

IN BRIEF

Early Signaling Events in Mechanosensing

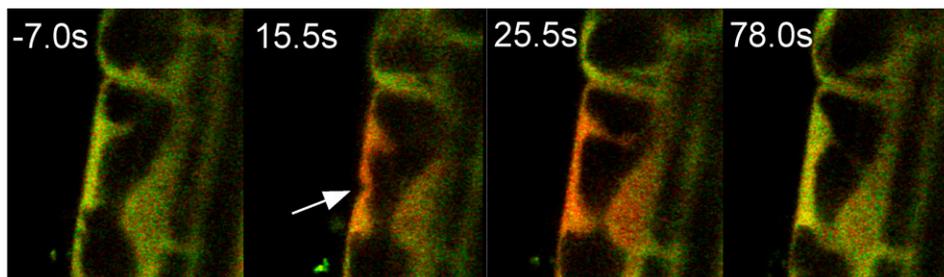
In order to survive and adapt to stresses such as herbivore attack, wind, and physical barriers to growth, plants are equipped to sense and respond to mechanical stimulation (for reviews, see Chehab et al., 2009; Monshausen and Gilroy, 2009). While details of the sensing and transduction of mechanical stimuli are not clear, transient calcium fluxes, pH changes, and reactive oxygen species (ROS) production are known to occur early in the process. Now, **Monshausen et al. (pages 2341–2356)** elegantly demonstrate that mechanically induced increases in cytosolic Ca^{2+} have stimulus-specific signatures and that they cause pH changes and ROS production. The authors achieve high spatial and temporal

of Ca^{2+} influx across the plasma membrane. When a plant root encounters a barrier, the root bends as it continues to grow. This results in stretching of cells on one side of the root and compression of cells on the other side. Monshausen et al. found transient cytoplasmic Ca^{2+} increases on the stretched sides of cells, showing that endogenous mechanical stresses and external stimuli are likely transduced by the same (or similar) mechanisms.

The authors examined pH changes and were able to show that surface alkalization and concomitant cytoplasmic acidification are intimately related to Ca^{2+} flux signatures. A monophasic response was seen within a few seconds of touching a single cell. By contrast,

nated those responses to touch or bending. Thus, Ca^{2+} influx into the cytoplasm is necessary and sufficient to cause pH changes and ROS production. Both pH and ROS can affect cell wall linkages, so the ability to alter them on a rapid time scale gives the plant a chance to adjust quickly to mechanical perturbations. All together, the authors assembled an impressive collection of tools that allowed them to define the relationships between early events in mechanosensing and to do so in living, intact plants.

Nancy R. Hofmann
Science Editor
nhofmann@aspb.org



Transient calcium increase upon touching. An *Arabidopsis* root epidermal cell is shown before (left panel) and after (right three panels; time elapsed is labeled) a touch stimulus. The arrow indicates the point of stimulation, red signal represents higher Ca^{2+} concentration, and yellow represents lower concentration. (Adapted from Figure 1 of Monshausen et al. [2009].)

resolution in planta using an array of fluorescent molecules to visualize rapid responses to touch, bending, and barriers to growth in *Arabidopsis thaliana* roots.

They found that when individual root epidermal cells were touched (simulating fungal attack, for instance), cytosolic Ca^{2+} increases occurred rapidly at the area of the stimulus, spread throughout the cell, and dispersed (see figure). In contrast with this monophasic effect, temporary bending of the entire root led to transient biphasic Ca^{2+} increases. Both of these responses were abolished by calcium channel blockers, suggesting the involvement

root bending led to biphasic surface alkalization of the affected region, and adding a barrier to growth resulted in surface alkalization on the stretched side. Furthermore, Monshausen et al. found that ROS production in the apoplast occurs on the same time scale. The pH and ROS responses, however, occur independently of each other. Stimulating either effect did not induce the other, and disrupting one did not affect the other.

Calcium ionophore treatments, leading to increased cytoplasmic Ca^{2+} concentrations, did induce pH changes and ROS production. Moreover, calcium channel blockers elimi-

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