Functional adaptation and phenotypic plasticity at the cellular and whole plant level*

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The ability to adaptively alter morphological, anatomical, or physiological functional traits to local environmental variations using external environmental cues is especially well expressed by all terrestrial and most aquatic plants. A ubiquitous cue eliciting these plastic phenotypic responses is mechanical perturbation (MP), which can evoke dramatic differences in the size, shape, or mechanical properties of conspecifics. Current thinking posits that MP is part of a very ancient "stress-perception response system" that involves receptors located at the cell membrane/cell wall interface capable of responding to a broad spectrum of stress-inducing factors. This hypothesis is explored here from the perspective of cell wall evolution and the control of cell wall architecture by unicellular and multicellular plants. Among the conclusions that emerge from this exploration is the perspective that the plant cell is phenotypically plastic.

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1. Introduction

Phenotypic plasticity has been defined broadly as any form of *environment-dependent phenotype expression* (DeWitt and Scheiner 2004). An alternative definition is *the production of environmentally adapted phenotypes by a specific genotype*. This phenomenology, which can confer great adaptability, is extensively expressed by plants because of three features that do much to distinguish them from animal life. First, all terrestrial plants (= embryophytes) and many aquatic plants are sedentary organisms, which means that each plant begins and ends its existence in very much the same physical location. One consequence of this lifestyle is that each plant typically experiences changes in its ambient environment throughout its lifetime, which for woody perennial species may last for thousands of years. Second, in contrast to vertebrates and many invertebrates, some multicellular algae and all land plants, including annual and biennial species, have an "open" ontogeny in which functionally equivalent organs are produced sequentially throughout the growing season. This iterative organogenesis results in the production of serially homologous organs that often develop and reach maturity under different environmental conditions or stimuli. Third, the basic metabolic requirements of all eukaryotic photoautotrophs establish intimate physiological linkages between external environmental variables and the acquisition of essential nutrients and irradiant energy. This feature is evident from the opportunistic growth patterns of roots, the solar-tracking of leaves, and the many phytochrome-mediated developmental responses to light conditions (Taiz and Zeiger 2002). For these and other reasons, it is not surprising that plants manifest "plastic" phenotypes, both as variation among organs produced by the same plant (in response to environmental variation during growth in a particular habitat) and in the form of morphological, anatomical, or physiological differences among conspecifics (in response to different large-scale habitat conditions). Indeed, although many examples of non-adaptive phenotypic responses to abiotic environmental variation are known (e.g. reduced leaf growth and nitrogen concentrations in plants experiencing low nitrogen availability results in plants with fewer seeds; see Sultan and Bazzaz 1993), the results of most transplant and common garden experiments show that character variation within individual species is typically dominated by environmental variation rather than genotypic differences.

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2. Mechanical perturbation

Although many physical environmental factors, such as light intensity and quality, or temperature, provoke or influence plant phenotypic expression, the most ubiquitous and influential developmentally are unavoidable mechanical forces. Broadly speaking these forces fall into one of two categories: (i) internally generated mechanical forces produced by cell, tissue, or organ expansion and growth, and (ii) externally applied mechanical forces resulting from the movement of air, water, neighboring organisms, falling debris, etc. Some workers have argued that growth-induced mechanical forces influence the frequency and orientation of cell division as well as overall cell shape (e.g. Sachs 1878; Thompson 1948; Lintilhac and Veseky 1981; Green 1992; Xu *et al*. 1995). Others have even suggested that internally generated forces may provide physical cues for patterns of cellular differentiation and histogenesis (Biro *et al*. 1980; summarized by Trewavas and Knight 1994).

Nonetheless, the roles played by internally generated mechanical forces remain somewhat controversial, although it is clear that these forces exist and that plant development is responsive to them. In contrast, it is generally agreed that externally applied mechanical forces are perceived and used by plants to alter their development and the physical properties of cell walls and tissues. Well over 80% of all vascular land plant species examined are reported to manifest pronounced morphogenetic responses to periodic or chronic mechanical perturbation (Jaffe 1973), a phenomenon that is called thigmomorphogenesis. Among the most common mechanical responses are overall aboveground growth inhibition, thicker and shorter internodes and petioles, a reduction in lamina surface area, a reduction in stem and leaf tissue stiffness and strength, an increase in root stiffness and strength, and changes in biomass allocation patterns to vegetative and reproductive organs (for examples of each of these phenotypic responses, see Jaffe *et al*. 1984; Telewski and Jaffe 1986; Ennos 1991; Gartner 1994; Crook and Ennos 1996; Niklas 1998). An additional response among woody species is the preferential deposition of wood within individual growth layers in response to predictable directional stem or root flexure (see Knight 1811; Jacobs 1954).

This general phenomenology is not limited to terrestrial plants, or even to those that are phyletically closely related to the land plants. For example, in his case study of phenotypic differences among specimens of the siphonous marine green alga *Caulerpa* (figure 1), Tandy (1933 – 1934) reports that, in comparison to their counterparts growing in sheltered conditions, plants inhabiting rocky wave-swept habitats

Figure 1. Growth habit of the marine siphonous green alga *Caulerpa mexicana*. The entire organism consists of a single cell that is incompletely partitioned and mechanically reinforced by internal transverse and horizontal strut-like outgrowths of the inner lining of the cell wall (not shown).

exhibit a reduction in the number of erect frond-like axes, increased "rhizome" branching and interweaving, irregular cushion-shaped growth forms, and an increase in the number and thickness of intracellular transverse cell wall struts.

Collectively and individually, these features are clearly functionally adaptive to dealing with the mechanical forces generated by wave activity.

In addition to mechanical perturbation, additional "touch" related responses have been reported. Among these are thigmotrophic phenomena (e.g. directional growth responses to touch, such as tendril coiling), reversible thigmotactic responses (e.g. changes in the swimming direction of *Euglena* and *Volvox* spp.), rapid nastic responses (e.g. *Mimosa pudica* and *Cassia sensitivum* leaf folding and *Dionaea* and *Aldrovanda* leaf-trap closure) as well as similar phenomena involving the propagation of physiologically induced action potentials (see Shimmen 2001), and touch-induced responses that involve the release of turgor-generated tensile or compressive stresses in specialized tissues or organs (e.g. spore ejection mechanisms of *Selaginella* and ferns, and "exploding" *Medicago* flowers and *Impatiens* fruits).

3. A general model for signal perception?

The aforementioned responses to touch are manifold and evident among diverse phyletically unrelated eukaryotic unicellular and multicellular photoautotrophs (e.g. *Euglena* and *Caulerpa*), which lends credence to the notion that the response mechanisms provoked by external mechanical forces are part of a much more extensive, complex, and perhaps very ancient "stress-perception response system" (Albrecht *et al*. 1993; Braam *et al*. 1997; Jaffe *et al*. 2002; Braam 2005). This possibility is supported by recent research showing that a variety of environmental stresses other than mechanical perturbation are perceived by similar (possibly) identical mechanisms (Humphrey *et al*. 2007; Martinac 2007; Pickard 2007). For this reason, the literature treating the topic of mechanoperception is extensive, albeit often confusing because some authors treat this general topic as if the same signal receptors and signal transduction pathways are involved in the perception of a broad range of physical stimuli other than mechanical stimulation (reviewed by Jaffe *et al.* 2002). Currently, little is known about mechanoperception or how mechanical signal transduction pathways evoke patterns of genomic expression or changes in metabolism or physiology (see however Nakagawa *et al*. 2007). Likewise, comparatively little is known about how the response systems to other environmental stresses operate. It is generally acknowledged that mechanoperception involves receptors located at the interface between the cell wall and cell membrane (Ingber 2003; Humphrey *et al*. 2007). It is also reasonably well established that other receptors are located within the endoplasmic reticulum. However, despite progress beyond these two broad generalizations (see Haswell 2007), there is little consensus about the details of "stress" perception because experimental evidence exists that other kinds of stress-receptors share these two features. What can be said with far greater certainty is that the molecular aspects of stress perception in general, and mechanical disturbance in particular, are critical to our understanding of plant evolution, because they shed light on how plants recognize and distinguish among different environmental stimuli.

Extensive research shows that touch genes (*TCH*) and related genes in *Arabidopsis* (as well as other genes in many other plant species) are up-regulated rapidly by three seemingly unrelated classes of stimuli that collectively can be considered "stress" inducing: (i) mechanical disturbance (such as vibration, touch and twisting); (ii) externally applied growth-altering substances (such as IAA, brassinosteroids and jasmonates); and (iii) abiotic environmental factors (such as temperature shock). Research also shows that regardless of its physical or chemical nature, each of these classes of stimuli activates calcium ion channels followed by dramatic increases in cytosolic Ca^{2+}. This phenomenology is consistent with the stretch-dependent and voltage-gated nature of Ca^{2+} channels, properties that permit a constellation of different kinds of stimuli to evoke similar or identical responses (Pickard 2007). Space does not permit a detailed discussion of the complexity of Ca^{2+} as a signal transduction component, but it is not surprising that the activity of mechanosensitive Ca^{2+}-selective channels increases in response to decreasing temperature (Ding and Pickard 1993). Örvar and colleagues (2000) proposed that temperature-induced changes in membrane fluidity and the subsequent activation of stretch-sensitive Ca^{2+} ion channels are the main cause of actin cytoskeleton rearrangements in plant cold-sensing epidermal cells. Likewise, Xiong and Zhu (2002) suggest that mechanoperception signaling is co-opted during osmotic stress signaling. That *any* mechanical, electrical or chemical change in the cell wall or plasma membrane is, in theory, capable of opening Ca^{2+} channels is not in doubt. Mechanical forces stretch, compress or twist the plasma membrane. Changes in turgor pressure or temperature alter the extent to which the plasma membrane is appressed to the cell wall. Osmotic stress affects plasma membrane electrical properties. Chemical substances, such as IAA, can change H^+-coupled ion transport systems and thus the physical or chemical properties of cell wall or plasma membrane constituents (Baluska and Hlavacka 2007). What is far less clear is how plant cells discriminate among different kinds of stimuli. From a purely theoretical perspective, we would expect organisms to evolve "signal specific" sensors that permit them to respond developmentally in adaptively different ways to different

environmental cues. Current models for mechanoperception that account for the ability to discriminate among the three classes of signals that cause Ca^{2+} ion channels to open have been proposed but much remains unknown (see Fasano *et al*. 2002; Demidchik and Maathuis 2007).

Importantly, all calcium ion channels are not the same. Each is a protein, made up of one or more polypeptides that form a hydrophilic pore in a membrane. Each allows Ca^{2+} ions to pass relatively unimpeded at a rate of about 106 s^{-1} or more. However, Ca^{2+} permeable channels can be either nonselective or highly selective for Ca^{2+}, depending on the pore size and on the charge density of the binding sites at their mouths, properties that depend on protein structure, which can vary among channels. Thus, there can be (and are) many types of Ca^{2+} channels on the same membrane. This variation in channel protein structure and size provides a mechanism whereby different signals can be perceived differently. In tandem with a recent model of mechanoperception, this holds some promise for general insights into signal perception (Jaffe *et al*. 2002; see also Telewski 2006; Demidchik and Maathuis 2007). This model of mechanoperception draws attention to the potential roles played by Hechtian strands and integrin-like proteins. Hechtian strands, which become visible during plasmolysis, connect the cell wall to the plasma membrane. These "cytoplasmic links" are implicated in signal transduction and cytoskeletal reorganization, in part because they can contain actin microfilaments and microtubules that are indirectly tethered to the cell wall by integrin-like proteins (Lang-Pauluzzi and Gunning 2000). The functional integration of integrinlike proteins and Hechtian strands posited by the model of Jaffe and others (2002) is supported by the observation that exposure of cells to peptides containing the integrin-binding RGD sequence (those with an Arg-Gly-Asp sequence) results in the loss of Hechtian strands, accompanied by a loss of signal transmission pathways between the cell wall and the plasma membrane (see Kiba *et al*. 1998).

The role of integrins in animal systems is well known. These proteins comprise a large family of cell surface adhesion receptors that typically bind to RGD peptides. They transfer signals from the extra-cellular matrix across the plasma membrane to the cytoplasm.Although integrins sensu stricto have not been isolated from plant cells, integrin-like proteins have been reported for higher plants as well as fungi. Additionally, an integrin-like protein in association with stretch-activated calcium channels is reported for the charophycean alga *Chara* (Wayne *et al*. 1992). It is therefore reasonable to suppose that integrin-like proteins function similarly in signal transduction pathways across a host of eukaryotic lineages. Because these proteins can vary structurally, they provide, in tandem with different calcium ion channels, an additional mechanism for discriminating among different stimuli.

4. The evolution and role of cell walls

The foregoing suggests that a very ancient "stress-perception response system" is intimately linked to the cell membrane, which in turn is in intimate contact with some sort of cell wall — here broadly defined to include any intra- or extracellular matrix made by the protoplast and adjoined to its cell membrane — that ultimately maintains the shape and size of unicellular organisms by means of an internal hydrostatic pressure generated by the protoplast. Among multicellular organisms, particularly plants, the infrastructure of cell walls serves as an endoskeleton. In both cases, the architecture of the cell wall is controlled by the protoplast it surrounds in adaptively plastic ways. Unicellular and multicellular organisms control organismic shape and size by controlling the architecture and mechanical properties of their cell walls (Green 1992; Stebbins 1992; Kutschera and Niklas 2007). Accordingly, if an organism expresses phenotypic plasticity, as virtually every organism does, adaptive responses to the environment reflect the plasticity of cell wall formation and subsequent controlled deformation.

Cell walls have evolved independently in diverse bacteria and in a host of phyletically unrelated unicellular and multicellular heterotrophs and photoautotrophs (Niklas 2004; Popper 2008). Its chemical composition, therefore, varies (often significantly) among different lineages. However, one of the most widely phyletically distributed cell wall chemical components is cellulose, which, for its density, is one of the strongest biopolymers measured in tension (Niklas 1992). The ability to synthesize this polysaccharide is found among certain Eubacteria, diatoms, tunicates, dinoflagellates, red and green algae, charophytes and their sister group, the land plants (Niklas 2004). This wide phyletic distribution suggests that the capacity to synthesize cellulose among eukaryotic lineages was the result of lateral gene transfer from endosymbiotic eubacteria-like organisms to the genomes of their host cells during the course of primary or secondary endosymbiotic events (Niklas 2004).

This lateral gene transfer hypothesis for the machinery of cellulose synthesis is supported by recent studies that show remarkable molecular homologies among functionally non-redundant cellulose synthase genes (*CesA*) across diverse prokaryotic and eukaryotic species. Ultrastructural comparisons of the trans-membrane complexes containing cellulose synthase proteins also support this hypothesis (Delmer 1999; Richmond and Somerville 2000; Nobles *et al*. 2001; Roberts *et al*. 2002; Römling 2002). For example, all members of the *CesA* gene family isolated from land plants encode for integral membrane proteins with one or two trans-membrane helices in the N-terminal protein region and three to six trans-membrane helices in the C-terminal region (Richmond and Somerville 2000). Likewise, all members of

this gene family share an N-terminal domain structure that includes a cytoplasmic loop consisting of four conserved regions (U1–U4), each of which contains a D residue or the QXXRW sequence. The D-D-D-QXXRW motif is predicted to code for glycosyltransferase functionality. Three other features are shared among land plant cellulose synthases: (i) a strongly conserved region (CR-P) between the U1 and U2 conserved regions, (ii) an N-terminal LIM-like zinc-binding domain, and (iii) the so-called hypervariable region between U2 and U3 (Delmer 1999). The hypervariable region is now known to have strong sequence similarity among closely related species. It is therefore a highly conserved region within specific clades (Vergara and Carpita 2001).

Molecular comparisons indicate that the CR-P insertion and the D-D-D-QXXRW motif evolved before the appearance of the monophyletic land plants—indeed, before the appearance of eukaryotes—because both of these features have been identified in *CesA* proteins from the green alga *Mesotaenium caldariorum* (Roberts *et al*. 2002) and in putative *CesA* proteins from cyanobacteria (Nobles *et al*. 2001). Thus, the genomic roots of cellulose biosynthesis are bacterial. It is also clear that gene duplication and functional divergence occurred after ancient *CesA*-like genes became embedded within eukaryote genomes, because eukaryotic *CesA* proteins are functionally non-redundant and because they are arranged in structurally well-defined trans-membrane structures, called terminal complexes (TCs), which are invariably involved with the assembly of cellulose. For example, among all land plants and some of their close algal relatives, TCs, as seen from the exterior surface of the plasma membrane, are solitary rosettes consisting of six granules.

Although the precise arrangement and number of the different cellulose synthases within an individual granule are currently unknown, research indicates that some *CesA* proteins (designated as *CesAi* proteins) initiate glucan chain formation by accepting glucose residues from a sugar nucleotide donor (most likely uridine 5'-diphosphate, or UDP), whereas other synthases further extend individual glucan chains (designated as *CesAe* proteins). Several investigators have also suggested that dimers of cellulose synthase are required in order to provide a cooperative cellobiose-generating system (Carpita *et al*. 1996; Albersheim *et al*. 1997; Kurek *et al*. 2003).

The presence of cellulose in the surfaces or walls of many different kinds of organisms is not surprising. Cellulose is relatively "cheap" for photosynthetic organisms to manufacture, extremely hard to digest, and, as noted, extraordinarily strong when placed in tension. The high density-specific tensile strength emerges from the participation in inter- and intra-chain hydrogen bonding of all available hydroxyl groups among adjacently aligned β-1,4-glucan chains, which aggregates cellulose chains into insoluble crystalline strands reinforced by the dispersion forces among stacked heterocyclic rings. In plant cell walls, the cable-like geometry of this unbranched covalent arrangement gives rise to extended structures called microfibrils, which are held together by structural proteins (e.g., extensin), a variety of pectins (e.g., homogalacturonan, rhamnogalacturonan, and arabinan), and hemicelluloses (e.g. xyloglucan, arabinoxylan, glucomannan, and xylan) (Cosgrove 1996; Popper 2008). In turn, microfibrils are aggregated into larger structures, called macrofibrils.

The mechanical properties of microfibrils is governed in part by their dimensions (width, thickness, and length). Microfibrillar width and thickness are determined by the arrangement of TCs and the number of cellulose synthase units per TC, both of which tend to be highly conserved for individual species (Tsekos 1999). For example, cellulose producing eubacteria and all phaeophytes and rhodophytes (e.g. *Pelvetia* and *Ceramium,* respectively) typically have single linear TC arrays similar to those reported for the marine tunicate *Metandrocarpa uedai* (Kimura and Itoh 1996). Likewise, many xanthophyte and chlorophyte species have stacked linear TC arrays (e.g. *Vaucheria* and *Oocystis,* respectively). In contrast, all embryophytes and some charophyte algae (e.g. *Nitella*) have solitary TCs arranged in hexagonal rosettes (when viewed from the exterior plasma membrane surface). Among embryophytes, as noted above, each granule contains six cellulose synthase units, each of which produces one glucan chain. The typical embryophyte microfibril is thus described as consisting of 36 glucan chains, collectively measuring 3.5 micrometers (μm) by 3.5 μm in width and thickness (although this has yet to be determined unequivocally).

Across many different natural and artificial sources, the degree of cellulose crystallinity is correlated with glucan chain length (Delmer 1999). The siphonous green alga *Boergesenia forbesii* holds the current record in this regard (i.e. 23,000 units per chain). However, microfibrillar length often exceeds the glucan chain length predicted on the basis of cellulose crystallinity, indicating that chain initiation and termination probably occur multiple times during the fabrication of individual microfibrils. Although various hypotheses have been proposed to explain glucan chain termination (e.g. chain cleavage to relax localized tension resulting from "out-of-step" synthases in adjoining granules), none satisfactorily explains how entire TCs are initiated or terminated.

Much remains to be learned about how TCs are globally coordinated to fabricate the cellulosic infrastructure of an entire cell wall. The most prevalent hypothesis is that TCs are guided by cortical microtubules. If this is true, cytoskeletal architecture controls microfibrillar deposition and cell wall texture such that a change in the architecture ought to produce different depositional patterns and wall textures.

This hypothesis is consistent with the parallel alignment of microfibrils and microtubules that is frequently reported for recently synthesized parts of plant cell walls (Wymer and Lloyd 1996; Taiz and Zeiger 2002). It also sheds light on anisotropic cell growth, because most researchers believe that cells enlarge by a process involving enzymatic stress relaxation and mechanical slippage (creep) of cellulose microfibrils, which make up the bulk of the load-bearing polysaccharide network in cell walls (Cosgrove 1996).

As noted above, cellulose is one of the strongest materials when placed in tension. Microfibrils thus are likely to function as "tensile cables," anchored together by other cell wall constituents. This mechanochemical configuration permits fully turgid cells, especially thin-walled ones, to retain their shape; that is, thin-walled cells are hydrostatic mechanical devices (Niklas 1992). Also, by virtue of preferential deposition of microfibrils in cell walls, individual cells or tissues (particularly the epidermis of multicellular plants) can mechanically control cell, tissue, or entire organismic shape and size (for a discussion about the mechanical role of the epidermis, see Kutschera and Niklas 2007). However, for cells to expand and permanently grow in size, the cell wall must be "relaxed" by allowing microfibrils to slip past one another. Likewise, changes in the orientation of microfibrils (affected by cytoskeletal reorientation of microtubules) are required to alter the direction of subsequent preferential cell expansion and growth. The deposition of transverse microfibrils in recently produced cell wall layers would predispose cells to expand longitudinally, whereas longitudinal microfibrils would favor transverse expansion.

Although the mechanics of cell wall expansion and isotropic growth are comparatively well understood (see Schopfer 2006), research using mutants indicates that microtubule and microfibril organization is only part of a much more complex story (Seagull 1991;Wiedemeier *et al*. 2002; Smith 2003). For example, the cells of the temperature-sensitive *mor1-1* mutant of *Arabidopsis thaliana* lose their orderly cortical microtubule arrangements at their restrictive culture temperatures. They also lose their capacity for anisotropic growth (which suggests a random arrangement of microtubules), yet retain parallel microtubule arrangements. Using the same mutant, Himmelspach and colleagues (2003) investigated whether well-ordered, preexisting microfibrils or cortical microtubules are essential for the resumption of normal (longitudinally aligned) microfibrils. Their protocol involved the transient disruption of microfibril organization with a brief treatment of the cellulose synthesis inhibitor 2,6-dichlorobenzonitrile, and the subsequent examination of the alignment of newly formed microfibrils as cellulose synthesis was recovered at the mutant's nonpermissive culture temperature. Despite the presence of disordered microtubules (and the initially random cell wall texture of the microfibrils), new microfibrills formed in transverse and longitudinal patterns. These and other experiments indicate that preexisting microtubule or microfibril templates may not be required for the resumption of prior microfibrillar organization. But this does not preclude the possibility that microtubules influence the direction of cellulose extrusion, which in turn dictates subsequent microfibrillar orientation. Given that recently formed portions of microfibrils are anchored in the cell wall, it is possible that TCs are dynamically propelled in the same direction in which they initially extrude microfibrills (Staehelin and Giddings 1982). If so, an initial parallel alignment of microtubules and microtubules may be a transient phenomenon.

5. Conclusions

A review of the literature indicates that (i) most aquatic and terrestrial plant species manifest some degree of adaptive phenotypic plasticity, (ii) the most ubiquitous environmental cue for this phenomenology is mechanical perturbation, (iii) this cue is one of many perceived by a very ancient "stress-perception response system", (iv) that operates at the cell membrane/cell wall interface across phyletically diverse and unrelated lineages of heterotrophs and photoautotrophs, (v) some physiological and structural elements of this interface appear to be shared among these lineages by virtue of lateral gene transfer from ancient endosymbiotic Eubacteria that evolved into modern-day mitochondria and chloroplasts, (vi) among these elements is the "machinery" required to synthesis cellulose and deposit it in cell walls in the form of microfibrils that act as "tensile cables", (vii) that are incorporated into the cell wall in concert with cortical microtubules and (viii) in a manner that permits cells to alter shape and size in response to external environmental cues. An additional conclusion is that multicellularity is not a prerequisite for morphological complexity or phenotypic plasticity, as is evident from the ecotypic variation of siphonous algae like *Caulerpa*.

References

Albersheim P, Darvill A, Roberts K, Staeheln L A and Varner J E 1997 Do the structures of cell wall polysaccharides define their mode of synthesis?; *Plant Physiol.* **113** 1–3

Albrecht T, Groth B, Xia Z Q, Luxem M, Liss H, Andert L and Spengler P 1993 Evidence for the involvement of jasmonates and their octadecanoid precursors in the tendril coiling response of *Bryonia dioica*; *Phytochemistry* **32** 591–600

Baluska F and Hlavacka 2005 Plant formins come of age: something special about cross-walls; New Phytol. **168** 499–503

Biro, R L, Hunt E R, Erner Y and Jaffe M J 1980 Thigmomorphogenesis: changes in cell division and elongation in the internodes of mechanically perturbed or etherel-treated bean plants; *Ann. Bot.* **45** 655–664

Braam J 2005 In touch: plant responses to mechanical stimuli; *New Phytol.* **165** 373–389

Braam J, Sistrunk M. L, Polisensky D H, Xu W, Purugganan M, Antosiewicz D M, Cambell P and Johnson K A 1997 Plant responses to environmental stress: regulation and functions of the *Arabidopsis TCH* genes; *Planta* **203** S35–S41

Carpita N, McCann M and Griffing L R 1996 The plant extracellular matrix: news from the cell's frontier; *Plant Cell* **8** 1451–1463

Cosgrove D J 1996 Plant cell enlargement and the action of expansins; *BioEssays* **18** 533–540

Crook M J and Ennos A R 1996 Mechanical differences between free-standing and supported wheat plants, *Triticum aestivum* L.; *Ann. Bot.* **77** 197–202

Delmer D P 1999 Cellulose biosynthesis: Exciting times for a difficult field; *Ann. Rev. Plant Physiol. Plant Molec. Biol.* **50** 245–276

DeWitt T J and Scheiner S M 2004 *Phenotypic plasticity* (New York: Oxford University Press)

Ding J P and Pickard B G 1993 Mechanosensory calcium selective cation channels in epidermal cells; *Plant J*. **3** 83–110

Demidchik V and Maathuis F J M 2007 Physiological roles of nonselective cation channels in plants: from salt stress to signaling and development; *New Phytol.* **175** 387–404

Ennos A R 1991 The mechanics of anchorage in wheat *Triticum aestivum* L. II. The anchorage of mature wheat against lodging; *J. Exp. Bot.* **42** 1607–1614

Fasano J M, Massa G D and Gilroy S 2002 Ionic signaling in plant responses to gravity and touch; *J. Plant Growth Regul.* **21** 71–88

Gartner B L 1994 Root biomechanics and whole plant allocation patterns: responses of tomato plants to stem flexure; *J. Exp. Bot.* **45** 1647–1654

Green P B 1992 Pattern formation in shoots: a likely role for minimal energy configurations of the tunica; *Int. J. Plant Sci.* (formerly *Bot. Gaz*.) **153** S59–S75

Haswell E S 2007 MscS-like proteins in plants; *Curr. Top. Membr.* **58** 329–359

Himmelspach R, Williamson R E and Wasteneys G O 2003 Cellulose microfibril alignment recovers from DCB-induced disruption despite microtubule disorganization; *Plant J.* **36** 565–575

Humphrey T V, Bonetta D T and Goring D R 2007 Sentinels at the wall: cell wall receptors and sensors; *New Phytol.* **176** 7–21

Ingber D E 2003 Tensegrity II. How structural networks influence cellular information processing networks; *J. Cell Sci.* **116** 1397–1408

Jacobs M R 1954 The effect of wind sway on the form and development of *Pinus radiata* Don; *Aust. J. Bot.* **2** 35–51

Jaffe M J 1973 Thigmomorphogenesis: the response of plant growth and development to mechanical stress; *Planta* **114** 143–157

Jaffe M J, Telewski F T and Cooke P W 1984 Thigmomorphogenesis: on the mechanical properties of mechanically perturbed bean Plants; *Physiol. Plant.* **62** 73–78

Jaffe, M J, Leopold A C and Staples R C 2002 Thigmo responses in plants and fungi; *Am. J. Bot*. **89** 375–382

Kiba A, Sugimoto M, Toyoda K, Ichinose Y, Yamada T and Shiraishi T 1998 Interaction between cell wall and plasma membrane via RGD motif is implicated in plant defense responses; *Plant Cell Physiol.* **39** 1245–1249

Kimura S and Itoh A 1996 New cellulose synthesizing complexes (terminal complexes) involved in animal cellulose biosynthesis in the tunicate *Metandrocarpa uedai*; *Protoplasma* **194** 151–163

Knight T A 1811 On the causes which influence the direction of the growth of roots; *Philos. Trans. R. Soc. London* **1811** 209–219

Kurek I, Kawagoe Y, Jacob-Wilk D, Doblin M and Delmer D 2003 Dimerization of cotton fiber cellulose synthase catalytic subunits occurs via oxidation of the zinc-binding domains; *Proc. Natl. Acad. Sci. USA* **99** 11109–11114

Kutschera U and Niklas K J 2007 The epidermal-growth-control theory of stem elongation: an old and new perspective; *J. Plant. Physiol.* **164** 1395–1406

Lang-Pauluzzi I and Gunning B E S 2000 A plasmolytic cycle: the fate of cytoskeletal elements; *Protoplasma* **212** 174–183

Lintilhac P M and Veseky T B 1981 Mechanical stress and cell wall orientation in plants. II. The application of controlled directional stress to growing plants, with a discussion on the nature of the wound reaction; *Am. J. Bot*. **68** 1222 –1230

Nakagawa Y, Katagiri T, Shinozaki K, Qi Z, Tatsumi H, Furuichi T, Kishigami A, Sokabe M, Kojima I, Sato S, *et al*. 2007 *Arabidopsis* plasma membrane protein crutial for Ca2+ influx and touch sensing in roots. *Proc. Natl. Acad. Sci. USA* **104** 3639–3644

Margulis L 1981 *Symbiosis in cell evolution* (San Francisco: W H Freeman)

Martinac B 2007 3.5 billion years of mechanosensory transduction: structure and function of mechanosensitive channels in prokaryotes; *Curr. Top. Membr.* **58** 26–57

Niklas K J 1992 *Plant biomechanics* (Chicago: University of Chicago Press)

Niklas K J 1998 Effects of vibration on mechanical properties and biomass allocation pattern of *Capsella bursa-pastoris* (Cruciferae); *Ann. Bot.* **82** 147–156

Niklas K J 2004 The cell walls that bind the tree of life; *BioScience* **54** 831–841

Nobles D R , Romanovicz D K and Brown R M Jr 2001 Cellulose in cyanobacteria. Origin of vascular plant cellulose synthase?; *Plant Physiol.* **127** 529–542

Örvar B L, Sangwan V, Omann F and Dhindsa R S 2000 Early steps in cold sensing by plant cells: the role of actin cytoskeleton and membrane fluidity; *Plant J.* **23** 785–794

Pickard B G 2007 Delivering force and amplifying signals in plant mechanosensing; *Curr. Top. Membr.* **58** 361–392

Popper Z A 2008 Evolution and diversity of green plant cell walls; *Curr. Opin. Plant Biol.* **11** 1 – 7

Richmond T A and Somerville C R 2000 The cellulose synthase superfamily; *Plant Physiol.* **124** 495–498

Roberts A W, Roberts E M and Delmer D P 2002 Cellulose synthase (*CesA*) genes in the green alga *Mesotaenium caldariorum; Eukaryotic Cell* **1** 847–855

Römling U 2002 Molecular biology of cellulose production in bacteria; *Res. Microbiol*. **153** 205–212

Sachs J 1878 Über die Anordnung der Zellen in jüngsten Pflanzenteilen; *Arb. Bot. Inst.Wurzburg* **2** 46–104

Schopfer P 2006 Biomechanics of plant growth; *Am. J. Bot*. **93** 1415–1425

Seagull R W 1991 Role of the cytoskeletal elements in organized wall microfibril deposition; in *Biosynthesis and biodegradation of cellulose* (eds) C H Haigler and P J Weimer (New York: Marcel Dekker) pp 143–163

Shimmen T 2001 Involvement of receptor potentials and action potentials in mechano-perception in plants; *Aust. J. Plant Physiol.* **28** 567–576

Smith L G 2003 Cytoskeletal control of plant cell shape: Getting the fine points; *Curr. Opin. Plant Biol.* **6** 63–73

Staehelin L A and Giddings T H Jr 1982 Membrane mediated control of cell wall microfibrillar order; in *Developmental order: its origin and regulation* (eds) S Subtelny and P B Green (New York: A R Liss) pp 133–147

Stebbins G L 1992 Comparative aspects of plant morphogenesis: a cellular, molecular, and evolutionary approach; *Am. J. Bot*. **79** 589–598

Sultan S E and Bazzaz F A 1993 Phenotypic plasticity in *Polygonum persicaria*. III. The evolution of ecological breadth for nutrient environment; *Evolution* **47** 1032–1049

Taiz L and Zeiger E 2002 *Plant physiology* (Sunderland: Sinauer)

Tandy G 1933 – 1934 Experimental taxonomy in marine algae, with special reference to *Caulerpa*; *Proc. Linn. Soc. London* 63–64

Telewski F W 2006 A unified hypothesis of mechanoperception in plants; *Am. J. Bot.* **93** 1466–1476

Telewski F W and Jaffe M J 1986 Thigmomorphogenesis: field and laboratory studies of *Abies frazei* in response to wind or mechanical perturbation; *Physiol. Plant.* **66** 211–218

Thompson D W 1948 *On growth and form* (Cambridge: Cambridge University Press)

Trewavas A and Knight M 1994 Mechanical signaling, calcium and plant form; *Plant Mol. Biol.* **26** 1329–1341

Tsekos I 1999 The sites of cellulose synthesis in algae: diversity and evolution of cellulose-synthesizing enzyme complexes; *J. Phycol.* **35** 635–655

Vergara C E and Carpita N C 2001 β-D-glycan synthases and the *CesA* gene family: Lessons to be learned from the mixed-linkage (1–3), (1–4) β-Dglucan synthase; *Plant Mol. Biol.* **47** 145–160

Wayne R, Staves M P and Leopold A C 1992 The contribution of the extracellular matrix to gravisensing in characean algae; *J. Cell Sci.* **101** 611–623

Wiedemeiyer A M D, Judy-March J E, Hocart C H, Wasteneys G O, Williamson R E and Baskin T I 2002 Mutant alleles of *Arabidopsis* RADIALLY SWOLLEN 4 and 7 reduce growth anisotropy without altering transverse orientation of cortical microtubules or cellulose microfibrils; *Development* **129** 4821–4830

Wymer C and Lloyd C 1996 Dynamic microtubules: Implications for cell wall patterns; *Trends Plant Sci*. **1** 222–228

Xiong L and Zhu J-K 2002 Molecular and genetic aspects of plant responses to osmotic stress; *Plant Cell Environ.* **25** 131–139

Xu W, Purugganan M M, Polisensky D H, Antosiewicz D M, Fry S C and Braam J 1995 *Arabidopsis* TCH4, regulated by hormones and the environment, encodes a xyloglucan endotransglycosylase; *Plant Cell* **7** 1555–1567

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