changes should consider the potential role of geomagnetic cues [20]. The rate of field drift can vary substantially across different regions of the Earth and through time. Thus, seemingly idiosyncratic variation in the movements and biogeographic patterns of geographically disparate and phylogenetically divergent populations might be unified by considering the role of geomagnetic drift [4].

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Plant Biology: Plants Turn Down the Volume to Respond to Cell Swelling

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Turgor manipulation to induce plant cell swelling is one of the classic experiments undertaken in biology courses in schools and at universities. However, only now do we start to understand the molecular mechanisms responsible for detecting plant cell swelling.

The ability to detect and respond to physical stimuli is essential for maintenance of homeostasis in all living systems. Mechanoperception is the ability to sense mechanical stimuli, which can have external (such as gravity, vibration or touch) and internal (such as osmotic pressure or inter- and intracellular tension) origins. Our knowledge regarding the mechanisms perceiving mechanical stimuli and translating them into biochemical signals is still limited and derives mostly from animals or single-celled organisms [1]; however, mechanoperception obviously also occurs in plants [2]. Every plant cell perceives both static and dynamic mechanical stimuli to appropriately

fine-tune growth, development and interaction with the environment. Such stimuli occur during graviperception, proprioception, touch, mechanical loading, and strains caused by self-loading and internal growth [3]. In parallel and in stark contrast to animals, plant cells need to contain turgor pressure arising from the osmotic flow of water [4]. This force within each plant cell pushes the plasma membrane outward against the cell wall, generating the mechanical stress and pressure levels found in road bike or car tires. Therefore, in order to contain these high turgor pressure levels, the cell walls surrounding all plant cells are normally sturdier than the extracellular matrix encompassing animal cells. Plant cell walls consist of polysaccharides and proteins, with cellulose microfibrils forming the main load-bearing elements ensuring successful containment of turgor pressure [5]. The consequence being that mechano-sensitive structures and processes (exemplified by plasma membrane stretching or shrinking) in plants are simultaneously affected by turgor pressure levels and the functional integrity of the cell walls. Research into the mechanisms responsible for adaptation to hyper-osmotic stress occurring during drought and leading to reduced turgor levels has been quite successful [6]. However, our knowledge is very limited when it comes to the molecular mechanisms detecting cell swelling derived from hypo-osmotic stress or weakened cell walls caused by pathogen-derived degrading enzymes. One reason for this is that intact plant cell walls limit the effects of hypo-osmotic stress applied. Therefore, a model system allowing simultaneous manipulation of turgor levels and cell wall integrity in a tightly controlled manner would represent a very useful tool to analyse mechanisms detecting plant cell swelling.

Unicellular organisms like *Saccharomyces cerevisiae* or *Escherichia coli* which, like plants, have cell walls, have been used as model systems to understand the molecular mechanisms monitoring and controlling turgor pressure as well as mechano-perception [7,8]. Representative molecular components involved include in yeast a plasma membrane-localized Ca^{2+} channel complex consisting of MID1 and CCH1 and mechano-sensitive channels of small conductance (MscS) found in bacteria. The MID1 CCH1 complex detects plasma membrane stretch induced by hypo-osmotic stress or yeast cell wall deformation, thus contributing to mechanoperception, hypo-osmotic stress detection and cell wall integrity maintenance [8]. MscS proteins have been described as safety valves since they prevent bacterial cells from bursting in case hypo-osmotic stress arises [9].

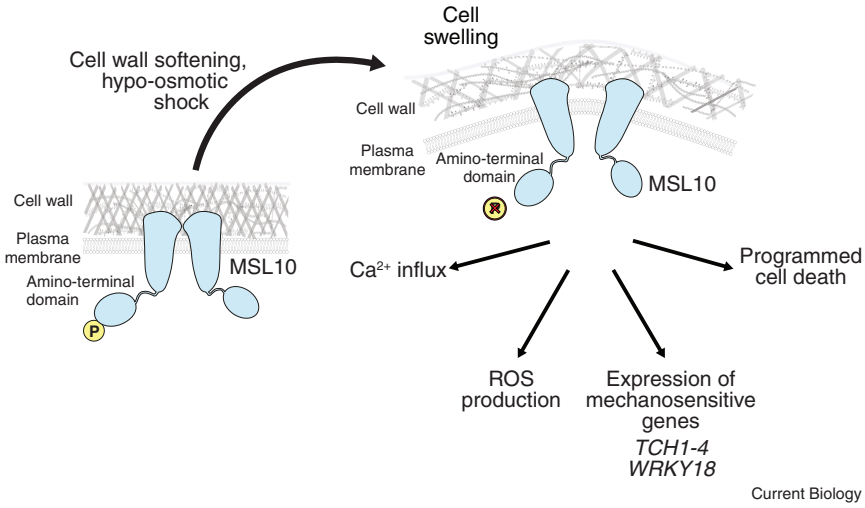

Figure 1. MSL10 mediates responses to *Arabidopsis* cell swelling.
Schematic summary of the experimental system developed by Basu and Haswell and of the role of MSL10 in detecting cell swelling and mediating responses to it.

Research into the mechanisms responsible for mechanoperception and turgor monitoring in plants has benefited from using translational research approaches. MID1-COMPLEMENTING ACTIVITY 1 (MCA1) and 2 from *Arabidopsis thaliana* partially rescue MID1 CCH1 loss-of-function yeast strains, and have similar functions in plants as the complex in yeast [10]. In plants, like in yeast, a dedicated cell wall integrity maintenance mechanism exists, monitoring the state of the cell walls and initiating adaptive responses if cell wall integrity is impaired. Cell wall integrity is impaired during exposure to biotic or abiotic stress, as well as developmental processes like etiolation. MCA1, peptide ligands and plasma membrane-localized kinases THESEUS1 (THE1) and FERONIA (FER) belonging to the *Catharanthus roseus* receptor-like kinase1-like (*Cr*RLK1L) family contribute to cell wall integrity maintenance [11]. A family of MscS homologs (MSLs) with 10 members has been identified in *Arabidopsis*, with several members mediating adaptation to hypo-osmotic stress [12]. Another member (MSL10) acts as a non-selective, membrane tension-gated ion channel [13], regulating cell death and jasmonic acid production [14]. While the available knowledge suggests that an MSL family member could act as a sensor for cell swelling, we have lacked until now conclusive evidence supporting this hypothesis.

In an exciting study published in this issue of *Current Biology*, Basu and Haswell report on a novel experimental system they have developed to investigate the mechanisms enabling plant cells to detect and respond to cell swelling [15]. They use a combination of osmotic and cellulose biosynthesis inhibitors to manipulate simultaneously turgor levels and the load-bearing cellulose microfibrils in the cell walls of *Arabidopsis* seedling roots (Figure 1). This allows them to induce cell swelling in a tightly controlled manner, and study responses to swelling *in vivo* without the (interfering) support provided by the normally sturdy cell walls. By investigating different responses (programmed cell death, reactive oxygen species production, expression of

mechano-sensitive genes and Ca^{2+} influx), the authors efficiently characterize the temporal dynamics of the processes induced by cell swelling.

An initial Ca^{2+}-influx is detectable approximately two seconds after swelling is induced, while ROS production becomes pronounced between 30–60 minutes. By characterizing transcript levels of touch-induced genes and a transcription factor, the authors show that transcriptional responses to cell swelling involve an early transient and a delayed longer-term response. They show that cell swelling induces programmed cell death and use different markers to conclude that cell swelling induces a type of programmed cell death observed in response to biotic/abiotic stress, differing from programmed cell death induced during development. The authors also include in these experiments seedlings containing gain- or loss-of-function alleles for MSL10. The resulting phenotypic data show conclusively how reducing MSL10 activity reduces the responses monitored, while increased MSL10 activity has the opposite effect. They proceed to show that dephosphorylation of MSL10 is required for cell swelling-induced programmed cell death.

The experimental system Basu and Haswell have developed will have a profound effect on research into the mechanisms responsible for perception of hypo-osmotic stress and cell swelling, as it enables us to finally move 'the immovable object' (the plant cell wall) in a controlled manner, while also bringing about controlled changes in turgor pressure levels *in vivo*. From an applied perspective, cell swelling occurs when plant pathogens release cell wall-degrading enzymes during early stages of infection [16]. So, investigating in more detail the processes regulating responses to cell swelling in crop species where the same experimental system can be easily applied will generate knowledge helping us to improve the performance of food crops. The results regarding the function of MSL10 are really exciting because they indicate that MSL10 activity enables the cell to detect swelling and induce adaptive responses. Bearing in mind that previous work has shown that MSL10 is a stretch-activated channel, the new data strongly support the notion that MSL10 translates mechanical stimuli resulting from cell swelling into chemical signals regulating downstream responses.

More importantly, this new study also raises additional intriguing questions and opportunities for follow-up experiments. Basu and Haswell showed that cell swelling induces Ca^{2+} influx, but MSL10 seems not to be directly responsible for this. It will be interesting to dissect the molecular processes and components responsible for this. Previous work has shown that plant cell wall integrity maintenance signalling is activated by cell swelling. Responses to cell wall integrity impairment involve signal transduction processes based on protein phosphorylation (THE1, FER), are turgor sensitive and involve both MCA1 and Ca^{2+}-based signalling processes [17–20]. These similarities raise questions regarding if and how processes mediated by cell wall integrity signalling and MSL10 interact. To summarize, by developing a novel experimental system to study plant cell swelling, characterizing the dynamic responses to swelling and establishing MSL10 as sensor required for control of the swelling-induced responses, the study by Basu and Haswell makes important contributions to the field.

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