



REVIEW PAPER

Plant vibrations at all scales: a review

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Abstract

Plant vibrations is a wide subject that covers topics ranging from the swaying of trees under wind to elastic waves made by an insect on a leaf to communicate with its neighbors. For this reason, the state of the art is somehow fragmented over several communities. This review aims at giving a general overview of the main results and challenges in plant vibrations. Several scales are considered, from the very small and local, in leaves or fruits, to large canopies of many plants.

Keywords: Damping, mechanics, modes, swaying, vibrations, waves.

Introduction

Plants, in the widest definitions, have been recognized as mechanical systems: this led to a definition of the general field of plant biomechanics (see, for instance, [Niklas, 1992](#)). Their mechanical characteristics such as their elastic stiffness have been widely documented. The deformation under gravity or wind loading, and the risk of loss of stability, for instance by lodging or buckling, could be assessed. More generally, even at the cell level, where turgor pressure is a key load, a mechanistic point of view has allowed a better understanding of how plants live and die ([Niklas and Spatz, 2012](#)). However, plants, and their substructures, have not only stiffness but also inertia. Because of this, they are susceptible to all dynamic effects such as elastic wave propagation and vibration.

The purpose of this review is to try and give a general understanding of the present knowledge and forthcoming issues in these aspects. The author is a mechanical engineer, as will be clearly apparent to botanists, who has been working in this domain for ~20 years, and has been fascinated by the variety of questions that arise in plant dynamics and vibrations.

The canonical case of plant vibration is that of the free oscillating motion of the stem of a plant after a gust of wind.

This is ubiquitous, but is only one of the many cases where dynamic effects play an important role. To obtain a more general view, one needs to consider the range of length scales involved. Below the level where plant sway motion occurs ([Fig. 1a](#)), dynamics are also present in subsystems ([Fig. 1b](#)), for instance in the swaying of branches, the flutter of leaves, or the oscillation of fruits. It may also play a role in wave propagation in stems excited by insects. At a scale above the plant level, dynamic interactions between plants occur when they touch each other in their oscillation. Finally, considering a large number of plants ([Fig. 1c](#)), one may also consider crop, kelp, or forest canopies as porous and elastic media that interact with the surrounding flow ([de Langre, 2008](#)).

As a consequence, there is a very large variety of motivations for the exploration of dynamic effects in plants. The most developed one is certainly plant, particularly tree, vulnerability to wind loading ([Gardiner *et al.*, 2016](#)). In such a case, the rapidly fluctuating nature of wind needs to be considered, not just its time average magnitude. A lot has been done to measure and model tree dynamics (see, for instance, [Moore *et al.*, 2018](#)). Branch dynamics followed, as it clearly appeared that a tree

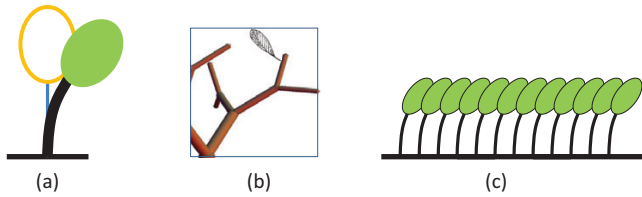


Fig. 1. A schematic view of the scales where vibrations occur in plants: (a) swaying at the plant scale; (b) motion of subsystems such as branches, leaves, or fruits; and (c) motion of a whole canopy, as a continuum.

sway involved such motion (James, 2003). In water, the strong oscillating loading by waves has also been considered as a dynamic loading (Denny, 2014).

However, the lower scale level has also retained growing attention. Leaf fluttering and, more generally, foliage motion has been studied within the scope of photosynthesis (Burgess *et al.*, 2016), gaseous exchange (Grace, 1978), water retention, or herbivore attacks (Yamazaki, 2011; Appel and Cocroft, 2014; Warren, 2015). Fruit motion, such as that of olives (Tombesi *et al.*, 2017) and citruses (Torregrosa *et al.*, 2014), is a rather specific domain, because motion is then caused artificially by a shaker, as a means of harvesting.

These levels of motion, from organ to whole plant, have also interested electrical engineers for their effects on Wi-Fi transmission (Pelet *et al.*, 2004). In relation to visual perception by humans, the graphic rendering community for video games and animated films has put great efforts into modeling plant motion (see, for instance, Diener *et al.*, 2009). Not only humans are visually affected by plant motion: primates and lizards are known to adapt their gestural language in the presence of moving plants (Peters *et al.*, 2007; Roberts and Roberts, 2015). However, plants are also wave-bearing systems: insects communicate using elastic wave propagation along stems (Cocroft and Rodríguez, 2005). Motion of canopies has been considered in crop science, for the purpose of avoiding lodging, but also in seed and pollen propagation and capture (Nathan and Katul, 2005). In addition to all these, plant motion has been identified as a major factor in plant thigmomorphogenesis and proprioception (Coutand *et al.*, 2009; Bonnesoeur *et al.*, 2016; Hamant and Mouliia, 2016; Nicoll *et al.*, 2019).

Vibrations are also a way for testing: the time of flight of acoustic waves or the frequency of acoustic resonance are reliable ways to infer elastic properties of wood for tree and log segregation (Apiolaza, 2009; Legg and Bradley, 2016) or to estimate the moisture content in the wood, which is related to wood color (Suyama, 2014). Recent developments include the use of vibrations for high-throughput phenotyping of plants (de Langre *et al.*, 2018; Nakata *et al.*, 2018), or ripening tests (Hou *et al.*, 2018).

Considering all this variety of scales and applications, some clarification is needed. Below we shall first recall the concepts in dynamics and vibrations that will be used thereafter. The plant scale level will be addressed in a subsequent section, followed by smaller scales, from leaf to fruits, and larger scales. Experimental methods, and some more advanced topics, are discussed in the final section.

Some useful concepts in vibrations

We first recall some elementary concepts and models in dynamics and vibrations. More details may be found in classical textbooks (Weaver *et al.*, 1990; Graff, 2012; Thomson, 2018).

Modes and waves

A first note must be made on the amplitude of the motions that are considered. If they are small enough, in comparison with the size of what is deformed, the whole framework of linear dynamics and vibrations is applicable. Provided the system (plant, fruit, canopy, etc.) is assumed to respond elastically and to have some inertia, some coupling may then occur between the spatial variations of deformations and their temporal variations. This is the general field of dynamics. This coupling may materialize in propagating (elastic) waves, such as those sent by insects to communicate through a stem: a local deformation is propagated. It may also materialize as vibrations, where deformations do not propagate but oscillate in place, such as in the swaying of a full tree. In the latter case, a very important concept of linear vibration theory can be used, which is that of vibration modes. A mode of vibration refers to a particular shape of free motion that can oscillate in time, eventually dying out. It is defined by its shape in space (the modal shape), its oscillation (the frequency), and the way in which it decays in time (the damping). Vibrations according to modes are observed when the system is left free to vibrate after an initial perturbation. An elastic systems has a very large number of modes, so that one, or another, or several simultaneously may be observed in a given situation of loading. For instance, referring to the tree as a model, we can observe bending modes and torsion modes, and more localized bending modes of branches. Modes are a fundamental part of linear vibrations, because they can be used to reconstruct any motion of the system by combining their response: they are intrinsic quantities. Actually all respond to excitations in a similar way, which is that of a mass–spring–damper oscillator, as illustrated in Fig. 2a. Therefore the canonical equation for vibration reads

$$M\ddot{X} + C\dot{X} + KX = F \quad (1)$$

where M is a mass, $X(t)$ is the modal motion of interest, \dot{X} and \ddot{X} are the corresponding velocity and acceleration, C is a damping coefficient, K is a stiffness, and $F(t)$ is the applied load. This equation applies to mass–spring systems, but also, quite generally, to any modal response. It is therefore useful to consider how a mode reacts to forcing, which can be an impulse loading such as with a hammer, a pull and release, a sinusoidal loading such as with a shaker, or a more complex quasi-random loading such as by wind. Impulse loading and pull and release both result in a free oscillation at the frequency of the mode $f_0 = 1/(2\pi)\sqrt{K/M}\sqrt{1-\zeta^2}$ with a damping factor $\zeta = C/2\sqrt{KM}$; Fig. 2b). A sinusoidal forcing results in an oscillation at the frequency of forcing, at an amplitude that depends on the frequency of forcing, f , with a high amplitude called resonance if the forcing and modal frequency are close (Fig. 2c). The response to random loading is a bit more

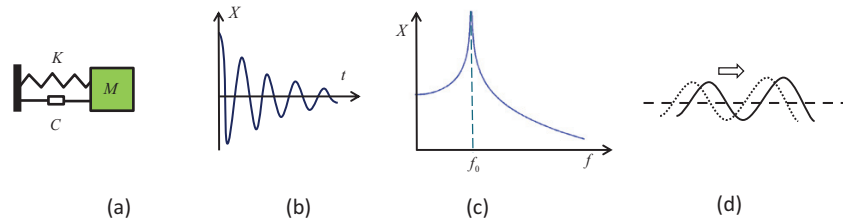


Fig. 2. Elementary concepts: (a) mass–spring–damper oscillator; (b) free oscillation; (c) resonance curve; and (d) propagating wave.

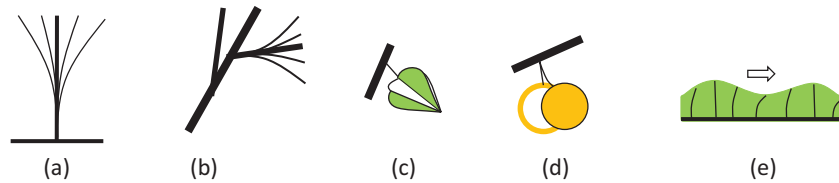


Fig. 3. A schematic view of dynamic deformations: (a) bending mode of a clamped-free beam in bending, or global swaying mode of a plant; (b) local bending mode of a branch; (c) torsion mode of a leaf; (d) pendular mode of a fruit; and (e) canopy wave or honami.

complex: the motion is also random, but its spectral content is higher in the range of the frequency of the mode. Damping reduces the time of free oscillation and the amplitude of response under oscillating or random forces.

In continuum systems that have both stiffness and inertia, elastic waves can propagate. In that case the velocity of propagation (Fig. 2d) depends on both the property of the system (stiffness and inertia) and the characteristics of the wave, such as its wavelength.

Models

Numerous models are in current use to represent these effects. Because it satisfyingly represents the response of a mode, the mass–spring–damper oscillator model above is much used. However, the meaning of the parameters and their relationship to what is known of the plant (geometry, stiffness, etc.) is not straightforward, except for some simple geometries such as a fruit or a leaf. When considering stem vibrations, particularly in pole-like trees, models of bending beams are quite useful. Here, the stiffness and mass are continuously distributed along a particular axis. For instance, in a straight beam, the transverse displacement $Y(x, t)$ satisfies

$$BY^{(4)} + m\ddot{Y} = F, \quad (2)$$

where B is a bending stiffness, m is a mass per unit length, $Y^{(4)}$ is the fourth derivative in space, \ddot{Y} is the acceleration, and $F(x, t)$ is now a local load. In the absence of load, this leads to bending modes that can be determined easily (Weaver *et al.*, 1990; Fig. 3a). For more complex geometries, for instance branched, numerical methods such as the Finite Element Method are needed to solve the differential equations. In terms of wave propagation, simple models are available to relate the velocity of the wave to the frequency of the excitation, when the bearing medium is a beam in bending (for a stem), or a plate (for a leaf), or a continuum canopy with interacting plants. Models also exist to take into account in a simple way the presence of the fluid surrounding the vibrating system (see, for instance, Blevins, 1977;

Päidoussis *et al.*, 2010; Axisa and Antunes, 2006). If the fluid is barely moving by itself, its presence can be taken into account by simple changes in the oscillator equation above; the mass would increase, the stiffness would increase by buoyancy (an important effect in water), and damping would also increase because of the viscosity of the fluid. If the fluid does move by itself, wind, or current, many phenomena may interfere with the dynamics of the solid: forcing by vortices, strong coupling between the solid motion and the flow that decreases the apparent stiffness and the damping, up to flow-induced instabilities. As an example of flow-induced instabilities in plants, one may cite leaf or kelp blade flutter, but also in some aspects crop canopy oscillations under flow. All these may and do happen for plants, and affect plant vibrations either as causes or as perturbations.

The characteristics of the modes (shape, frequency, and damping) may also be obtained from experiments. Considering the complexity of the geometries, and of materials, this is often the only way to obtain reliable data. Exciting the mode can be done by impact, pull and release test, sinusoidally shaking (shaker), or, more complex, a natural random loading. Measuring the motion involves traditional techniques in vibration engineering such as accelerometers, strain gauges, optical target monitoring, electromagnetic tracking, and laser vibrometers. However, video image processing has developed a lot, allowing both high speed and high spatial resolution, with simple portable devices, at the cost of intensive image processing.

So far we have essentially defined these motions by the displacement in the plant. However, strain of tissues which can be derived by taking the spatial gradients of the displacement are of interest for fracture, but also in models of thigmomorphogenesis (Coutand *et al.*, 2009). As noted in Tadriss *et al.* (2018) for foliage dynamics, displacement may be relevant for light capture, but velocities are the quantities of interest for perception (human or animal) and Wi-Fi interactions, and accelerations for water and insect retention.

At this stage, one may expect some general trends on dynamics in plants, considering their specificities and differences

from more classical mechanical systems in engineering. First, plants are rather softer systems, by both their material and geometries, than many man-made systems of comparable size. As such, the frequency of free oscillation f_0 is expected to be lower. In fact, most frequencies found at the plant scale or organ scale are of the order of 1 Hz or 10 Hz, which is quite low in vibration engineering for systems of the size of plants. Secondly, because of the complex architecture of plants, one may expect a multitude of modes to play a role. For instance, whereas a simple beam has well-separated bending modes, in a tree with 10^4 leaves there will be vibration modes for all and every leaf, at very similar frequencies: the modal density is huge. Finally, because of their flexibility, plant deformations are expected to be of the order of their dimensions, even under small loads, and the limits of the framework of linear vibrations and waves may be reached. Still, dynamics and vibrations are worth studying in plants, and reveal astonishing features.

Dynamics at the plant scale

Schematically representing a plant by a flexible system of stems and leaves anchored in the ground, a mode of vibration can be observed corresponding to the whole swaying of the plant (Fig. 1a). In such a mode, schematically, the strongest bending occurs in the lower part of the plant, the upper part of the plant thus being rotated during the sway. The frequency of the mode will depend on the stiffness of the stem, on the inertia of the whole body, and of course on the size of the plant. This mode will be found at all scales, from the small shoot to the largest trees. It is actually a double mode, as the plant may oscillate in any direction.

Experiments

Measuring the frequency of this mode is rather straightforward: exciting the plant by impact, or more efficiently by pull and release, and counting the time of a period. Even a shaker can be used, looking for resonance. Strain gauges on trees, accelerometers, or, quite easily now, videos are easily used and processed, as the motion affects the whole plant. Some examples are given in Farquhar *et al.* (2000); Rudnicki *et al.* (2001); Brüchert *et al.* (2003); Moore and Maguire (2005); Schindler (2008); Kane and James (2011); Rodriguez *et al.* (2012); Kane *et al.* (2014); and Kovacic *et al.* (2018). Measuring the damping requires that the sway is not too damped, so that its decrease is observed over a few periods or, if artificially forced resonance is considered, that a fine analysis of the resonance response is done. Even for such a simple motion of the plant, the accurate determination of damping is always much more difficult than that of the frequency: the idealized model of linear damping does not really apply for such complex systems, and damping is often found as a consequence to depend strongly on the amplitude of motion. Moreover, the high level of damping often does not allow fitting the parameters on a long enough signal of free decay. The modal shape, finally, is easily obtained from video analysis, although this may only give a partial knowledge of the motion, as some parts may be hidden. However, this is not an important issue as the plant does move as a whole in its upper part. The

motion may be more complex than that idealized above; for instance, a whole plant motion may include some torsion, as in trees with asymmetric crowns (Skatter and Kucera, 2000; James, 2003).

To draw a general picture of what is known about these modes in plants is somewhat oversimplifying, but some trends appear. First, the frequency of oscillation f_0 depends on the size of the plants but within only about one order of magnitude, which is not much considering the variety of sizes: for instance a few Hertz for wheat in Py *et al.* (2006) and 10 times less for trees in Moore and Maguire (2004). Secondly, the modal damping ζ varies a lot between species and individuals. It is clearly affected by the foliage, the stem lignification, and the complexity of the architecture: dampings of the order of 5–20% are common in plants on the first mode of swaying (Milne, 1991; Brüchert *et al.*, 2003; Spatz *et al.*, 2004; Speck and Spatz, 2004; Moore and Maguire, 2005; Spatz and Theckes, 2013; Gardiner *et al.*, 2016). This allows a few oscillations before stopping. Removing leaves on a giant reed (Speck and Spatz, 2004) or preventing crown contact by pruning shows that damping is not caused by just one mechanism: interaction with the surrounding fluid, internal dissipation, or contact with other plants. For aquatic plants, overdamping with the damping coefficient >1 is common, so that no free oscillation is generally possible.

Models

In terms of modeling, an immediate parallel can be made to the classical clamped beam and its first mode of vibration (see Fig. 3a). In such a model, the mode shape and frequency can be computed, and the mode shape resembles what is observed in plants.

The frequency f_0 of a uniform beam is of the order of $\sqrt{B/mL^2}$ where m is the mass per unit length of the beam, B is the bending stiffness, and L is the length. In a plant, the mass is not uniformly distributed, nor is the bending stiffness, which depends on the diameter of the stem, but this formula gives a first-order approximation. The more important result is the dependence on the size of the plants. Assuming that the mass per unit length m scales as the cross-sectional area and that the bending stiffness B scales as that of a cylindrical beam, which scales as the D^4 , the frequency should vary as D/L^2 (Gardiner, 1992; Moore and Maguire, 2004). The other parameters, the density and the stiffness of the tissue, are not expected to vary much across species or individuals. The length and diameters are generally thought to be related by simplified allometry laws where the diameter D varies as L^β , and, as a result, the frequency would vary as $L^{\beta-2}$. The value of β varies enormously among plants but, if a value of 1.5 was assumed (McMahon and Kronauer, 1976; Moulia and Fournier-Djimbi, 1997; Rodriguez *et al.*, 2008), the frequency would only weakly vary with length, as $L^{-1/2}$. This first-order model may be and has been considerably refined, considering beams of variable sections, local loads of crowns, and more realistic geometries with numerical methods (Fournier *et al.*, 1993; Kerzenmacher and Gardiner, 1998; Sellier *et al.*, 2006; Murphy and Rudnicki, 2012; Pivato *et al.* (2014). Interestingly, as the frequency of the first mode of oscillation of a tree also depends on the mass of the foliage, it is affected by the presence of intercepted rain (Selker

et al., 2011). Root anchoring, which is not a perfect clamp but has some rotational stiffness (Neild and Wood, 1999), does not seem to influence the frequency a lot, except in water-saturated soils. Numerical modeling of the whole plant by Finite Elements does provide accurate information on these modes (Sellier *et al.*, 2006; Rodriguez *et al.*, 2008), but requires some detailed knowledge of the geometries, which is often not available. For plants underwater, the stiffness is greatly affected by buoyancy forces, without which the plant would often not even stand up. Moreover, the inertia to be considered includes then the added mass, which corresponds to the entrained mass of water in the motion and depends a lot on the geometry. For these reasons, the frequencies do not follow the same trend as in air, and ad-hoc modeling is necessary, and possible (Stewart, 2004, 2006). In the case of oscillatory flow such as induced by waves, the dynamics of the blade-like plants or part of plants may be quite complex (Luhar and Nepf, 2016; Leclercq and de Langre, 2018).

The modeling of the damping of plant-level modes is complex, as several mechanisms dissipate the energy of the oscillations (Spatz and Theckes, 2013). A first is the dissipation that occurs inside the tissues of the plant as they deform in the oscillations (see Spatz *et al.*, 2004). A second mechanism is the interaction of the plant with the external fluid and, to a lesser extent, with the soil where it is rooted. The former will increase with the interaction area: a deciduous tree will be more damped in summer than in winter, because of the presence of leaves. The latter will increase with the ability of roots to move and to experience friction. Finally, the apparent damping of this first mode is also increased when some of the motion on this mode is transmitted to other modes, without return (Spatz *et al.*, 2007; Theckes *et al.*, 2011, 2015). This is particularly the case when frequencies are close, as in branched architectures (Rodriguez *et al.*, 2008). For instance, in a model branched system, Theckes *et al.* (2015) showed theoretically and experimentally that the damping induced by the transfer to branch modes could vary from 0 to 2%, from small to large oscillations (as a function of the size of the system). Note that this differs from the linear coupling between modes that is found when their damping is high: here, the transfer of energy requires that the amplitudes of motion are large enough that the motion in one mode excites another one.

To summarize, a lot is known about the modes of vibrations at the plant scale. For trees, this allows mechanistic models of wind-induced damage to be built (Gardiner *et al.*, 2008). The role of dynamic effects in the response of a tree to wind depends on the wind loading (Gardiner *et al.*, 2016). For instance, in a canopy, the loading is due to low-frequency eddies, and the trees are excited far from their resonant frequency (Schindler and Mohr, 2018, 2019). Research now includes specific problems that appear for complex geometries, such as the role of branch architecture, or interactions with neighboring plants (Schindler *et al.*, 2013).

Smaller scales: branches, leaves, and fruits

Branches

As noted in the Introduction, much of the knowledge on vibrations in plants comes from the domain of trees. If one tries to analyze further than the global motion of the plant, a more

complex dynamic landscape arises. Experimentally, when a plant is excited locally, such as by an impact or by pull-release on a branch, or by shaking at higher frequencies, some modes are found that have higher frequencies and more localized mode shapes (see, for example, Castro-García *et al.*, 2008; Rodriguez *et al.*, 2012; Spatz and Theckes, 2013; Der Loughian *et al.*, 2014). These experiments require that the plant motion is measured at more than one point, ideally at all points by image analysis (Barbacci *et al.*, 2014). It was recognized (James, 2003; Rodriguez *et al.*, 2012) that there was a somehow decoupled motion of branches, provided they were small enough when compared with the trunk. More precisely, a branch could sway almost independently of others, in addition to the motion it had as part of the whole-plant motion. Because of the difference in mass, the oscillation of an individual sufficiently small branch would not cause the motion of the whole plant. In an idealized view (Rodriguez *et al.*, 2008), each level of branching provides a new set of localized modes, that only affect the branches further down the branching pattern.

Modeling these higher modes may also be done using simple beam models (Fig. 3b). For instance, if a branch sways on an almost still trunk, the canonical clamped beam model applies. Again the scaling analysis may provide some information on the frequencies of the modes in a given plant as one goes higher in branching orders. Rodriguez *et al.* (2012) showed that the frequencies of higher modes increased very slowly with the branching order. This proximity in frequencies allowed a possible energy transfer; see the damping by branching mechanism discussed in the previous section.

Leaves

Leaves, due to their small individual masses and sizes, compared with the whole plant, can often be considered as local, independent subsystems (Vogel, 2012). This means that their proper dynamics are independent from one another, and do not affect the global (trunk) or even semi-global (branch) modes, though of course their mass needs to be taken into account in these higher scale modes, as they are carried in such motions. A leaf, isolated from a dynamic point of view, may be considered in terms of its global motions. In an idealized scheme, it may oscillate up-down, sideways, and in torsion (Fig. 3C). In these motions, the bending occurs in the petiole (Niklas, 1991; Vogel, 1992) while the lamina contributes by its inertia. Measuring these modes becomes more complex than those at higher scales. Because of their flexibility, only non-contact techniques may be used, namely laser or videos. Considering the huge variety of geometries, no general trend may be given for the frequencies except a clear decrease with size, and a dependency on the turgor pressure, that affects the stiffness of the petiole (Gonzalez-Rodriguez *et al.*, 2016). Damping seems to originate mainly with the interaction with air, but friction with other leaves may exceed this (Tadrist *et al.*, 2018). Some autonomous motions of the leaves, called fluttering, exist in the presence of wind (Tadrist *et al.*, 2015). Modeling leaf modes requires a good knowledge of the petiole stiffness in bending and torsion, and of the inertia of the lamina. If these are measured separately, combining them in a mass-spring model gives

satisfactory results. An issue which is specific to leaves is their response to wind excitation. An individual leaf may be set into motion by several distinct mechanisms. First, turbulent fluctuations in local wind velocities result in randomly fluctuating pressures on the lamina. This causes a motion of the leaf, in its bending mode (up–down for a horizontal leaf), generally of small amplitude. Secondly, a strong coupling between the leaf and the flow of air exists and may cause vibrations, if the air velocity is high enough. This is a fluid–solid instability called torsion flutter, and can be modeled using methods common in aerospace engineering (see [Tadrist et al., 2015](#)). In some reduced ranges of velocities, a third mechanism may play a role, called vortex-induced vibrations ([Shao et al., 2012](#)), where the leaf motion is coupled to its own wake.

If one needs to consider the dynamics of the whole set of leaves, the foliage, some wider analysis is needed. It is then found that the absolute motion in the foliage is dominated by individual leaf flutter at low wind velocities, and by the response of the whole branches to wind turbulence at higher wind velocities ([Tadrist et al., 2018](#)).

In water, the configuration is quite different (see, for instance, [Puijalon et al., 2008](#); [Miller et al., 2012](#); [Albayrak et al., 2014](#)). The forces due to the presence of water totally dominate the inertia, and the destabilizing forces are very strong, even at low velocities.

Fruit

Fruit, more particularly orchard fruit such as olives or oranges, are also small-scale mechanical subsystems of the plant. Most of the interest in the dynamic motion is motivated by harvesting using harmonic shaking. Similarly to a leaf, the simple motion where the fruit oscillates as a pendulum attached by the stem is evident ([Fig. 3d](#)). Experimental measurements showed a frequency that is reasonably uniform in a tree, due to a small variability in fruit mass, and a rather low damping ([Castro-Garcia et al., 2017](#)). Providing a harmonic excitation of the support (the tree), a resonance can be achieved and high amplitude of the response results in high stress in the attachment, with cumulative fatigue damage, and thereby harvesting ([Tsatsarelis, 1987](#); [Tombesi et al., 2017](#)). This simple view does not contain the further refinements of the approach: the highest level of harvesting is actually achieved when the shaker frequency is set not at the frequency of resonance of the fruits but at twice its value ([Torregrosa et al., 2014](#)). In that case, large amplitudes of oscillation of the fruit can be obtained by a non-linear resonance effect.

Pollen

Vibrations have been shown to play a role in the release of pollen ([Urzay et al., 2009](#); [Timerman et al., 2014](#)). In that case, the motion of the stamen, induced by wind, is necessary to create the appropriate conditions for the ejection of pollen grains from the anther: large amplitudes of oscillation result in large inertia forces that are sufficient to shed pollen grains. Note that for these motions to exist, it is necessary that the oscillating stamen is not much damped in its main mode of

oscillation, which is a strong constraint on its structure and close environment. Wind-induced vibrations may also play a role in the ability of plants to capture air-borne pollen grains, as the collecting reproductive surfaces, in their motion, intersect the incoming flow more efficiently ([Krick and Ackerman, 2015](#); [McCombe and Ackerman, 2018](#)).

Larger scales: canopies

We have so far considered here plants as isolated individuals. However, they often grow in the vicinity of neighbors, and this affects their dynamic behavior. One may distinguish two limiting cases, for the sake of simplicity. The first one is that of two similar plants that interact; the second is a continuum of multiple plants.

In the interaction between two plants, a canonical case is that of crown interactions in trees. As trees move with large amplitudes under wind, crowns may touch ([Rudnicki et al., 2001, 2008](#)). This induces energy transfer between trees, and between tree-scale modes and branch-scale modes; by this, dissipation, and therefore apparent damping, will increase. For crops such as alfalfa, interaction through contact in leaves leads to an added effective stiffness, increasing the apparent frequency of oscillation, but also damping ([Doaré et al., 2004](#)).

In a denser and more continuous setting, the canopy, oscillations under wind have been observed and described by [Inoue \(1955a, b\)](#), ([Finnigan and Mulhearn \(1978\)](#)), and [Finnigan \(1979\)](#). Experimentally measuring the motion of a canopy requires a large set of data, from video analysis (see, for instance, more recently [Py et al., 2005](#); [Hobbs et al., 2007](#)), and for an artificial canopy ([Barsu et al., 2016](#)). Not considering scales smaller than the plant, a relationship exists between the frequency of oscillation and the wavelength of the oscillation. Without interaction between plants, the frequency is constant with the wavelength. With interaction, it increases as the wavelength decreases. The corresponding dispersion relationship may be coupled with that of the fluid dynamics, to analyze flow–canopy coupling ([Py et al., 2006](#)). This also exists in water ([Ghisalberti and Nepf, 2006](#); [Gosselin and de Langre, 2009](#)). These phenomena of wave propagation are referred to as honami ([Inoue, 1955a](#)) in the presence of wind, and monami in water flow ([Fig. 3e](#)). However, the main factor affecting wind-induced damage on crops does not seem to be due to dynamic effects ([Gardiner et al., 2016](#)). For tree canopies, the response seems to be much more decoupled, because the frequencies of eddies normally fall well below the resonance frequencies.

Advanced topics

The evolution of experimental methods

A large number of methods are available to measure vibrations, and waves, in plants (see, for instance, [de Langre, 2008](#) for wind-induced motion, and [Legg and Bradley, 2016](#) for acoustic waves). The choice of an appropriate method depends strongly on the scale of the system of interest (plant, leaves, or canopies), on the quantity to measure (local or global), and on the

environment (indoor or outdoor). Some specificities of plants, in terms of vibration measuring techniques, are the complexity of the geometries, the high flexibility, and, of course, the outdoor environment. Classical techniques have been used for decades on plants (strain gauges, accelerometers, displacement transducers, inclinometers, and optical target monitoring). They are often intrusive by their loads and the wirings, and are not well adapted to light systems such as twigs, leaves, or fruits. Laser vibrometers are commonly used now, for instance in Casas *et al.* (1998), to measure motion without contact.

Recent developments in technology are rapidly changing the experimental techniques. Using the new possibilities of data storage on cards and battery autonomy, continuous measurement of oscillations over months can now be done on several trees in the natural environment (Gougherty *et al.*, 2018). Small and light autonomous accelerometers will become available to be used more systematically in the outdoor environment. However, the major developments in vibration measuring techniques for plants are in the field of optics: video cameras, even with a high rate of frames per second, are commonly available, with growing data storage facilities. This allows capturing the motion of whole plants, organs, or canopies, and then, by image processing, deriving the relevant parameters of interest. Real-time analysis becomes feasible. Many of the recent papers cited in this review use video capture as the method of vibration measurement (Miller *et al.*, 2012; Torregrosa *et al.*, 2014; Luhar and Nepf, 2016; de Langre *et al.*, 2018; Kovacic *et al.*, 2018; Leclercq and de Langre, 2018; Nakata *et al.*, 2018; Tadrist *et al.*, 2018).

Interactions with hosts

Plants are essential components of the habitat of many species. Birds rest on branches, monkeys jump from branch to branch, and insects communicate. These hosts may at first be considered as sources of excitations for the vibrations of the plants (Casas *et al.*, 1998). In some cases, such as for orangutans (Thorpe *et al.*, 2007; Van Casteren *et al.*, 2013), their mass needs also to be taken into account in the dynamics of the branches, not just by the transient weight loading it causes. The domain of insect-plant dynamic interaction has been extensively explored to understand inter-insect communication or prey-predator interactions (reviewed in Coccoft and Rodríguez, 2005). For insects, propagating vibratory signals through the plant structure may be more efficient than communicating through air. Considering the size of insects, the typical range of vibrations they can induce on the plant is of the order of hundreds of Hertz. These frequencies are quite far above those mentioned above for modes of whole plants or even smaller subsystems. They will therefore excite more local modes (for instance, local undulations of a lamina), and a wave propagation approach then becomes more relevant. A stem, for instance, excited far above its first mode of bending behaves as a wave-bearing system. These are well-known models: waves propagate with velocities that depend on their frequencies, allowing a rich signal content (Casas *et al.*, 2007; Miles, 2016). Insects also take advantage of possible resonances of the modes in the plants they excite (Polajnar *et al.*, 2012). Leaves are indeed sensitive,

in their growth, to high-frequency excitation, as a mechanism to fight against chewing (Appel and Coccoft, 2014), and their motion under wind may also deter herbivores (Warren, 2015).

Phenotyping

As modal and wave propagation parameters depend on the mechanical and geometrical characteristics of the plants, they may be used to infer some properties. At the plant scale, following Der Loughian *et al.* (2014), some recent work has shown that the frequency of oscillation of the first mode (de Langre *et al.*, 2018), or of part of the stem (Nakata *et al.*, 2018), may be used as a relevant way to phenotype individual plants. In fact the frequency, in combination with geometrical information that can be measured simultaneously, can be used to characterize a combination of mass and stiffness, or their evolution. For instance, in the simple beam model above, measuring f_0 and L allows one to derive B/m . The frequency is also a measure of the margin to buckling (Timoshenko and Gere, 2009).

Impacting leaves by an acoustic field is also efficient to evidence the changes in local properties due to water stress, (Sano *et al.*, 2015), and fruits can be tested by high-frequency probes (Hou *et al.*, 2018). In that case, it is the property of the bulk of the fruit that is involved in the response, not that of the fruit-stem pendular system. From the wave propagation properties, the ripeness of the fruit may be inferred. In wood, as the velocity of elastic waves depends on both density and modulus of elasticity, direct measurement of this velocity can be done by the time of flight along a given distance, following an impact (see Legg and Bradley, 2016). This can be used for early selection of trees in a breeding program (Apiolaza, 2009) or for moisture and wood color estimates (Suyama, 2014). More generally, the evolution in time of dynamic properties such as frequencies, damping, or wave velocity may give useful information on the evolution of the plant. For instance, tree phenology has been monitored over a whole year using tree oscillation frequencies (Gougherty *et al.*, 2018).

Visual rendering and communication

The motions of plants are central to the perception of the environment. Using the knowledge on plant vibration to build realistic animated virtual scenes is by itself a challenge: real-time computation is necessary in video games requiring simple models. Even in animated films where the time constraint is less severe, it is quite difficult to build a full model of a plant environment. A simple plant-scale mode sinusoidal animation is clearly inefficient to give a realistic impression. The inclusion of higher modes, such as in Diener *et al.* (2006, 2009) and Zhao and Barbič (2013), is already a significant improvement, with a small increase in cost as only a few modes are needed. To include foliage motion is more problematic. This is a field of intense research. In a more indirect way, plant motion is known to affect visual communication between animals; chimpanzees have been observed to adapt their gestures in a mating context to the presence of wind, which moves the surrounding plants (Roberts and Roberts, 2015). Similar features have been

observed for communication by tail motion in lizards (Peters *et al.*, 2007).

Simple rules

Considering the immense variety of geometries and materials in the systems we have mentioned above, it might not seem possible to give ‘rules of thumb’ or simplified equations that would be applicable to vibrations in plants, in general. Some elements may, nevertheless, be given that, we hope, would be of some use to biologists and botanists.

First, for particular systems, such as trees, well-established correlations exist, because of the very large set of experimental data collected over years. A strong correlation has been found between the geometry and the frequencies of the first mode of bending (see, for instance, Moore and Maguire, 2004).

Secondly, some general rules of vibration engineering apply and may be adapted: the frequency of oscillation of a mechanical system scales as $\sqrt{K/M}/(2\pi)$ where K is a stiffness and M is a mass (see above). Whereas the mass of plants is a well-studied quantity, it is difficult to estimate the stiffness. However, the stiffness of a system can be deduced from its deformation under a given load. Let δ be the deformation under gravity, in the direction of the motion of interest, for instance the maximum deformation in a plant as we rotate it so that gravity acts transversally to the stem. In that case, δ scales as Mg/K where g is gravity. As a consequence, the frequency can be approximated as $\sqrt{g/\delta}/(2\pi)$. To estimate the frequency of bending of a plant or a leaf, a simple test of static deformation is needed.

Finally, because in plants the damping of the modes is often of the order of ≥ 0.1 , the amplitude of vibration will not differ too much from the deformation under a static load of the same magnitude, except right at resonance.

Conclusion

The field of plant biomechanics has, over the years, progressively evolved to consider dynamics, not just statics. This came from questions raised by various fields of plant or animal biology, as exemplified in this review. A lot of the classical tools of vibration engineering, both in experiments and in models, have been applied with success to plants. They are now commonly used in the fields of forestry, insect communication, and video rendering. A new point has been reached recently with the ability to measure vibrations using videos, even at high frequencies. By this, dynamic motion of both small (leaf or under) or large systems (full plants and canopies) can now be measured, and post-processed, efficiently. Vibration testing, which used to require advanced technology and skilled technicians, may now be done as an additional part of many programs in plant science. This opens up the possibility to build much richer models of plant vibrations, that include several scales, and their interactions with other plants or hosts. The ability to gather, almost in real time, a large quantity of data, for instance, opens the fields of phenotyping by vibrations, or correlation between plant motion and insect behavior, to cite just two examples.

A question that remains open is the biological role of vibrations in plants and, if there is a role, how plants adapt to modify or control vibrations. It must be noted first that vibrations are present in any system that has some mass and some stiffness. As soon as biomass is present in a plant, and some stiffness is created, for instance to stand against gravity, the possibility of vibrations exists. Some of these vibrations are clearly beneficial, from a biological point of view, in pollen release and capture (Timerman *et al.*, 2014; McCombe and Ackerman, 2018), and in deterring herbivores (Warren, 2015). Oscillations of kelp blade under flow are probably beneficial for nutrient exchange. Vibrations that occur naturally, under wind, might also be used by plants to read their own shape (Hamant and Moulia, 2016). This would require some mechanoperception of frequencies, beyond the well-known perception of the deformation. Leaf flutter might be beneficial in reducing the temperature of outer leaves, but it increases drag and therefore mechanical stresses (see Vogel, 2009). More generally, a dynamic response will be more severe than a purely static one, though, as noted above, the level of damping present in plants limits this effect. The most common way that plants limit vibration is probably to always have a sufficient level of damping, through several independent mechanisms: interaction with the outer fluid, soft tissues, and energy transfer to higher orders of branching.

To conclude, vibrations are naturally present in plants, in many forms, and plants have managed to find a benefit in some cases and to limit the costs in others.

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