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REVIEW

Methodological advances in predicting flow-induced dynamics of plants using mechanical-engineering theory

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Summary

The modeling of fluid–structure interactions, such as flow-induced vibrations, is a well-developed field of mechanical engineering. Many methods exist, and it seems natural to apply them to model the behavior of plants, and potentially other cantilever-like biological structures, under flow. Overcoming this disciplinary divide, and the application of such models to biological systems, will significantly advance our understanding of ecological patterns and processes and improve our predictive capabilities. Nonetheless, several methodological issues must first be addressed, which I describe here using two practical examples that have strong similarities: one from agricultural sciences and the other from nuclear engineering. Very similar issues arise in both: individual and collective behavior, small and large space and time scales, porous modeling, standard and extreme events, trade-off between the surface of exchange and individual or collective risk of damage, variability, hostile environments and, in some aspects, evolution. The conclusion is that, although similar issues do exist, which need to be exploited in some detail, there is a significant gap that requires new developments. It is obvious that living plants grow in and adapt to their environment, which certainly makes plant biomechanics fundamentally distinct from classical mechanical engineering. Moreover, the selection processes in biology and in human engineering are truly different, making the issue of safety different as well. A thorough understanding of these similarities and differences is needed to work efficiently in the application of a mechanistic approach to ecology.

Key words: flow, plant biomechanics, vibration

Introduction

The plant canopy interacting with wind

Organisms, aerial or aquatic, natural or cultivated, often grow in the form of canopies. In such organizations, the height and density of organisms vary at a much larger scale than does the size of the organism itself. This review focuses on the case of a terrestrial canopy interacting with wind. Very distinct cases exist, ranging from the short wheat canopy to the high rain-forest canopy. Let us first consider a crop canopy, as discussed by Py and colleagues (Py et al., 2006). In terms of geometrical and mechanical characteristics, it can be stated that the typical density is approximately 100 specimens per square meter, the vertical height is 1 m and the diameter of individual stems or size of leaves is of the order of a few millimeters. The natural frequency of oscillations of plants is of the order of 1 Hz, and the flow velocity is of the order of $1\,m\,s^{-1}$. The density of the surrounding fluid is three orders of magnitude smaller than that of the plant tissue. Wind in the presence of canopy differs significantly from wind over a flat surface (Fig. 1). The wind profile shows a double boundary-layer profile – one in the canopy, and one above the canopy – that causes the wind fluctuations to be strongly organized in the form of coherent eddies (Finnigan, 2000). Flexible plants forming the canopy are known to move in wind. This motion has many consequences (de Langre, 2008): when of large amplitude, it can induce breaking or permanent bending, but even low-amplitude motion has a strong influence on growth (Moulia and Combes, 2004), gaseous exchanges inside the canopy are modified by the motion (Farquhar and Eggleton, 2000) and, finally, seed or pollen dispersal, or photosynthesis, are affected not only by wind but also by wind-induced motion (Nathan et al., 2002). Quantifying this motion, and modeling the influence of the biomechanical characteristics of the plants is essential for the understanding of these issues. Similar phenomena are found in the case of canopies made of trees, but at different scales of time and length. It can be stated, therefore, that the problem of the mechanical interaction of a plant canopy (PC) with wind has some importance in the field of plant biomechanics and, more generally, for plant ecology.

The steam generator bundle interacting with water

The other system considered hereafter is well known in nuclear engineering. The steam generator (SG) is a key component of most modern reactors; it allows the transfer of thermal energy initially produced by the nuclear reaction from the primary circulating loop to the secondary one. Owing to the considerable flux of energy to transfer, SGs are among the largest heat exchangers in the world. They typically convey 300 MW between the two circuits they interface. In the most widespread design (pressurized water reactors), this is made possible by a bundle of ~5000 tubes, 20 m long. These tubes, with a diameter of ~2 cm, are very densely packed, with a distance between them of approximately half a diameter. They allow the transfer of heat from the internal fluid, coming from the nuclear core, to the external fluid, which ultimately is boiled to form vapor that will activate the turbine, generating electricity. These long U-shaped tubes are held by supports along their span and have typical natural frequencies of 10 Hz. The external water and steam flow runs at up to $5\,m\,s^{-1}$. In the region of interest here, the U-bend part (Fig. 1),

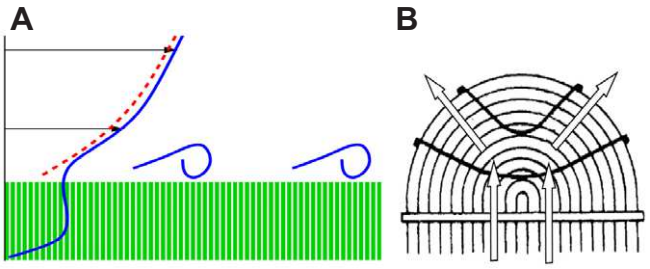


Fig. 1. Air and water flows in disparate study systems. (A) The plant canopy (PC) experiencing wind, with the corresponding wind profile and structured eddies (blue) and boundary layer profile (broken red line). (B) The upper part of the bundle of U-tubes in a steam generator (SG). White arrows indicate water flow.

the tubes are semi-circular and the flow is mainly radial and therefore perpendicular to the tubes (Fig. 2). As for the crop canopy, flow across such a flexible system results in a vibratory motion. Here, the possible consequence of the motion is damage by fatigue or wear at the support. Wear, and subsequent leakage of the internal flow to the external circuit, have in fact significantly affected ~40% of the reactors in existence (Diercks et al., 1999). Approximately 10,000 tubes have been plugged around the world for this reason, and many SGs have been replaced, at a cost of ~$100 million each (Païdoussis, 2006). More generally, the complete fracture of a damaged tube is a safety issue. The interaction of flow with these tubes is also of interest for the understanding of particle transport and deposition in the heat exchanger (Srikantiah and Chappidi, 2000).

Fluid–structure interactions: elementary concepts

Some general concepts of the modeling of flow-induced vibrations are necessary in order to understand the approaches used to analyze the two cases presented above. First, the frequencies involved in the flow and in the moving structure have to be compared. In plants and SG tubes, the typical frequencies of motion are above the 1 Hz value: hence any variation of flow velocity at lower frequencies only has a quasi-static effect. This defines the range of interaction with the mean flow, where it is sufficient to consider the static drag force acting on the structure. This static drag affects the static deformation of the structure, such as the mean bending of the crop canopy under wind. Under very high mean flow, static damage can occur, such as tree branch breakage in storms or SG tube bending in extreme accidental cases. This occurs in a similar way for corals (Madin and Connolly, 2006). The effect of flow fluctuations of higher frequencies is more complex; see for instance the book by Païdoussis and colleagues for a general presentation (Païdoussis et al., 2011). The flow exerts oscillating forces that can come from the fluctuating part of the flow velocity, by turbulence or large eddies, or that result from a coupling between the flow and the flexibility of the solid structure. The forces cause vibratory motion, predominantly at the natural frequency of the structure, and corresponding oscillating stress. This results in damage by fatigue or wear. The relationship between the oscillating stress and the corresponding damage differs with the material, biological or metallic. Moreover, transient dynamic effects can cause overshoots of stresses, causing fractures or local buckling; this is a typical mechanism for lodging, windbreak or windthrow of trees.

A comparative point of view

It is often the case, both in biological and engineering sciences, that a comparative analysis of systems points out similarities and differences that allow the derivation of some general conclusions. The point of view taken here is not to compare the two systems, one from nuclear engineering and one from plant biomechanics, but to compare how they have been modeled. In fact, it happens that the author of this paper has worked on both over the years. In some sense, it is hoped that the understanding of the similarities and differences in the methods used will be useful for the development of mechanistic approaches to ecology, which is the focus of this present special issue. More specifically, the scope of the paper is the adequate use of mechanical engineering to build efficient predictive methods in ecology, with particular attention to the issue of individual-level and group-level models.

A comparative analysis of the fluid–structure interaction approaches

Defining an equivalent continuum

In both systems, the first question that appears in the modeling of the mechanical behavior is whether to consider individuals (plants, tubes) or some equivalent a continuum. Owing to the large number of individuals, and their similarities, some kind of homogenization

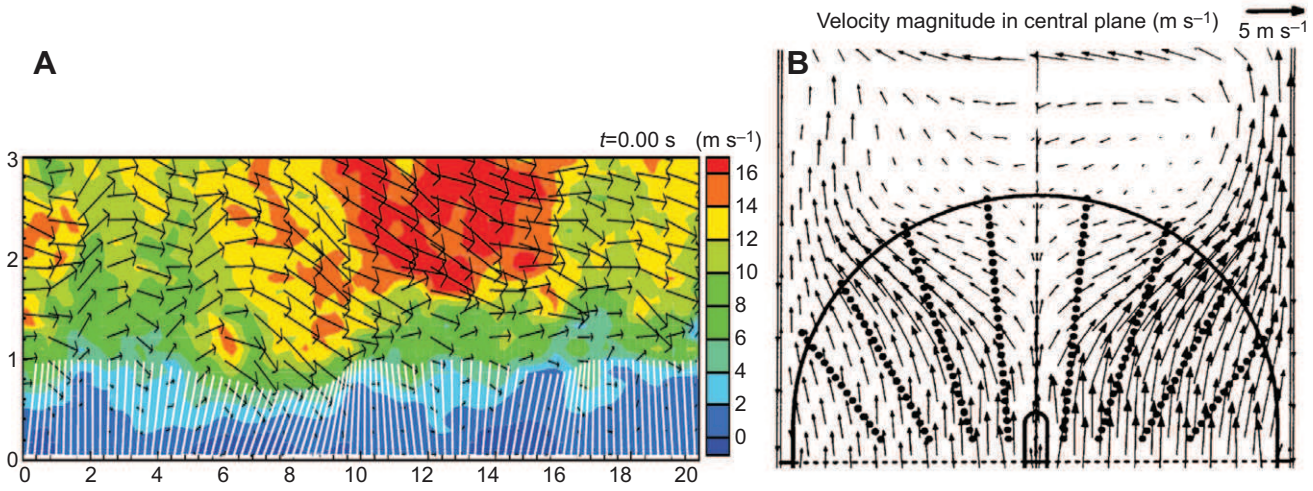


Fig. 2. Modeling the flow using an equivalent continuum medium. (A) Instantaneous flow over and through an alfalfa canopy [reproduced, with permission, from Dupont et al. (Dupont et al., 2010)]. (B) Mean flow through the bundle of a SG (modified from Pettigrew and Taylor, 2003a).

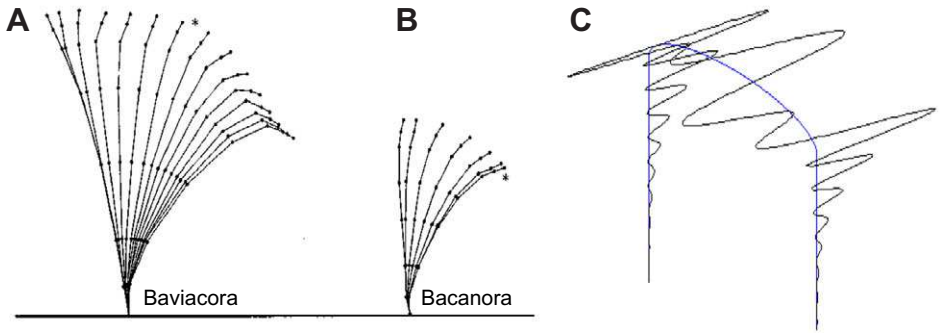


Fig. 3. Modeling the dynamic behavior of individuals. (A,B) The first modal shapes of wheat stalks (modified from Farquhar et al., 2000). (C) The modal shape of a U-tube with supports (modified from Adobes and Gaudin, 2004).

approach seems possible. In the SG, the classical approach is to compute the flow through a fixed porous medium (Belliard and Grandotto, 2002). The main characteristic of the porous medium is the volume porosity, which is the fraction of the volume occupied by the fluid, typically 0.5. Also needed is a measure of the quantity of fluid–solid interface per unit volume. In practice, this is done through the use of a hydraulic resistance matrix, which gives the friction exerted by the flow on the porous medium as a function of the fluid velocity. Porosity plays an important role in the mass balance equation and in the hydraulic resistance matrix used in the momentum balance equation. Similarly, in PCs, a volume porosity is defined, typically 0.99. To quantify the surface of interaction per unit volume, the leaf area index (LAI) is often used, where the surface of interaction is referred to the projected area of the plant on the ground. A typical value for a tree is 10. This also allows the definition of the flow resistance in the canopy and thereby computation of the flow (see Fig. 2 for two examples). Both approaches, in the SG and the PC, are similar in principle, although the ranges of parameters are quite different: the case of the SG is dominated by porosity effects, whereas that of the PC is dominated by LAI effects (Doare et al., 2004; Dupont et al., 2010). For both systems, this definition of an equivalent continuum allows the computation of the flow with a simple approach. Nevertheless, debates exist on the reliability of this approach to compute flow through tubes or trees close to the edges, a general caveat found in all homogenization procedures; in fact, when quantities vary on a length-scale of the order of the distance between individuals, the averaging procedure used to define the equivalent continuum fails. For instance, the fluid forces on the first tree of a forest edge or on the external tube of a steam generator might not be accurately predicted with this method, and local effects are typically ignored in this approach. Edge effects are always a specific problem in mechanical engineering. For SGs, outer tubes are *a priori* less prone to flow-induced vibration as the flow is less confined, but local jet effects have been observed. A corresponding issue in ecology would the differential behavior of edge plants in a crop canopy that are not mechanically constrained on one side.

Variability

A second question that arises is that of variability. In fact, the next step in trying to model the response to flow is to apply the flow-induced forcing to a given individual vibrating system (Fig. 3). In the SG case, one would expect that all tubes are very similar, as they are man-made. Unfortunately, this is not the case in terms of their dynamic characteristics, which depend strongly on the support conditions: these conditions vary from tube to tube over the years owing to the build-up of deposits and local contact effects. Similarly, plants differ mechanically from one another even in well-controlled growing conditions. Vibration tests on a series of alfalfa plants showed variability in terms of frequency and damping (Doare et al., 2000). At this stage, the two questions to be answered are: first, can an average individual be defined that will allow the assessment of the average behavior and, second, can an extreme case be defined that will allow one to assess the extreme behavior? In SG tubes, no average individual can be defined as the nominal support condition is never observed, and the number of combinations of possible support conditions is huge. Only a statistical approach, using Monte-Carlo simulations for instance, can be used to derive the probability density function of the response (Payen and de Langre, 1996; Delaune et al., 2000). In a PC, a comparative analysis of alfalfa and wheat showed that, although the variability was much larger in alfalfa than in wheat, using an average plant was legitimate and efficient in both cases (Py et al., 2006). Then, the problem of what the most vulnerable plant, or tube, might be in the PC, or SG, differs somewhat between the two cases. In the SG, leakage of a single tube is itself a problem in the short term, so that understanding what combination of parameters might lead to damage is essential. In a PC, the lodging of a single plant is a different issue. It might have an insignificant instantaneous effect, for instance on forest biomass production, but a considerable long-term ecological effect – for instance, in creating a gap where a faster-growing species can grow. The Monte-Carlo approach mentioned above can probably be used to identify the rate of gap formation. More generally speaking, from an ecology point of view, it can produce useful results in terms of pointing out distinct behaviors that depend on the characteristics of populations. It should also be noted that, in both SGs and PCs, it is the average behavior that affects the efficiency, thermal or agricultural. Finally, a plant canopy can range from a uniform monoculture of wheat to a natural jungle canopy or a coral bed. Mechanical and geometrical variability is indeed very different in these cases. Using a Monte-Carlo method allows the taking into account of large ranges of variations of the parameters, but large numbers of simulations will then be needed to obtain reliable statistics.

Time scales

An issue that also arises in both systems is that of the multiple time scales present. In the SG case, with frequencies of motion of the order of 10 Hz, the vibratory period of motion is at the scale of the inverse of the frequency, ~0.1 s. Simultaneously operating conditions are stable over days, and the wear process occurs over months. In a PC, the plant motion is at the scale of 1 s, and wind conditions are generally stable over a day or two, and growth occurs over months or even years in trees, integrating information from the instantaneous strain over time. In both cases, a careful decoupling of the two time-scales is necessary: all flow and mechanical conditions are assumed to be constant for the modeling

of flow-induced motion (short times), and cumulative models are used to take into account the slow variation of these conditions (long times). In that sense, wear or fatigue models, such as those of Delaune and colleagues (Delaune et al., 2000), and growth models such as those of Moulia and colleagues (Moulia et al., 2006), are very similar in principle.

Length scales

The question of multiple length scales also exists in both systems. A proper modeling, as described above, requires going from the modeling of the flow pattern in the SG or PC to the modeling of the dynamic response of individual plants or tubes, taking into account local effects at even smaller scales. These slender individual components have several, and quite different, scales of length: their length-to-diameter ratio can be of the order of 100:1 or even 1000:1, and even smaller length scales are also involved, such as gaps at the supports of SG tubes, of the order of 0.1 mm (Axisa et al., 1988), or the thickness of leaves, which play a role in the stiffness of interplant contact (Doaré et al., 2004). In both systems, the ratio of large-to-small scales can exceed 10,000. This can only be taken into account, as for the time-scales, by articulating models over scales. For PCs, this requires the use of plate models for leaves, spring models for contacts and beam models for stems (Niklas, 1992). In SGs, beam models and nonlinear spring models are necessary (Axisa et al., 1988). These can also be used for nonlinear contacts between plants (Doaré et al., 2004).

Adaptation

Both systems can also be analyzed in terms of adaptation – here meaning the ability to adjust to specific stresses of the environment. For a PC, the natural adaptation to wind-induced motion is thigmomorphogenesis, resulting in a higher allocation during growth of biomass to roots, and to shorter stems (Telewski, 2006; Moulia and Combes, 2004). The consequence is, evidently, reduced vibration and damage risk. Moreover, for tree canopies, the management of edges can be used to reduce risks as trees grow (Dupont and Brunet, 2008). For SG tubes, the adaptation process is more complex. A first part is natural in the sense that the evolution of parameters during the system life-time might reduce the risk of damage in highly stressed regions. For instance, wear increases the gaps between tubes and their support, which, in some conditions of turbulent excitation, results in a lower wear rate. Ultimately, wear can thus be self-limited (Hassan et al., 2005). In that sense, there is therefore no true age-dependent degradation in a SG tube as the mechanical vibratory load that the tube supports plays a central role in the degradation, and the load can change strongly over time. The second part of the adaptation process is plugging, an operation by which the flow inside a weak tube is suppressed by the use of plugs at both ends. Then, a rupture of the tube does not provoke leakage. Of course, if too many tubes are plugged, the efficiency of exchange is diminished. Here, a significant difference appears between the two systems: thigmomorphogenesis is a complex biological process that involves mechanoperception of strains, transmission of signals and adapted growth. Its fundamental mechanisms, particularly in the dynamic range, are not clear as of today. By contrast, adaptation in SG tubes is a well-controlled process. Self-limited wear can be easily modeled (Axisa et al., 1988; Delaune et al., 2000), and plugging results from well-defined procedures (Diercks et al., 1999).

Evolution

In terms of evolution, some parallels can also be drawn, with required caution, and in a purely descriptive sense. SGs have only existed for ~50 years, but the evolution of their design has been significant, as a result of the analysis of the problems of flow-induced wear. New designs involve simple cures, such as adding supports to the tube, called anti-vibratory bars, and using materials less prone to fretting wear. Yet, the search for higher efficiency in thermal exchange has led to a denser packing of tubes, which was not compatible with reduced vibratory risk. A trade-off issue appeared that is classical in design. For plant canopies, the reduction in the height of crops is relevant here; the selection of shorter wheat, including dwarf wheat varieties, and the use of chemical agents to reduce height, does have a positive influence on yield. It can nevertheless be counter-productive on wind-induced motion for several reasons: first, shorter plants move less and therefore the beneficial effect of plant motion on internal gaseous exchange in the canopy is lost; second, their static deformation is also reduced, so that they do not benefit from drag reduction by flexibility; and finally, as the stem constitutes a much smaller part of the plant, any motion of the tip results in higher deformation of the stem, and therefore a higher possibility of fracture or buckling. Here again, a trade-off issue appears between improved agricultural productivity and increased risk of losses.

Some methodology issues

Transfers from mechanical engineering to plant biomechanics

The striking similarities between the two problems of flow-induced vibration and damage suggest that many models and methods developed in mechanical and nuclear engineering are somehow applicable to the biomechanics of PCs. In terms of computational methods, this has been the case in the modeling of flow, where the numerical methods for simulating high-Reynolds flow over canopies – for instance large eddy simulations – are almost identical to those used in standard engineering computation (Dupont et al., 2010). Similarly, finite-element codes developed for nuclear engineering have been used for the computation of the dynamic properties of plants (Rodriguez et al., 2008). These cases are illustrated in Fig. 4. Similarly, many results on the dynamics of flows in and above canopies have been derived by using the classical methods of hydrodynamic stability theory (Finnigan, 2000; Ghisalberti and Nepf, 2002; Py et al., 2006; Gosselin and de Langre, 2009). As an illustration, Fig. 5 shows how the interactions between a canopy and air or water flow differ by using such methods. Some other fields of applications seem to be unexplored, but promising and include: a probability approach for the analysis of the biomechanics of extreme events, optimization procedures in design in relation to evolution and models for cumulating damage of distinct origins, such as fatigue and creep. Progress in these fields requires a significant investment in terms of interdisciplinary work.

Nonlinear mechanics

A first challenge stems from the fact that plants are soft slender structures and are generally much more deformed under fluid loading than are man-made structures. This is quantified by the dimensionless Cauchy number (de Langre, 2008). For instance, the order of deformation, defined simply as displacement divided by length, is typically 0.001 in the SG case and 0.1 in the PC case. Unfortunately, most methods and codes used in mechanical engineering are based on the simplifying assumption that deformation is small, allowing one to work with linearized

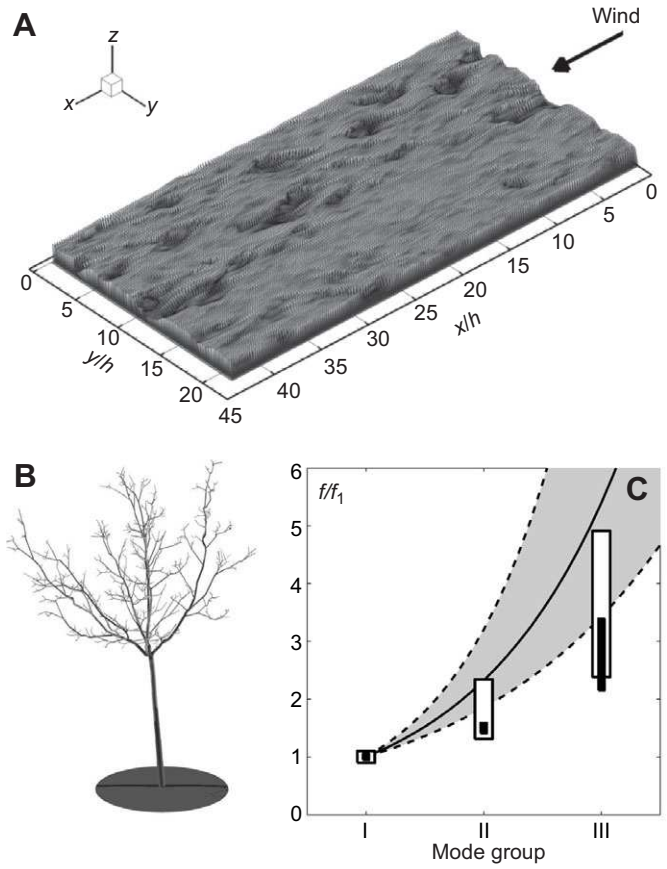


Fig. 4. Computations using standard models of mechanical engineering. (A) Flow-induced motion of a crop canopy, using the large eddy simulation technique (Dupont et al., 2010). (B) A plant-specific modal shape of a walnut tree based on the digitized geometry and computation using a finite-element code from nuclear engineering (Rodriguez et al., 2008). (C) Comparison between the dimensionless frequencies (f/f_1, f_1 being the frequency of the first mode) computed using plant-specific data (in black), frequencies measured on the actual tree (in white) and frequencies derived from the allometry parameters defining the slenderness of branches and the branching organization.

equations. To model the consequent reduction of drag by elastic reconfiguration, which is an important nonlinear effect in the interaction of flow and a canopy, it is necessary to use rather advanced models of structural mechanics under large deformations (see Fig. 6) (Gosselin et al., 2010). Nevertheless, these models exist, even in standard codes used for nuclear engineering or aerospace engineering (Stanford et al., 2008). Fig. 7 shows in a more advanced approach the sequence of breakage events in a tree under increasing flow intensity, using the same code (Lopez et al., 2011).

Geometries and materials

An important difficulty that arises in the development of a mechanical approach to plant motion is that of properly taking into account geometries and materials. This is a general issue in biomechanics, and more generally in the modeling of natural systems, even in geophysical sciences. Several approaches are possible. The first is the equivalent of what is referred to as the 'patient-specific approach' in human biomechanics (referred to as 'plant-specific' hereafter). In practice, samples are described in fine detail, both in their geometry and in the characteristics of materials (Py et al., 2006; Sellier et al., 2006; Rodriguez et al., 2008). This allows the building-up of a reasonable model of a given plant in a given state. When a canopy needs to be modeled, the plants are assumed to be identical. The plant-specific approach allows validations of intermediate modeling steps; for instance, the computed response to wind of a given tree can be directly compared with a measured quantity on this same tree. The second approach relies on the use of allometry laws that have been derived on a large number of samples. An average plant or canopy is then built, with idealized characteristics. In previous studies (Py et al., 2006; Dupont et al., 2010), the alfalfa canopy was modeled from the allometry laws based on the analysis of many plants (Fig. 8). In another study (Rodriguez et al., 2008), the modal characteristics of trees were shown to derive only from allometry parameters, using an invariant scaling relationship (Fig. 4C). A combined solution exists, where specific geometries and materials that satisfy allometry laws are generated randomly. But the most suitable solution is certainly probabilistic as material and geometries evolve with time and instantaneous environmental conditions, so that a deterministic biomechanical approach only gives one partial result. Considering the number of parameters involved and the nonlinear relationship between parameters and response, a probabilistic approach needs to be based on multiple simulations, for instance using a Monte-Carlo technique (see Fig. 8) (Delaune et al., 2000).

Growth

The true limit in the transfer of mechanical-engineering methods to the modeling of plants is the difficulty of taking into account the history of growth. A plant in a given environment is shaped in its geometry and material by its history of growth. Fundamentally, plants are able to differentiate directly their phenotypes in response to environmental stimuli. In a canopy, there exist differences between plants at the canopy edge and those inside the canopy. Edge plants have been exposed to a higher level of fluid loading during their growth, so that they might have different geometrical or material characteristics. This in turn can influence the flow, as well as the mechanical response to fluid forces. Similarly, tubes at the edge of a SG tube bundle have had a distinct history of flow forces and therefore of wear, but their geometry and material were identical to the rest at the initial stage. This issue is related to the

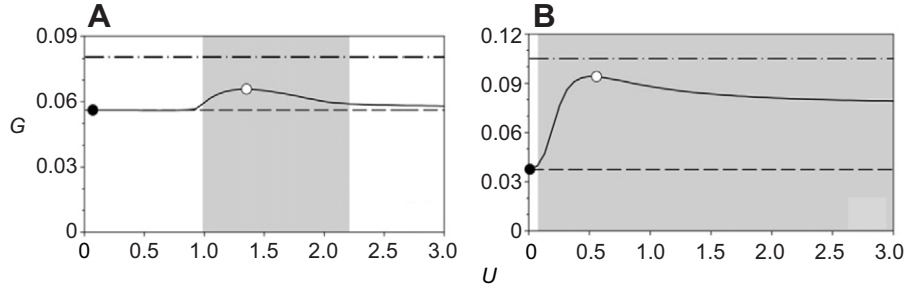


Fig. 5. Modeling the interaction between a flexible canopy and the flow using standard flow-instability theory (modified from Gosselin and de Langre, 2009). The two graphs show the magnitude of the instability (growth rate, G) as a function of the dimensionless flow velocity (reduced velocity, U). (A) In air, the strong coupling region, in gray, is limited to a small range of velocities. (B) In water, the coupling is spread over a large range of velocities.

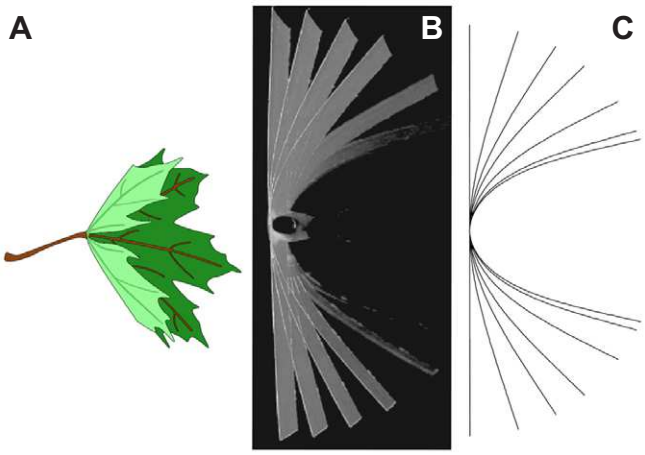


Fig. 6. Modeling the large deformation of plant organs under flow. (A) Schematic view of a reconfigured leaf experiencing wind (modified from Vogel, 1989). (B) Experiments on flow-induced bending of a plate and (C) a simulation of the same problem using nonlinear geometrical effects (Gosselin et al., 2010).

existence of several time scales, as mentioned in the preceding section. Of course, models of the effect of mechanical strain on growth are needed at this stage. This is a vast field of research that will have applications in understanding the ecology of a large variety of systems as they grow, for instance kelp (Gaylord et al., 2012), coral (Madin and Connolly, 2012) or sea grasses (Ghisalberti and Nepf, 2002).

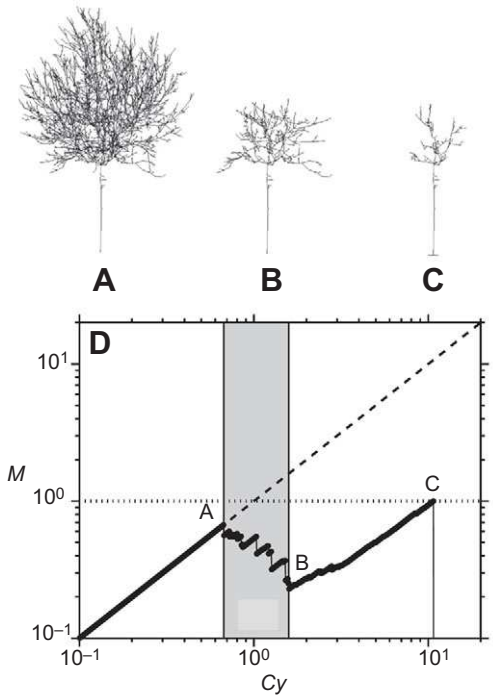


Fig. 7. The computed flow-induced pruning of a walnut, using a finite-element computation of stresses and a model of brittle behavior (Lopez et al., 2011). (A–C) Three stages of the tree: (A) initial stage, (B) after breakage of the main branches and (C) before breakage of the trunk; (D) the corresponding evolution of the moment (*M*) at the base at the function of the Cauchy number (*Cy*), which increases with the flow velocity. This sequence of breakage events results in a significant reduction of the load on the tree.

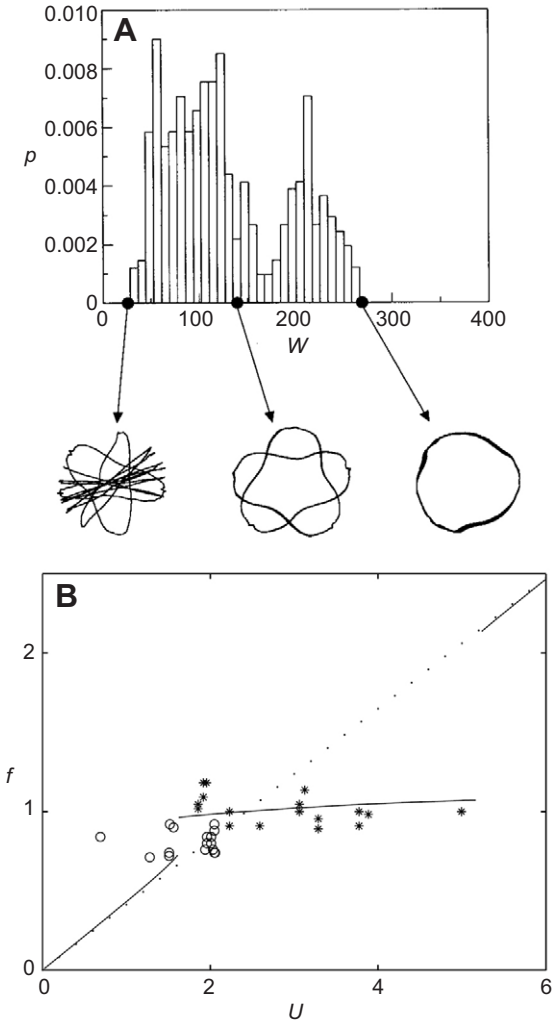


Fig. 8. Taking into account the variability in the properties of individual components. (A) The probability density function (*p*) of the wear work rate (*W*, the product of the impact force by the sliding velocity) following a large number of simulations of tube motions, in a Monte-Carlo approach (Delaune et al., 2000). The probability density function shows a large variety of possible responses of the system. (B) A comparison between experimental (symbols) and model (line) of the local frequency (*f*) of oscillation of a crop canopy under flow, as a function of the flow velocity (*U*) (modified from Py et al., 2006). The model is based on the characteristics of the average plant.

Conclusions

The use of a biomechanical approach to understand ecological issues requires first the building-up of sound biomechanical models. In the case of the effect of wind on the canopy, this biomechanical approach is not yet well established. Considerable work remains, but many approaches used in mechanical engineering are available (Table 1). Their transfer is in some cases straightforward, for instance in the computation of flows or elementary structural mechanics effects. Advanced issues can also be addressed now by using methods developed in mechanical and nuclear engineering, as has been shown for instance in the case of nonlinear structural mechanics for flexibility effects or in the case

Table 1. A summary of important remaining issues where engineering methods can be applied to plant biomechanics and ecology

Phenomenon	Modeling approach	Engineering example	Biological example	Present state and expected developments	Ecological applications
Large static deformation under flow	Geometrical nonlinearities	Membrane wings (Stanford et al., 2008)	Drag reduction in leaves (Vogel,1989)	Corresponding numerical and experimental methods not commonly used in plant biomechanics	Defoliation during storms
Dynamic deformation	Linear vibration theory	Modal shape of a U-tube (Adobes and Gaudin, 2004)	Modal shape of a wheat stalk (Farquhar et al., 2000)	Standard methods now abundantly used	Dynamic interactions between insects and plants
Dynamic deformation with contact	Numerical integration with local nonlinearity	U-tube with loose support (Axisa et al., 1988)	Oscillation of alfalfa with contact (Doaré et al., 2004)	Not commonly used in modeling of plants under flow	Interaction by abrasion between tree crowns of competing species
Evolution of properties with time or damage	Decoupling of time-scales	Fretting wear (Delaune et al,. 2000)	Growth (Moulia et al., 2006), flow-induced pruning (Lopez et al., 2011)	Need for coupled models of growth and mechanical response under flow	Shaping of canopies by dominant winds
Flow through poro-elastic medium	Numerical integration with volume force	Flow through U-tube bundle (Pettigrew et al., 2003)	Flow through crop canopy (Dupont et al., 2010)	Need for systematic description of plant canopies using porosity models with deformation	Nutrient transport in dense sea grass canopies
Variability	Monte-Carlo simulation	Effect of gap in wear test machine (Delaune et al., 2000)	Effect of plant height variability on the risk of lodging	Not commonly used in modeling of plants under flow	Plant population damage under extreme weather events

of damage propagation. At this stage, it seems inefficient to go in the direction of a detailed plant-by-plant analysis, where the exact geometrical and material characteristics of the plant are used. Similarly, all methods based on the classical assumption of small deformations miss an essential feature of plant biomechanics, which is their large deformation under flow. Incorporating growth models directly in the biomechanics of plants is certainly a very promising direction, and in that sense plant biomechanics is going to diverge significantly from mechanical engineering. Moreover, for instance in the way that variability is analyzed, some differences have appeared that are related to the different functions involved, biological or mechanical. At a larger scale, if it is desired to address ecological questions, it seems that a true understanding of the interaction of plant systems with flow in their environment would greatly benefit from methods used in system engineering for man-made components. The true challenge is in finding a well-balanced adaptation of our engineering knowledge to these plant systems. The comparative analysis of the SG and the PC shows that this is indeed possible and fruitful. Moreover, as in many cases of applications of methods from mechanical engineering to biomechanics, the benefit might also be substantial in the field of mechanical engineering itself, in terms of the generality of the methods (Crimaldi, 2012).

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