



A general review of the biomechanics of root anchorage

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Abstract

With few exceptions, terrestrial plants are anchored to substrates by roots that experience bending and twisting forces resulting from gravity- and wind-induced forces. Mechanical failure occurs when these forces exceed the flexural or torsional tolerance limits of stems or roots, or when roots are dislodged from their substrate. The emphasis of this review is on the general principles of anchorage, how the mechanical failure of root anchorage can be averted, and recommendations for future research.

Keywords: Drag, mechanical failure, plant adaptation, plant evolution, roots, wind damage.

Introduction

Previous research has shown that the capacity of a root system to provide anchorage stability can be understood phenomenologically in terms of the degree to which root systems respond to the mechanical forces transmitted to them by their shoot systems (Pfeffer, 1893; Dittmer, 1937; Stolzy and Barley, 1968; Nass and Zuber, 1971; Coutts, 1983; Anderson et al., 1989; Ennos and Fitter, 1992; Ennos, 1993, 2000; Gartner, 1994; Stokes et al., 1995, 1996, 1997; Crook and Ennos, 1996; Stokes and Mattheck, 1996; Niklas, 1999). Nevertheless, shoot-root system interactions are influenced by a number of abiotic and biotic factors, including soil conditions and overall plant size, that are complex and difficult to analyze (Wiersum, 1957; Eavis, 1972; Kramer, 1983; Marshall and Holmes, 1988; Vogel, 2012; Gardiner et al., 2016). The goal of this paper is to provide an overview of some of the more important aspects of root mechanics and anchorage stability.

Despite all that has been learned, in comparison with what is known about the biomechanics of aerial plant organs, we are still comparatively ill informed about the mechanics of roots and how terrestrial plants are stabilized against dynamic forces. The lack of extensive data on root systems is understandable in part because subterranean portions of the plant body are difficult to access and evaluate. Consequently, from a purely practical perspective, the aboveground portions of land plants have received the most attention. In addition, understanding the mechanics of root systems presents substantial theoretical and experimental difficulties. In addition to the physical properties of roots (e.g. tissue elastic moduli, and the size, shape, geometry, and number of roots) (Ennos, 1993, 2000), root anchorage is dictated by the characteristics of the soil and the depth to which roots grow (Coutts, 1983; Marshall and Holmes, 1988; Stokes et al., 1997). Indeed, the synergism between the mechanical behavior of above- and belowground plant organs is extremely complex, particularly since the mechanics of the former is influenced by wind speed and direction, and because the behavior of the latter is influenced by the presence of other neighboring plants, soil type, and the degree to which the soil is hydrated-a feature that can change over short periods of

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time (Marshall and Holmes, 1988; Gartner, 1994; Holmes, 2015; James, 2003; Gardiner *et al.*, 2010, 2016; Albrecht *et al.*, 2016). Nevertheless, despite the complexity of the shoot–root–soil system, understanding the dynamic interactions between aerial and subterranean portions of the plant body is essential to conceptualizing important ecological phenomena such as soil erosion and stem and root lodging.

The purpose of this paper is to provide a review and summary of the current understanding of root lodging. The authors are hopeful that this review will be a useful resource for future researchers, both as a ready reference and as an indicator of research that is still needed to attain a comprehensive understanding of complex root—soil interactions that influence root lodging.

General principles

It is important to highlight the general principles that pertain to all terrestrial plants and to arborescent plants in particular: (i) aboveground organs sustain two general categories of mechanical forces, namely gravity-imposed static loads and windinduced dynamic loads (Vogel, 1981; Niklas, 1992); (ii) these forces, and the stresses and strains they induce, can interact and affect one another (Gardiner *et al.*, 2010, 2016); (iii) static loads increase slowly as a plant grows in size such that growth patterns can be adjusted developmentally to compensate for increasing static loads (Niklas, 1992; Niklas and Spatz, 2000); (iv) in contrast, dynamic loads can change hourly and sometimes dramatically, and are therefore intrinsically unpredictable (Gardiner *et al.*, 2010, 2016); (v) as a consequence, plants generally fail as a result of dynamic loads (Coutts, 1983; Anderson *et al.*, 1989); (vi) plant tissues are effective at resisting pure bending loads, but are more susceptible to failure when the loading is combined with shear or torsional loading (Niklas and Spatz, 2012); (vii) the younger parts of a plant (composed of primary tissues) typically have a lower stiffness than their older counterparts composed of secondary tissues; and (viii) the mode of failure of root tissue typically takes on one of two forms: root tissue failure near the ground level or failure of the soil–root subsystem.

Collectively, these principles bear directly on the dynamic behavior of the shoot-root-soil system (Fig. 1). For example, the magnitude of wind-induced drag forces (F) exerted on the aerial portions of a plant is proportional to the product of the canopy sail area (A) and the square of the ambient wind speed (U): $F \propto AU^2$ (Vogel, 1981). Regardless of whether this drag force is reduced by leaf and stem flexure or by mechanical 'pruning' (Niklas and Spatz, 2000), it invariably exerts a bending moment at the base of the shoot-root junction $(M_{\rm B})$, which equals the product of the drag force and the lever arm (L) through which the drag force is exerted: $M_B = FL$ (Niklas and Spatz, 2012). Therefore, mechanical stability requires that the root-soil system provides a restoring moment $(M_{\rm R})$ that equals the bending moment $(M_{\rm R}=M_{\rm B})$; that is, anchorage failure may occur when $M_{\rm R} < M_{\rm B}$ (Coutts, 1983; Ennos and Fitter, 1992; Gartner, 1994; Stokes et al., 1995, 1996, 1997; Gardiner et al., 2010).

Many biotic and abiotic factors contribute to the magnitude of the restoring moment $M_{\rm R}$ (Fig. 1). The ability of a



Fig. 1. Schematic of different kinds of roots in a 'conventional' anchorage system. (A) Four kinds of roots are illustrated (a, lateral roots; b, tap roots; c, sinker roots; d, fibrous roots). (B and C) A two-dimensional finite element model illustrating stresses within the roots and within the surrounding soil. (D). A bending moment (M_B) is generated by a drag force (F), which is proportional to the product of the square of the canopy sail area (A) and wind speed (U). The bending moment equals the product of the drag force and the lever arm over which it is exerted (L), and must be counterbalanced by a restorative moment (M_R) to ensure mechanical stability. The magnitude of the restorative moment depends on the depth of burial of the root system (d), the flexural and torsional stiffness of roots (EI and GJ), and the physical properties of the soil (density, ρ ; hydration, h; compaction c; and shear modulus, τ), which influence the friction coefficient (f) at the root–soil interface. Open triangles indicate directions of local bending forces.

section of root tissue to contribute to a restoring moment $M_{\rm R}$ is determined by the distance away from center of rotation of the shoot-root system (x), and the amount of restoring force that it can apply (R). This can be represented algebraically as $M_{\rm R}=Rx$. When evaluating the system from this standpoint, it becomes clear that the most robust root system is one that can maximize both the restoring force and the mechanical leverage of that force.

Additionally, a plant may have strategies for reducing the applied bending moment. Since $M_{\rm B} \propto A U^2 L$, and because the wind speed is uncontrollable, changes in the sail area and height due to flexure of the plant's stems or leaves can be used to reduce the applied bending moment (more about this in 'Minimizing the applied moment').

Maximizing the restoring force

The limiting restoring force that is applied to the system arises from either the root tissue, the root—soil interface, or the broader regions of soil that are indirectly affected by the root ball. As such, the tissue properties of the root, geometric characteristics of the root, friction and adhesion interface between the root and the soil, and soil material properties are of the utmost importance in maximizing the strength of a root-soil system (see for example Fig. 2).

The restoring force of the root tissue

Depending on the orientation of a given section of root tissue relative to the center of rotation, the root tissue can apply either a bending, torsional, tensile, or compressive load (see Fig. 3). Lateral roots oriented normal to the direction of the prevailing wind will experience torsion and therefore twist along their lengths as well as bend to varying degrees, whereas lateral roots that are upwind and downwind of the prevailing wind will bend primarily upward and downward, respectively (Coutts, 1983; Anderson *et al.*, 1989; Ennos, 2000). Tap and sinker roots whose axes intersect the center of rotation will flex in complex patterns.

Internal tissue stresses are dependent upon the applied loads and the material and geometric characteristics of the roots. The restorative bending load is proportional to the product of the bulk tissue elastic modulus (E) and the second moment of area (I) (i.e. flexural rigidity=EI). The restorative torque is proportional to the product of the bulk tissue shear modulus



Fig. 2. The partially exposed root system of a sugar maple (*Acer saccharum*) (A and B) and the appearance of three roots (I–III) experiencing different loading conditions (C–E) as a result of the drag forces (F) created by prevailing winds and eccentric self-loading. (C and D) Schematics of a polar and a lateral view of roots I–III showing transverse root geometries, bending and restorative moments (MB and MR), tensile and compressive bending stresses (σ + and σ -, respectively), and shear stresses (τ). (E) The formula for the second moment of area of an isosceles trapezoid, which approximates the geometry of roots I and III. The plane of bending (n) is denoted by a dashed line. [B–D are adapted from Niklas (1999) with permission of the American Journal of Botany.]

(*G*) and the polar second moment of area (*J*) (i.e. torsional rigidity=*GJ*). The restorative tensile or compressive load is proportional to the product of *E* and the area of the root (A_r) (i.e. tensile rigidity= EA_r). For example, a circular section of root with diameter *r* will have a flexural rigidity of $E \cdot \frac{\pi}{4}r^4$, a torsional rigidity of $G \cdot \frac{\pi}{2}r^4$, and a tensile rigidity of $E \cdot \pi r^2$.

Significant research has been performed in understanding both the tissue (McGarry, 1995; Operstein and Frydman, 2000; Hamza et al., 2006; Johnson et al., 2010) and the geometric characteristics (McCully, 1999) of roots. One example of this involves a large sugar maple, Acer saccharum, which was available for detailed anatomical study (Fig. 2; Niklas, 1999). Differences in the strength and stiffness (measured in bending and torsion) were determined for wood samples removed from the most recent (youngest) growth layers at different points along the lengths of three large lateral roots emerging at different compass directions from the base of this tree. These roots were selected because their orientation with respect to the direction of the prevailing wind could be determined (Fig. 2A, B) based on wind velocity measurements taken over four consecutive growing seasons (from 1996 to 1999) and because the tree canopy had been pruned heavily on one side such that the prevailing dynamic and static loading conditions on each root could be reasonably assumed (Fig. 2C, D). Specifically root I was predominantly exposed to bending, causing its upper surface to experience tensile stresses (σ +) and its lower surface to be subjected to compressive stresses (σ -); root II was predominantly subjected to torsional stresses (τ) ; and root III was predominantly exposed to bending in the opposite direction to that of root I such that the location of tensile and compressive stresses was reversed.

Analyses of wood samples removed from different portions of the three roots revealed that the compressive strength (σ_c),



Fig. 3. A coconut palm root system exposed by the erosion of beach sand during Hurricane Inike (1992). The remains of a hotel foundation destroyed by Inike is seen to the right of the root system.

elastic modulus (*E*), and torsional modulus (*G*) decreased, on average, from the base of the trunk toward the tip of each root. Each of these variables maximized at ~1 m (where root taper was maximized) from the base of the trunk. These trends were correlated with longitudinal changes in the second moment of area (*I*) and the polar second moment of area (*J*), which were sufficient in magnitude to mask the effects of differences in *E* and *G* on flexural and torsional rigidity, both of which decreased from the base of the trunk to the tip of each root (Niklas, 1999).

Two features of this study are of particular interest: (i) the stiffness of the wood in the most recent growth layer; and (ii) the transverse geometry of each root. The stiffness and compressive strength of wood samples removed from the lower surface of the most recent growth layer in root I (which experienced compression as a result of bending) were greater than those measured for samples taken from the opposing side (which experienced tension). The opposite was observed for root III. In addition, the thickness of the most recent growth layer was greater on the bottom of root I and on the top of root III (see Fig. 2D). Further, the compressive strength and shear modulus of wood samples removed from the most recent growth layer in root II (which experienced torsion) were greater than those of samples removed from roots I and III. These trends in the material properties of wood are notable because the differences in wood strength and stiffness in roots I and III were adaptive with respect to the kinds of stresses experienced in the youngest growth layers of wood.

Turning to the geometry of roots, the transverse sections near the base of roots I and III conformed roughly to isosceles trapezoids in which the largest sides were oriented toward the maximum compressive stresses. This geometry and orientation affect the second moment of area of both roots (Fig. 2C, D). As in all geometries, the second moment of area of an isosceles trapezoid, $I_{\rm n}$, increases as the cube of the dimension orthogonal to the plane of bending (i.e. $I_n \propto d^3$) (Fig. 2E). More importantly, a trapezoid minimizes compressive stresses near its large base (which is where maximal compressive stresses occur in roots I and III) because the neutral plane is closer to its larger than its smaller base. In contrast to roots I and III, the transverse geometry of root II, which predominantly experienced torsion, was circular. This cross-section may be adaptive in the context of torsion because it can minimize the polar moment of area for any given surface area.

This example illustrates how individual roots in the same anchorage system can adaptively respond to chronic mechanical perturbation induced by dynamic loading. In particular, the differences in root transverse geometry and in the material properties of the wood in roots I–III are examples of the phenomenon known as thigmomorphogenesis (Knight, 1803, 1811; Jacobs, 1954; Telewski, 2006), which has been reported for >80% of all of the species examined (Jaffe, 1973). Studies of the molecular events preceding developmental changes in stems and leaves have implicated the role of mechano-sensing stretch-activated ion channels and the cytoskeleton–plasma membrane–cell wall in the mechano–perception of wind and additional mechanical loads (Telewski, 2006; Chehab *et al.*, 2009). It is reasonable to posit that similar phenomenologies occur in the derivative cells of root vascular cambium.

The restoring forces of the soil and root-soil interface

Root depth and geometry combine with soil features such as density, hydration, compaction, and soil shear strength (d, ρ , *h*, *c*, and τ , respectively) to determine the overall strength of the root-soil system (Coutts, 1983; Marshall and Holmes, 1988; Anderson et al., 1989; Crook and Ennos, 1996; Ennos, 2000). Specifically, the interaction between root architecture and soil type plays a key role in the robustness of the root anchorage system. Roots more effectively resist bending and twisting as root depth, soil density, compaction, and soil shear strength increase. In contrast, bending and twisting become more likely as the strength of soil decreases with increasing hydration and decreasing compaction. The latter occurs for the following three reasons: (i) hydration reduces particulate cohesion and softens cemented aggregates; (ii) the development of macroscopic swelling causes uneven strains throughout the soil profile; and (iii) rapid hydration of dry soils can compress air trapped within the soil before advancing downward, whereupon it can reach pressures that exceed the tensile strength of the soil, resulting in its explosive release and soil failure (Marshall and Holmes, 1988). Other important abiotic factors are soil suction and the friction (f) generated at the root-soil interface. These two factors, along with root size and number, influence the extent to which roots can be pulled along their lengths out of the soil (Anderson et al., 1989).

Roots can actually modify the effective bulk mechanical properties of the soil. Experimental tests using different root architectures indicate that roots can enhance soil shear strength (Ghestem *et al.*, 2014), and fracture toughness and bond energy (Zhang, 2008). Additionally, this phenomenon can be advantageously implemented through the use of soil ballasting (Mamo and Bubenzer 2001; Dupuy *et al.*, 2005*a*, 2007; Gyssels *et al.*, 2005; Stokes *et al.*, 2007; Li *et al.*, 2016). In certain circumstances, the presence of roots is believed to increase the strength of the soil, improve soil stability, and decrease soil erosion. In fact, trees and plants are sometimes even used as landslide prevention and mitigation features in landslide-prone environments (Mamo and Bubenzer, 2001; Stokes *et al.*, 2007; Li *et al.*, 2016; Hales and Miniat, 2017).

One example of this ballasting effect is found by investigating an arborescent monocot, the coconut palm (*Cocos nucifera*), which survived the effects of Hurricane Iniki in 1992. Inspection of the soil within the 'root ball' of the specimen shown in Fig. 3 revealed a cement-like soil consistency surrounding the living roots, presumably because of the effects of organic exudates from the surfaces of roots on the aggregation of soil particles. This phenomenology has been reported for the root systems of other species (Price, 1911; Shane, 2011).

Maximizing the mechanical leverage of the restoring force

The second main factor in the restoring moment of anchorage systems is the mechanical leverage of the restorative force. This leverage is typically achieved through the architecture of the root system. Root system architectures vary widely between plant species, many of which have been covered in detail (Ennos, 2000). Attempts have been made to characterize root architecture, such as X-ray microcomputed tomography (μ -CT) (Mairhofer, 2012), visual scoring of architectural traits in maize (Trachsel *et al.*, 2011), and genetic mapping of root traits in maize and rice (Husakova *et al.*, 2013; Muthreich *et al.*, 2013). The root system architecture plays a key role in the restorative moment that can be applied by the root system, and understanding and manipulating key architectural features is pivotal for future plant advancement (Rogers and Benfey, 2015). Although there are many types of root architectures, many of which have been covered in detail in previous review papers (e.g. Ennos, 2000), it is worth mentioning a few examples here, and discussing how specific architectural strategies affect the mechanical leverage of the root system.

Plate root systems

Plate root systems, such as those seen in *A. saccharum*, act as shallow cylindrical volumes that can resist overturning moments. Plate root systems aim to maximize their mechanical leverage by growing horizontally away from the center of rotation to maximize the effective moment arm of the resistance forces. As such, the mechanical leverage of this system is dependent of the radius and depth of the plate. Sensitivity studies of many of the plate root system parameters have been investigated, including overall plate geometry and the effect of soil on the root plate system (Blackwell *et al.*, 1990; Cucchi *et al.*, 2004; Fan and Tsai, 2016).

Tap root systems

Where plate root systems increase their leverage by growing horizontally outward, tap root systems aim to maximize their mechanical leverage by growing downward. These systems act like pilings to resist the overturning moment of the plant. One example of this root system can be shown in a case study of the columnar cactus Pachycereus pringlei, which was studied to explore the hypothesis that the ability to resist wind-throw decreases with increasing plant size (Niklas et al., 2002). Seventeen conspecifics differing in size were examined to determine the scaling relationship among shoot height, basal stem diameter, and root anchorage. In addition, the root system of one specimen measuring ~5 m in height was excavated in detail to measure the dimensions of its lateral, tap, and sinker roots, and the material properties of the tissues in the youngest growth layers in these roots. Excavation of the root system revealed that the columnar shoot was subtended by a woody tap root measuring 1.15 m in depth and 0.20 m in width at its junction with the shoot. The tap root was connected to an extensive but shallow system of lateral roots, three of which comprised the bulk of the lateral anchorage system (designated as 1L, 2L, and 3L) (Fig. 4). The largest of these lateral roots (1L) branched into four roots (1L1-1L4), the largest of which (1L1) measured 5.15 m in length and 0.064 m in diameter at its base. The lateral roots 2L and 3L measured 3.89 m and 4.11 m in length and 0.09 m and 0.10



Fig. 4. Schematic silhouettes of the shoot and taproot of a specimen of *Pachycereus pringlei* (shown to the left) and a polar-view schematic of its extended root system. Black circles indicate the locations of sinker roots. The notion 1L, 2L, and 3L distinguish among the three principal lateral roots and their subsidiary lateral roots (e.g. 1L1, 1L2, and 1L3). [Adapted from Niklas et al. (1999) with permission of the Journal of Experimental Botany.]

m in basal diameter, respectively. The depth of burial of the proximal and most distal lateral roots varied between 0.05 m and 0.20 m, respectively. A total of eight sinker roots were observed near the base of the three lateral roots.

Examination of the anatomy of all three types of roots revealed a core of wood and a peripheral complex of tissues consisting of periderm, cortex, and secondary phloem. The number of alternating ray and axial tissue panels in the xylem and phloem increased toward the vascular cambium; that is, the number of rays increased as secondary growth proceeded. The rays and living peripheral complex tissues contained large amounts of starch. A comparison of spatially and chronologically equivalent tissue samples from the youngest growth layers within the wood revealed that the volume fraction of axial tissue increased toward the distal ends of all three types of roots. Mechanical tests of all wood samples showed that the volume fraction of axial tissue correlated positively with Young's elastic modulus (*E*) and the breaking stress measured in bending ($\sigma_{\rm B}$). By virtue of their tapering, the second moment of area (I) and second polar moment of area (J) of all root types increased proximally toward the base of the shoot.

Coronal root systems

Coronal root systems, as often seen in monocots such as wheat and maize, grow in the shape of a downward-facing cone (or crown, hence the 'coronal' moniker), and aim to balance the geometric attributes of plate root- and tap root-like systems. To quantify the robustness of coronal root architectures, systems have been developed to predict the risk of failure (Baker *et al.*, 1998). It has been found that in general, wider angle cone patterns are more robust in certain wheat cultivars (Crook and Ennos, 1994, Piñera-Chavez *et al.*, 2016).

Other root architectures

Root architectures vary widely between species, and many do not fall into one of the three main categories discussed above. Many species, such as *Mallotus wrayi*, fall in the 'intermediate system' definition, sharing features of two or more of the three main architectures (Crook *et al.*, 1997; Ennos, 2000). Investigation into more novel architectures, such as the so-called flying buttress root system in *Rhizophoria mangle* (Méndez-Alonzo *et al.*, 2015), or the brace root systems of *Zea mays* (Foth, 1962; Hetz *et al.*, 1996), demonstrate alternative methods of maximizing the mechanical leverage of root systems.

Minimizing the applied moment

Plants also adopt strategies to minimize the overturning moment that the root system has to resist. As previously discussed, wind-induced loading will cause an overturning moment equivalent to the product of the height above the base at which the load is applied (L) and the drag force (F), which is in turn the product of the sail area (A) and the square of the ambient wind speed (U). When this load is applied, the plant will bend, and the lever arm of the gravity-induced loading of the weight of the plant will increase, thereby increasing the applied moment.

Plants are also able to modify the drag forces applied to their aboveground organs by changing the overall area exposed to

the wind (Gillies *et al.*, 2002). This can be achieved through a decrease in the area of the wind-exposed leaf area (Vogel, 1989) or changing bending orienting parallel with the direction of the wind (Speck, 2003). However, the latter strategy has the potential to increase the gravity-induced bending moment adversely at the base of the shoot-root junction (see Fig. 5). For example, let us consider a stem with weight *W*. If a wind-induced drag force is applied to a single leaf at the top of the stem causing the center of gravity of the plant to deflect by Δx , the resulting overturning moment at the root-shoot junction can be defined as $M_{\rm B} = AU^2L + W\Delta x$. It should also be noted that the wind profile varies between different environments, and significant research has been performed on determining the wind profile that is exerted on different plant species (Massman, 1987; Grant and Nickling 1998).

One example of a drag-reduction strategy can be found in *Cocos nucifera*. Inspection of the leaf base of old and decaying *C. nucifera* leaves reveals a cross-hatched infrastructure of vascular tissues and associated fibers that girdle the stem (see Fig. 6). Measurements of the fibrous components of this infrastructure indicate that their torsional shear modulus (*G*) and Young's elastic modulus (*E*) are, on average, 3.1 GN m⁻² and 13.4 GN m⁻², respectively (unpublished data), which are comparable with those of many types of wood (Niklas and Spatz, 2010).

The cross-hatched, chevron-like arrangement of the fibrous components within the living tissues of petioles is mechanically complex because it provides an opposing system of comparatively rigid guywires operating within a less stiff matrix of parenchymatous ground tissue. This system benefits mechanically from the overall external geometry of the base of the leaf, which consists of an annulus-like component surrounding the stem and a lever-like component. Collectively, the two

Methods for characterizing root morphology

Morphological characteristics are typically more influential than material properties (von Forell *et al.*, 2015), but characterization of the root morphology has been a long-standing challenge in root lodging research. Many methods have been developed for characterizing root morphology. These have ranged from relatively low-tech methods involving a shovel (Trachsel *et al.*, 2011) or pressurized water (Stoeckeler and Kluender, 1938; Böhm, 1979; Gross, 1995, Lindsey *et al.*, 1995), to sophisticated imaging techniques involving CT scanning (Gregory *et al.*, 2003; Lontoc-Roy *et al.*, 2005; Mooney *et al.*, 2012) or ground-penetrating radar (Barton and Montagu, 2004; al Hagrey, 2007). A very thorough review article on root characterization summarizes this field up to the year 2008 (Danjon and Rubens, 2008).

Methods for imaging root morphology have progressed rapidly in recent years. A 2012 book, *Measuring roots*, includes sections on both lab and field studies of root morphology (Mancuso, 2012). Morphology assessment methods described within this book include electrical impedance (Repo *et al.*,

Fig. 5. When firmly anchored plant stem deflects from its original position (dashed outline) and orients itself parallel to the direction of the wind, the drag force potentially decreases, but the gravity-induced moment at the shoot–root junction increases due to the increased moment arm of the gravity-induced load.

components of the leaf base look much like an offset wrench (Fig. 7A). Finite element analyses of this geometry reveal that the bending and torsional stresses in the longitudinal and radial directions reach their maxima along the upper rim of the annulus, extending outward along the rim of levered portion of the petiole. The smallest stresses are predicted to occur along the lower surfaces where the annulus merges with the levered portion of the petiole (Fig. 7A). Moderate stress intensities are predicted internally within the leaf base.

Computer simulations (KJN, unpublished) using the aforementioned material properties and geometry of the base of the petiole indicate that both contribute significantly to reducing the effects of drag forces on anchorage stability primarily because of leaf flexure. The silhouette of a coconut palm measuring 7.16 m in height was used to simulate the appearance of the plant when subjected to a sustained wind speed of 33 m s^{-1} (the equivalent of a category 1 hurricane) (Fig. 7B, C). Computations show that the canopy sail area is reduced to 32% of its original area, whereas stem height is reduced by 9%. As a consequence, the drag-induced bending moment exerted at the base of the stem was estimated to be <44% of the force that would have occurred had no leaf flexure taken place. Two additional components contributed to these results: (i) a reduction in the drag coefficient; and (ii) a reduction in the height of the foliage 'crown' as a result of stem flexure. The importance of leaf flexure was corroborated by laboratory experiments using isolated leaves, which indicated that individual leaves can flex \geq 90° without experiencing shear failure.

One additional feature is worth mentioning. The dislodgement of a palm's root system does not have invariably fatal consequences provided that roots maintain access to water. This fact is attributed in part to the capacity of fleshy roots to tolerate significant bending and twisting before they undergo mechanical failure.





Fig. 6. Fibrous leaf bases girdling a palm stem.



Fig. 7. Finite element simulations of wind-induced movements at the base of a palm leaf (A) and computer simulations predicting the profile of a palm exposed to a hurricane category 1 wind speed (B and C). (A) The base of the palm leaf consists of a torus (that surrounds the stem) and a funnel-like cantilevered petiole (that supports the rest of the leaf). The intensities of bending stresses are indicated by different colors. The intensities of tensile and compressive stresses are shown in red and blue, respectively (see scales to the left). (B and C) Silhouettes of a coconut palm exposed to calm wind conditions (B taken from a photograph of a real specimen) and the same palm exposed to an oncoming high intensity (hurricane category 1) unidirectional wind speed (based on computer simulations using the mechanical responses of the leaf base shown in A). The leeward deflections of leaves (and the downwind flexure of the stem) were used to compute the drag force exerted on the specimen [see Niklas and Speck (2001) for protocols.]

2012), confocal microscopy (Pollastri *et al.*, 2012), and a review of three-dimensional (3D) quantification methods (Fang *et al.*, 2012). Additional methods have included a 3D optical imaging system for plants grown in a transparent agar (Clark

et al., 2011), a similar 2D imaging system that tracked root morphology over time (Lobet *et al.*, 2011), and a 2D computer vision-assisted analysis system for analyzing flatbed scanner images of roots (Le Bot *et al.*, 2010).

Rich data sets obtained from root morphology studies have enabled the creation and validation of realistic 3D models of root morphology. A review on this topic was published that included comparisons of six different modeling platforms (Dunbabin *et al.*, 2013). More recent advances include integrated parametric models (Barczi *et al.*, 2018) and a functional– structural root modeling framework (Schnepf *et al.*, 2018).

Advanced root modeling studies

As computational power increases, the ability to create more realistic computational models becomes feasible. In 2005, Dupuy et al. used parametric variation and finite element modeling to look at the restorative forces that can be withstood in four different soil types, and found that the ideal root system architecture is different for each soil type (Dupuy et al., 2005a). Additionally, the failure mode varies between soil types (Dupuy et al., 2007). Modeling suggested that the root system architecture and mechanical properties of the soil can actually modify the shape of the slip surface and the location of the center of rotation, thereby potentially increasing the robustness of the anchorage system (Fourcaud et al., 2008). The effective bulk mechanical properties of soil can also be modified through tilling, thereby changing features of the root-soil system architecture by increasing features such as the root penetration into the soil, root density, and root diameter (Dexter, 1978; Somerville, 1979; Bian et al., 2016).

A series of three experiment-informed computational studies (Yang et al., 2014, 2017, 2018) were carried out to investigate specifically the root anchorage of Pinus species. The first study incorporated a tissue failure model and demonstrated that the model was sufficiently detailed to capture experimentally measured behavior patterns (Yang et al., 2014). The second paper introduced the RootAnchor model, which consists of individual root segments, modeled as Timoshenko beams (Timoshenko, 1930). Virtual models were based upon an existing data set of actual root morphology. This study reported a ranking of factors from greatest to least influence: tap roots, windward shallow roots, perpendicular shallow roots, windward sinker roots, and leeward shallow roots. A subsequent, more detailed sensitivity analysis using similar modeling techniques revealed that the morphological traits played a dominant role in tree anchorage. The key factors were found to be tap root depth, the rate of root taper, and the diameter of shallow roots on the windward side of the tree (Yang et al., 2018).

Thigmomorphogenesis

As plants grow, they constantly respond to stimuli, and can change their growth and effective mechanical properties as a result. As previously mentioned in discussing the root system of *A. saccharum*, root systems and root system architectures are no exception to this phenomenon. For example, research performed on tomato plants found that periodic horizontal loading of the aboveground stems resulted in larger root–stem dry weight ratios (Gartner, 1994). Similarly, investigations have been performed on the possibility of manipulating the root anchorage robustness of *Pinus pinaster* through the removal of the tap roots in seedlings (Khuder *et al.*, 2007).

Dynamic effects

One of the least understood aspects of root anchorage is the damping of harmonic oscillations resulting from windinduced motion. Damping causes a decrease in the amplitudes of free oscillations and thus reduces the danger of a resonance catastrophe in high winds (Jacobs, 1954; Mayhead, 1973; Milne, 1991; Peltola et al., 1993; Moore and Maguire, 2004; Spatz et al., 2007). Setting aside dissipative mechanisms in the root-soil system, there are two principal sources of damping: fluid damping and structural damping within the material (e.g. wood in the case of trees). Fluid damping (the dissipation of energy into the surrounding soil) depends on the square of the velocity of the plant's movement relative to the surrounding medium. Viscous damping depends on the physical properties of plant tissues. Although the mathematics of complex harmonic oscillations are reasonably well developed, their application to tree harmonics is very poorly understood, in large part because of the geometric complexity of canopy architecture and the heterogeneity in the material properties of different levels of branching (owing to the anatomical transitions between primary growth in twigs and secondary growth in older branches).

Agronomic studies

A great deal of agronomic research has been conducted to determine how to reduce root lodging in crops—especially cereal crops. Research in this area tends to focus on individual crops such as rice (Miyasaka, 1970), maize (Stamp and Keil, 1992*a*, *b*; Sanguineti *et al.*, 1998), and wheat (Crook and Ennos, 1993, 1994; Berry *et al.*, 2003). In contrast to the more mechanistic approaches described above, agronomic research often focuses on how nutrients and farm management practices influence root lodging (Liebhardt *et al.*, 1965; Crook and Ennos, 1996; Scott *et al.*, 2005; Bian *et al.*, 2016). A review article on root lodging in cereals provides an excellent overview of research in this field (Berry *et al.*, 2004).

Future research

While much progress has been made, a great deal of additional information will probably be necessary to form a more complete understanding of the factors influencing root lodging. The following sections highlight a number of areas in which further research is needed, as well as methodological approaches for accelerating progress on these topics.

Knowledge gaps

The creation of accurate computational models will require reasonably accurate material properties. However, at present, relatively little is known about the mechanical tissue properties of roots. Should roots be approximated as linearly elastic or non-linearly elastic? What is the role of viscoelastic damping in root tissues and between roots and soil? Furthermore, what is the distribution of material properties within roots and do spatial distributions of material properties serve structural purposes? A substantial amount of additional research will be required to address these issues.

Thus far, almost no research has been performed on the failure mechanics of root tissues. Many biological systems have developed fracture resistance strategies (Bertram and Gosline, 1987; Bruet *et al.*, 2008). It is not yet clear if roots manifest similar strategies, or perhaps new, uncharacterized strategies. Do roots fail by brittle fracture, plastic fracture, or fatigue-induced fracture? Can roots recover from partial fractures, and if so, how quickly? At present, this area of research is largely unexplored.

Minor roots are typically neglected in root biomechanics research, but the cumulative effect of hundreds or thousands of small roots could have a significant impact on root lodging. In particular, certain root configurations could support the formation of a robust root ball, while other root arrangements may discourage root ball formation. However, little is known about the process of root ball formation and the effect of minor roots on root lodging.

One area of serious concern is the methodologies used to measure biomechanical characteristics of root systems and their architecture. As with any developing field, standardized, repeatable, and reliable measurement techniques are of the utmost importance to ensure translational research.

New technologies

Several new initiatives and technologies can be expected to inform future research. Of particular note in this area is the ROOTS initiative from the US Department of Energy ARPA-E program. The ROOTS program has provided over US\$24 million to root imaging research, including new techniques such as thermoacoustic imaging, MRI, X-ray CT imaging, and backscatter X-ray imaging (https://arpa-e.energy. gov/?q=programs/roots). These research projects will probably produce valuable new data sets and techniques that can be used to advance our understanding of root lodging.

Accelerating empirical research through computational simulations

Modern computational power has the potential to accelerate research progress on the biomechanics of root lodging. Even when information about material properties and root architecture is lacking, simulations can serve as 'computational experiments' which can provide valuable insights. This approach often allows research to progress more quickly and at a fraction of the cost of empirical studies. For example, computational models can be used to perform parametric and global sensitivity analyses (Dupuy *et al.*, 2005*b*, 2007; von Forell *et al.*, 2015; Yang *et al.*, 2018), studies which are often not possible in an experimental setting. Results from sensitivity analyses can be used to rank-order model parameters according to their predicted influence on system response. Once rankings are obtained, empirical studies can be designed to (i) verify model predictions; and (ii) target the parameters and effects with the strongest predicted influence. Used in this way, computational models can significantly accelerate research progress by circumventing costly and time-consuming empirical studies (Dupuy et al., 2005*a*, *b*, 2007; Yang *et al.*, 2014, 2017, 2018).

Concluding remarks

Arborescent plants can experience mechanical failure of the root system as a result of wind-induced drag forces. The mode of failure typically takes on one of two forms: root tissue failure near the ground level or failure of the soil–root subsystem. Of these modes, failure of the soil–root subsystem is quite difficult to analyze because it is contingent upon complex interactions between roots and soil. This challenge is exacerbated by the fact that soil conditions can be highly variable (e.g. soil compaction, composition, and moisture content all affect both the soil mechanical properties and the soil–root interactions). It is clear from previous studies that root anchoring features and strategies vary among species. Even within species, anchoring strategies can vary due to local conditions.

Although a great deal has been learned about root lodging, substantial knowledge gaps remain. One such gap is understanding the effects of chronic dynamic oscillations on stem and root tissue fatigue and how stems and roots are affected by these oscillations as well as how the roots may dampen these oscillations. Research in this area is imperative if we hope to understand fully the ways in which plant anchorage systems respond to dynamic loadings.

The use of computational models has increased over recent years and is anticipated to play a greater and greater role in root lodging research. With these models comes the opportunity to perform detailed parametric sensitivity studies. This approach can greatly improve the utility of our models and provide valuable insights that can be used to design empirical studies that are more closely focused on significant factors and effects.

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