy being scattered all along the trunk. Modes related to group of subtrees localized at a constant number of lateral branching (fixed N, changing P) were found to be localized higher in the tree as the modal frequency increased. But the intercalation of modes both in terms of spatial localization and frequency is obvious. The modal analysis of idealized trees thus suggests that the localization of modes in the structure depends of the tree architecture via its branching pattern (sympodial vs. monopdial).

# TEST OF THE SCALING LAWS ON MODELS OF REAL TREES

The scaling laws for modal frequencies (Eqs. 16 and 17) and localization of the centers of kinetic and bending energy (Eqs. 21 and 22) were then applied to the two "real" tree models (i.e., the sympodial walnut and the monopodial pine, Fig. 1). The results were then compared with the modal characteristics computed using 3D finite element models (see section *Modal analysis of a walnut and a pine tree*; Fig. 2).

**Determination of biometrical parameters for the scaling** *law*—Orthogonal regressions (SAS version 9.1, procedure Insight Fit) were applied to estimate slenderness allometric coefficients,  $\beta$ , and branching ratios,  $\lambda$  and  $\mu$ , from the MTG tree databases of the walnut and pine geometries. Slenderness coefficients,  $\beta$ , were estimated from the linear orthogonal regression  $\log(d) = \beta \log(l) + k$  (Niklas, 1994). Lateral branching ratios,  $\lambda$ , were estimated from linear orthogonal regression  $(d_N)^2 = \lambda (d_{N-1})^2$ and axial branching ratio,  $\mu$  (in monopodial tree), from  $(d_{1,P})^2 = \mu (d_{1,P-1})^2$ . Regression coefficients, root mean square errors, coefficients of determination, and 90% confidence intervals (Dagnelie, 2006) are reported in Table 4.

Case of the walnut tree—Parameters were estimated using data from the first three order branches with diameters and lengths larger than 1 cm and 1 m, respectively (Fig. 7A, B). A highly significant, tight allometric relation was found between *l* and *d* (Fig. 7A), capturing 87% of the total variance, with only two outlying points corresponding to the trunk and to a cut branch. The relation between  $d_{N+1}$  and  $d_N$  was a little bit more biased, but still a highly significant  $\lambda$  could be defined. The sympodial branching pattern of the walnut implies an axial branching ratio  $\mu$  equal to 0. The angle of branching has been found to vary between 0° and 40°, a mean angle of branching,  $\alpha = 20^\circ$ , was retained.

*Case of the pine tree*—Parameters were estimated using data from the first two order branches (Fig. 7C–E). The slenderness  $\beta$  (Fig. 7C) and the longitudinal area reduction  $\mu$  (Fig. 7E) were statistically significant. The axial branching ratio  $\lambda$  (Fig. 7D) was also significantly different from zero, but the relation between the cross-sectional area of the parent segment and of lateral branches was very poor [the slope of the regression model with the intercept is not significantly different from zero with probability p(>F) = 0.13]. The mean angle of branching was  $\alpha = 30^{\circ}$ .

Application of scaling laws—Using the parameters corresponding to the two real trees (Table 4), we applied the scaling laws derived in the *Theoretical considerations* section to the case of each real tree, then compared the results to the modal characteristics computed using the 3D finite element models

TABLE 4. Slenderness coefficients  $\beta$ , lateral and axial branching ratios  $\mu$ and  $\lambda$ , respectively, and branching angles  $\alpha$  estimated from walnut and pine tree geometries (orthogonal regression coefficients, confidence intervals at 90% level [CI), coefficients of determination [ $R^2$ ], and root mean square of the residual errors [ $\sigma_{res}$ ]). Tree geometries are from Sinoquet et al. (1997) and Sellier and Fourcaud (2005), respectively. Note that for  $\lambda$  and  $\mu$ , the regressions were obtained with no intercept so that the  $R^2$  value cannot be compared directly with that related to a standard linear regression, and significance levels are to be related to a null hypothesis where the dependant variable is equal to zero (for a more detailed discussion, see Freund and Littel, 1991).

Tree	β	λ	μ	α
Walnut	1.37	0.25	0	20°
CI	1.25<β<1.49	0.22<λ<0.29		
$R^2$	0.87	0.74		
$\sigma_{res}$	0.2	0.008		
Pine	1.38	0.038	0.74	30°
CI	1.25<β<1.52	0.032<λ<0.044	0.71<µ<0.79	
$R^2$	0.85	0.59	0.97	
$\sigma_{res}$	0.086	11.92	5.33	

defined in the section *Modal analysis of a walnut and a pine tree* (Fig. 8).

*Case of the walnut*—Figure 8A displays the frequencies of the three groups of modes (I, II, and III, see Fig. 2A, C and section *Modal analysis of a walnut and a pine tree*) estimated using the 3D FEM vs. the group number *N*. On the same graph, the dotted lines show the frequencies predicted using Eq. 16 with the 90% confidence range of parameters as in Table 4. The same comparison is held for the values for the height of the bending and kinetic energy centers (using Eqs. 21 and 22), in Fig. 8B and C. Though the geometry of the real walnut is much more complex than that of the idealized fractal sympodial tree, the prediction using the scaling laws quite closely brackets the range of modal characteristics of the FEM model. The positions of the centers of bending and kinetic energy are particularly well estimated, with the exception of two points.

*Case of the pine*—As emphasized previously, the case of the monopodial tree is much more complex, due to the double index dependence related to the two kinds of branching, axial and lateral. We will focus on the characteristics of the modes labeled II in the section *Modal analysis of a walnut and a pine tree* (see Fig. 2B, D), corresponding to the motion of lateral subsets. In terms of the double index reference, these are modes involving [2,*P*] subsets. The scatter of modal characteristics is higher in the pine tree than in the walnut tree (Fig. 8D–F). The scaling law derived from idealized fractal monopodial tree still brackets from 60 to 75% of the outputs of the FEM model. But half of the confidence intervals from the scaling laws does not contain any output of the FEM model.

Moreover, modes of group I' cannot be predicted, using the scaling laws applied to subsets of the tree because the corresponding deformation cannot be defined as the deformation of a subset. For instance, the frequencies of I' are in the order of 2.4 Hz for the pine tree, while those corresponding to subset [1,2] are about 1.16 Hz.

#### DISCUSSION

An approach of the complex oscillatory behavior of trees through modal and scaling analyses-Despite its standard use in mechanical engineering (Gerardin and Rixen, 1994), modal analysis has only been used in a few studies to analyze the dynamic characteristics of trees in relation to their 3D architecture (Fournier et al., 1993; Moore and Maguire, 2005; Sellier et al., 2006). Compared to the analysis of the vibrational behavior of separated elements of the tree such as trunk, branches (e.g., Mc-Mahon and Kronauer, 1976; Spatz et al, 2007), modal analysis takes into account the additional fact that as a whole, the tree is a mechanical structure. As a consequence, elastic strain energy is almost instantaneously distributed over the whole tree structure, and vibrations involving the whole tree can occur. Such vibrations can involve several parts of the tree together and can thus be more complex than that of isolated parts. Indeed, models connecting a large number of small damped oscillators connected together-each oscillator modeling a branch subsystem-have been proposed recently (James et al., 2006). However, such models are not parsimonious, and their behavior may be difficult to analyze quantitatively. Under the classical assumption



Fig. 7. Biometrical relations in the walnut and the pine trees. (A, C) Allometric relations between length and diameter of branches in (A) the walnut and (C) the pine tree. (—) Orthogonal regression  $D \sim L^{\beta}$ , with  $\beta = 1.37$  (A) and  $\beta = 1.38$  (C). (B, D) Branches cross-sectional areas before and after a lateral branching in (B) the walnut and (D) the pine tree. (—) Orthogonal regression  $(d_N)^2 = \lambda(d_{N-1})^2$ , with (B)  $\lambda = 0.25$  and (D)  $\lambda = 0.038$ . (E) Cross-sectional areas of the trunk before and after a branching in the case of the monopodial pine tree. (—) Orthogonal regression  $(d_{1,P})^2 = \mu(d_{1,P-1})^2$ ,  $\mu = 0.74$ . Gray areas in the graphs correspond to the 90% confidence level (see Table 4). ( $\bigcirc$ ) measured data from Sinoquet et al. (1997) and Sellier and Fourcaud (2005).

of relatively small displacements, this complex behavior can be analyzed as the superposition of a (large) set of much simpler free-vibration modes with characteristic modal frequency and modal deformation and modal inertial mass. These modes are mechanical attributes of the whole tree structure, its intrinsic dynamical characteristics independent of any particular load. They characterize the vibrational excitability of a given tree. A given load, say, a turbulent wind with specific frequencies and spatial distributions, will excite only the modes with compatible frequencies and modal shapes. Becausee universal wind spectra have been obtained showing that mechanically active wind loads in trees typically occur in the 0-10 Hz band (Stull, 1988), and the drag mainly applies to the leaf-bearing terminal segments, it is possible to focus on the subset of modes in this frequency band and with modal deformations involving significant displacements of the branch tips, as done in this study.

Because they are based on very detailed and extensive architectural and mechanical data, modal analyses can also provide guidelines for defining simpler models, as illustrated through scaling analysis (and discussed later).

Before discussing the major insights on tree mechanics obtained through this method, we should discuss its limitations. In its strict definition, modal analysis only deals with small displacements, as is the case for trees submitted to moderate winds. But with large winds, large displacements occur, and geometric nonlinearities such as strong streamlining or branch collisions have to be taken into account (de Langre, 2008). Such nonlinear behaviors are still a very active area of research in the mechanics of fluid–structure interactions (de Langre and Axisa, 2004). However, some numerical methods for predicting flow-induced vibrations in nonlinear cases still involve modal analysis (Axisa et al., 1988), meaning that modal analysis is still a robust starting point for the analysis of the dynamic excitability under strong winds.

**Branches are important to the tree dynamics**—The detailed FEM modal analysis of entirely digitized trees with a very large contrast in their mechanical architecture and modal behavior confirmed and extended previous reports: modes involving significant branch deformation could have frequencies very close to—and even rank in between—modes deforming mainly the trunk (Fournier et al., 1993; Moore and Maguire, 2005; Sellier and Fourcaud, 2005; James et al., 2006; Sellier et al., 2006). As many as 25 modes could be found with frequencies between one and two times the most basal mode involving the trunk and



Fig. 8. Comparison of the prediction from the scaling laws with the finite element results on the true tree geometry: (A) frequencies, (B) centers of kinetic energy  $(\bigcirc)$ , (C) centers of bending energy (O) of modes of the walnut tree, and (D) frequencies, (E) centers of kinetic energy  $(\bigcirc)$ , (F) centers of bending energy (O) of modes [2,*P*] of the pine tree.  $(\bigcirc$  and O) are results from the FEM on true tree geometries; gray areas are predictions from the scaling laws, Eqs. 12, 13, 18, and 19, using idealized tree models.

with a typical modal spacing as low as 0.1 Hz, consistent with the results of James et al. (2006) and Spatz et al. (2007).

Although these modes are complex, they can be classified using their frequencies and modal deformation. In this study, no modes involving an inflection in their modal deformation, I' (i.e., second modes of the trunk, I' in our labeling), could be observed within the 25 first modes in the walnut tree, whereas for the pine tree, I' only rank 17th and 18th (i.e., 14 modes II involving first order branches ranked in between the fundamental mode of the trunk I and its I' mode). This is quite in contrast with claims from the literature, mostly about adult conifer trees, on which only first I and second I' bending modes of the trunk have been reported (e.g., White et al., 1976; Mayer, 1987; Hassinen et al., 1998; Kerzenmacher and Gardiner, 1998). However, in these studies only the strains in the trunk were measured or modeled; therefore, only modes involving significant deformation of the trunk could be recorded. Indeed, when analyzing the vibration modes of an adult maritime pine (Pinus pinaster) using finite element analysis, Fournier et al. (1993) also found that modes concentrated in frequency and that modes of the second group ranked between the first and the second bending modes of the trunk. Branch deformation is thus an important aspect of trees dynamics whatever the architectures and size (see also Fournier et al., 1993; Sellier and Fourcaud, 2005; Moore and Maguire, 2005; Spatz et al., 2007).

Scaling laws can be defined—As hypothesized, and despite the aforementioned complexity of the 3D architecture and modal structure of real trees, scaling laws based on the assumptions of (1) idealized allometric fractal trees and (2) symmetric modes of branches, are able to explain a large part of the spatial and temporal characteristics of the modes involving the successive orders of branches relative to the first mode deforming the trunk (Fig. 8). The distribution of modal characteristics was particularly well predicted in the case of the tree with highest modal density and where the branch modes are the most salient, i.e., the sympodial walnut tree. Moreover, in both trees, scaling laws were able to predict correctly the relative ranking of the different types of modes (Fig. 8A), validating the hypothesis that the dimensional analysis of the symmetric modes of idealized fractal trees can capture a large part of the scaling of modal settings in real trees (frequencies and localization of bending and kinetic energy), although more advanced analysis may be conducted for monopodial trees.

Such scaling law has two major uses. From a methodological and practical point of view, the overall dynamics of a complex tree can be reduced to (1) the measurement or estimation of the most basal mode, which is the easiest to characterize and has been studied or modeled in numerous studies (e.g., Gardiner, 1992; Spatz and Zebrowski, 2001); (2) a standard description of the branching mode, i.e., sympodial vs monopodial mode (Barthelemy and Caraglio, 2007); and (3) three simple biometrical parameters that have been measured in many biomechanical and ecological studies (e.g., McMahon and Kronauer, 1976). This compact description of the overall dynamics of a complex tree is to be compared with the extensive work on detailed 3D digitizing (Sinoquet and Rivet, 1997) followed by complete modal analysis. It would be interesting though to test these scaling laws in trees of other species and other sizes, so that the accuracy in the prevision through these simplified laws could be assessed more completely.

From a more fundamental perspective, these scaling laws give direct insights into the significance of tree architecture and geometry for its modal behavior and thus to its excitability to wind and its possible mechanoperceptive control, as discussed next.

*Effects of architecture and biometrical characteristics on modal content: Tuning and compartmentalization*—Both area reduction ratios and the slenderness coefficient affect the relative frequency and the location of modes (see Eqs. 16 and 21), whereas the branching angle only affects the spatial localization of the modes. In all the cases, the effects of the parameters are nonlinear and mixed.

For example, in the case of the sympodial tree, variations in  $\lambda$  and  $\beta$  both influence the value of the frequency of a given group of modes. In the natural ranges estimated from our data (Table 4), a decreasing  $\lambda$  (i.e., a higher reduction in the crosssectional area at branching) increases the relative frequency of a given group of mode. A decreasing  $\beta$  (i.e., a tree with higher slenderness) also increases the relative frequency of a given group of mode. It should be noted here that both  $\lambda$  and  $\beta$  have been reported to be under similar control of wind mechanoperception through thigmomorphogenetic secondary growth responses (Telewski, 2006; Watt et al., 2005). Thus, thigmomorphogenetic responses may be able to tune the multimodal frequencies range of the whole tree, whatever the genetic specific traits of its architecture. It is, moreover, striking that two trees as geometrically different as an old walnut tree and a young pine tree could present fundamental modes in the range of 1–1.5 Hz with a large number of their branch modes in the 2.5-3 Hz band, consistent with many reports in the literature (B. Roman, Ecole Superieure de Physique et Chimie Industrielles de Paris (ESPCI), personal communication). This similarity in modal frequencies may point toward some modal tuning controlling the biometrical parameters of the trees (and thus of the scaling laws). The effectiveness of this acclimation process remains to be studied, but the current study provides useful tools to do so.

Last but not least, a very unexpected salient conclusion that is captured by the scaling laws is that branching and secondary growth are tuned so that the reduction of cross sectional area at branching points ( $\lambda$  and eventually  $\mu$  in monopods), induce a clear structural compartmentalization of the modal spatial distribution and a scaling similarity between successive modes. Whatever the architecture, modes have been found to be more and more local as their modal frequency increases. And both their modal frequencies and modal mass are scaled recursively to that of the first mode of the whole tree. These compartmentalization and scaling similarity are not mechanical necessities. As previously stated, the elastic strain energy underlying modal behavior is distributed almost instantaneously over the whole structure; so that structural compartmentalization and scaling similarities result from a specific biomechanical design of the trees during their architectural development. This specific biomechanical design of the trees requires a consistent tuning of both (1) branching symmetries within the architecture and (2) the secondary growth balance between parent and axillary branches (as reported by Watt et al., 2005. Moreover, this consistent tuning should be efficient in highly different architectural patterns (monopods vs. sympods) and is thus very likely to have resulted from adaptation.

These structural compartmentalization and scaling similarities are probably important in making the overall biological control over the multimodal dynamics of the tree more tractable, whatever its size. Assessing how this gain in control may be beneficial for species adaptation and individual acclimation to wind should be the matter of specific future investigations. Indeed, scaling laws give only approximations, and clear differences were found in the modal spatial patterning between monopodial and sympodial trees. Moreover, trees in a forest stand may have more significant shoot abrasion or crown asymmetry. At last, competition for resources and photomorphogenetic responses to shade may interact with the mechanoperceptive acclimation to wind (Fournier et al., 2005). But some elements affecting the biomechanical significance of multimodal scaling of trees to the response to wind load can already be directly discussed from our results.

Significance of multimodal dynamics and scaling laws to the responses of trees to wind—Wind excites trees through the drag force applied to the constitutive elements of the trees, branches, and possibly leaves or needles. From surface area considerations, most of the drag thus occurs at in the distal, possibly leafy, segments of the tree. All the modes in this study have a common characteristic: their larger displacements sits on the extremities of the tree. Therefore, they should reciprocally all be excited by a force applied at the extremities, such as the wind-drag force (Gerardin and Rixen, 1994). Moreover, because wind spectra usually have a large frequency band (Raupach et al., 1996) overlying most of the modal frequencies of the considered modes, several modes may be excited directly by highly fluctuating winds. As a consequence, the two types of tree architectures studied here should have a dense multimodal response to gusts involving a very significant contribution of branches of all the orders.

James et al. (2006) and Spatz et al. (2007) have argued that dynamics including branch deformation with close modal frequencies could be beneficial to the tree by enhancing aerodynamic dissipation through a mechanism called multiple resonance damping or multiple mass damping. A prerequisite for this mechanism to occur is a multimodal behavior of the tree, with high modal density in the frequency range and significant branch deformations, exactly what was found here for trees with contrasting architectures. This dense multimodal dynamics, a consequence of the branched structure, can then be interpreted as a strategy to prevent the trunk from bending excessively until the rupture. It should be noted, however, that the high modal density observed in our two trees did not reach the almost perfect tuning in the modal frequencies of branches larger than 0.5 m reported by Spatz et al. (2007) for a (monopodial) Pseudostuga menziesii tree. A similar result in our study would have meant either  $\lambda$  and  $\mu = 1$  or  $\beta = 2$ , which can be rejected statistically in our two trees (Table 4). However in our study, possible variations in the longitudinal Young's modulus along the branch (that have been reported by Spatz) were not considered. It would be interesting to further investigate if the distribution

1536

of wood stiffness along branches could be controlled to further enhance the modal density.

Modes can also be characterized in terms of the localization of their bending centers, i.e., the zone of significant bending of the tree. The first bending modes result in deformation on the trunk, while higher frequency modes result in deformations localized in higher orders of branching in the tree, with a different spatial pattern in monopodial and sympodial trees. This compartmentalization may have consequences for windbreaks. Indeed, some studies have reported branch breaks occurring before trunk or roots breaks, with obvious benefit for wind resistance (Cullen, 2002; Watt et al., 2005). Such mechanical modal compartmentalization of the wind hazards would then present analogies with compartmentalization strategies in front of hydric stresses (Meinzer et al., 2001) and perhaps pathogens (Shigo, 1986). But this mechanical modal compartmentalization of the wind hazards remains to be confirmed experimentally over a larger range of situations and species.

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#### Appendix 1.

Because the derivation of scaling laws for the bending and kinetic energy centers are similar, only the case of the bending energy center is detailed here.

First is considered the case of the sympodial tree. The mode associated with the subgroups of the group *N* is related to  $2^{N-1}$  subsets of the tree, deforming like the first mode, and the rest of the tree is supposed to be at rest. The bending energy center of a mode of group *N* is assessed from all the centers related to each subset. Subsets of the group *N* are grouped by two and related to a subset of the group N - 1. The relation between these centers is derived using the angle of branching,  $\alpha$ , the branching ratio,  $\lambda$ , and the elevation of the branching bifurcations,  $z_N$ , see sketch on Fig. 9A. It reads

$$z_{N}^{\rm B} - z_{N-1} = \lambda^{1/2\beta} \cos \alpha \left( z_{N-1}^{\rm B} - z_{N-2} \right), \qquad (24)$$

so that 
$$z_N^{\rm B} = z_{N-1} + (\lambda^{1/2\beta} \cos \alpha)^{N-1} z_1^{\rm B}$$
. (25)

Using the same process, in the case of the monopodial tree, see the sketch in Fig. 9B, it is found that

$$z_{N,P}^{\rm B} - z_{N-1,P} = \mu^{(P-1)/2\beta} \left( z_{N,1}^{\rm B} - z_{N-1,1} \right), \tag{26}$$

this gives, as Eq. 21 is still valid in the case of the monopodial tree

$$z_{N,P}^{\rm B} = z_{N-1,P} + \mu^{(P-1)/2\beta} \left(\lambda^{1/2\beta} \cos \alpha\right)^{N-1} z_{1,1}^{\rm B}.$$
 (27)

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Fig. 9. Sketches illustrating the positions of bending centers of several modes in (A) the sympodial tree and (B) the monopodial tree.