To respond or not to respond, the recurring question in plant mechanosensitivity

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INTRODUCTION

Mechanosensing is an important factor regulating plant growth and development (Hamant, 2013). Mechanical cues may be internal signals produced during tissue or cellular expansion (Ingber, 2005; Hamant et al., 2008) or external signals from the environment, mainly from wind (Mouila et al., 2011). To understand the influence of wind on plant development, different methods have been used in the laboratory to simulate the mechanical effect of wind, like bending, touching, shaking, or brushing the aboveground parts of plants. These mechanical stimulations result in a thigmomorphogenetic syndrome generally characterized by reduction in stem height, modification of the mechanical properties of the stem, increase in root biomass and local increases in stem radial growth depending on the species (Telegewski, 2006).

These physiological responses that alter the growth trajectory and form of the plants are thought to be involved in a long-term process of acclimation, tending to reduce the impact of subsequent mechanical stimulation (Mouila et al., 2006; Telegewski, 2006). However, less is known about how plants respond to rapid recurrent mechanical stimulations. Wind typically induces repeated flexing of plant organs at different frequencies (De Langre, 2008). Plant stems may oscillate at frequencies in the range of 1–5 Hz in wind, corresponding to 60–300 bends per minute (Rodriguez et al., 2008; Der Loughian et al., 2014). In temperate climates, windy and calm days alternate on a time scale of several days (Stull, 1988). If every response to each mechanical stimulus was of the same magnitude, plants would invest greatly in withstanding mechanical perturbation to the detriment of growth. Plants thus need to permanently fine-tune their response to mechanical stimulation in order to avoid the cost of a constitutive protection system. This holds especially true for trees because of their long-term growth period and their high stature. There is some experimental evidence that plants reduce their responsiveness to mechanical signals as a function of their mechanical history. This acclimation of mechanosensitivity has been named accommodation (Mouila et al., 2011) in reference to the cellular accommodation that bones undergo in response to external mechanical loading (Schriefer et al., 2005). Here we summarize and discuss experimental observations of plants responding to recurrent mechanical simulation. Regulation of plant responsiveness to recurrent cold and drought stress is compared to mechanosensitivity accommodation. Finally, preliminary evidence and speculation about the molecular mechanisms involved in such processes are discussed.

SATURATION AND DESENSITIZATION, WAYS TO DEAL WITH SUCCESSIVE MECHANICAL STIMULATION

When studying variation in plant responsiveness to successive mechanical stimulations, two parameters need to be taken into account. (i) The intensity of the mechanical stimulation should be quantified so it can be reproducibly and repeatedly applied. (ii) The kinetics of plant responses to single and successive stimulations should be characterized.

Formerly, a first approach to investigate plant mechanosensitivity was to quantify and compare the effect of different magnitudes or numbers of mechanical stimulations. When Phaseolus vulgaris internodes are rubbed repeatedly (following a standardized method), the amount of mechanical stimulation correlates positively with the extent of internode elongation, but the sensory function becomes saturated even with small amounts of rubbing
(Jaffe et al., 1980). To mimic the effect of wind, mechanical experiments on tree species are usually done by bending the stem for a few seconds then releasing it. This transient stimulus (which will be here called bending) has the added advantage of allowing the experimenter to control how much strain is applied, so the physical stimulus perceived by plant cells is known (Coutand and Moulia, 2000; Coutand et al., 2009). In such experiments on Ulmus americana, no increment in the secondary growth response was detected after three weeks when stimulation frequency was increased from 5–80 bends a day (Telewski and Pruyn, 1998). In another set of observations on Prunus persica, stems were bent in a controlled manner eight times a day. Over the 6 weeks of the experiment, the stimulus of repeated bending affected growth less, even when the actual strains applied were increased slightly over time to compensate for stem radial growth (Coutand et al., 2008). Altogether, these results suggest that saturation of either the mechanosensory or the response systems was reached. However, because the responses were measured at the end of several weeks of treatment, it was not possible to exclude the possibility that plant sensitivity was adjusted with each successive bend and that only some of the first mechanical treatments were responsible for the observed responses. In poplar, controlled stem flexing at a sub-saturation level was coupled with kinetics analyses of the responses to each successive bending. The result was a rapid reduction in responsiveness of both radial growth and gene expression (Martin et al., 2010). In particular, these experiments showed that the second bending, 24 h after the first, was markedly weaker in inducing four early mechanoresponsive genes encoding, respectively, two calmodulins, a C2H2 transcription factor (Figure 1A) and a xyloglucan endotransglycosylase. As the abundance of these genes transcripts returned to basal levels before 24 h (Martin et al., 2009), the expression levels observed could only have been due to the second bending and not due to response saturation. These data demonstrated that a single bending is sufficient to initiate a change in plant responsiveness, in this case a down-regulation or desensitization, to subsequent bending. In Arabidopsis, an even faster desensitization occurred after unquantified successive touch stimulation (Arteca and Arteca, 1999). As soon as 1 h after the first stimulation, a second touch was less effective in inducing ACS6 expression, a gene encoding 1-aminocyclopropane-1-carboxylic acid (ACC) synthase enzyme (Figure 1A). In the conditions described above

![Desensitization kinetics set up in response to recurrent mechanical stimulations applied at high frequency in case of wind induced Ca\(^{2+}\) cytosolic concentration in Nicotiana tabacum (Knight et al., 1992) or at low frequency in case of touch-induced ACS6 expression in Arabidopsis (Arteca and Arteca, 1999) and bending-induced ZFP2 expression in Populus tremula x P. alba (Martin et al., 2010). (B) Hypothetical mechanisms for the short-term or long-lasting desensitization: (i) alterations of perception through sensor turnover, modification or inactivation, (ii) negative feedback from long-term accumulation of signaling molecules or transcription factors and (iii) information storage through epigenetic regulation.](image-url)
after the second bending of the poplar stem, about seven days without any bending stimulus were necessary to recover the full capacity for induction of gene expression (Figure 1A, Martin et al., 2010), suggesting that this state of desensitization to mechanical loads lasts for several days. Such desensitization was also observed in case of the typical defensive leaf-folding reflex of Mimosa plants (Gagliano et al., 2014). However, in this case, the resensitization was assessed with a mechanical disturbance different from the one responsible of the desensitization.

The above kinetics could be said to more closely mimic the alternation between windy and calm days in nature rather than oscillations in the wind at frequencies between 1 and 5 Hz (Rodriguez et al., 2008). The effects of mechanical treatments that recur at short intervals were investigated by analyzing rapid cellular events. Knight et al. (1992) showed that wind-induced mechanical stimulations of Nicotiana seedlings generate peaks of elevated cytosolic calcium concentrations. The amplitudes of calcium peaks diminished when stimulations were repeated every 5 s until cells became refractory to further stimulation. Full desensitization was attained after about 6–7 stimulations (about 30 s of intermittent stimulation) and full responsiveness was recovered less than 60 s later when stimulation was decreased (Figure 1A). However, attenuation of this type of calcium response was not detected in Arabidopsis roots when the two touch stimuli were separated by 20 s (Monshausen et al., 2009).

Intuitively we would expect down-regulation of sensitivity upon prolonged mechanical or recurrent stimulation to be a key component of any biological sensory process. However, kinetics and mechanistic data are still lacking to fully describe desensitization. Moreover, the link between the decrease in responsiveness of mechanoresponsive genes and the regulation of mechanoperception is yet to be elucidated.

FINE-TUNING SENSITIVITY, A RECURRING THEME

Modifying plant responsiveness is not restricted to recurrent mechanical stimuli as other abiotic stimuli act in a similar way. However, a plethora of terminologies have been used to describe these different stress situations which may mask some of the similarities. Generally, altered physiological responses to recurrent abiotic stress that allow a plant to maintain its performances despite the stress, is referred to as “acclimation” or “hardening.” For biotic stress, the term “priming” is usually preferred, and is defined as “the phenomenon whereby previous exposure makes a plant more resistant to future exposure” (Bruce et al., 2007). When the response to a stimulus is modified at the cellular or molecular level, authors predominantly use terms to describe the state of sensitivity of the cells. For example, to describe how peaks of cytosolic free calcium concentration decrease with repeated stimulation/stress, the terms “attenuation” or “desensitization” are used (Knight et al., 1992; Plieth et al., 1999). Bruce et al. (2007) suggested the general term of “stress imprint” to designate “a genetic or biochemical modification of a plant that occurs after stress exposure that causes future responses to future stresses to be different.” This is less anthropomorphic than the concept of “memory” or “training,” but many authors are using “plant stress memory” to encapsulate the idea that plants store information related to a first stress exposure, leading to increased or decreased responses to subsequent exposures (Galis et al., 2009; Stork et al., 2009; Ding et al., 2013).

The time-courses of desensitization–resensitization phenomena have barely been investigated. The kinetics of the generation of peaks in intracellular calcium concentration in response to cold were studied in Arabidopsis roots with regimes of recurrent cold stimulation at a range of intervals on the time-scale of several minutes. As in wind-stimulated Nicotiana seedlings (Knight et al., 1992), attenuation of the height of calcium peaks was observed and desensitization started minutes after the first stimulation and lasted for a minimum of 30 min before re-sensitization occurred (Plieth et al., 1999). However, this desensitization was overridden if the intensity of the subsequent stimulus was increased (i.e., with a decrease in the temperature). These phases of desensitization or attenuation at the calcium level could avoid an over-mobilization of internal and external stores of calcium which would hamper any further response.

Exposing Arabidopsis plants to cold temperatures (+4°C) also triggers rapid modifications in gene expression. One example is the up-regulation of genes encoding members of the AP2/EREBP family of DNA-binding proteins, the cold binding factors (CBFs; Gilmour et al., 1998). Using the accumulation of CBF transcripts as a marker, Zarka et al. (2003) found that the cold-sensing mechanism can be desensitized within a few hours of exposure to a low temperature. In the case of desensitization to +4°C, resensitization (i.e., recovery of CBF induction at this same temperature), took between 8 and 24 h of re-exposure to warm temperatures. As for the calcium response, the desensitized state could be overridden by a further decrease in temperature.

In the phenomena described above, desensitization is a way for plants to avoid over-responding, using excess signaling molecules (e.g., calcium) or saturating the sensing machinery. However, in the case of plant defense (Galis et al., 2009; Conrath, 2011) or dehydration (Ding et al., 2012), adjustments in plant sensitivity can also make plants more responsive to subsequent exposures, in what we could call hypersensitization. For example, Arabidopsis plants trained by a first exposure to a dehydration stress wilt more slowly than untrained plants when they are exposed a second time. When the plants are subjected to cycles of 2 h of dehydration and 22 h of rehydration, “trainable” genes (e.g., RD29B, RAB18) produced higher transcript levels in response to subsequent stresses than to the initial stress, whereas “non-trainable” genes expressed similar transcript levels for each stress event (e.g., RD29A and COR15A). This “transcriptional memory” persisted for at least 5 days and was lost after 7 days (Ding et al., 2012). More recently, a large-scale transcriptional analysis revealed there are 1963 such “memory” genes in the Arabidopsis transcriptional network triggered by dehydration stress (Ding et al., 2013).

To conclude, different plant species modify their sensitivity to abiotic stresses at the physiological, cellular and molecular levels with very different kinetics. However, it should be noted that the different mechanisms have some features in common despite the very different environmental cues. For example, at the level of the molecular response, desensitization is usually rapid and lasts for several days.
HOW TO CONTROL DESENSITIZATION
If desensitization occurs in response to a variety of recurring biotic and abiotic cues, how have the common features of responsiveness regulation emerged in these different signaling pathways? What are the underlying mechanisms? Three potential mechanisms could be proposed depending on the kinetics of their occurrence (Figure 1B).

ALTERATIONS OF PERCEPTION THROUGH SENSOR TURNOVER, MODIFICATION OR INACTIVATION
The natures of potentially numerous touch, cold, and osmotic sensors are still to be fully elucidated. As discussed by Telewski (2006), abiotic stimuli cause membrane deformation by modifying turgor pressure or membrane fluidity, and some are also sensed as mechanical stimuli by living cells. Two classes of putative mechanosensors are currently under investigation, stretch-activated channels and transmembrane proteins inserted into the cell wall/plasma membrane/cytoskeleton (CWPMC) network (Monshausen and Gilroy, 2009; Haswell and Monshausen, 2013).

Two types of stretch-activated channels have been identified so far. Mid1-complementing activity (MCA) proteins are calcium channels (Nakagawa et al., 2007; Yamanaka et al., 2010) and MscS-like (MSL) family members are non-selective channels identified based on homology to bacterial MscS (Kung, 2005; Haswell et al., 2008). Is the rapid desensitization of calcium influx after repeated cold and mechanical sensing linked to the gating kinetics of these channels? In bacteria, results of patch-clamp experiments have indeed shown that MscS channels are inactivated after prolonged exposure to membrane tension (Koprowski and Kubalski, 1998; Levina et al., 1999). In plants, the only gating kinetics obtained for a stretch-activated channel was for the Arabidopsis MSL10 channel, but no inactivation of the channel was detected (Maksaev and Haswell, 2012).

The initial sensor of mechanical stress could also be a component of the CWPMC network like receptor-like kinase (RLK) transmembrane proteins (Monshausen and Gilroy, 2009; Haswell and Monshausen, 2013). Whereas a direct link between membrane protein kinases and mechanosensing has not been established, several reports suggest that the cytoskeleton, through its tethering with transmembrane proteins, could be involved. In the Arabidopsis meristem, cortical microtubules re-oriented rapidly (within 6 h) in the presence of a mechanical stress (Hamant et al., 2008). A more recent study demonstrated that katanin, a microtubule-severing protein, is required for cell responsiveness to the mechanical stresses generated by growth in Arabidopsis meristem cells (Uyttewaal et al., 2012). This provides the outline for a model in which microtubule dynamics allow the cell to respond efficiently to mechanical forces (Nick, 2013).

NEGATIVE FEEDBACK FROM LONG-TERM ACCUMULATION OF SIGNALING MOLECULES OR TRANSCRIPTION FACTORS
Peaks of cytosolic calcium accumulation are a common feature in many stress signaling pathways. As this calcium response is attenuated by repetitive stimulation, Ca\(^{2+}\) influx and efflux transporters regulating calcium homeostasis could be considered as components of a “mechanical memory.” Cyclic nucleotide-gated channels (CNGCs) can mediate fluxes of Ca\(^{2+}\) ions, and binding of Ca\(^{2+}\)/calmodulin inactivates CNGCs (Hua et al., 2003; Ali et al., 2006). Thus, the negative action of calmodulin or calmodulin-like proteins on CNGC activity could diminish plant responsiveness through a direct feedback pathway restricting Ca\(^{2+}\) influx into plant cells. Genes encoding calmodulin or calmodulin-like proteins are up-regulated early after touch or stem bending (Depège et al., 1997; Lee et al., 2005; Martin et al., 2009), but the involvement of CNGC channels has not been directly addressed in relation to mechanical loading. Glutamate receptors are nonselective cation channels activated by glutamate and glycine (Qi et al., 2006; Stephens et al., 2008) that mediate an increase in cytosolic Ca\(^{2+}\) upon cold stress and touch (Meyerhoff et al., 2005). When a second glutamate treatment was applied after the first stimulus, no additional Ca\(^{2+}\) response was observed, suggesting that these receptors remain in a putative desensitized state for 1 h (Meyerhoff et al., 2005). Again, the potential role of such glutamate receptors in the mechanotransduction pathway needs to be established.

The desensitization process could also involve transcription factors exerting a negative feedback control on the first stages of the mechanotransduction pathway. In poplar, PtaZFP2, a gene encoding a C2H2 transcription factor, is rapidly up-regulated after stem bending (Martin et al., 2009). In PtaZFP2-overexpressing poplars, the up-regulation of several mechanosensitive genes was much weaker after stem bending than in wild-type plants (Martin et al., 2014). Thus, PtaZFP2 negatively modulates poplar responsiveness to mechanical stimulation. Among the genes downstream of PtaZFP2, CML42, a calmodulin-like encoding gene, and WRKY53 and WRKY40, transcription factor encoding genes are up-regulated. The Arabidopsis homologs of these poplar genes have been described as negative regulators of plant defense responses (Xu et al., 2006; Vadassy et al., 2012). Thus, in concert with these molecular suppressors, PtaZFP2 could reduce the reactivation of the mechanical signaling pathway when stems are bent again.

INFORMATION STORAGE THROUGH EPIGENETIC REGULATION
One intriguing result is that desensitization of the expression of mechanosensitive genes to mechanical stimuli lasts at least three days (Martin et al., 2010). Bruce et al. (2007) suggested epigenetic changes could be a mechanism for long-term information storage after various abiotic stresses. Chromatin remodeling during drought and cold stresses, which alters accessibility of genes to proteins regulating transcription, has received more attention recently (Kim et al., 2008, 2010a; Chinnusamy and Zhu, 2009; To and Kim, 2014). For example, the dynamics of the chromatin status of four stress-responsive candidate genes were analyzed during recovery (i.e., rehydration) of Arabidopsis from drought stress (Kim et al., 2012). These studies focused on changes in acetylation (ac) and methylation (me) of lysine (K) residues of histone H3 N-terminal tails. While the proportion of H3K9ac was reduced rapidly during rehydration, H3K4me3 decreased more gradually and was maintained at low levels on the drought-inducible genes even up to 5 h after rehydration. As H3K4me3 is correlated with
positive gene responsiveness, the authors suggested that this epi-
genome mark of stress memory might help plants respond more
effectively to subsequent stresses (Kim et al., 2012; To and Kim,
2014). Indeed, in the Arabidopsis H3K4 methyltransferase mutant
atx1, which is defective in methylyating H3K4, the responsiveness
do not increase as much as in wild-type (Ding et al., 2011,
2012).

In an example of cold sensing, the hos15 Arabidopsis mutant
showed modifications in both histone deacetylation and cold
tolerance (Zhu et al., 2008). HOS15 is a WD-40 protein similar
to human transducin-beta like protein, a component of
repressor complexes involved in histone deacetylation. Apart
from an analysis of DNA methylation in Bryonia internodes
stimulated by rubbing (Galaud et al., 1993), information about
epigenetic regulation during plant responses to mechanical
loads is scarce. However, some structural features of the aforemen-
tioned poplar transcription factor PtaZF2 indicate that it could
be involved in histone modification. The PtaZF2 protein con-
tains a DLN-box (Gourcilleau et al., 2011), also known as an
ERF-associated amphiphilic repression motif (Ohta et al., 2001;
Kazan, 2006). Recently, transcription factors containing this motif
were reported to exhibit repression activity via histone deacetyla-
tion and stimulation of heterochromatin formation in Arabidopsis
(Causier et al., 2012), so this is preliminary evidence on which
to base wider study of epigenetic regulation of responsiveness
to mechanical stimuli.

CONCLUSION

The regulation of plant mechanosensing could be an important
part of acclimation to wind by modulating the magnitude and
duration of the response and preventing costly investment in
reducing or redirecting growth. Modulation of responsiveness
could also occur in response to internal mechanical signals pro-
duced during tissue or cellular expansion or maturation as part of
morphogenesis. The mechanisms underlying this phenomenon are
largely unknown essentially because there is so little data on
the nature of the presumed mechanosensors or the timing of the
regulation. Although some mechanisms are beginning to be iden-
tified for other abiotic stresses, they remain largely hypothetical
in the case of mechanical stimulation such as bending caused by
wind. More high-resolution description of the timing of plant
responses at the tissue and cellular level would help to demon-
strate the importance of mechanosensing regulation for plant
acclimation.

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REFERENCES

Ali, R., Zielinski, R. E., and Berkowitz, G. A. (2006). Expression of plant
cyclic nucleotide-gated cation channels in yeast. J. Exp. Bot. 57, 125–138. doi:
10.1093/jxb/erj012.
Arteca, J. M., and Arteca, R. N. (1999). A multi-responsive gene encoding 1-
aminocyclopropane-1-carboxylate synthase (ACS6) in mature Arabidopsis leaves.
Plant Mol. Biol. 39, 209–219. doi: 10.1023/A:1006177902093

Bruce, T. J. A., Matthes, M. C., Napier, J. A., and Pickett, J. A. (2007). Stressful
‘memories’ of plants: evidence and possible mechanisms. Plant Sci. 173, 603–608.
doi: 10.1016/j.plantsci.2007.09.002

Causier, B., Ashworth, M., Guo, W., and Davies, B. (2012). The TOPELESS interac-
tome: a framework for gene repression in Arabidopsis. Plant Physiol. 158, 423–438.
doi: 10.1104/pp.111.186999

Chinnusamy, V., and Zhu, J. K. (2009). Epigenetic regulation of stress responses
in plants. Curr. Opin. Plant Biol. 12, 133–139. doi: 10.1016/j.pop.2008.12.006

Conrath, U. (2011). Molecular aspects of defence priming. Trends Plant Sci. 16,
524–532. doi: 10.1016/j.tplants.2011.06.004

Couillard, C., Dupraz, C., Jasouen, G., Ploquin, S., and Adam, B. (2008). Mecha-
nical stimuli regulate the allocation of biomass in trees: demonstration with young
Prunus avium trees. Ann. Bot. 101, 1421–1432. doi: 10.1093/aob/mcn054

Couillard, C., Martin, L., Leblanc-Fournier, N., Decourteix, M., Julien, J. L.,
and Mouila, B. (2009). Strain mechanosensing quantitatively controls
diameter growth and the level of expression of the PtaZF2 mechanosen-
sitive gene in poplar. Plant Physiol. 151, 223–232. doi: 10.1104/pp.109.138164

Coutand, C., and Mouila, B. (2000). Biomechanical study of the effect of a controlled
bending on tomato stem elongation: local strain sensing and spatial integration
of the signal. J. Exp. Bot. 51, 1825–1842. doi: 10.1093/jexbot/51.352.1825

De Langre, E. (2008). Effects of wind on plants. Annu. Rev. Fluid Mech. 40, 141–168.
doi: 10.1146/annurev.fluid.40.111406.102135

Depege, N., Thonat, C., Coutand, C., Julien, J. L., and Boyer, N. (1997).
 Morphological responses and molecular modifications in tomato plants after
mechanical stimulation. Plant Cell Physiol. 38, 1127–1134. doi: 10.1093/oxford-
journals.pcp.a029097

Der Loughian, C., Tadrist, L., Allain, J. M., Diener, J., Mouila, B., and de Langre, E.
(2014). Measuring local and global vibration modes in model plants. C. R. Méc.
342, 1–7. doi: 10.1016/j.crmec.2013.10.010

Ding, Y., Avramova, Z., and Fromm, M. (2011). Two distinct roles of ARA-
BIDOPSIS HOMOLOG OF TRITHORAX1 (ATX1) at promoters and within
transcribed regions of ATX1-regulated genes. Plant Cell 23, 350–363. doi:
10.1090/bpc.110.080150

Ding, Y., Fromm, M., and Avramova, Z. (2012). Multiple exposures to drought
'train' transcriptional responses in Arabidopsis. Nat. Commun. 3, 740. doi:
10.1038/ncomms1732

Ding, Y., Liu, N., Vilouvet, L., Riethoven, J. J., Fromm, M., and Avramova, Z. (2013).
Four distinct types of dehydration stress memory genes in Arabidopsis thaliana.
BMC Plant Biol. 13:229. doi: 10.1186/1471-2229-13-229

Gagliano, M., Rento, M., Depczynski, M., and Mancuso, S. (2014). Experience
teaches plants to learn faster and forget slower in environments where it matters.
Oecologia 175, 63–72. doi: 10.1007/s00442-013-2873-7

Galaud, J. P., Gaspar, T., and Boyer, N. (1993). Inhibition of internode growth
due to mechanical stress in Bryonia dioica. Oecologia 101, 1421–1432. doi:
10.1007/BF00305486

Galis, I., Gasquerel, E., Pandey, S., and Baldwin, I. T. (2009). Molecular mechanisms underlying plant memory in JA-mediated defence responses. Plant Cell Environ. 32, 617–627. doi: 10.1111/j.1365-3040.2008.01862.x

Gilmore, S. J., Zarka, D. G., Stockinger, E. J., Salazar, M. P., Houghton, J. M.,
and Thomashow, M. F. (1998). Low temperature regulation of the Arabidopsis CBF
family of AP2 transcriptional activators as an early step in cold-induced COR
gene expression. Plant J. 16, 433–442. doi: 10.1046/j.1365-313x.1998.00310.x

Gourcilleau, D., Lenne, C., Armenise, C., Mouila, B., Julien, J. L., Bronner, G.,
et al. (2011). Phylogenetic study of plant Q-type C2H2 zinc finger proteins and expression analysis of poplar genes in response to osmotic, cold and mechanical stresses. DNA Res. 18, 77–92. doi: 10.1093/dnares/ dar001

Hamant, O. (2013). Widespread mechanosensing controls the structure behind
the architecture in plants. Curr. Opin. Plant Biol. 16, 654–660. doi:
10.1016/j.pbi.2013.06.006

Hamant, O., Heisler, M. G., Jonsson, H., Krupinski, P., Uyttewaal, M., Bokov, P.,
et al. (2008). Developmental patterning by mechanical signals in Arabidopsis. Science
322, 1650–1655. doi: 10.1126/science.1165594
Maksaev, G., and Haswell, E. S. (2012). MscS-Like10 is a stretch-activated ion channel. *Plant Physiol.* 159, 1790–1798. doi: 10.1104/pp.112.198150

Moulaï, B., Der Loughian, C., Bastien, R., Martin, L., Rodriguez, M., Gourcilleau, D., et al. (2011). “Integrative mechanobiology of growth and architectural development in changing mechanical environments,” in *Mechanical Integration of Plant Cells and Plants Springer, Series: Signalling and Communication in Plants*, ed. P. Wojtaszek (Berlin: Springer-Verlag), 269–302.

Nakagawa, Y., Katagiri, T., Shinozaki, K., Qi, Z., Tatsumi, H., Furuchi, T., et al. (2007). Arabidopsis plasma membrane protein crucial for \( \text{Ca}^{2+} \) influx and touch sensing in roots. *Proc. Natl. Acad. Sci. U.S.A.* 104, 3639–3644. doi: 10.1073/pnas.0607730104

Nick, P. (2013). Microtubules, signalling and abiotic stress. *Plant J.* 75, 309–323. doi: 10.1111/pj.12102

Ohta, M., Matsu, K., Hiratsu, K., Shishih, H., and Ohme Takagi, M. (2001). Repression domains of class II ERF transcriptional represers share an essential motif for active repression. *Plant Cell* 13, 1959–1968. doi: 10.1105/tpc.13.8.1959

Plieth, C., Hansen, U., Knight, H., and Marc, R. K. (1999). Temperature sensing by plants: the primary characteristics of signal perception and calcium response. *Plant J.* 18, 491–497. doi: 10.1046/j.1365-313X.1999.00474.x

Qi, Z., Stephens, N. R., and Spalding, E. P. (2006). Calcium entry mediated by GLR3.3, an Arabidopsis glutamate receptor with a broad agonist profile. *Plant Physiol.* 142, 965–971. doi: 10.1104/pp.106.088899

Rodriguez, M., De Langre, E., and Moulaï, B. (2008). A scaling law for the effects of architecture and allometry on tree vibration modes suggests a biological footing to modular compartmentalization. *Am. J. Bot.* 95, 1532–1537. doi: 10.1105/tpc.107.055216

Stork, W., Diezel, C., Halitschke, R., Galis, I., and Baldwin, I. T. (2009). An ecological analysis of the herbivory-elicted JA burst and its metabolism: plant memory processes and predictions of the moving target model. *PLoS ONE* 4, e6497. doi: 10.1371/journal.pone.0006497

Stull, R. B. (1988). *CML42-mediated calcium signaling coordinates responses to spodoptera exigua* herbivory. *Proc. Natl. Acad. Sci. U.S.A.* 105, 9444–9449. doi: 10.1073/pnas.105.23.9444

Vadassery, J., Reichelt, M., Hause, B., Gershenzon, J., Boland, W., and Mithöfer, A. (2000). Acidification of the leaf apoplast is localized to actively growing regions of the Arabidopsis root. *Planta* 211, 319–327. doi: 10.1007/s00425-002-0732-0

Yang, X., Chen, C., Fan, B., and Chen, Z. (2006). Physical and functional interactions between pathogen-induced Arabidopsis WRKY18, WRKY40, and WRKY60 transcription factors. *Plant Cell* 18, 1310–1326. doi: 10.1105/tpc.105.037523

Yamaoka, T., Nakagawa, Y., Mori, K., Nakano, M., Imamura, T., Katoaka, T., et al. (2010). MCAI and MCA2 that mediate \( \text{Ca}^{2+} \) uptake have distinct and overlapping roles in Arabidopsis. *Plant Physiol.* 152, 1284–1296. doi: 10.1104/tpc.109.147371
Zarka, D. G., Vogel, J. T., Cook, D., and Thomashow, M. F. (2003). Cold induction of Arabidopsis CBF genes involves multiple ICE (inducer of CBF expression) promoter elements and a cold-regulatory circuit that is desensitized by low temperature. Plant Physiol. 133, 910–918. doi: 10.1104/pp.103.027169

Zhu, J., Jeong, J., Zhu, Y., Sokolchik, I., Miyazaki, S., Zhu, J. K., et al. (2008). Involvement of Arabidopsis HOS15 in histone deacetylation and cold tolerance. Proc. Natl. Acad. Sci. U.S.A. 105, 4945–4950. doi: 10.1073/pnas.0801029105

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