



Mechanosensing and Plant Growth Regulators Elicited During the Thigmomorphogenetic Response

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The influence of mechanical bending or flexing of trees, due primarily to wind, on tree growth and development has been observed and reported for hundreds of years. This response was defined as the thigmomorphogenetic response in 1973. In general, the response of trees and other plants to bending is a reduction in extension/height growth, increase in radial growth, and increased allocation from above-ground to below-ground tissues accompanied by changes in biomechanical properties of the xylem. Within the last 50 years, significant advancements have been reported in characterizing the response of trees to this mechanical perturbation. Current research has advanced the understanding of how plants respond after mechanopreception via molecular signaling and physiological changes in growth regulation. This review provides insight into these subcellular reactions of thigmomorphogenesis and a summary of recent advances.

Keywords: wind, touch, thigmomorphogenesis, mechanosensing, mechanopreception, growth regulators

INTRODUCTION

External mechanical loading induces mechanical perturbation (MP) of trees and nonwoody plants via wind, rain, the brushing or touching of passing animals, pushing through soil, or accumulation of ice or snow and is known to induce a cascade of physiological, developmental, anatomical, and morphological responses termed *thigmomorphogenesis* (Table 1) (Jaffe, 1973). The reaction to MP by the mechanosensing response network has been shown to be dose dependent (Jaffe et al., 1980; Braam and Davis, 1990; Telewski et al., 1997; Telewski and Pruyun, 1998; Bonnesoeur et al., 2016; Kašpar et al., 2017). After perceiving a mechanical force, a series of signaling and subsequent growth regulator responses are triggered. This review article addresses the current state of knowledge concerning this physiological response pathway. The alteration of plant structure and function (anatomy, morphology, and mechanical properties) has been addressed in a previously published reviews (Telewski, 1995, 2006, 2012, 2016a,b; Jaffe et al., 2002; Gardiner et al., 2016).

MECHANOSENSING AND GROWTH REGULATORS SIGNALING

Action Potential

The first detectable response is a change in action potential and electrical resistance, which develops across the cell membrane within seconds after MP (Lund, 1931; Sibaoka, 1966; Asher, 1968; Pickard, 1971; Desbiez, 1973; Jaffe, 1976; Frachisse et al., 1985; de Jaegher and Boyer, 1989; Choi et al., 2016). The next measurable change occurs as an increase in intracellular Ca²⁺ functions as a secondary messenger of the mechanical signal in plants in response to numerous abiotic and

TABLE 1 | Thigmo-mechanoresponse cascade flow diagram of the physiological responses after the induction of a mechanical perturbation.

	Thigmo-Mechanoresponse Cascade Response	Growth
1–10 s	Increase in action potential and electrical resistance	
	↓	
1–2 min	Phloem transport stops Increase in intracellular Ca ⁺⁺ Increase in H ₂ O ₂ and other ROS	
4–8 min		Elongation Growth ceases
	↓	
5–15 min	Transcription of 1-aminocyclopropane-1-carboxylate synthase 6 (ACS6)	
10–30 min	Expression of calmodulin and calmodulin-related genes (TCH1, TCH2, TCH3) and xyloglucan endotransglycosylase (TCH4) 1-aminocyclopropane-1-carboxylate (ACC) accumulation	
30–60 min		Recovery of shoot growth
	↓	
1–2 h	TCH1, TCH2, TCH3, and TCH4 expression Returns to base levels Cessation of DNA methylation Phytoalexin-like substances peak Lipoxygenase (LOX) mRNA transcription Callose synthesis and deposition in phloem	
	↓	
2–9 h	Full recovery of DNA methylation Peak in S-adenosylmethionine (SAM) synthesis Peak in ethylene synthesis	
6–24 h		Increase in radial growth by vascular cambium
	↓	
24 h	Callose and ethylene return to pre-MP stress levels	

biotic stresses (Blume et al., 2000; Dodd et al., 2010; Batistič and Kudla, 2012; Choi et al., 2016). Such an accumulation of intracellular Ca²⁺ has been reported in plants and plant tissues exposed to MP (Thonat et al., 1993; Haley et al., 1995; Knight, 2000; Ishihara et al., 2017). For this reason, it is currently unclear if stretch-activated Ca²⁺ channels

(Ding and Pickard, 1993; Pickard and Fujiki, 2005) function in the primary perception or are triggered by the mechanosensing network proposed by Baluška et al. (2003, 2005). The function of stretch-activated channels is to facilitate the transport of Ca²⁺ across the cell membrane into the cell in response to MP (Ding and Pickard, 1993; Pickard and Fujiki, 2005). An

increase in cytoplasmic calcium in response to MP has been documented in several plant systems (Toriyama and Jaffe, 1972; de Jaegher and Boyer, 1990; Knight et al., 1991, 1992; Trewavas and Knight, 1994; Legué et al., 1997; Pickard and Fujiki, 2005). Confirming the role of cytoplasmic calcium in mechanoperception, de Jaegher and Boyer (1990) were able to block the thigmomorphogenetic response by treating MP plants with EGTA, a calcium ion chelator, which also blocked peroxidase activity and ethylene biosynthesis, both of which are known to be involved downstream of the initial perception of MP.

Reactive Oxygen Species

Hydrogen peroxide (H₂O₂) and other reactive oxygen species (ROS), also known as active oxygen species (AOS), are part of the defense response of plants that function as signaling molecules to a variety of stimuli. Fungal attack involves the mechanical insertion of a fungal penetration peg through the host cell wall stimulating ROS and AOS production by the host plant (Sutherland, 1991; Mehdy, 1994; Gus-Mayer et al., 1998). The release of ROS also occurs when transferring cell cultures or physical stirring cultures (Apostol et al., 1989; Legendre et al., 1993). Yahraus et al. (1995) induced an oxidative burst in *Glycine max* (L.) Merr. cells in response to osmotic stress (altered turgor pressure) and direct MP. Levels of soluble and cell wall-bound basic peroxidases increased 24 h after MP of *Bryonia dioica* Jacq. (Boyer et al., 1979). The induction of ROS and increase in cytosolic Ca²⁺ appear to be concurrent, and ROS have been suggested to regulate Ca²⁺ channel gating (Mori and Schroeder, 2004). Additionally, stress-induced H₂O₂ induces ethylene biosynthesis in plants (Van Breusegem et al., 2001), which is subsequently involved in a number of stress responses, which are addressed below. Tomatoes overexpressing glutathione peroxidase, a part of the ROS-scavenging system, exhibited a significantly reduced thigmomorphogenetic response (Herbette et al., 2011), further confirming the important role of ROS in the thigmomorphogenetic response. MP also has been shown to induce the defense and stress signaling molecule, nitric oxide (NO), in the leaves of *Arabidopsis thaliana* (L.) Heynh. (Garcés et al., 2001). NO induces stomatal closure and may protect the plant from desiccation during windy conditions when the boundary layer is stripped from the leaf surface. Subsequent research has shown that the touch-inducible gene *CML24/TCH2*, which codes for a Ca²⁺-binding protein (Braam and Davis, 1990; Delk et al., 2005; Lee et al., 2005), is required for NO accumulation (Tsai et al., 2007; Ma et al., 2008).

Gene Up-Regulation

Shortly after the sensing of an MP and the resulting action potential has been generated, a series of genes are transcribed. The rapid up-regulation (expression) of calmodulin and calmodulin-related genes (*TCH1*, *TCH2*, and *TCH3*) was observed in *A. thaliana* (L.) Heynh. (*Arabidopsis*) 10–30 min after mechanoperception of a touch, wind, or rain stimulus and returning to base levels by 1–2 h (Braam and Davis, 1990). *Arabidopsis TCH4* encodes for a xyloglucan endotransglycosylase and was coexpressed with the other *TCH* genes (Xu et al., 1995). The expression of xyloglucan endotransglycosylase in

response to wind was located in cells undergoing expansion (Antosiewicz et al., 1997). Galaud et al. (1993) observed a cessation of DNA cytosine methylation in *B. dioica* 1 h after the application of MP, with full recovery of methylation 3 h after MP. The authors also reported a peak in production of S-adenosylmethionine, a substrate for DNA methylation and a precursor for ethylene biosynthesis, co-occurred with the cessation of DNA methylation.

Touch, wind, and wounding all induced increased lipoxygenase (LOX) mRNA transcription in *Triticum aestivum* L. seedlings (Mauch et al., 1997). The MP induced response occurred within 1 h after treatment, and the amount of transcript was reported to be strongly dose-dependent. LOXs are involved or implicated in a number of metabolic pathways associated with plant growth and development, abscisic acid (ABA) biosynthesis, senescence, mobilization of lipid reserves, wound responses, resistance to pathogens, formation of fatty acid hydroperoxides, synthesis of jasmonic acid, and traumatic acid (Mauch et al., 1997). Controlled bending of young *Populus tremula* × *Populus alba* cv 717-1B4 stems stimulated an up-regulation of jasmonic acid and other plant abiotic stress and defense signaling pathways (Pomiès et al., 2017).

Phloem Transport

MP of stems of *Phaseolus vulgaris* L. and *Gossypium hirsutum* L. cv. “Stoneville 213” blocks phloem transport within 1–2 min after perturbation with full recovery of transport requiring 20–175 min (Jaffe and Telewski, 1984; Jaeger et al., 1988). Callose plugs are involved in blocking phloem sieve plates and slowing down or blocking phloem transport and have been observed in response to MP in stems of *P. vulgaris* and *Pinus taeda* L. 1 h after MP. The callose plugs peak after 9 h and reabsorbed after 25 h (Jaffe and Telewski, 1984). The rapid response of blocked phloem transport and the formation of callose plugs have not been directly linked. The mechanism of rapid phloem transport is still unknown. Callose deposition also occurs within 5 min of gravity stimulation in *Zea mays* L. and *Pisum sativum* L. Deposition of callose occurred first on the upper side of displaced stems, and after 2–3 h, the pattern was reversed. The callose inhibitor, 2-deoxy-D-glucose, blocked callose formation and considerably reduced gravitropic bending in both species (Jaffe and Leopold, 1984).

Plant Growth Regulators

Ethylene biosynthesis has been reported to be a fairly ubiquitous response to a number of environmental stresses including mechanical stress and serves as a signaling molecule (see Abeles et al., 1992; Bleecker and Kende, 2000). Both 1-aminocyclopropane-1-carboxylate synthase (ACS6) and 1-aminocyclopropane-1-carboxylate (ACC) are involved in the ethylene biosynthetic pathway and are stimulated by MP in *Arabidopsis* leaves peaking at 5–15 min and 15–30 min, respectively (Arteca and Arteca, 1999). MPs induced by wind, touch, and dynamic flexing have all been shown to induce ethylene formation in vascular plants. It was the first plant growth regulator to be implicated in the response to MP (Goeschl et al., 1966; Brown and Leopold, 1973; Robitaille and Leopold,

1974; Hiraki and Ota, 1975; Jaffe and Biro, 1979; Biro and Jaffe, 1984; Prasad and Cline, 1985; Telewski and Jaffe, 1986; de Jaegher et al., 1987; Telewski, 1990; Emery et al., 1994; Onguso et al., 2006; Love et al., 2009). Researchers were also able to mimic the effects of MP with the application of exogenous ethylene (Mitchell, 1977; Biro et al., 1980; Erner et al., 1980; Telewski and Jaffe, 1981; Erner and Jaffe, 1983; Prasad and Cline, 1985). More recently, Pomiès et al. (2017) reported that a single MP either up- or down-regulated (differential expression) 6% (2,663 genes) of the *P. tremula* × *P. alba* cv. 717-1B4 genome, including ethylene synthesizing genes. However, Boyer et al. (1983) reported MP reduced ethylene production but increased the ability for conversion of ACC to ethylene, suggesting an increased expression or increased activity of ACC synthase in *B. dioica*. The application of exogenous ethylene and overexpression of ACC oxidase stimulate cambial growth in *P. tremula* × *Populus tremuloides*, whereas *etr1-1* (ethylene receptor mutant) transformed plants did not respond to ethylene application. When exposed to MP, the *etr1-1* transformed plants exhibited no increase in radial growth and suppressed tension wood formation, as well as no reduction in height growth, indicating ethylene is key to a response to MP (Love et al., 2009). However, Johnson et al. (1998) reported *Arabidopsis* ethylene mutants *ert1* and *ein2*, which are deficient in sensing or responding to ethylene, did respond to MP; specifically, there was a normal thigmomorphogenetic reduction in inflorescence height growth in response to MP similarly to wild-type plants. The authors did not report any data for inflorescence diameter growth. The authors concluded, "...the ERT1 and EIN2 protein functions are not required for developmental and molecular responses to mechanical stimulation." Anten et al. (2006) using transgenic *Nicotiana tabacum* L. modified with the *Arabidopsis* ERT1 allele reported similar results to those of Johnson et al. (1998). The conclusion regarding the role of ethylene in the thigmomorphogenetic response was again presented as "...a fully functional ethylene pathway is not required for aspects of thigmomorphogenesis." (Chehab et al., 2011). As presented earlier, Paul-Victor and Rowe (2011) did not observe any change in the basal diameter of *Arabidopsis* inflorescence exposed to MP compared to control plants, whereas inflorescence height is significantly reduced in response to MP. The role of ethylene in response to MP appears to effect secondary growth and subsequent development and differentiation of the vascular cambium and may not impact elongation or height growth associated with the primary growth of the apical meristems of inflorescence stalks in *Arabidopsis* (Anten et al., 2006; Telewski, 2006). Contrary to Chehab et al. (2011) study on inflorescence spikes, Okamoto and Takahashi (2019) observed that MP inhibits root elongation in *Arabidopsis*. The application of ACC reduced the root elongation of *Arabidopsis*, whereas the application of either silver ions or salicylic acid restored the growth in the MP roots.

Auxin has also been implicated in the thigmomorphogenetic response (Boyer, 1967; Mitchell, 1977; Hofinger et al., 1979; Erner and Jaffe, 1982; Jedrzejuk et al., 2020). MP reduced the endogenous level of auxin in *B. dioica*, and the application of exogenous auxin restored the growth rate in MP plants (Boyer,

1967). A reduction in auxin content after MP was reported in MP plants of *Solanum lycopersicum* L., *Plantago major* L., and *Solanum tuberosum* L. (Saidi et al., 2010; Onoda and Anten, 2011; Markovic et al., 2016). The MP-induced reduction in stem elongation during primary growth is the result of increases in the activity of indoleacetic acid (IAA) oxidase, phenylalanine ammonia-lyase, cinnamyl alcohol dehydrogenase, or defense-related peroxidase (Cipollini, 1998; Saidi et al., 2010; Jedrzejuk et al., 2020). Auxin is known to exhibit cross-talk interaction with ethylene. Erner and Jaffe (1982) hypothesized the accumulation of auxin-like plant growth regulators resulted from ethylene production earlier in the thigmomorphogenetic response and was responsible for the reduction in internode (shoot) elongation. However, this hypothesis was challenged by the subsequent observation that ethylene mutants still respond to MP with a reduction in shoot elongation (Johnson et al., 1998).

A role for ABA has also been reported in thigmomorphogenesis with higher levels of ABA reported in response to MP (Jeong and Ota, 1980; Erner and Jaffe, 1982; Beyl and Mitchell, 1983). ABA is a growth antagonist, and its increase in response to MP could facilitate the observed reduction in extension growth in response to MP. In addition to its role in NO accumulation, the *CML24/TCH2* gene also has been shown to be required in the ABA responses (Delk et al., 2005) and has been suggested to be linked to ABA's role in thigmomorphogenesis (Chehab et al., 2011).

MP leads to a significant reduction in endogenous gibberellin (GA) (Suge, 1978; Takahashi and Suge, 1980). Unfortunately, no time course of GA content was conducted. MP in *P. vulgaris* was observed to decrease after 29 days of daily application of bending for 1 min (Suge, 1978). MP in cucumber decreased growth and increased the number of pistillate flowers, a process regulated by a reduction in GA. The application of GA₄₊₇ to MP plants nullified the effect of MP on growth and floral sex expression. The application of silver nitrate, an antiethylene agent, reversed the effect of MP on floral sex expression but did not restore normal growth (Takahashi and Suge, 1980). The endogenous levels of GA₄, GA₁₂, GA₁₅, and GA₃₄ declined significantly in MP *Arabidopsis*. The decrease in GA content was reported to be consistent with the decreased rate of inflorescence extension growth and leaf morphology. The application of exogenous bioactive form of gibberellic acid (GA₄) reversed the decreased rate of extension growth in MP plants. MP also induced the expression of *AtGA2ox7*, which encodes an enzyme involved in GA catabolism. The loss-of-function *Arabidopsis* *ga2ox7* did not respond to MP (João et al., 2015). The authors suggest *ga2ox7* is a key regulator of thigmomorphogenesis, and MP-induced changes in morphology are dependent on GA catabolism.

In terms of thigmo-responses, jasmonates (JAs) were first implicated in the thigmonastic coiling response of tendrils (Falkenstein et al., 1991; Weiler, 1993). The octadecanoid 12-oxo-phytodienoic acid, a precursor for JA, increased several-fold in response to MP, inducing a thigmomorphogenetic response in beans, and the application of coronatine triggered a thigmomorphogenetic response (Stelmach et al., 1998). MP *Medicago truncatula* Gaertn. plants exhibited higher levels of JA

and reduced height growth compared to control plants (Tretner et al., 2008). A study on the allene oxide synthase (AOS) mutant in *Arabidopsis* further implicated the role of JA in the thigmomorphogenetic response. The AOS mutation disrupts JA and other oxylipin synthesis. AOS mutant plants did not exhibit a thigmomorphogenetic response when exposed to MP (Chehab et al., 2012).

Cytokinin content was elevated in the xylem exudate of MP *Helianthus annuus* L. stems; however, it was reduced in the leaves of MP plants (Beyl and Mitchell, 1983). The entire field elucidating the role of plant growth regulators in the post-mechanopreception–thigmomorphogenetic response is still open for investigation. The increasing number of metabolic mutants in *Arabidopsis* available for study will help clarify the role different growth regulators, signaling compounds, and cytoskeleton structure have in the thigmomorphogenetic response.

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 symplast. Following mechanopreception, a cascade of physiological responses occurs, involving up- or down-regulation of gene expression and plant growth regulators. 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) and 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 stem's 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 reduce 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. Research into the mechanosensing and biochemical/physiological response of plants to MP has advanced significantly over the past 60 years. More recent advances in molecular biology and genetics have accelerated this understanding. The literature cited in this review is a compilation of many studies which investigate a multitude of different plant species reflecting a broad diversity of plant growth forms and strategies, from short-lived annuals of both dicot and monocot taxa to long-lived woody perennials, sessile

plants to vining plants to arborescent plants. As reviewed here, differences in results for different physiological systems might be simply a result of different biological requirements needed to support a specific plant organ, growth form, or ecological strategy. For example, *Arabidopsis* is a short-lived sessile annual composed of a rosette of leaves and a flower spike. The only structure that rises above ground level and is potentially exposed to wind is its floral spike upon which most MP studies in this species have been conducted. This organ is an ephemeral structure of primary growth tissues lacking secondary growth and specialized in supporting flowers/reproduction. *B. dioica* and *Cucurbita pepo* are both vining plants that have secondary growth but rely on other plants or objects for mechanical support. Monocotyledonous angiosperms such as *Triticum* and *Zea* do not possess a vascular cambium. The annual dicotyledonous angiosperms including *Phaseolus*, *Helianthus*, *Nicotiana*, and *Medicago* possess a vascular cambium but do not achieve great height growth. Within arborescent taxa, within the same species, differences in parentage and genetic lines can result in different degrees of growth responses to MP, which has been reported in both dicotyledonous angiosperms and coniferales (conifers). This has been clearly demonstrated in hybrid *Populus* clones and *Pinus taeda* half-sib families. This latter fact provides some potential for tree selection and breeding programs to identify traits that convey increased resistance to wind-induced damage to forest plantations such as wind-throw or stem snap (Telewski and Moore, 2016).

With a few notable exceptions (for reviews, see Telewski, 1995, 2006, 2012, 2016a,b), the majority of arborescent woody tree species that fall within the dicotyledonous angiosperms and conifers exhibit some degree of a thigmomorphogenetic response when exposed to wind or other MP. Variations within this response reported in past studies likely arose due to the type and intensity of the MP applied to the plant and the underlying genetics and life history. Standardizing force application has contributed significantly to understanding the amount of force required to induce a response in trees (Coutand et al., 2000). The application of clonal or half- or full-sib technology will also reduce variability within a study group/population. This will potentially lead to the identification of potential gene candidates to further elucidate the variability in the thigmomorphogenetic response. Such an approach can be further advanced by incorporating specific genetic mutations and gene silencing techniques to isolate and identify key elements in the response pathway. Further investigation into the role of ACC and ethylene in the response of woody plants to determine if their role in the thigmomorphogenetic response is restricted to radial, secondary growth of the vascular cambium and not a reduction in height growth controlled by the apical meristem will be critical. Likewise, further elucidation of the timing and role that down-regulation of GA has on the inhibition of height growth is needed. Previous studies have reported a cessation of height growth shortly after MP with a recovery within an hour afterward. Does this growth cessation involve the down-regulation of GA, or is down-regulation involved later in the response pathway? Currently, no studies have investigated the role of mechanopreception and growth regulation in the

development of roots in trees, although changes in morphology and anatomy have been reported. It would be interesting to determine if the response to wind and other MP induces similar responses in roots or if there are subtle differences given the nature of the root's structure and function in anchorage as opposed to withstanding bending and sway of the branches and trunk. Ultimately, a better understanding of the interactions of gene expression and growth and development could be applied

for trait selection in tree improvement programs to increase the stability of forest and plantations to withstand the projected increase in winds associated with frontal and cyclonic storm systems forecast in climate change models.

AUTHOR CONTRIBUTIONS

FT is solely responsible for this publication.

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Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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