

Effects of Wind on Plants

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Abstract

This review surveys the large variety of mechanical interactions between wind and plants, from plant organs to plant systems. These interactions range from leaf flutter to uprooting and seed dispersal, as well as indirect effects on photosynthesis or insect communication. I first estimate the relevant nondimensional parameters and then discuss turbulence, plant dynamics, and the mechanisms of interaction in this context. Some common features are identified and analyzed in relation to the wind engineering of manmade structures. Strong coupling between plants and wind exists, in which the plant motion modifies the wind dynamics. I also present some related biological issues in which the relation between plant life and wind environment is emphasized.

*[V]oici la lourde nappe/Et la profonde boule et l'océan des blés
[Like a sheet/The deep swell on a sea of wheat]
Charles Péguy (1873–1914)*

1. INTRODUCTION

Plants and wind are two essential elements of the human environment. Plant motion is a visual manifestation of the reality of wind, as is illustrated in the poetry of all cultures. It is also used to scale wind velocity, as stated in the Beaufort scale: At force 2, “leaves rustle.” Plant windthrow has been a concern for humankind over the ages because of its impact on food availability and habitat. Plant growth is affected by wind, as can be seen in flag trees. In fact wind-plant interactions cover a much larger range of mechanisms than those commonly experienced at a human scale, from thermal effects on a leaf to long-range dispersal of seeds. The aim of this review is to provide the fundamental concepts that allow the treatment of a variety of phenomena and models. This first section explores a variety of interactions that may exist. Section 2 then applies dimensional analysis to obtain and estimate the relevant nondimensional parameters pertaining to the interaction. In Sections 3 and 4 the dynamics of wind and plants are analyzed separately. Section 5 proposes a framework to model the response of plants to wind loading. Fully coupled cases in which the motion of the plant modifies the wind dynamics are examined in Section 6. Finally, Section 7 focuses on biological effects resulting from these interactions.

1.1. The Extent of the Literature

Some of the earliest work on the subject goes back to the description of honamis (Inoue 1955), which refers to traveling waves on wheat. Since then, abundant literature has been produced on the subject of wind and plants. The list of references provided at the end of this review only covers a small fraction of the papers on the subject. I have deliberately chosen to restrict the bibliography to recent work and older but essential articles.

Previous surveys in this series (Raupach & Thom 1981, Finnigan 2000) focused on the effect of vegetation on wind, in particular on its turbulent features, rather than on the reverse. This point of view was fully justified because of the need to gain precise knowledge about turbulence near and inside plant canopies, as all biological and ecological mechanisms are influenced by the structure of this turbulence. Many recent reviews exist on specific aspects of the direct or indirect effects of wind on plants. They address the topics of crop dynamics (Berry et al. 2004, Cleugh et al. 1998) and tree dynamics (Gardiner 1995, Moore & Maguire 2004) under wind, seed dispersal by wind (Kuparinen 2006), the ecological effects of wind (Ennos 1997), the effect of wind on plant growth (Mouliat et al. 2006, Telewski 2006), and plant evolution under wind constraint (Niklas 1998). More general concepts may be found in the earlier reviews by Mayer (1987) and Van Gardingen & Grace (1991), as well as in an essential book on plant biomechanics by Niklas (1992) or in books specifically devoted to trees (Mattheck 1998). Several conference series are also dedicated, wholly or in part, to the subject, such as the Wind and Trees series (see Coust & Grace 1995, Mitchell 2007, Ruck et al. 2003), as well as the Plant Biomechanics series (Salmen 2006, Telewski et al. 2003). When looking at the journal titles in the Literature Cited below, one clearly sees that the scientific community working on the effects of wind on plants is quite dispersed, from botany to meteorology and from forestry

to image production and entomology. This dispersion certainly does not help in the understanding of coupled phenomena, but it suggests that unsuspected scientific challenges exist at the intersection between these disciplines.

1.2. The Variety of Plants and Ecological Systems

Systems of interest range far beyond the simplest fluttering leaf, which is the most common experience of wind effects on plants. This is exemplified in the types of plant systems considered in recent papers. Trees under wind are analyzed either as individuals (e.g., Sellier et al. 2006) or as canopies (Rudnicki et al. 2001). Investigators have also studied the effect of wind on their branches (Watt et al. 2005), leaves (Roden 2003), seeds (Nathan et al. 2002), or, indirectly, the structure of roots (Tamasi et al. 2005). Similarly, crops vary from wheat (Berry et al. 2003) to corn (Flesch & Grant 1991), alfalfa (Doaré et al. 2004), rice (Oladokun & Ennos 2006), barley (Berry et al. 2006), sunflower (Smith & Ennos 2003), and reed (Speck 2003). Noncrop plants include daffodils (Etnier & Vogel 2000). Ecological systems considered in most existing studies correspond to temperate climates although they constitute only a small proportion of the existing diversity on Earth. The rainforest (Clair et al. 2003) and to a much lesser degree dry African systems (Stigter et al. 2002) are progressively being examined.

1.3. The Variety of Motivations

The most important motivation for the analysis of wind effects on plants is certainly the optimization of biomass production for food, material, or energy production. Forestry applications are central, such as windthrow, which refers to tree uprooting, and the evolution of populations (Gardiner & Quine 2000). Note that recent large-scale storms over forests in Europe, such as those in 1999, resulted in economic losses equivalent to a yearly yield. Agricultural issues involve the risk of lodging, the permanent windthrow of crop, which causes losses of the order of 70% of the yield (Berry et al. 2004). Researchers are also analyzing in detail other aspects, such as the dispersion of seeds, spores, and pollens (Nathan et al. 2002).

More fundamental biological issues have created the need for data and models of wind-plant mechanical interactions to help understand the effects of wind on the essential functions in a plant. Wind directly influences photosynthesis and gaseous exchanges at the leaf scale as well as leaf temperature (Stokes et al. 2006). Wind also modifies light shedding inside a plant canopy through the displacement or flutter of the outer leaves, thereby modifying photosynthesis (Roden 2003). Wind controls the deposition of particles on leaves, leading to abrasion or chemical effects. Wind-induced motion of plants affects the behavior of borne insects and their communication (Cocroft & Rodriguez 2005). More complex but essential biological mechanisms relate wind-induced strains and motion to growth and posturing (Moulija et al. 2006), adaptation, and long-term evolution (Niklas 1998).

The industry of video games and animated-film production has recently provided a strong motivation for the development of models of wind-induced motion of plants

(Diener et al. 2006). The proper rendering of outdoor scenes under wind is essential to creating a sense of reality and plays a large role in the quality of the product. Moreover, real-time animations in video games require that the dynamics is reproduced in its essential features using the simplest possible models to save computational time. In this industry, the plants of interest originate from all type of vegetations, from urban trees to rainforest or even imaginary landscapes.

These three types of motivations—namely biomass production, biological science, and image production—certainly differ. They nevertheless share the urgent need for quantitative data and models of the effects of wind on plants.

1.4. The Variety of Scales

According to the examples mentioned above, the range of physical parameters is indeed quite large (**Figure 1**). The length scales of interest start at 10^{-6} m, which is the size of small airborne pollen. Seeds scale at 10^{-3} m, whereas plant organs such as leaves, flowers, branches, and plants themselves range from 10^{-2} m (small leaves) to 10^2 m (the largest trees). Finally the size of populations commonly scale at 10^3 m. Hence a range of 9 orders of magnitude, from 10^{-6} to 10^3 m, is not uncommon for a given plant system. Similarly, the smallest time scales are approximately 10^{-2} s for photosynthesis responses and leaf flutter. The period of plant and branch swaying is typically from 10^{-1} to 10 s. Leaves fall in approximately 10 s, whereas seed transport may last 10^3 s. Larger time scales include growth (from 10^2 to 10^5 s), life cycle (from 10^7 to 10^{10} s), and evolutionary scales (up to 10^{15} s). This defines a range of 17 orders of magnitude. A given plant experiences most of these time and length scales during its lifetime: Its size changes, seasons modify its architecture, and biological materials and subcomponents grow or are removed.

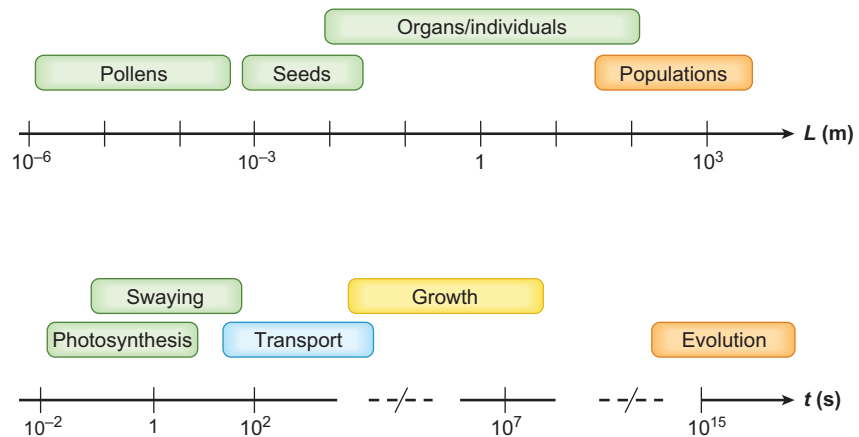


Figure 1

Typical length (*top panel*) and time (*bottom panel*) scales in the interaction of wind and plants.

2. NONDIMENSIONAL PARAMETERS

In view of the immense variety of interactions, a preliminary dimensional analysis appears necessary. In addition to the parameters related to wind and to plant dynamics considered separately, there exist nondimensional parameters pertaining to the interactions. They may be derived from elementary dimensional analysis. For a given reference wind velocity U and density ρ_F , using the modulus of elasticity E and density ρ_S for the solid, two nondimensional parameters, arise

$$\mathcal{M} = \frac{\rho_F}{\rho_S}, \quad C_Y = \frac{\rho_F U^2}{E}, \quad (1)$$

which are the mass ratio and the Cauchy number, respectively, commonly used in the mechanics of fluid-structure interactions (Blevins 1990, Chakrabarti 2002, de Langre 2002, Dowell 1999, Paidoussis 2003).

The mass ratio is of the order of 10^{-3} for all cases of wind-plant interactions, as the density of vegetal material is typically 10^3 times higher than air. As \mathcal{M} scales the added mass caused by the fluid motion resulting from the solid motion, this inertial effect is usually negligible, except for some plane structures, such as leaves in which geometric effects play a central role (Blevins 1990).

The Cauchy number C_Y , which characterizes the deformation of an elastic solid under the effect of flow, is defined as the ratio of the dynamic pressure and the modulus of elasticity. For a modulus of 10^8 Pa, corresponding to soft living vegetal tissues, and for a wind velocity of 10 m s^{-1} , corresponding to very high wind conditions at a plant level, the Cauchy number is of order 10^{-6} . As this implies that no deformation can be expected in the plant, the Cauchy number defined in Equation 1 is clearly inappropriate, common knowledge showing strong deflections in plants. In fact the slenderness of plants needs to be taken into account in the deformability: Most vegetal structures are slender in order to access light and carbon. A slenderness number S therefore needs to be defined as the ratio of the maximum to minimum cross-sectional dimensions of the system L and ℓ . The deformation of a slender beam in bending under a transverse surface load being proportional to S^3 (Niklas 1992), the convenient set of dimensionless numbers now reads

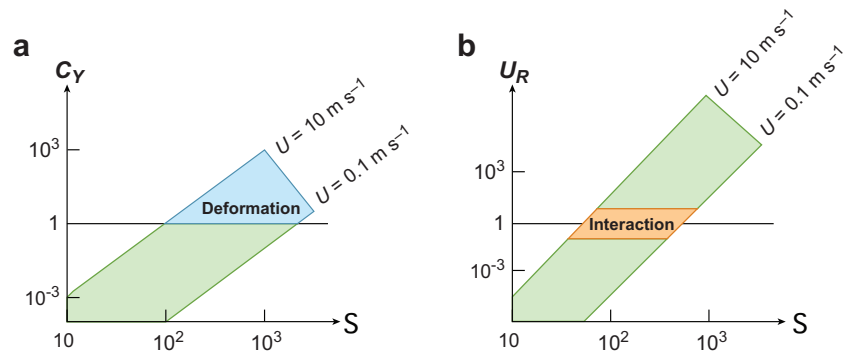
$$\mathcal{M} = \frac{\rho_F}{\rho_S}, \quad S = \frac{L}{\ell}, \quad C_Y = \frac{\rho_F U^2 L^3}{E \ell^3} = \frac{\rho_F U^2}{E} S^3. \quad (2)$$

Figure 2a illustrates the influence of slenderness on the order of magnitude of the Cauchy number. As a slenderness of more than 100 is not uncommon in stems, one may expect a Cauchy number of order unity for a wind of 10 m s^{-1} . Therefore, in contrast to most structures encountered in classical wind engineering (Simiu & Scanlan 1996), in which the slenderness may also be large (antennas, cables) but the stiffness is usually two orders of magnitude larger, one can expect a significant static deformation of a plant under the action of wind. This is an important specificity of wind effects on plants.

The reduced velocity, denoted U_R , is also used commonly in flow-induced vibrations, specifically when considering dynamical effects (see Blevins 1990, Hémon 2006, Paidoussis 2003). It may be defined as the ratio of the period of free vibration of

Figure 2

The effect of slenderness on dimensionless numbers relevant to wind effects on plants. (a) The Cauchy number may exceed 1, which corresponds to large plant deformation. (b) The reduced velocity may become of order 1, which corresponds to strong dynamical coupling.



the solid, T , over the advection time across the solid, here ℓ/U . Considering that the period of oscillation of a slender beam scales as $(L^2/\ell)\sqrt{\rho_S/E}$, the reduced velocity is easily expressed using the preceding parameters as $U_R^2 = C_Y S/\mathcal{M}$. When the reduced velocity is of order unity, one may expect dynamical interactions, such as resonances or lock-in, as the two time scales become close. As illustrated in **Figure 2b**, this may occur in a large range of wind velocities and plant slenderness.

3. WIND IN THE PRESENCE OF PLANTS

The presence of plants affects the characteristics of wind, so data used in wind engineering for manmade structures are often inappropriate for plants. This is a long-studied issue (Finnigan 2000, Raupach & Thom 1981), and this section presents only the main results.

3.1. The Canopy Model

Vegetation is present in a large proportion of emerged land. With a vertical scale ranging from 10^{-2} m to 10^2 m, it affects wind in the lower part of the atmospheric boundary layer. Moreover vegetation, natural or cultivated, often grows in the form of dense populations that form canopies. These may be defined as sets of plants such that the scale of variation of height and density is much larger than the scale of a plant. Canopies may be homogeneous and may be formed by one type of plant at the same stage of growth, such as a wheat-crop canopy. They also may be much more varied in content, such as a rainforest in which a large number of species coexist. Both these examples differ from the case of an isolated plant or a less-dense plant stand, such as trees in the African savannah. The plant canopy is therefore a reference case, which has large applicability.

A recent review in this series (Finnigan 2000) fully documents flow and turbulence at the scale of the plant canopy itself. The specificity of turbulence in canopies has been recognized early—see the reviews by Raupach & Thom (1981) and Van Gardingen & Grace (1991)—the leading motivation being the understanding of gaseous exchanges

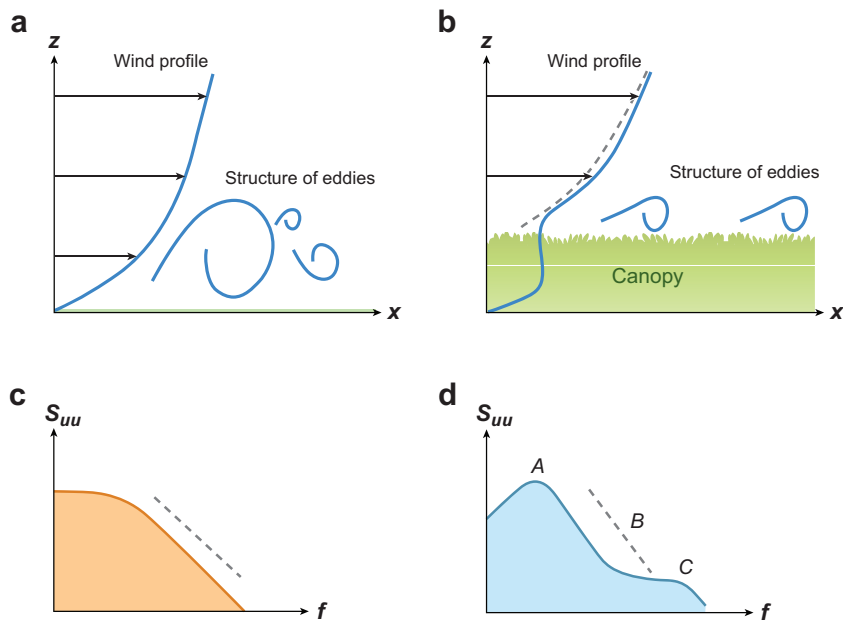


Figure 3

Main differences between boundary layer flow (*a, c*) and canopy layer flow (*b, d*). (*Top panels*) Wind profile and structure of eddies. (*Bottom panels*) Spectrum of fluctuations of the horizontal velocity, S_{uu} . The canopy layer velocity spectrum (*d*) differs from the boundary layer spectrum (*c*) in three aspects. First, it shows a more pronounced peak at a central frequency, which is that of the mixing-layer instability (**A**). Second, because of the drag on all elements of plants in the canopy, the dissipation cascade is enhanced, showing a steeper decrease with frequency (**B**). Finally this interaction with the plants, as well as the possible swaying of branches or leaves, causes the emission of vortices at higher frequencies, resulting in a possible second peak in the spectrum (**C**).

in the presence of wind, which are essential to biomass production. Surprisingly, early experiments showed that the diffusion of scalars in or close to the canopy may occur in the direction opposite the descending gradients, contrary to classical diffusion models. Researchers then collected large sets of experimental data on wind close to and inside canopies, both in wind tunnels and outdoor conditions. These investigations allowed, in the late 1990s, the emergence of a much clearer picture of the flow dynamics at the scale of the canopy [see an essential paper by Raupach et al. (1996)].

In the absence of vegetation, the distribution of time-averaged wind horizontal velocity is logarithmic with height (**Figure 3a**). In a canopy, wind exists in the form of an inner boundary layer, termed the canopy layer here (**Figure 3b**). This flow profile then connects to the outer boundary layer above the canopy, termed the boundary layer profile here. In terms of turbulence characteristics, the canopy layer case displays strong differences compared to the boundary layer. In the latter, fully developed turbulence results in the classical Kolmogorov cascade from large to small scales.

Figure 3c illustrates the corresponding spectrum of horizontal fluctuating velocity. Conversely, in the canopy layer, fluctuations are mainly generated by a mixing-layer instability that develops from the inflectional wind profile (**Figure 3b**) (Raupach et al. 1996). This results in large coherent structures being convected above the canopy. They are triggered by gusts at a larger scale that locally increase the shear level in the inflectional profile and allow the instability to develop. This schematic picture of flow and turbulence in a canopy is qualitatively supported by numerous indoor and outdoor experiments, but quantitative data are specific to each environment.

3.2. Recent Advances in Experiments and Numerical Simulations

Since Finnigan's (2000) review, new experimental results have led to an enhanced knowledge of the characteristics of wind in the presence of plants. The main features of turbulence as described above have been confirmed in particular cases: non-neutral atmospheric conditions (Brunet & Irvine 2000), indoor and outdoor experiments (Zhu et al. 2006), and the transition between the boundary layer case and the canopy layer case at the upstream edge of a canopy (Morse et al. 2002). Simultaneously, investigations on underwater canopies have revealed the existence of a mixing-layer instability in shallow water (Ghisalberti & Nepf 2002).

Numerical simulations of wind flow over and inside vegetation have significantly progressed in recent years. Computations including vegetation effects differ essentially through the specific modeling of turbulence and, therefore, the spatial and temporal scales they can simulate. The fact that the length scales of interest are usually much larger than plant organs (stems, leaves) is taken into account through a porosity for the fluid domain and through dissipation. Modeling vegetation in $k-\varepsilon$ turbulence schemes requires that the dissipation mechanism mentioned above, in which the Kolmogorov cascade is modified, is somehow taken into account. This is done through additional terms in the budget equation for k and for ε (Foudhil et al. 2005, Katul et al. 2004, Liang et al. 2006). More refined models consider two distinct frequency bands for k , corresponding to the two mechanisms pictured in **Figure 3d** (Wilson 1988). Such models allow for the analysis of wind structures in the presence of plants at the scale of a kilometer, as in an urban forested park (Dupont & Brunet 2006).

A finer simulation of temporal and spatial flow structures in the presence of canopies requires the use of large-eddy simulations. These are still at the development stage, beginning with the work of Shaw & Schumann (1992). Recent results in three-dimensional configurations, such as a forest edge (Yang et al. 2006), show that the structure of turbulence and its evolution can be properly simulated. Two-dimensional large-eddy-simulation computations, although less physical, are also of interest in terms of qualitative simulations of processes such as coupling with the motion of a canopy using an immersed boundary method (Ikeda et al. 2001). Clearly, the simulation of wind dynamics in the presence of plants is rapidly evolving and giving useful results, both in terms of applications, via statistical approaches, and in terms of understanding the physics of fluctuations, via large-eddy simulations.

4. PLANT MOTION

Researchers have developed a large number of models to simulate the motion of plants or plant organs. These models range from simple mass-spring oscillators to more complex finite-element descriptions. They differ in the botanical structure they seek to represent (e.g., tree, leaf, crop, canopy, and seed) and in the physical quantity they are designed to yield (e.g., amplitude of motion, frequency, maximum stress, and damping). For specific applications, I refer the reader to the reviews mentioned in Section 1. I focus here more on methodological aspects than on results particular to a type of plant or plant population, aiming to propose a formulation that connects most of the existing models.

4.1. Measuring Motion in Vegetation

Most of the present knowledge on the wind-induced motion of vegetation is based on experimental data, thereby strongly influencing model developments. Although the motion of plants under wind is certainly perceivable to the eye, its measurement is not straightforward for several reasons. Most plants are light and flexible structures compared to most devices used in displacement monitoring: Except for trees, adding a few grams or a small spring on a plant or a plant organ does modify its dynamics. The characteristics of plants change rapidly in time, such as through growth and water loss. Plants also display complex geometries, contacts between substructures, and several length scales in the same individual. Finally, measuring in an outdoor unbuilt environment adds specific constraints in terms of the portability and protection of apparatus, power supply, and control of experimental conditions.

Notwithstanding these difficulties, investigators have made considerable effort to obtain data on plant motion, by resorting to surprisingly inventive approaches. Various solutions have been found, depending on the size of the plant, the amplitude of motion, and the accessibility. **Figure 4** describes these solutions for individual plants, canopies, and particles.

Investigators commonly use classical methods for the vibration analysis of an individual plant. These methods allow the measurement of a local deformation, displacement, rotation, velocity, or acceleration by implementing a strain gauge (Watt et al. 2005), an optical target monitoring (Hassinen et al. 1998, Speck & Spatz 2004) or an electromagnetic tracking system (Rudnicki & Burns 2006), an inclinometer (Sellier et al. 2006), a Doppler velocimeter, or an accelerometer. All these techniques are well adapted for large plants and have been developed essentially for trees. Some applications exist for lighter plants, such as crops (Berry et al. 2003), although their effect on plant dynamics may be difficult to assess. More recently researchers have used image-processing techniques based on video recording for individual plants (Doaré et al. 2004, Farquhar et al. 2000b).

For measuring the motion of a whole canopy (**Figure 4b**), image correlation (similar to particle image velocimetry) from video is well suited, as shown by Py et al. (2005, 2006) for wheat and alfalfa crops and by Diener et al. (2006) for a small tree. The use of radar-based techniques, which have wider applications in agronomy monitoring, allows the detection of the motion of crops and trees (Brown et al.

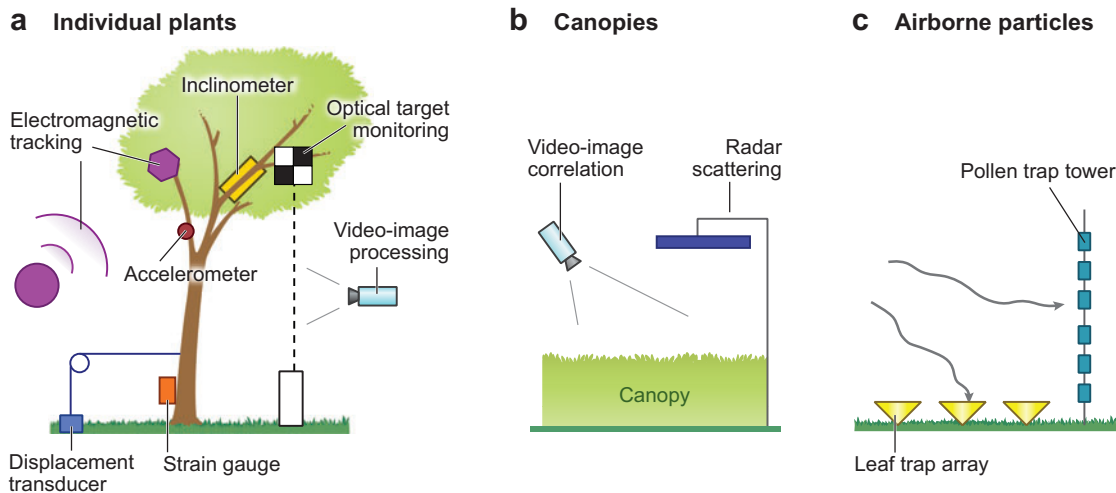


Figure 4

Techniques used for the measurement of wind-induced motion in vegetation. (a) For the motion of individual plants, researchers have used strain gauges (Watt et al. 2005), displacement transducers, optical target monitoring (Hassinen et al. 1998, Speck & Spatz 2004), inclinometers (Sellier et al. 2006), electromagnetic tracking (Rudnicki & Burns 2006), accelerometers, and video-image processing (Doaré et al. 2004, Farquhar et al. 2000b). (b) For the motion of canopies, they have used video-image correlation (Diener et al. 2006; Py et al. 2005, 2006) and radar scattering (Brown et al. 2003). (c) For the motion of airborne particles, they have used leaf trap arrays on the ground (Staelens et al. 2003) and pollen trap towers (Bullock et al. 2006).

2003). Video or radar experiments on canopies have the immense advantage of being nonintrusive and yield data for many points at the same time.

When the motion of wind-borne plant organs is of interest (**Figure 4c**), experimental approaches differ: The large number of moving objects as well as the motion amplitude require specific techniques [see Bullock et al. (2006) for pollens and seeds and Staelens et al. (2003) for leaves]. Tracking seems a natural method, but it is by far less efficient than particle trapping.

4.2. Geometry and Porosity

A first step in the modeling of plant motion is the description of its geometry. Plants are individually designed structures, genetically defined, and immense varieties of characteristics are present, even in a given species. Still, considerable knowledge exists on the architecture of plants and on laws that govern the length and diameters of segments (McMahon & Kronauer 1976, Moullia & Fournier 1997, Niklas 1992). Moreover, a given individual plant can now be fully described in its geometry using digitalizers, and a theoretical framework exists to formulate its architecture (Moullia & Sinoquet 1993).

To model the wind response of complex vegetation geometries, such as trees or canopies, one needs to take advantage of the existence of distinct spatial scales: The size of elements that provide most of the interaction with wind, such as leaves, is much smaller than the scale of variation of the displacement of interest, such as in the trunk. The wind load is then integrated over fine scales, using a standard procedure of volume averaging over a reference volume, Ω_0 . This requires first the definition of local averaged quantities to describe the geometry. In the simplest form, such quantities are the volume porosity, $\beta = \Omega_S / \Omega_0$, and the area density, $\varepsilon = A_S / \Omega_0$, where Ω_S and A_S are the volume and interface area of the solid in the reference volume Ω_0 , respectively. These local properties may be related to parameters used in the description of plants: The leaf area density (leaf area divided by plant volume) is a spatial average of ε over a whole plant or canopy, or parts of them. The leaf area index (leaf area divided by plant base area) is equivalent to the leaf area density multiplied by the plant height H . As a typical value of leaf area index for canopies is 10, the order of magnitude of leaf area density and therefore of ε is $10/H$. The volume porosity β is small, typically less than 10^{-2} , as plants comprise slender and thin elements. The same concepts of porosity and volume averaging have been applied to water flow through channels obstructed by submerged plants (see Hoffmann 2004).

4.3. Elementary Oscillator Model

The study of plants as mechanical objects precisely defines the field of plant biomechanics. It covers a wide area of subtopics, as shown in a classical book by Niklas (1992). Here, I consider only the mechanics relevant to the understanding of motion under wind. Researchers soon recognized that the response of plants to wind was essentially dynamic: A purely static approach, ignoring inertia, fails to explain windthrow (Gardiner & Quine 2000, Mayer 1987). In terms of dynamical models, three aspects need to be considered (see, for instance, Bruchert et al. 2003).

The first aspect is stiffness, the relation between static loads and deflections. A plant is a slender structure, fixed at its base, and as such it is often considered a cantilevered beam with a tapered section. One can use a similar representation for branches or petioles of leaves (Niklas 1991, Vogel 1992). The rotary stiffness of the root plate may also contribute to the global stiffness (Baker 1995).

The second aspect to consider is inertia, which is strongly dependent on plant architecture and organization: Rotary inertia is present in the root plate, inertia of the main stem is usually not negligible, and leaves or crown structures also bring mass. For instance, in a plane tree, the leaves may account for 70% of the total mass (Baker 1995). In pine saplings (Sellier et al. 2006) or in Douglas fir (Watt et al. 2005), the mass of needles and finer upper branches accounts for approximately 50% of the total mass.

Finally, dissipative phenomena play a central role in the response. Damping (see Moore & Maguire 2004) is caused by the interaction of fine structures such as leaves with air, contact with other trees, root interaction with soil, and dissipation in the plant material: It is therefore plant dependent. Typical values of the dimensionless modal damping are 0.10 in trees (Watt et al. 2005), 0.30 in alfalfa (Doaré et al. 2004),

and 0.15 and 0.30 for giant reed with and without leaves, respectively (Speck & Spatz 2004). These are large values compared with dampings of manmade structures in the wind, such as antennas or cables, which are typically 10 times lower.

The modeling of stiffness, mass, and damping varies among authors and among plants. Most models refer to a single-mode approximation of the statics and dynamics. The motion of the plant is then defined by a reference frequency of free oscillations f_0 , a modal mass m , a reference damping ξ , and a modal displacement shape $\varphi(P)$. The displacement of any point P in the plant is then expressed as $\mathbf{X}(P, t) = q(t)\varphi(P)$, the function $q(t)$ satisfying an oscillator equation,

$$m\ddot{q} + c\dot{q} + kq = f(t), \quad (3)$$

where $c = 2\xi\omega m$, $k = m\omega^2$, $\omega = 2\pi f_0$, and $f(t)$ is a wind-induced load. Here c , m , and k are the damping coefficient, the mass, and the stiffness, respectively. Provided that the wind load f is properly modeled, one can then derive the whole dynamics of the plant using the standard vibration theory (Gérardin & Rixen 1994).

4.4. Multimodal Dynamics

Depending on the complexity of the botanical structure and on the degree of refinement needed, one or more degrees of freedom are necessary to represent plant dynamics. This may be the case, for instance, to take into account damping mechanisms involving transfers between modes (Spatz & Pfisterer 2006) or the presence of higher frequencies in the response (James et al. 2006). A more general formulation than Equation 3 involves considering the displacement of any point P resulting from a modal superposition $\mathbf{X}(P, t) = \sum_n q_n(t)\varphi_n(P)$. Each modal displacement $q_n(t)$ then satisfies a modal oscillator equation identical in form to Equation 3, with appropriate modal mass, stiffness, and damping. The modal characteristics may be either measured through the vibration modal analysis technique or computed, provided adequate modeling of the stiffness, mass, and damping is used. Even for complex architectures, the characteristics of the first few modes may be derived by computations (see, for instance, Sellier et al. 2006). Still, damping remains the most unknown parameter.

The organization of the vibrational modes of a plant is highly dependent on its architecture. For trees, rules may be derived regarding the frequencies, based on the biometrical relations that exist between the length and diameter of branches of successive orders. The order N of a branch here is the number of branching between the branch and the ground. A simple case is illustrated in **Figure 5** (Rodriguez et al. 2007). In an idealized branched tree, the length L_N and diameter D_N of a segment of order N define the length and diameter of the two branches of order $N + 1$ that emanate from the next branching point as follows (McMahon & Kronauer 1976): (a) The sum of cross-sectional areas of segments is equal before and after branching, and (b) the length of a segment is related to its diameter through a constant ratio D/L^α , where α varies between 1 and 2 [see the discussion by Moulia & Fournier (1997) on these laws]. The combination of these two rules yields $L_{N+1} = L_N/2^{1/(2\alpha)}$ (McMahon & Kronauer 1976). **Figure 5a** represents such an idealized branched tree. The subset of the tree emanating from its first branching is then identical to the whole tree,

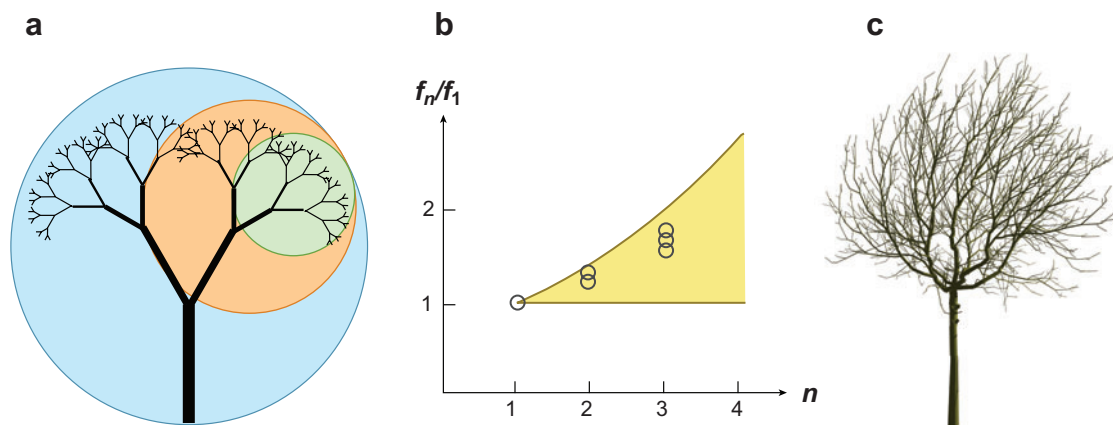


Figure 5

The effect of the architecture on the free vibration frequencies of a tree. (a) Idealized branched tree showing that the subsets (*orange and green*) are self-similar to the whole tree (*blue*). (b) Evolution of the normalized frequency of free vibration modes with the rank of the mode. The yellow zone is defined by the scaling laws associated with the iterations laws for the idealized tree in the range $\alpha = 1$ to 2. Circles represent frequencies of modes for a walnut tree, computed using a finite-element discretization (Rodríguez et al. 2007). Several frequencies exist at a given rank, corresponding to three-dimensional motion and multiple branches. (c) First modal shape of the walnut tree, fully digitized, corresponding to $n = 1$ in panel b.

with a scaling of lengths and diameters that can be derived from the two rules above. Considering that frequencies of beams in bending vary as D/L^2 , the first frequency of the tree, f_1 , and its second frequency, f_2 , which is also the first of the subset, are related by $f_2/f_1 = 2^{(2-\alpha)/(2\alpha)}$. A similar relation holds for higher modes, the iteration process of branching being self-similar. This is illustrated in **Figure 5b**, which compares the above scaling results for f_n/f_1 for an idealized tree to a finite-element computation of modes for a real walnut tree. Although the real geometry of the walnut tree shown in **Figure 5c** is quite different from the idealized tree in **Figure 5a**, the ratios f_2/f_1 and f_3/f_1 fall within the domain predicted by the scaling law (Rodríguez et al. 2007).

4.5. Canopies and Poroelasticity

Modeling the dynamics of a canopy considered as a continuum requires a completely different framework: In this case plants are not individualized, but their characteristics and their interactions are homogenized in the characteristics of the continuum. This approach falls in the general context of poroelastic systems. A simple model (Farquhar & Eggleton 2000) arises when identical plants described by a single-mode approximation are grouped in a one-dimensional geometry. Using the single-mode approximation in the vertical direction, the horizontal displacement of any point of the canopy reads $\mathbf{X}(x, z, t) = q(x, t)\varphi(z)$. The modal displacement $q(x, t)$ becomes space dependent. Coupling between plants through contact may be incorporated,

leading to a wavelike equation (Doaré et al. 2004):

$$k'q - r' \frac{\partial^2 q}{\partial x^2} + c' \frac{\partial q}{\partial t} + m' \frac{\partial^2 q}{\partial t^2} = f(x, t), \quad (4)$$

where the derivation of the parameters k' , r' , c' , and m' requires an averaging process. For instance, the averaged mass reads $m' = m/d^2$, where d is the average distance between plants (Py et al. 2006). As shown below, this formulation is well adapted to studying the case of a propagating wind gust.

5. WIND LOAD AND PLANT RESPONSE

Whereas wind and plant dynamics are analyzed separately above, here I propose a description of the interactions in the framework of modal analysis. Models such as those presented by Wood (1995), Baker (1995), Saunderson et al. (1999), Kerzenmacher & Gardiner (1998), and Spatz & Bruechert (2000) may be seen as particular cases of this approach.

5.1. Drag on Plants

Wind on a plant surface causes local skin friction and pressure drag. The net drag load on a plant, or on part of a plant, may be measured in a wind tunnel with a load cell. Researchers have done this for leaves (Vogel 1989), models of leaves (Schouveiler & Boudaoud 2006), wheat spikes (Farquhar et al. 2000a), and even whole tree crowns (Vollsinger et al. 2005).

Depending on the scale of interest, the plant or subsets of the plant may be regarded either as a bluff body surrounded by air flow such as an individual leaf or as a porous body with through flow such as a tree crown, as discussed in Section 4.2 with regard to the concept of porosity. In the first case, a drag load is commonly expressed as

$$\mathbf{F} = \frac{1}{2} \rho AC_D |\mathbf{U} - \dot{\mathbf{X}}| (\mathbf{U} - \dot{\mathbf{X}}), \quad (5)$$

where the drag factor AC_D depends on the geometry and the Reynolds number. Note that we do not separate the reference area A and the drag coefficient C_D , as only their combined effect matters. Section 6 discusses the dependence of the drag coefficient on wind-induced changes in plant configuration. The use of Equation 5 with a time-varying wind velocity \mathbf{U} and plant velocity $\dot{\mathbf{X}}$ allows one to derive a time-varying load \mathbf{F} . Alternatively when using a porous medium model, one can define a local volume drag load as

$$\mathbf{f} = \frac{1}{2} \rho \varepsilon c_D |\mathbf{U} - \dot{\mathbf{X}}| (\mathbf{U} - \dot{\mathbf{X}}). \quad (6)$$

In a canopy, the combined drag coefficient εc_D essentially varies with z and may be derived from the variation of the Reynolds stress, $\varepsilon c_D = (\overline{u'w'})_{,z} / u^2$ (Kerzenmacher & Gardiner 1998). The drag coefficient c_D is found to be of the order of 0.1 for trees (Kerzenmacher & Gardiner 1998). Note that a point load, as defined by Equation 5, may be considered as a particular volume distributed load given by Equation 6, so only this case is mentioned further.

From this local definition of wind load over the porous media, one can easily derive the modal wind load for mode n by a modal projection, as in G eradin & Rixen (1994), integrating over the whole volume

$$f_n = \int \mathbf{f} \cdot \varphi_n \, d\Omega. \quad (7)$$

Elementary cases of interest are easily recovered by choosing specific forms of the modal shape: the net drag on using a translational mode $\varphi = e_x$, the moment on root plate with $\varphi = (z/L)e_x$, and the torsional load using $\varphi = r e_\theta$ in cylindrical coordinates.

5.2. Modal Response

The dynamics of a given mode n excited by wind is then defined by combining Equations 3, 6, and 7:

$$m\ddot{q} + c\dot{q} + kq = \int \frac{1}{2} \rho \varepsilon c_D |\mathbf{U} - \dot{q}\varphi| (\mathbf{U} - \dot{q}\varphi) \cdot \varphi \, d\Omega, \quad (8)$$

where the modal subscript n has been omitted for clarity, and mode coupling has been ignored.

On removing all time-dependent terms, one can derive the static contribution of each mode and the total static response as well by superposition. For each mode, damping in still air and flow-induced damping are also found by assuming $\mathbf{U} = 0$ and $\dot{q} \ll |U|$, respectively. Another important case arises when wind velocity fluctuations are taken into account. The fluctuations u such that $U(t) = U + u(t)$ are known only through their spectral characteristics, such as S_{uu} , as described in Section 3. In that case, the plant velocities are usually considered to be of smaller amplitude, so load does not depend on \dot{q} . When fluctuations are assumed to be small, u^2 terms may be neglected versus Uu terms, and the general framework of linear spectral analysis may be applied. The methodology to derive the spectral characteristics of the response, such as the power spectral density of displacement at a given point, from the spectral characteristics of wind is then a standard procedure as in the prediction of turbulence-induced vibrations in hydrodynamics and wind engineering (Axisa et al. 1988, Blevins 1990, de Langre 2002, Dowell 1999, H emon 2006, Pa idoussis 2003, Simiu & Scanlan 1996).

Specific features exist in the case of wind over plants (Baker 1995, Gardiner 1995, Mayer 1987). First, wind loads are strongly correlated over a plant. This results from the comparison of the plant size, L , to the size of eddies that contribute to the excitation. Second, by contrast to the large structures of interest in wind engineering (such as bridges or antennas), damping is high and modes may be close to each other, which may not allow standard simplifications in the combination of modal responses (Axisa et al. 1988). Finally the large deformability of plants causes large amplitudes of motion, so nonlinear effects due to geometry or contact with other plants, such as crown clashing in trees, may come into play. In such cases, the equation of motion may also be solved using modes but in the time domain, via a standard procedure in flow-induced vibrations (e.g., Axisa et al. 1988).

5.3. Propagating Load on Canopies

As mentioned above in Section 2, the low-frequency content of the wind spectra is associated with propagating gusts over a canopy resulting from a mixing-layer instability. If one considers the response of a given plant, the spectral description presented above for the modal response is adequate, as propagating gusts are simply seen as low-frequency events. The global response of the canopy may also be sought, in which load varies both in space and time. The spectral procedure is still applicable to propagating loads, through the use of complex correlation functions to derive the modal admittances. Alternatively one may use a simple model in which the load is time independent in a moving frame of reference (Doaré et al. 2004, Farquhar & Eggleton 2000). In such a frame defined by $X = x - Ut$, the modal equation for the canopy reads

$$(mU^2 - r)q'' - cUq' + kq = f(X), \quad (9)$$

where primes are derivatives with respect to X . The dependence in space is then equivalent to the time dependence of an oscillator: Resonance conditions may occur for specific wavelengths of the gust. Moreover, the motion of the canopy behind a gust resembles the evolution of a damped oscillator, in which the time variable is replaced by $-X$. Nonlinear effects due the interactions between plants are easily taken into account (see Doaré et al. 2004).

5.4. Wind Dispersal as a Particular Case of Modal Response

One may represent the case of airborne organs in the framework of modal superposition (Equation 8). This only requires that the modes used in the modal superposition are the three rigid-body modes. They are defined by a frequency equal to zero, a modal mass equal to the particle mass, and modal shapes equal to the unit vectors in the three directions (x , y , and z).

The simplest model for particle dispersal, referred to as ballistic by Kuparinen (2006), may also be derived from Equation 8 by considering time-independent velocities \dot{q}_x and \dot{q}_z for the horizontal and vertical rigid-body modes, respectively, and a time-independent point load resulting from a constant velocity U . The resulting angle of descent is given by the ratio of these two velocities, which reads $\dot{q}_z/\dot{q}_x = w/U$, where $w^2 = 2mg/\rho AC_D$ is the terminal descent velocity. For small particles, the influence of the Reynolds number is of course essential to the value of C_D .

For light particles with small terminal velocities (such as spores or seeds), the case of most interest involves particle uplifting, which occurs when the instantaneous, upward vertical wind velocity exceeds the terminal descent velocity. This results in long-distance dispersal (Kuparinen 2006), which plays a key role in the propagation of species: Only a few propagules with long-range motion are needed for this phenomenon to take place. Simulating this propagation requires models in which all fluctuating components of the wind are represented. This is the case for the Lagrangian stochastics method (see Nathan et al. 2002), which is based on the tracking of a given particle's trajectory, subjected to local wind velocities that vary in time and space. From the knowledge of wind spectral characteristics, one may

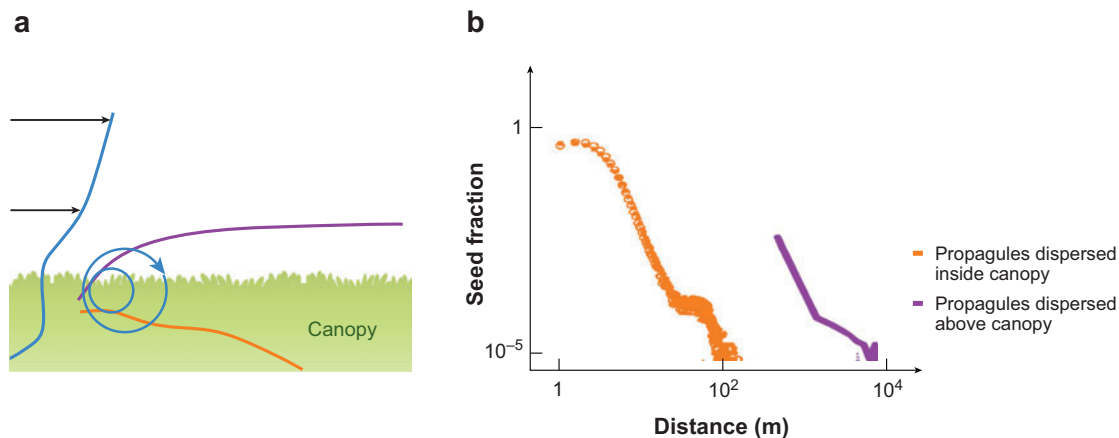


Figure 6

The dynamics of the long-distance dispersal of seeds from a canopy. (a) Two types of trajectories of propagules. (b) Computed fraction of seeds as a function of distance to the tree of origin for a yellow poplar. Most propagules are dispersed inside the canopy (*orange*), and their spreading function decreases with distance, up to approximately 100 m. A small proportion of propagules (*purple*) is ejected by mixing-layer eddies above the canopy, where higher-flow velocity carries them away. This results in a second peak in the spreading function, with distances of the order of kilometers. Figure adapted from Nathan et al. 2002 and Nathan & Katul 2005.

generate time samples of the wind velocity encountered by a particle and compute its resulting motion through Equation 8. A striking result of these simulations is that the dispersal function then shows a pronounced secondary peak at large distances (Figure 6): Some seeds are propagated upward and then carried away by the flow above the canopy, whereas most stay inside the canopy and fall at a short distance (Nathan et al. 2002).

6. FULLY COUPLED MODELS OF WIND-PLANT INTERACTIONS

In the models presented above, the plant or plant organ responds to wind loading, but the response does not modify the loading. In this section, I present two cases in which it is essential to account for the action of plant motion on wind.

6.1. Honami Lock-In: A Reduced Velocity Effect

As described in Section 3, a mixing-layer instability develops above a canopy, creating large-scale coherent fluctuations. The most amplified wavelength is classically derived by a linear temporal stability analysis of the inflectional velocity profile and scales with the mixing-layer thickness (Ho & Huerre 1984). A more refined linear stability analysis is possible that includes both the flow and the flexible canopy, as in the recent study of Py et al. (2006). In such a model, the drag resulting from

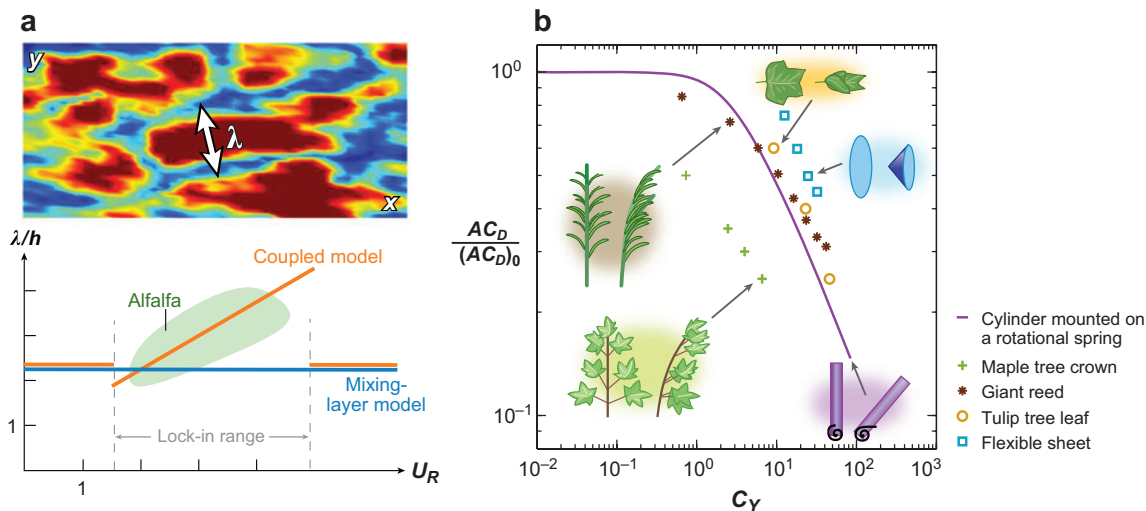


Figure 7

Fully coupled effects in wind-plant interactions. (a) Honami lock-in, scaled by the reduced velocity (Py et al. 2006). (Top panel) Experimental data of the instantaneous velocity magnitude of plants on an alfalfa field under wind displaying a wavelength λ . (Bottom panel) Comparison between experimental data on alfalfa (green zone) and theoretical prediction of a wavelength lock-in effect (orange lines) using the coupled model. The simple mixing-layer model (blue line) fails to capture this effect. (b) Reconfiguration, with a variation of the drag factor with the Cauchy number. The line represents a model of a cylinder mounted on a rotational spring; plus signs represent maple tree crown (Vollsinger et al. 2005); asterisks, giant reed (Speck & Spatz 2004); open circles, tulip tree leaf (Vogel 1989); open squares, flexible sheet (Schouveiler & Boudaoud 2006).

flow fluctuation affects the canopy dynamics and is simultaneously incorporated into the linearized momentum equation. The temporal stability analysis associated with these coupled equations shows a surprising lock-in feature in a specific range of flow velocities: The wavelength of the instability no longer scales with the mixing-layer thickness (Figure 7a). This range is defined by a reduced velocity U_R of order unity. The wavelength then scales with U_R , as the frequency of the instability locks on the frequency of the canopy. Experimental data of honamis on wheat fields and alfalfa fields confirm this effect (Py et al. 2006). The fundamental mechanism of lock-in, which is essentially linear (de Langre 2006), is found in many flow-induced vibration issues, such as in vortex-induced vibrations. Galloping, which is probably the cause of the vibration of elongated leaves such as grass in light crosswind, also depends on the reduced velocity, the essential nondimensional parameter that scales the ratio of two time scales: advection and oscillation.

6.2. Drag Reduction: A Cauchy Number Effect

The lock-in phenomenon discussed above is linear by nature. Coupling also arises through nonlinearities, when the body-shape change needs to be of order unity

to affect the wind load. Here, we assume the drag induced by wind varies as $F = \rho U^2 AC_D/2$. It has often been reported that the U^2 variation of drag does not apply for plants. This has been expressed in terms of a Vogel exponent, noted b , so that the dependence of drag load with velocity scales as U^{2+b} . A value of $b = -1$ is not uncommon so that the drag load increases linearly with the velocity. Some Reynolds number effects may be the cause for the smallest plant components, but most observations relate this reduction to significant deformations of the plant. Such shape change may take different forms, from a simple pronounced bending to wrapping, and they fall under the generic name of reconfiguration (Vogel 1989). It is an essential mechanism by which vegetation reduces stress induced by external flow, in air or water (see Harder et al. 2004). According to the dimensional analysis in Section 2, reconfiguration is expected to depend on the Cauchy number, which controls the shape changes of the plant due to flow.

For a nonporous body (as defined in Section 4), flow-induced deformation may affect drag through two distinct mechanisms. First, as noted by most authors, deformation induces a reduction in the effective cross-flow area, A , which does directly reduce the total drag load. Second, the deformed shape may be more streamlined, so the pressure recovery in its wake is improved, also reducing drag. These combined effects are fully discussed by Alben et al. (2004) for the model case of a thread in a soap film, a 2D model for fluid flow, and by Vollsinger et al. (2005) for a tree crown in a wind tunnel: They are found to be of similar magnitude. **Figure 7b** shows typical experimental data of the evolution of the drag-reduction ratio $AC_D/(AC_D)_0$ with Cauchy number. Data on plants correspond to a maple tree crown in a wind tunnel (Vollsinger et al. 2005), a giant reed in outdoor wind (Speck & Spatz 2004), and a tulip tree leaf under an air jet (Vogel 1989). The Cauchy number has been estimated by setting $E = 10^8$ Pa and $S = 125, 400$, and 200. Experimental data for a flexible disk, which is an idealized leaf geometry, are also shown (Schouveiler & Boudaoud 2006). All these evolutions display a strong decrease of drag for a Cauchy number of order unity.

As an elementary model of this effect, one may consider a rigid cylinder of length L and diameter D mounted on a rotational spring of stiffness C , which allows deformation by bending in the flow direction (**Figure 7b**). Assuming that the drag depends on the velocity normal to the cylinder, the drag-reduction ratio varies as $AC_D/(AC_D)_0 = \cos^2\theta$, where θ is the angle of inclination. Using the equilibrium of moments between drag and rotational stiffness, one yields $C_Y = \rho U^2 D/C = 4\theta/\cos^3\theta$. **Figure 7b** shows the relation between drag and Cauchy number using this model. It is found to qualitatively represent the reconfiguration effect observed in the experimental data.

7. BIOLOGICAL AND ECOLOGICAL EFFECTS

The above sections consider plants as mechanical structures, with some peculiar features such as their large flexibility but ignore their functions as living individuals, parts of larger living systems. These functions are affected by wind, either directly or indirectly. Tèlewski (1995) has proposed a systematic classification. Three particular cases are presented here.

7.1. Wind and Photosynthesis

Photosynthesis is an essential biochemical process in the life of plants. Its efficiency depends on the flux of light absorbed by the leaf and the gaseous exchange through the stomata, small apertures on the leaves' surface. Wind does affect photosynthesis through several mechanisms (Sinoquet et al. 2001, Smith & Ennos 2003).

Wind first affects exchanges by convection, as the leaf surface is swept by wind. Although the Reynolds number on a leaf based on wind velocity and leaf cross-wind length does not exceed 10^4 , the boundary layer is generally turbulent, which significantly enhances convection exchanges. This is because of the roughness of veins, the shape of edges, the canopy turbulence, and in some cases the wind-induced flutter of the leaf, such as in aspen poplar (Grace 1978). A second indirect effect of wind on photosynthesis is through light shedding. Wind-induced motion of leaves and plants plays a significant role in the shedding of light inside a plant canopy (Tong & Hippias 1996). As photosynthesis is a time-dependent mechanism with short time scales, it is clearly affected by plant motion. The flutter of leaves is also involved: Oscillations of the leaf plane reduce light interception by the most exposed leaves and simultaneously spread light to lower leaves inside the canopy (Roden 2003).

7.2. Wind and the Growth and Death of Plants

It is common knowledge that plants in windy conditions display different growth than those in calm conditions: Trees are bent leeward, and roses grow shorter. Moreover, wind is often the cause of irreversible damage to plants, from leaf tearing to branch breaking and windthrow. Each of these effects cannot be seen as purely biological (when growth is concerned) or mechanical (when damage occurs): The plant that grows is mechanically strained, and the plant that is damaged has grown in windy conditions.

Wind effects on plant growth result from several competing effects, as emphasized by Smith & Ennos (2003) in the case of sunflowers. For instance, wind affects the photosynthesis mechanism, which is essential to plant growth (as discussed above), but simultaneously it also causes motion, which itself affects growth. Experiments can separate these effects by preventing plant motion with supports or, conversely, by causing deformation without wind, using a direct mechanical stimulus. Several distinct mechanical effects on growth may thus be identified. Jaffe (1973), in a seminal paper, documented thigmomorphogenesis, which is the effect of motion on growth: A mechanically stimulated plant stem does grow shorter and, generally speaking, stronger. Therefore, plants are able to tune their height and slenderness biologically as a response to the mechanosensing of wind. Coutand & Mouli a (2000) have shown that this surprising effect is a global plant response to a local strain: A small local bending of a tomato plant during 30 s causes growth to stop for approximately 1 h. Field experiments have confirmed this effect, such as those by Ennos (1997) and more recently over a wide range of wind velocity by Mouli a & Combes (2006).

Even long-term loading affects growth: Branches of trees exposed to wind are significantly thicker (Watt et al. 2005), and the root system of a wind-exposed tree is denser and asymmetric (Tamasi et al. 2005). Trees develop flexure wood in branches

affected by wind, so flexibility and the ability to sustain large deformation are enhanced. Trees also develop reaction wood that allows their architecture to bear high permanent stress. The mechanism of perception of loads by the plant is still an open question (Telewski 2006). Moreover, for a given plant under given conditions, the combination of all these effects in a particular growth pattern raises the issue of plant posturing, as discussed in detail by Moulia et al. (2006): How does a plant architecture evolve in terms of a combined muscular-skeletal system? This is a fascinating new control problem in which both sensors and actuators evolve in time in relation to the constraint.

Windthrow, and more generally wind-induced damage, constitutes the essential motivation for research on wind effects on plants (Cucchi et al. 2005). Its understanding involves most of the issues raised in this review. Whether the phenomenon is uprooting, leaf tearing, or stem breaking, it may be seen as the result of a threshold being reached by a state value (for instance, a critical bending moment in stem breaking). It therefore requires the development of improved knowledge for a given system, not only on wind, wind loads, and the dynamic response to wind loads, but also on other loads such as those induced by snow on trees and rainwater on crops. Also required is knowledge on the threshold value and its dependence on ecological and meteorological conditions. For instance, the lodging of wheat is affected as much by wind intensity as by the rainfall that modifies root resistance and loads the spikes (Berry et al. 2004). A probabilistic approach is often needed to account for threshold crossing by rare events. This goes far beyond the scope of this review and is actually closely related to many fields of wind engineering (Simiu & Scanlan 1996). Efficient models exist for trees and crops (e.g., Baker 1995, Berry et al. 2003, Cleugh et al. 1998, Cucchi et al. 2005, England et al. 2000, Gardiner & Quine 2000, James et al. 2006).

7.3. Wind, Plants, and Insects

The interactions between plants and animals are numerous, from feeding to hosting. Wind affects these functions in numerous ways, indirectly, for example, by material hardening through thigmomorphogenesis or directly by the dynamical response. For instance, insect communication often uses vibrational transmission through the plant structure (Cocroft & Rodriguez 2005). The frequencies involved in this communication between individuals on the same plant have to differ from those of the vibrational response of the plant to wind excitation, which vary with wind velocity. Considering that spiders communicate at 30 Hz and insects at frequencies as low as 100 Hz (Cocroft & Rodriguez 2005), this may cause a real problem. The mechanical interactions between wind, plants, and insects comprise a still largely unexplored field: How does wind-induced motion affect insect hosting? How does it affect the possibility of pollenization through insects?

8. CONCLUDING REMARKS

Although the effects of wind on plants are manifold, even in the restricted context of mechanics, we can identify several common features. First, the fluid mechanics

of wind in the presence of plants and the solid mechanics of plants are themselves quite specific: Wind turbulence is different from its counterpart in classical boundary layers, and plant structural dynamics is different from its counterpart in manmade structures. Second, the interactions that cause the motion of plants or of parts of plants are caused by mechanisms that are well-known in flow-induced vibration, but several important specific features raise challenging questions: the range of length scales in a given medium (from leaves to canopies), the complex three-dimensional geometries (from individual plant architecture to seed dispersal in a rainforest), and the magnitude of deformation (from fluttering leaf to streamlined tree crown). Future research should emphasize four directions.

First, experiments need to be performed, as always. Data exist, and significant efforts have been made in that direction over the years, but mainly for large individuals (trees) and by using point measurements. Significant improvement is expected as experimental techniques will be developed that allow the measurement of the motion of plants and the dynamics of wind, simultaneously, over large sets of points, and for plant systems of various sizes. Considerable progress has been made in fluid mechanics in the transition from point to full field measurements. Similar progress can be expected in wind-plant interactions.

Second, researchers should explore poroelasticity effects. The complexity of geometries and the range of length scales in a given system have progressively led to the introduction of the concepts of porosity in flow through vegetation. A further step now needs to be taken in the direction of poroelasticity, in which the dynamics of plants is also averaged in space. Fundamental concepts exist that allow one to account for the architecture of elastic structures to build a homogenized model.

Third, small systems are still virgin territory. The large majority of studies discussed in this review focus on trees and most of the remaining ones on crops. This is justified by the immense practical interest in these plants. Because of their size, experiments and models are more accessible. Still, many phenomena exist at smaller scales, in particular in relation to biological and ecological issues. Although seeds and pollens are now abundantly studied, not much is known about the effects of wind on grass, flowers in trees, or light stems carrying insects. Here, experimental data are lacking, and the physical mechanisms of interactions remain to be explored.

Finally, methodology issues need to be addressed head on. Most of the numerous results obtained so far in this field have come from the application of mechanical sciences to biological systems, which is the object of biomechanics. This is a fruitful approach, and much progress can still be done, in particular in the three directions mentioned above. Still, in the case of wind effects on plants, this method is probably more limited than in the biomechanics of animal and human systems for the following reason: The plant or the canopy that responds to wind is also defined by wind. Its selection, its design, and its growth are all related to the environment, of which wind is a key element. Therefore, it seems necessary to go beyond biomechanics (i.e., the mechanics of living systems) to mechanobiology (i.e., the biology of mechanical systems).

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