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Thigmomorphogenesis: the response of plants to mechanical perturbation

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Tigmomorfogenesi: la risposta delle piante alle perturbazioni meccaniche

Riassunto. Gli effetti di perturbazioni meccaniche (MP), che causano il piegarsi degli organi della pianta, sulla crescita e sviluppo della pianta stessa sono stati osservati e descritti da centinaia di anni. In generale, la risposta delle piante a perturbazioni meccaniche consiste in una diminuzione nella crescita in estensione/altezza, un aumento della crescita radiale, e un'aumentata allocazione verso le parti aeree rispetto a quelle radicali. L'azione del vento, ad esempio, produce chiome più compatte, modificazioni anatomiche a livello non solo dello xilema e differente conformazione degli apparati radicali. L'effetto è comunque diverso a seconda della specie. Dal punto di vista bio-meccanico la diminuzione del modulo elastico conferisce al fusto la capacità di essere più flessibile, assorbendo una maggiore quantità dell'energia piegante imposta dal carico meccanico. Negli ultimi 50 anni sono stati fatti dei significativi passi in avanti nel caratterizzare la risposta di varie specie vegetali a MP e la risposta di crescita è stata definita tigmomorfogenesi. La ricerca attuale si è concentrata sul meccanismo meccano-percettivo e processo fisiologico, sulla bio-meccanica, sulle modificazioni nella morfologia, anatomia e allometria, sull'induzione di resistenza ad altri stress biotici ed abiotici e sulle applicazioni nelle pratiche forestali, agricole ed ortoflorofrutticole., Questo articolo presenta una prospettiva storica sulla tigmomorfogenesi e riassume i recenti avanzamenti nel comprendere la risposta delle piante a MP.

Introduction

Galileo (1638) proposed the principle of similitude which stated that if a structure was not able to adjust its shape and/or material properties as size increases it would be susceptible to failure under static self-loading or dynamic loading such as wind. In order for an organism to adjust its shape and/or mechanical properties, it needs to perceive the mechanical load imposed upon its structure. This is facilitated in all living organisms, from bacteria to humans, including plants, via a sense of touch, mechanosensing, or mechanoperception (see Ingber a,b, 2003; Kung, 2005; Telewski, 2006; Chehab *et al.*, 2009; Chehab *et al.*, 2011; Coutand, 2010; Monshausen and Haswell, 2013; Moulia *et al.*, 2015 for reviews). The ability of a plant to sense and respond to mechanical loads by altering growth has played a significant role maintaining mechanical stability with regard to gravity and wind and has subsequently influenced the evolution of land plants. The ability of land plants to cope with self-weight and wind-induced drag occurred by the Devonian period indicating natural selection for elastic stability occurred early in the evolution of land plants (Niklas, 1998a).

In a physical sense, touch can be defined as the application of a mechanical force upon and/or establishing contact with another object. The sensing of a mechanical force by living organisms has facilitated the evolution of not only of a sense of touch, but also a sense of balance or orientation with respect to gravity, and the sense of perceiving or hearing sound waves. Plants respond to gravity in what is referred to as the gravitropic response, a process usually facilitated by the sedimentation of statoliths within a living cell or possibly a change in internal pressures on plant tissues as a plant is displaced with respect to the gravitational vector (see Sack, 1991; Boonsirichai *et al.*, 2002; Haswell, 2003; Baluška and Volkmann, 2011 for review). Plants, such as the Venus Fly Trap (*Dionaea muscipula*), and the sensitive plant (*Mimosa pudica*) sense touch and respond rapidly by moving leaves in the thigmonastic response and vines and ten-

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drils grow towards a support once the stem or tendril comes into contact with a potential support in a process known as thigmotropism (see Jaffe *et al.*, 2002; Braam, 2005; Chehab *et al.* 2011 for review). The prefix 'thigmo' comes from the Greek for 'touch'. Plants can also respond to the sensation of touch by altering their growth patterns. These patterns can be influenced by wind, ice and snow loading, raindrops, and rubbing by passing animals (referred to hear as mechanical perturbation, abbreviated MP). In this case, the phenomenon is known as thigmomorphogenesis

The earliest recorded observation of the impact of wind on plant growth and form was reported by Theophrastus in 300 BC (Einarson and Link, 1976) when he observed trees growing in windy environments to be shorter in height with denser wood compared to trees growing in more sheltered environments (fig, 1). Knight (1803) was the first to conduct an experiment to quantify the effect of wind on growth and development in trees when he tethered apple trees to prevent wind induced sway and compared their growth to untethered trees. The tethered group of trees grew taller and had less radial growth than their untethered conspecifics. The importance of wind sway on the growth and development influencing tree form was recognized by Metzger (1893) and subsequently supported by the experimental observations reported by Jacobs (1954), and Larson (1965) prior to Jaffe's landmark publication where he coins the term thigmomorphogenesis (Jaffe, 1973) to describe the response of plants to touch. Prior to 1973, most studies on the impact of wind as MP focused on trees whereas studies on applied static mechanical loads focused on applying tension and were conducted on non-arborescent species, vines and tendrils (Newcombe, 1895; Hibbard, 1907; Bordner, 1908).

Fig. 1 - Wind-blown Frasier fir (*Abies fraseri*) trees exhibiting the flag-form growth form growing on a ridge in the Appalachian Mountains, U.S.A.

Fig. 1 - Alberi di Abies fraseri mostrano la tipica forma a bandiera su un crinale dei monti Appalachi.

During the period of the mid to late 19th century a great deal of attention was given to the mechanical growth theory proposed by Sachs (1873). For the most part, researchers of the time investigating mechanical loading relied on tension as an applied force on the growth and development of plant stems to test Sachs' theory resulting in the reporting of conflicting results. Reviews of these earlier works can be found in the publications of Newcombe (1895), Hibbard (1907) and Bordner (1908). Hibbard (1907) concluded that tension has some impact on the growth, development and lignification of some twining petioles, that the effect on tendrils 'has not yet been accurately determined' and tension 'has no influence on the increase in mechanical tissues in any stems examined.' In his experiments, Hibbard (1907) reports tension had no influence on tissue formation in *Helianthus annuus, Ricinus communis, Brasica oleracea,* or *Phaseolus multiflorus,* whereas *Vinca major* showed an increase in growth. Tension applied to the roots of *H. annuus* and *R. communis* stimulated a small increase in 'mechanical tissue' in the main and lateral roots. The application of a compressive force on stems of *H. annuus, V. major,* and *Fuchia speciosa* developed 'mechanical tissue'. Bordner (1908) replicated Hibbard's (1907) study and reported the application of tension to actively growing stems of herbaceous plants resulted in an increase in breaking strength (Modulus of Rupture), increased bast fiber and/or xylem production. Gilchrist (1908) reported sunflowers mechanically flexed to simulate swaying freely in the wind (resulting in alternating tension and compression in the stem tissues) exhibited increased radial growth at their base, similar to the results reported in studies on arborescent species. All three of these authors were students working in the laboratory of F.C. Newcombe. Newcombe (1895) had concluded; "The formation of such growths as have been recounted in this paper is no longer to be explained by simple mechanics…" and that "…the plant has the ability to respond to (mechanical) stress, but the notion of stress is complex, and will doubtless by future research be subdivided." Although these results are, for the most part, consistent with the thigmomorphogenetic response, interest in continuing research in the area of mechanical stress or wind effects on plants waned for the remainder of the first half of the 20th century.

When studies on the effect of wind on plant growth were considered, most researches prior to the studies of Jacobs (1954) attributed the stunted growth form to be the result of increases in plant desiccation, transpiration, nutrient stress, or leaf cooling (Shreve, 1914; Hill, 1921; Martin and Clements, 1935; Rao, 1938; Daubenmire, 1974;; Van Gardingen and Grace, 1991; Telewski, 1996; Ennos, 1997). Although wind can and will alter other foliar physiological processes, especially net photosynthesis, and transpiration via disturbance of the boundary layer which directly impacts leaf temperature, vapor pressure deficit, and diffusion gradients for carbon dioxide and water vapor (Van Gardingen and Grace, 1991; Ennos, 1997; Cleugh *et al.*, 1998), Telewski (1995) considers these as secondary stresses, whereas the direct mechanical movement of plant parts is considered the primary stress. Different wind speeds produce different rates of transpiration, and the rate of transpiration can be initially high with subsequent reductions over time (Martin and Clements, 1935). To emphasize the potential for different responses of plant growth in response to different wind speeds, Wadsworth (1959) determined an optimal wind speed for relative plant growth was around 1 m s^{-1}, the rate of growth decreasing at wind speeds above and below this threshold. The potential complex interaction between primary MP and secondary alteration of the leaf boundary layer on leaf development has been addressed indicating a plant can respond differently to MP versus alteration of the leaf boundary layer (Smith and Ennos, 2003; Anten *et al.*, 2010).

With only a few exceptions, interest in the effect of MP on plant growth was not renewed until the third quarter of the 20th century by the studies of Jacobs (1954), Wadsworth (1959), Whitehead (1962; 1963), Larson (1965), Boyer (1967), Bannan and Bindra (1970), Neel and Harris (1971), Burton and Smith (1972), and Jaffe (1973). Since that time, great advances in defining the thigmomorphogenetic response and understanding the developmental and molecular basis of the response to MP have been made.

Understanding how plants respond to the application of a mechanical load or touch is essential at both the fundamental and applied scientific levels. It is helpful in addressing how plants perceive the sense of touch, how loading alters plant growth and development, ecological fitness, and how that altered growth may impact the stability, yield, and quality of crops and appearance of a plant as well as the quality of its wood and fibers. Since the 1970s, the literature focused on thigmomorphogenesis has expanded greatly helping to define aspects of growth anatomically, morphologically, allometrically, and biomechanically as well as at the physiological and molecular level of response. This review will provide a summary of advances in the study of thigmomorphogenesis at these various levels of development and response.

Morphology and Allometry

Besides the previously reported observations by Theophrastus (Einarson and Link, 1976) and Knight (1803) the importance of wind sway on the growth and development influencing tree form was recognized by Metzger (1893) and subsequently supported by the experimental observations reported by Jacobs (1954), and Larson (1965). These studies were conducted prior to Jaffe's landmark publication in which he coined the term thigmomorphogenesis. Jaffe's studies were conducted on herbaceous plants in which the mechanical stimulus was applied by physically rubbing the plant, not by the application of wind (Jaffe, 1973) and similar to the application of the mechanical stimulus by Boyer (1967). In these studies, and subsequent studies, with few exceptions (Cordero 1999; Smith and Ennos, 2003; Bossdorf and Pigliucci 2009; Anten *et al.*, 2010), plants exposed to wind, rubbing, or mechanical flexing exhibited either a reduction in height growth, usually an increase in radial growth in the direction of the applied force or both, the net result being an increase in stem taper (fig. 2). In addition to changes in stem morphology, MP results in a reduction in leaf size and a shortening of branches resulting in a more compact crown with reduced wind-induced drag (see Biddington, 1986; Jaffe and Forbes 1993; Mitchell and Myers, 1995; Telewski, 1995, 2006, 2012, 2016; Mitchell, 1996; Jaffe *et al.*, 2002; Braam, 2005; Chehab *et al.*, 2009; Coutand, 2010; Chehab *et al.*,2011; Rosell *et al.*, 2012; Mitchell, 2013; Thomas *et al.*, 2015; Gardiner *et al.*, 2016 for reviews).

Anatomy

The earliest anatomical studies on plant responses to mechanical loading (tensile or compressive stress) conducted in the last quarter of the 19th century and first quarter of the 20th century reported if changes in anatomy were to occur, they would be observed as increases in the 'mechanical' tissues; collenchyma, sclerenchyma and xylem (for reviews see Newcombe, 1895; Hibbard, 1907; Bordner, 1908). Gilchrist (1908) reported that mechanical swaying of sunflowers (*Helianthus annuus*) induced by an electric motor to simulate wind sway increased the development of xylem in the plane of sway. Subsequent studies have confirmed mechanical stimuli of flexing or touch increase the production of xylem in the plane of sway in woody species (both conifers and dicotyledonous angiosperms), thus increasing the cross-sectional area of the stem in the direction of the applied mechanical load (see Telewski 2016 for review). The new xylem cells produced by the vascular cambium in the plane of flexure are characterized as having thicker cell walls, shorter axially and have larger cellulose microfibrillar angles (tracheids in conifers and fibers in angiosperms) with tracheids and vessels having smaller lumen cross sectional areas. This type of wood is known as flexure wood (Telewski, 2016). In porous wood angiosperms, flexure wood is characterized with fewer and smaller diameter vessels with an increase in the lignin monomer ratio of syringyl:guaiacyl (Telewski 2016).

Fig. 2 - Loblolly pine (*Pinus taeda*) seedlings, control (left) and exposed to 20 flexures per day (right). Note that the application of MP reduces height growth, needle leaf extension and reduces the overall profile of the crown to wind drag.

Fig. 2 - Figura. 2 - Piantine di Pinus Taeda*, controllo (a sinistra) e sottoposte a 20 flessioni al giorno (a destra). Si noti che l'applicazione di MP riduce la crescita in altezza , la lunghezza degli aghi e riduce il profilo complessivo della chioma esposta al vento*

However, as Telewski (2016) noted, not all species responded with an increase in xylem production in response to the mechanical stimulus. In some instances, the difference was likely due to the genetic diversity within a species. Some half-sib lines of loblolly pine (*Pinus taeda*) exhibited an increase in radial growth in the plane of applied flexing, where as other lines showed a decrease in radial growth perpendicular to the applied flexing force. All lines exhibited a decrease in the rate of height growth in response to flexing so that all lines exhibited greater stem taper

(Telewski and Jaffe, 1981; Telewski, 1990). In the case of the pioneer tropical rainforest species *Cecropia schreberiana*, the reported difference in response to wind of reduced radial growth may be a function of the ecological position the species holds in succession, and a function of its ontological stem anatomy. Stem stiffness can be accomplished in a number of ways, not just via an increase in material in the direction of loading which appears to be normal for the majority of species tested. Cordero (1999) explains that the seedlings of *Cecropia schreberiana* have a very large pith filled with turgid parenchymatous cells which "could help to reduce local buckling because of its high stability" of the thin-walled, turgid cells. As the seedlings mature into later ontological stages, they increase the cross sectional area of stiffer, denser xylem (fibers and vessels). The overall reduced growth rate in these seedlings is apparently due to a reduction in the maximum photosynthetic and respiration rates in the wind-exposed seedlings (Cordero 1999).

The thigmomorphogenetic response also can manifest itself differently in non-arborescent plants with different life histories and traits. The response of the inflorescence of Arabidopsis is a good example. Arabidopsis produces a rosette of leaves that are prostrate to the ground surface and produces an upright inflorescence. Plants brushed twice daily produced shorter inflorescences than control plants (Braam and Davis, 1990). Paul-Victor and Rowe (2011) reported that mechanically induced sway of developing Arabidopsis inflorescences were shorter but not significantly different in stem diameter than non-perturbed controls. However, anatomically, the stems of the mechanically flexed inflorescences produced less pith and intrafascicular tissues and more cortical tissues compared to control inflorescences.

In the common bean (*Phaseolus vulgaris*) MP applied to stems primary growth was characterized by a reduction in epidermal and cortical cell elongation and a reduction in the number of cells in the primary vascular bundles and pith tissues. Secondary growth was characterized by an increase in xylem production by the vascular cambium and an increase in cortical cell size (Biro *et al.*, 1980). Similar to the results reported by Gilchrist (1908) for MP *Helianthus annuus*, Patterson (1992) reported flexing the stems of *H. annuus* seedlings resulted in an increase in the formation of collenchyma and secondary xylem and a decrease in the amount of cortex and pith. These changes in stem anatomy result in altered mechanical properties which will be discussed below.

Wind and other mechanical perturbations impact stem anatomy by reducing pith autolysis (Carr *et al.*, 1995). Pith autolysis occurs within stems, petioles and flower stalks when cellulose degrading enzymes digest the cell walls of the pith and the carbohydrates are redistributed to growing regions of the plant resulting in a hollow stem (Aloni and Pressman, 1981; Hubermann *et al.*, 1993). Pressman *et al.*, (1984) reported MP of celery (*Apium graveolens*) petioles increased pithiness. However, when combined with drought stress or the application of gibberellic acid (GA3) which also increased the degree of pithiness, MP reduced the amount of pith autolysis.

Mechanical perturbation also influences leaf development. In arborescent species of both conifers and angiosperms, MP results in a reduction in the leaf area of individual leaves (Telewski, 1995; Niklas, 1996). Wind exposed maple leaves have shorter, thinner petioles with less lignified mechanical tissues resulting in a more flexible petiole (Niklas, 1996). MP induced by a unidirectional flexing of oak (*Quercus robur*) saplings resulted in leaves with lower stomatal density and larger epidermal cells (Reubens *et al.*, 2009). Venning (1966) reported wind increased the formation of collenchyma in the petioles of celery. However, Pressman *et al.* (1984) reported only a small decrease in celery petiole elongation in response to MP.

In the prostrate rosette plant *Arabidopsis thaliana* 'Columbia', exposure to brushing as the applied MP resulted in shorter petioles compared to control plants (Braam and Davis, 1990). In the prostrate rosette plant, *Plantago asiatica* exposed to trampling (stepping on a plant once per day) resulted in an increase in petiole diameter, a decrease in leaf blade width and increase in the length to width ratio of the leaf blade. When *Plantago major* was exposed to either wind or mechanical brushing the different MP treatments produced different leaf developmental responses compared to non-MP controls (Anten *et al.*, 2010). Both treatments reduced growth. However, brushing evoked the development of leaves with longer petioles with no change in petiole diameter, and more elliptical and thinner leaf blades (similar to *P. asiatica* response to trampling). Wind induced an opposite response. Anten *et al.* (2010) concluded leaves which developed in response to wind were better acclimated to reduce transpiration, whereas leaves developed in response to brushing were better able to reduce mechanical stress allowing for reconfiguring of the plant structure.

The leaves of the monocot *Festuca arundinacea* grown under windy conditions develop anatomical features similar to leaves grown under drought conditions. This includes more but smaller stomata, more epidermal appendages, and more marginal sclerenchyma. These changes are an acclimation to maintain a positive leaf water balance as well as the ability to withstand additional mechanical stress (Grace and Russell, 1977). Similarly, leaves of *Zea mays* growing in the wind developed a thicker cuticle, more but smaller stomata, and were thicker and wider than leaves from plants grown in the absence of wind. Hyaline sclerenchymatous cells developed in rows on leaf margins of wind-exposed plants, along with a thicker cuticle. Vessels in wind exposed leaves were larger in diameter and more frequent as were phloem elements. A three-fold increase in the number of fibers per bundle, but lower total dry weights was also observed (Whitehead and Luti, 1962). The sheaths of mechanically flexed rice (*Oryza sativa*) had significantly larger stomata than control plants (Zhao *et al.*, 2013).

Roots

Wind, the most common form of MP in the environment is a major cause of plant mechanical failure, especially the failure of the roots resulting in windthrow and crop failure in the form of lodging. Exposure and preconditioning of plants to wind actually improves root anchorage and mechanical properties to resist windthrow or lodging. Field observations include increases in annual growth ring width at the base of structural roots in thinned stands of *Pinus strobus* (Wilson, 1975), *Pinus sylvestris* (Fayle, 1976), and *Picea glauca* (Urban *et al.*, 1994) where stand thinning increased wind exposure. Roots increased in structural mass on the leeward side of *Picea sitchensis* compared to the windward side with respect of the prevailing wind direction (see Telewski, 1995; Gardiner *et al.*, 2016 for review). The authors reported the wind exposed trees with shallow root plates formed buttressed roots with greater cambial growth vertically and laterally at a point above the biological center (pith) of the root resulting in the formation of a T-beam in cross-section. These T-shaped root cross sections were more pronounced on the leeward side of the tree and greatest 0.5 m from the center of the trees. Roots on the windward side of the tree developed a cross-sectional shape similar to I-beams, a configuration which provides the tree with resistance to vertical flexing. Nicoll *et al.* (2008) employed field data to model the influence of wind on the acclimation of increased anchorage provide by roots. They reported that in wind exposed trees, the lateral roots increased in number and strength on the windward side of *Pinus peuce* trees.

Under experimental conditions, conifers exposed to a unilateral wind in a wind tunnel increased the number of lateral roots in both the leeward and windward directions. The sum of cross-sectional area of lateral root bases was greatest on the windward side, with Sitka spruce (*Picea sitchensis*) producing greater root branching, with longer woody tips of greater diameter on the windward side compared to the leeward side, improving anchorage of the wind-exposed trees (Stokes *et al.*, 1995). In a subsequent study where MP was applied by mechanically flexing stems of Sitka spruce seedlings, Stokes *et al.* (1997) reported flexed trees significantly increased root growth reported as coarse root mass, coarse root to fine root ratio, and total root to shoot ratio, with an increase in the cross-sectional area and mass of lateral roots growing in the plane of flexing. The lateral roots were elliptical in cross section with the long axis of the ellipse in the vertical direction, similar to the field observations of wind exposed trees reported by Nicoll and Ray (1996). Studies on deciduous angiosperms also concluded that MP induced by mechanically induced unidirectional flexing also altered both stem and root growth. English oak (*Quercus robur*) exhibited the greatest effect by producing more first order roots and deeper second order roots. Lateral roots on the leeward side of MP trees had a higher elastic modulus under tension compared to other lateral roots in MP or control trees. Black locust (*Robinia pseudoacacia*) produced more fine roots and shallow horizontal roots in response to flexing. The authors concluded that the modifications in root growth in response to MP potentially increase resistance to being up rooted or being overturned (Reubens *et al.*, 2009).

Non-arborescent species also respond to MP by altering root growth. Tomato plants exposed to a flexing treatment had higher root to shoot dry weight ratio than control plants. However, no changes in the diameter, elastic modulus, strength or number of laterals of the tap roots between MP and control plant were reported and no difference in the force required to uproot MP plants compared to controls was observed (Gartner, 1994). Wind under field conditions also influenced the growth of roots of *Helianthus annuus* and *Zea mays* when compared to staked plants. Both species were reported to increase the rigidity and bending strength in roots in response to wind sway by 40-50% and an increase in the root to shoot ratio in free swaying plants of both species compared to staked controls (Goodman and Ennos, 1997). Whitehead and Luti (1962) also reported wind exposure increased the root to shoot ratio and increased root length in *Zea* plants. When grown under experimental conditions in a greenhouse and exposed to a unidirectional flexure of their stems, both *Helianthus annuus* and *Zea mays* produced asymmetrical root systems with thicker, more rigid and more numerous first order roots within the plane of flexure. In *Helianthus*, the tap root became elliptical in cross section with the long axis parallel to the plane of flexure, similar to the pattern observed in the base of the stem. However, the increase in rigidity, strength and stiffness was only observed in the leeward roots of flexed *Helianthus*. Flexed *Helianthus* plants exhibited greater anchorage strength compared to control plants making them more difficult to uproot. In *Zea*, the leeward roots were thicker and more numerous than the roots on the windward side of the same plant. The roots on the windward side of flexed *Zea* plants were stiffer (Goodman and Ennos, 1998). Mechanical flexing increased root length, surface area, volume, biomass and root to shoot ratio in *Oryza sativa*. The MP treatment also increased methane oxidation capacity by the roots of *Oryza sativa* (Zhao *et al.*, 2013).

Stem Biomechanics

Changes in morphology, allometry, and anatomy in response to MP ultimately alter the biomechanical properties of plants. Particularly pronounced in trees, reductions in plant height growth and branch length, along with reductions in leaf size and crown area facilitate a reduction in the force applied as drag imposed upon the stem and roots (fig. 3) (Telewski and Jaffe, 1986a,b). Additional streamlining of tree crowns (flag or banner trees) in regions of strong prevailing winds also serves to reduce drag (Telewski, 2012; Gardiner *et al.*, 2016). MP has been shown to alter the mechanical properties of wood in both conifers and dicotyledonous angiosperms to the extent the elastic modulus (E), a measure of resistance to being deformed or a material's resistance to bending, is reduced. The decrease in the elastic modulus provides the stem with the ability to be more flexible, absorbing more of the bending energy imposed by mechanical load. However, as part of the thigmomorphogenetic response cambial growth in the plane of bending also increases resulting in an increase in the second moment of cross sectional area (I). The mathematical product of the elastic modulus times the second moment of cross sectional area of the stem provides for the flexural stiffness (EI) of the stem. Since I is calculated for a stem of circular cross section as I =Pi × r where r = the radius, a small increase in r greatly increases I. Therefore, in plants which increase radial growth while lowering E in response to MP (which includes the majority of trees), have a stiffer trunk which is better equipped to absorb bending energy (see Telewski 2016 for review). The alteration of wood biomechanical properties is not restricted to the trunk of trees but also is manifest in branches and their junctions to the main trunk. Branch junctions in trees growing in windy environments were shown to have a lower wood density and higher cellulose microfibrillar angles (MFA), whereas the wood in the stem surrounding the branch junction was higher in both wood density and MFA. The tissue within the branch junction is optimized to provide for deformation and increased flexibility in order to protect against branch to stem load transmission damping, whereas the stem tissue surrounding the branch junction has increased toughness to resist fracture (Jungnikl *et al.*, 2009).

Fig. 3 - Loblolly pine (*Pinus taeda*) seedlings exposed to 20 flexures per day (back) compared to control, non-flexed seedlings (front) exposed to the same wind velocity in a wind tunnel.
Fig. 3 - Piantine di Pinus taeda *sottoposte a 20 flessioni al giorno (sfondo) comparate al controllo non flesso (primo piano) esposte alla stessa velocità del vento in una galleria del vento.*

A decrease in E and an increase in I in response to MP have been reported in non-arborescent species which possess a secondary vascular cambium including *Phaseolus vulgaris* (Jaffe et al, 1984), *Helianthus annuus* (Goodman and Ennos, 1997), and *Nicotiana tabacum* (Hepworth and Vincent, 1999). In the sessile rosette species *Arabidopsis thaliana*, the stem of the inflorescence exposed to brushing also exhibited a decrease in E. However, stem diameter decreases in response to MP and as a result both I and IE decreased significantly resulting in a more pliable flower stalk (Paul-Victor and Rowe, 2011).

The Mechanosensing Mechanism

Over the course of the past 30 years research on a mechanosensing mechanism in living organisms has focused on two key cellular structures; 1. The cytoskeleton (Ingber 2003a,b) composed of tublin microtubules (Hush and Overall, 1991; Wymer *et al.* 1996; Hamant *et al.*, 2008) and actin microfilaments (Ingber 2003a,b; Baluška *et al.* 2003; Chehab *et al.*, 2011; 2005) and 2. Membrane-bound stretch activated mechanosensitive ion channels (Edwards and Pickard, 1987; Ding and Pickard, 1993; Kung, 2005; Pickard and Fujiki, 2005; Haswell, 2007; Sharma *et al.*, 2007; Haswell *et al.*, 2008; Haswell *et al.*, 2011; Hamilton *et al.*, 2015). Both of these structures are logical candidates or more likely function together, to provide the living cell a means for mechanosensing. Since the cytoskeleton and stretch activated mechanosensitive ion channels function at the level of the plasmamembrane, cell surface area regulation and membrane tension provide insight into the role of membrane tension in cell biomechanics and the potential role of membrane tension in mechanoperception in both plants and animals (Morris and Homann, 2001). The stretching and relaxation of the cell membrane in response to changes in the mechanical environment of cells as a component of mechanosensing fits well with reports of the role of stretch-activated membrane channels in the response of plants to mechanical stresses (Edwards and Pickard, 1987; Ding and Pickard, 1993; Kung, 2005; Pickard and Fujiki, 2005; Haswell, 2007; Sharma *et al.*, 2007; Haswell *et al.*, 2008; Hamilton *et al.*, 2015). The perception of a mechanical signal by cells is a rapid process with a rapid translation of the mechanical force into a biochemical or bioelectric message (Baluška *et al.*, 2003; Ingber, 2003a, b). Significant progress has been reported in the elucidation of the molecular basis of mechanosensory perception and transduction in animal systems, particularly the physical coupling between the cytoskeleton and cell membrane, which provides a continuous structural/mechanical network throughout the cell (see Janmey, 1998; Gillespie and Walker, 2001; Jaffe *et al.*, 2002; Baluška *et al.*, 2003; Ingber, 2003a,b; Telewski, 2006; Chehab *et al.*, 2011 for reviews).

The cytoskeleton, bound to the plasma membrane, quite possibly provides for tensile forces tugging the membrane and activating the mechanosensitive ion channels when a cell is mechanically stimulated based on Ingber's tensegrity model (Ingber 2003a,b). The two major elements of the cytoskeleton have their own unique mechanical properties. Microtubules are stiff and resist bending forces. Microfilaments are flexible and relatively strong providing resistance against buckling under compression and fracture under tension. Research indicates that of the two components, microtubules are more critical to mechanosensing than microfilaments. Microtubules were observed to reorient in response to MP in peas (*Pisum sativum*) roots (Hush and Overall, 1991) , shoot meristems of Arabidopsis (Hamant *et al.*, 2008), epidermal cells of *Lolium rigidum* leaves (Cleary and Hardham, 1993), and in protoplasts from tobacco (*Nicotiana tabacum*) (Wymer *et al.*, 1996). Wymer *et al.* (1996) demonstrated the importance of microtubules in mechanosensing by applying the microtubule-disrupting agent amiprophos-methyl to protoplasts before and during the application of MP (via centrifugation), resulting in elongation of the protoplasts, but without deference to the direction of the applied force. Similarly, the application of colchicine blocked the response of agar embedded chrysanthemum (*Dendranthema morifolium*) protoplasts to applied MP. Plasmolyzed cells treated with Arg-Gly-Asp (RGD) motifs (which disrupt adhesion of the plasma membrane-cell wall) disrupted mechanoperception after the cells were returned to normal turgor supporting the role of the cytoskeleton-plasma membrane-cell wall interface (CPMCW) interface in mechanosensing. However, cells treated with cytochalasin B, which disrupts microfilament formation, still responded to MP (Zhou *et al.*, 2007). These studies support a putative role of the microtubules in mechanosensing over microfilaments within the cytoskeleton (see Landrein and Hamant, 2013 for review).

Supporting the putative role of microtubules in mechanosensing, Perrin *et al.*, (2007) reported the novel microtubule-associated protein WVD2, a maltose binding protein, plays a significant role in mechanosensing in gravitropism of Arabidopsis roots and in the thigmomorphogenetic response of *Arabidopsis* inflorescences. One of the suite of touch-inducible genes, calmodulin-like 24 (*CML24*) was also reported to influence cortical microtubule orientation and mechanosensing in Arabidopsis roots (Wang *et al.*, 2011). However, *CML24* has also been associated with modulating actin microfilaments resulting in a more disorganized cytoskeleton in growing pollen tubes (Yang *et al.*, 2014).

As presented above, there is mounting evidence that supports the mechanism of mechanosensing includes aspects of both the CPMCW, specifically the microtubule component of the cytoskeleton, in combination with mechanosensitive stretch activated plasma membrane bound ion channels. However, there exists the need to further elucidate this mechanism and more fully understand its function in plant response to the mechanical environment.

Practical Applications

An understanding how plants respond to MP has a broad impact on commercial applications in the fields of forestry, agriculture, horticulture, and floriculture. This was first recognized in the forestry profession by Metzger (1893) who identified wind as having a significant influence on stem development and taper, and subsequently by Jacobs (1954) and Larson (1965). Since this time, numerous studies and reviews have reported on the influence of MP on tree growth and development (Telewski, 1995; 2012; Gardiner *et al.*, 2016), forest and plantation stand stability (Gardiner *et al.*, 2016; Mitchell, 2013), thinning and harvesting (Mitchell, 2013), urban forestry (Dahle *et al.*, 2014), and wood quality (Telewski, 2016).

While investigating the horticultural practice of staking nursery stock to prevent lodging and the practice of staking newly transplanted trees in landscapes, Neel and Harris (1971) reported on the influence of MP induced by wind sway on tree growth. Upon a detailed analysis of several tree species Harris *et al.* (1973) recommended modifying nursery practices regarding the staking of trees to take into consideration species differences in their response to MP or staking. Trees newly planted in a landscape, should they require staking to prevent being blown over, should be staked loosely to permit movement of the trunk and root collar to induce a thigmomorphogenetic response to increase stability (fig. 4a, b).

Fig. 4 - A properly staked tree in the landscape which provides for stem movement in the wind, but will prevent overturning in the wind.

Fig. 4 - Un albero correttamente ancorato in modo da consentire il movimento del fusto in caso di vento, ma impedendone il ribaltamento.

Much has been written regarding the negative impact of wind on crop plants, specifically the complicated influence of wind altering transpiration, leaf temperature, photosynthesis, leaf abrasion and lodging resulting in reduced crop yields (see Biddington, 1986; Cleugh *et al.*, 1998; Gardiner *et al.*, 2016 for reviews). Strong prevailing winds can also cause nursery stock to lean decreasing its commercial value (fig. 5). Although not always a consequence of MP, a common direct negative effect of thigmomorphogenesis on plant growth is a reduction in reproductive potential and crop yield (Latimer, 1991a; Jaffe and Forbes, 1993; Mitchell and Myers, 1995; Mitchell, 1996). The reduction in yield is associated with a reallocation of growth from shoots to roots while delaying flowering (anthesis) and number of flowers in response to MP (Niklas, 1998b; Cipollini, 1999). The role of jasmonic acid (JA) in the thigmomorphogenetic response has been reported to be in part, responsible for the observed delay in flowering (Chehab *et al.*, 2012).

However, MP can also be applied to improve plant performance by what is known as mechanical conditioning (Latimer 1991b). This is especially true of

Fig. 5 - Wind-induced lean in nursery stock.
Fig. 5 - Effetto del vento su alberi allevati in vivaio

crops raised or grown in greenhouses (Beyl and Mitchell, 1977; Mitchell and Myers, 1995). As Jaffe and Biro (1979) stated regarding thigmomorphogenetic studies, the plants referred to as controls without exposure to MP are not growing under normal or prevailing conditions as most plants growing outside of the protective environment of a greenhouse or growth chamber are exposed to the common sources of MP under field conditions including exposure to wind, rain, brushing by passing animals etc, as well as an inability to properly provide for self-support if the plants were grown too close together. This observation was restated by Biddington (1986) in his review of thigmomorphogenesis. Plants raised in a greenhouse prior to being planted out usually require a period of hardening which acclimates the plant to cooler temperatures, possibly higher light levels, but also exposes it to an increased level of MP. If transplanted directly to the field or garden without MP hardening to precondition to mechanical loading, plants will not be able to withstand the physical stresses to which they will be exposed (Biddington, 1986; Mitchell and Myers, 1995; Mitchell, 1996; Garner *et al.*, 1997). The application of MP to plants growing in a greenhouse in order to precondition them for transplant into the field has been recommended since the mid-1970s (Takaki *et al.*, 1977; 1978; Biddington and Dearman, 1985; Liptay, 1985; Latimer, 1990; 1991a; 1991b; Latimer and Thomas, 1991; Johjima *et al.*, 1992; Pontinen and Voipio, 1992; Latimer and Beverly, 1993; Autio *et al.*, 1994; Mitchell and Myers, 1995; Garner and Björkman, 1996; 1997; Garner *et al.*, 1997; Latimer, 1997). Plants preconditioned to MP before being set out in the field are better able to survive transplant shock than non-preconditioned plants (Liptay, 1985; Latimer *et al.*, 1991). A few studies have shown that plants will respond differently to MP depending on the season (Heuchert and Mitchell, 1983; Autio *et al.*, 1994).

The application of MP as a replacement for chemical treatments to control height growth in greenhouse grown plants was suggested in a review of the subject by Latimer (1991a) and by Miller and Telewski (1991) in a study to control plant form and marketability in Easter lilies (*Lilium longiflorum*). Vernieri *et al.* (2003) conducted a thorough comparison of the influence of different methods of applying MP and the chemical Topflor® to control height growth in *Salvia splendens* seedlings. They concluded that although MP did not provide as strong of a control over excessive elongation growth compared to chemical treatments, MP was effective as an alternative to chemical use. Of the MP treatments applied, brushing with a plastic pole four times a day every three hours from 9:00 to 18:00 provided the best results, followed by an impedance treatment (placing a metallic screen over the seedlings at night, and finally shaking using an orbital shaker at 220 rpm four times a day every three hours from 9:00 to 18:00. Koch *et al.* (2011) employed MP as a means to control extension growth in the production of potted herbs where the application of chemical growth inhibitors is prohibited on plants for consumption. MP has also been used to improve the quality and marketability of garden roses instead of growth retardants (Morel *et al.*, 2012). The application of MP to tissue culture production increased the robustness of explants for handling and survival (Sarmast *et al.*, 2014).

It has been suggested that exposure of plants to MP improves their resistance to other environmental stresses such as drought or freezing (Jaffe and Biro, 1979; Suge, 1980; Jaffe and Telewski, 1984). However, neither drought nor freezing stress tolerance was observed in MP plants in studies published by Biddington and Dearman, (1985; 1988) or Pardossi *et al.*, (1988). MP has been shown to confer resistant to pests and herbivory. Aphid populations were smaller on plants exposed to MP (Van Emden *et al.*, 1990). MP induced by brushing conferred greater resistance to attack by western flower thrips (*Frankliniella occidentalis* Pergande) and two-spotted spider mites (Tetranychus urticae Koch) (Latimer and Oetting 1999). Wind at 3 m/s for two hours per day also increased resistance to mite predation and anthracnose infection in common beans. The increased resistance observed in bean plants is related to the MP activation of the phenylpropanoid pathway (Cipollini, 1997). MP induced the expression of a pathogenesis-related transcript specific for a basic class of IV chitinase in sugar beet which is also involved in conferring resistance to the fungal pathogen *Cercospora beticola* (Nielsen *et al.*, 1994). The role of jasmonate in thigmomorphogenesis has also been implicated in mediating pest resistance in plants. The role of JA and its synthesis is known to play a key role in signaling and in the response of protecting plants from both necrotrophic fungi and herbivory (Farmer and Ryan, 1990; 1992; Gundlach *et al.*, 1992; Turner *et al.*, 2002). Arabidopsis plants exposed to MP conferred greater resistance to either fungal infection by *Botrytis cinerea* or herbivory by the cabbage looper (*Trichoplusi ni*). The active oxygen species (AOS) *Arabidopsis* mutant exposed to MP did not exhibit a thigmomorphogenetic response and also did not exhibit any resistance to either fungal pathogen or insect herbivore (Chehab *et al.*, 2012). Additionally, resistance to biotic stresses in response to MP are likely also conferred via the accumulation of reactive oxygen species (ROS) acting as signaling molecules under both abiotic and biotic stress conditions (Herbette *et al.*, 2011).

Summary and Conclusions

Thigmomorphogenesis is one of several plant responses to touch requiring a cellular level mechanosensing mechanism involving the cytoskeleton connected to the plasma membrane and cell wall. The plasma membrane contains mechanosensitive ion channels which facilitate signaling via the movement of Ca++ between the apoplast and synplast. Following mechanopreception, a cascade of physiological responses involving gene expression and plant growth regulators either up or down regulation occur. These physiological changes further influence cell expansion and division in meristematic regions altering the developing anatomy and morphology and ultimately allometry of both above and below ground plant organs. In general, the growth response is characterized by a decrease in height or extension growth (primary growth), an increase in radial growth (secondary growth) which increases stem taper. The change in growth pattern also results in a reallocation of growth from shoots to roots increasing the root-to-shoot ratio and decreasing reproductive potential by reducing flower number and delaying time to flowering. Changes in the anatomy and cellular structure modify the biomechanical properties of the stem lowering the stems resistance to bending (thus increasing the ability of the stem to absorb bending energy), but increasing overall stem stiffness by increasing overall stem diameter. Shorter stems and branches and smaller leaves reduce the profile presented to wind and thus reduces drag on the plant crown. Because the thigmomorphogenetic response shares many similarities with other plant stress responses, plants exposed to MP also exhibit greater resistance to other biotic and abiotic stresses.

This is an idealized description of thigmomorphogenesis and a few exceptions presently exist that do not match exactly the above series of events, particularly with regard to growth response. One exception can be accounted for as a result of genetic variability within plant populations or between different taxa. Plant growth form, habitat, and seral stage occupied by a given plant also appear to dictate individual taxa responses to MP. For example, plants with a basal rosette growth form will respond differently than large, arborescent taxa. The need for further clarification and characterization of the influence of genetic variability and adaptation to specific mechanical environments in plants merits further investigation.

Another exception in regard to plant response to MP concerns the method of applying MP. Initially, when defined by Jaffe (1973), thigmomorphogenesis was the response of plants to rubbing back and forth between the thumb and forefinger which applied pressure to the surface of an internode. The rubbing technique has since been applied by a number of researchers. Subsequently, the term thigmomorphogenesis was more uniformly applied to MP treatments which resulting in the application of pressure to a plant, usually resulting in an alternating motion inducing compression and tension. Therefore, thigmomorphogenetic MP treatments reported subsequently in the literature included the application of wind-induced bending, brushing, impedance (pushing through soil or pushing against a covering), touch induced by rain or watering, ice and/or snow accumulation, vibration, and shaking (either in a circular or back and forth direction). Initially, the shaking of plants, (which does induce an alternating stem compression and tension), and including wind and vibration, was termed seismomorphogenesis (Mitchell *et al.*, 1975; Mitchell and Myers, 1995). Treatment with vibration was later termed vibromorphism (Mitchell and Myers, 1995) and likely should include the influence of sound on plant growth, separate from thigmomorphogenesis. Independent of exposure to vibration or sound, the application of different forms of MP have been reported to induce differing results under experimental conditions raising the question whether plants can differentiate between different forms of MP. This is an area which merits further investigation.

Abstract

The influence of mechanical perturbation (MP) resulting in the flexing of plant organs on plant growth and development has been observed and reported for hundreds of years. In general, the response of plants to MP is a reduction in extension/height growth, and increase in radial growth and increased allocation from above ground to below ground tissues. Within the last fifty years, significant advances have been made in characterizing the response of multiple plant species to MP and the growth response was defined as thigmomorphogenesis. Current research has focused on the mechanoperceptive mechanism and physiological pathway, biomechanics, changes in morphology, anatomy and allometry, induction of resistance to other abiotic and biotic stresses, and practical applications in the fields of forestry, agriculture, and horticulture. This review provides a historical perspective of thigmomorphogenesis and a summary of recent advances in understanding the response of plants to MP.

Key words: touch, wind, thigmomorphogenesis, mechanosensing, biomechanics, anatomy, morphology.

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