

# 17 Touch-Responsive Behaviors and Gene Expression in Plants

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**Abstract** The abilities of plants to perceive stimuli in their environment are often overlooked. Yet hints of exquisite sensitivities abound. Indeed, although it is not generally appreciated, probably all plants can perceive and respond to simple mechanostimulation like touch. We will briefly review some of the more spectacular touch responses of specialized plants and then discuss developmental and molecular responses to touch that occur in nonspecialized plants. Many of these data and concepts have recently been reviewed by Braam (*New Phytol.* 165:373–389, 2005).

## 17.1

### Specialized Plants – Touch Responses That Catch Attention

Fast reactions are easy to see and therefore the touch responses of plants like Venus' flytrap, sundew and *Mimosa* are well recognized. Venus' flytrap (*Dionaea muscipula*) and sundew (e.g., *Drosera rotundifolia*) use touch-sensitive responses to carry out carnivory by cleverly trapping insects; these touch responses enable them to thrive in nitrogen poor soils. Venus' flytrap awaits potential prey by spreading wide its specialized bi-lobed leaves edged with needle-shaped tines (Fig. 17.1a). Trigger hairs on the ventral leaf surface must be touch-stimulated multiple times to induce trap closure (Curtis 1834). Recent examination of the changes that take place in leaf geometry upon rapid closing reveal that the rapid closure comes from a snap buckling of the leaves as they transition from open to closed state (Forterre et al. 2005). The signaling that must occur between the trigger hairs and the closure response is still somewhat mysterious; however, intercellular electrical changes are detected and may act as intermediary signals (Burdon-Sanderson 1873; Jacobs 1954; Jacobson 1965; Simons 1981; Fagerberg and Allain 1991).

The sundew attracts insects with its glistening mucilage-laden tentacles (Fig. 17.1b). Insects that alight upon the tentacle surfaces find themselves bound by the gluey mucilage. The agitated movements of the insect attempting to loosen itself from the sticky surface lead to touch-induced tropic and nastic movements of neighboring tentacles (Darwin 1893; Lloyd 1942). An indentation of the leaf generates a cup-shaped enclosure (Fig. 17.1b) where the meal is dissolved. The selective sensitivity of the tentacles is remarkable. Darwin (1880, 1893) reported that the tentacles are capable of

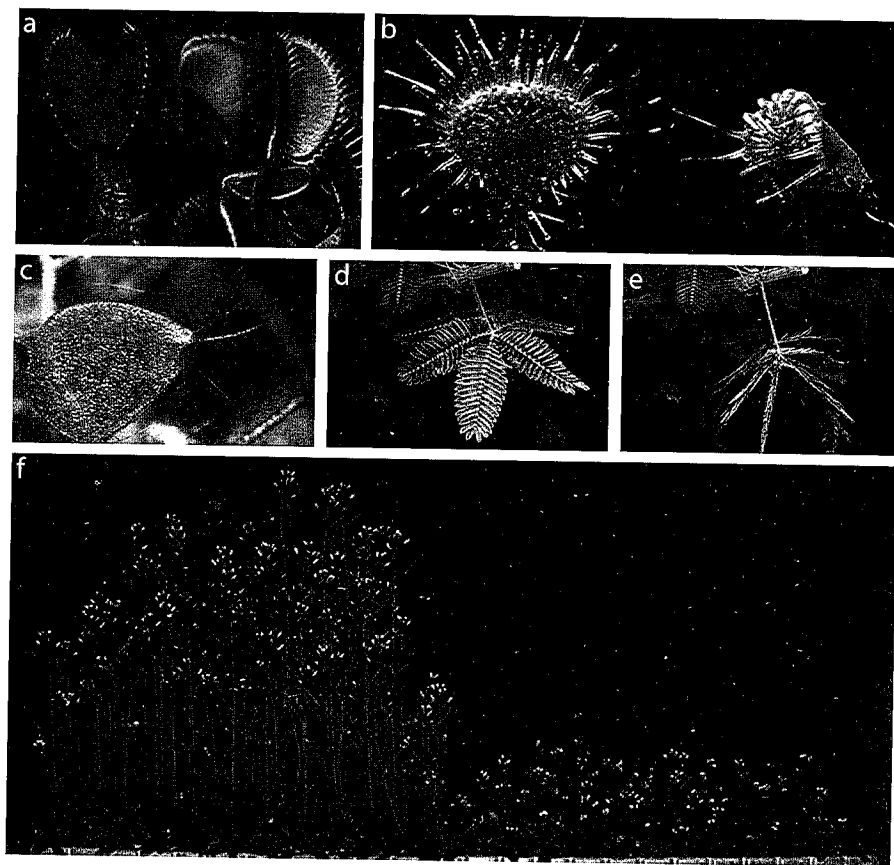


Fig. 17.1. a Potential prey nears a *Dionaea muscipula* (Venus' flytrap). b Open *Drosera* (sundew) leaf before and after touch stimulation. c *Utricularia inflata* (bladderwort) side view with tentacles visible at right near trap door. The doubly compound leaves of *Mimosa pudica* (sensitive plant) d open before stimulation and e closed after stimulation. f Repetitive touch stimulation leads to a delay in flowering and an inhibition of inflorescence elongation in *Arabidopsis*. The plants on the right were touched twice daily; the plants on the left are untreated controls. (Reproduced with permission of the New Phytologist Trust; Braam 2005)

detecting a strand of human hair weighing less than a microgram and yet rain droplets have little effect in activating the movements.

The trap of the bladderwort (*Utricularia*) may operate with similar mechanisms described recently for Venus' flytrap (Forterre et al. 2005). This aquatic rootless plant uses a thin-walled hollow sac and a watertight trapdoor as its prison and digestion chamber (Fig. 17.1c) (Lloyd 1942). The outer walls are curved inward, pulled perhaps by the negative hydrostatic pressure inside the bladder. Touch-sensitive appendages extend out near the trapdoor. When these triggers sense touch, by waterfleas or other small

creatures that have ventured close to the bladder opening, the door bursts open within 30 ms and water, and any unfortunate creatures caught in the current, rushes the chamber as the outer walls flip from concave to slightly convex in shape.

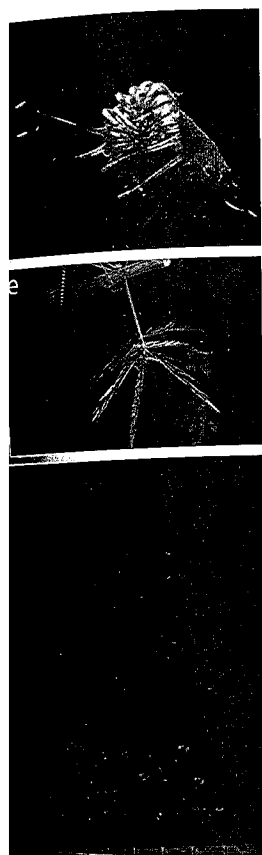
The touch-induced leaflet movements of the sensitive plant (*Mimosa pudica*) are more likely to occur for protective rather than aggressive purposes and adjacent, but untouched, leaflets fold up (Fig. 17.1d,e). If all the leaflets of the compound leaf undergo this movement, as in response to a strong mechanical stimulation such as wounding, the whole leaf nearly disappears (Simons 1981; Malone 1994). Electrical, hydraulic and chemical signals have all been implicated in carrying the long-range information that enables responses even in unwounded leaves (Ricca 1916; Houwinck 1935; Simons 1981; Fromm and Eschrich 1988; Malone 1994; Fleurat-Lessard et al. 1997; Stahlberg and Cosgrove 1997).

## 17.2

### Thigmotropism – Vines, Tendrils and Roots

Vines, tendrils and roots show expert thigmotropic behaviors. The *Monstera* vine uses both darkness and touch as growth and differentiation signals. The young vine searches the forest floor for darkness and grows toward dark shadows, a behavior called skototropism, to reach the base of its chosen host tree (Strong and Ray 1975). Upon touching the tree, the vine turns to grow upward and undergoes morphogenetic alterations such as leaf development and expansion as it ascends (Strong and Ray 1975).

Tendrils coiling also enables plants to reach sunlit heights that would otherwise require the expensive generation and maintenance of a tall supporting trunk. The touch-sensitive tip coiling behaviors of tendrils begin within seconds to minutes; not as fast as the trapping responses described before, but with a time frame that selectively enables winding around and attachment to stable objects perceived in the local environment (Jaffe and Galston 1968). Indeed, tendrils that respond to transient touch stimulation are able to reverse their behavior by unwinding (Jaffe and Galston 1968). Tendrils are highly sensitive, being able to perceive stimuli of a few milligrams or less (Darwin 1906; Simons 1992). In addition, tendrils are capable of distinguishing potentially productive and nonproductive perturbations; tendrils fail to coil in response to water droplets (Jaffe and Galston 1968). Tendrils can be thigmotropic, displaying coiling in a direction dependent upon the site of stimulation, or thigmonastic in that the direction of the coiling is predetermined and the touch stimulation simply triggers the response (Jaffe and Galston 1968). Octadecanoids and auxin



(a) Open *Drosera*  
(b) Open *Drosera* (bladderwort) side  
ground leaves of *Mimosa*  
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(indole-3-acetic acid) have been implicated as mediators of the differential growth effecting coiling (Jaffe and Galston 1968; Jaffe 1985; Weiler et al. 1993, 1994; Stelmach et al. 1998; Blechert et al. 1999).

Root tips are also highly sensitive to touch stimulation; perception of touch is thought to enable roots to avoid obstacles as they penetrate soils. Darwin (1880) and more recently Massa and Gilroy (2003) have observed that when root tips encounter an impenetrable surface such as a glass plate, the root tip flattens and turns 90° to grow over the surface until it is once again allowed to display positive gravitropism and turn to grow downward. Remarkably, perception of touch appears to delay the gravity-induced downward movement of columella cell starch granules and in this way may interfere with root gravitropism (Massa and Gilroy 2003).

### 17.3

#### Thigmomorphogenesis – Plasticity of Shoot Growth

Not only do the roots of nonspecialized plants sense and respond to touch, but the shoots are also mechanosensitive and mechanoresponsive. Mechanical perturbations, like touch or wind, generate gradual morphogenetic alterations in most, if not all, plants (Jaffe 1973). Plants subjected to repetitive mechanical stimuli develop with shorter and often stockier phenotypes (Fig. 17.1f). These changes occur slowly over time and therefore are not often recognized, but they can result in quite dramatic morphogenetic alterations. Jaffe, who conducted much of the pioneering work on this phenomenon, called the touch-induced changes in growth “thigmomorphogenesis” (Jaffe 1973). Thigmomorphogenesis likely evolved as an adaptive response to environmental stresses like wind and often results in increased rigidity or increased flexibility, depending upon the species, and may therefore improve resistance to further mechanical perturbation (Jaffe et al. 1984; Biddington 1986; Telewski and Jaffe 1986; Depege et al. 1997; Coutand et al. 2000).

Mechanical perturbation, like wind or touch, is likely perceived through the resulting longitudinal strain experienced by the shoot tissue. The extent of thigmomorphogenetic changes correlates strongly with the degree of longitudinal strain (Coutand et al. 2000). Furthermore, because thigmomorphogenetic alterations can affect subsequent strain, there are likely direct feedback pathways at play. The degree of thigmomorphogenesis would thus be tailored appropriately to the degree required for acclimation to the condition. For example, tobacco plants engineered to have weakened xylem composition would be predicted to have reduced tensile stiffness and should experience greater strain than wild-type plants. However, these transgenic tobacco are nearly indistinguishable from the wild-type control

in overall stiffness because the transgenics generate additional xylem tissue as apparent compensation for the material defects (Hepworth and Vincent 1999). These experimentally induced conditions are probably closely related to those that occur during natural progressive plant growth. Increased tissue strain would undoubtedly occur as plant size increases if there were no accompanying compensatory changes. Indeed, increased height in *Arabidopsis* is correlated with enhanced xylem production (Ko et al. 2004). The tissue alterations are likely induced by growth-associated strain increases. Consistent with these ideas, enhanced cambium differentiation can be induced by applying weight to immature *Arabidopsis* inflorescences (Ko et al. 2004), and cultured callus cells differentiate with cambium-like characteristics when subjected to compressive forces (Lintilhac and Vesecky 1984; Barnett and Asante 2000). Similar compensatory changes likely occur at a cellular level and can be observed when cell wall composition is altered by either mutation or inhibitors. Reduction in cellulose leads to enhanced pectin deposition (His et al. 2001); loss of lignin results in overaccumulation of cellulose (Hu et al. 1999). Thus, plants likely use strain as a measure of structural integrity at both the tissue and the cellular levels and can activate pathways that reinforce walls, tissues or organs in compensatory manners. The mechanosensory pathway is therefore undoubtedly critical for overall plant growth and development.

## 17.4

### Mechanosensitive Gene Expression

What are the growth alterations that result in thigmomorphogenesis and how are they triggered? One clue may come from the dramatic changes in gene expression documented to occur very rapidly in plants subjected to mechanical perturbation. The first touch-inducible genes were discovered rather unintentionally (Braam and Davis 1990) and since then many genes have been found to show mechanosensitive expression regulation (reviewed in Lee et al. 2005). Microarray technology permits a deliberate approach to investigating the prevalence of touch-inducible genes in the plant genome. The Affymetrix chip (Affymetrix, Santa Clara, CA, USA) for the *Arabidopsis thaliana* genome enables the probing of 22,810 genes for inducible expression. Over 2.5% of the total, 589 genes, are upregulated in expression at least twofold within 30 min of a touch stimulation (Lee et al. 2005). Expression of 171 genes is reduced (Lee et al. 2005).

In addition to many genes of unknown function, genes encoding potential calcium ( $\text{Ca}^{2+}$ )-binding proteins, cell wall synthesis and modification enzymes, protein kinases, transcription factors and disease-resistance proteins are most highly enriched in representation among those with twofold

or greater touch-inducible expression (Lee et al. 2005). Because calmodulin (CaM) and CaM-like proteins were among the first touch-inducible genes discovered (Braam and Davis 1990), it was not unexpected that these would be among those identified by the microarray as touch-inducible. Overall there is a 3.3-fold enrichment of Ca<sup>2+</sup>-binding protein encoding genes among the genes upregulated at least twofold by touch (Braam and Davis 1990). Furthermore, Ca<sup>2+</sup> has been implicated as a second messenger in mechanosensory signaling (Batiza et al. 1996; Calaghan and White 1999). Touch and wind trigger rapid cellular Ca<sup>2+</sup> increases in plants (Knight et al. 1991). Thus, expression upregulation of Ca<sup>2+</sup>-binding protein genes may be the result of a feedback pathway designed to produce more Ca<sup>2+</sup> receptors when stimuli that use Ca<sup>2+</sup> as a second messenger are perceived. Furthermore, because these proteins are potential Ca<sup>2+</sup> sensors (McCormack and Braam 2003), they may function to transduce Ca<sup>2+</sup> signals into cellular responses through Ca<sup>2+</sup>-dependent changes in target protein activities. The microarray and subsequent real-time PCR data indicate that expression levels of at least one *CAM* (*CAM2*) of the seven *CAMs* and 14 of the 50 *CMLs* are significantly upregulated by touch stimulation (Lee et al. 2005). The physiological functions of these touch-inducible genes encoding potential Ca<sup>2+</sup> sensors remain largely unknown. However, transgenic plants with reduced *CML24/TCH2* protein accumulation are defective in germination and seedling responses to abscisic acid, day-length regulated transition to flowering and growth inhibition induced by various salts (Delk et al. 2005).

Thigmomorphogenesis and the accompanying changes in structural properties would be predicted to require cell wall modifications. Cell walls are a major determinant of plant tissue integrity and form and thus changes occurring in thigmomorphogenesis likely involve alterations to the wall. Indeed, genes encoding cell wall synthesis and modification enzymes are among those most highly represented in the group of touch-inducible genes, undergoing a 2.5-fold increase in enrichment among the touch-inducible genes (Lee et al. 2005). Thus, touch-inducible expression of cell-wall-associated enzymes may underlie mechanostimulus-evoked morphogenetic changes.

Transcription factors and protein kinases are regulatory proteins whose production levels are often themselves regulated in response to diverse stimuli. Since these proteins can act as cellular switches to control physiological changes, their genes are typically among those most highly altered in expression in microarray experiments. Indeed, the touch-inducible gene cluster includes approximately twofold enrichment in both transcription factor and protein kinase genes (Lee et al. 2005).

Perhaps more unexpectedly, a major class of genes upregulated in expression by touch includes those that have been implicated in disease resistance (Lee et al. 2005). There is some evidence that suggests that

repetitive mechanical stimulation can lead to enhanced disease resistance (Biddington 1986); however, the basis of this potential resistance is not well understood. Notably a number of the disease-resistance-related genes upregulated in expression by touch are members of the nucleotide binding site (NBS) leucine-rich repeat (LRR) gene family. This family contains the majority of plant disease-resistance genes (R genes) identified to date (Cannon et al. 2002). The NBS domain is thought to contribute in signal transduction, and the LRR domain may be responsible chiefly for elicitor recognition (Cannon et al. 2002). The upregulation of expression of these genes suggests a potentiation of defense in touch-stimulated plants. Whether this potentiation results in an enhanced resistance response by plants is still to be determined.

It is also intriguing that many of the touch-inducible genes have been associated with the jasmonic acid (JA) pathway. In addition to genes encoding enzymes involved in JA biosynthesis, other touch-inducible genes are those that have been used as JA-dependent resistance markers, including those encoding proteinase inhibitors that block digestive enzymes of some insect herbivores. Recent literature indicates that plant defense responses against insect herbivores and some microbial pathogens are coordinated by JA signaling pathways (Howe 2001). JA-mediated defenses are typically preceded by accumulation of JA in response to biotic stress (Wasternack and Hause 2002). Whether touch results in the accumulation of JA and/or the establishment of an enhanced disease resistance state awaits further study.

Touch-inducible genes provide important tools for investigating how plants perceive mechanical stimuli; however, to date, most genes found to be touch-inducible in expression are also upregulated in expression by other types of stimuli. The original *TCH* genes, encoding CaM2, CML12, CML24, and XTH22, are not only upregulated in expression by various forms of stimuli that have mechanical properties, such as touch, wind and wounding, but also by stimuli such as cold, heat, and darkness that, at least superficially, do not appear to be mechanical in nature (Braam 1992, 2000; Sistrunk et al. 1994; Xu et al. 1995; Polisensky and Braam 1996). To address the question whether all touch-inducible genes share this property of being upregulated by diverse stimuli, microarray experiments were done using darkness as a stimulus (Lee et al. 2005). More than half of all touch-inducible genes were also upregulated in expression by darkness, and the coregulation was most apparent in those genes with the greatest fold touch inducibility (Lee et al. 2005). Indeed, among the top 60 touch-inducible genes with at least tenfold upregulation, only four were not at least twofold upregulated in plants treated with darkness (Lee et al. 2005). All but three of the 68 genes that are most strongly upregulated by darkness are also touch-inducible (Lee et al. 2005). These findings are consistent with an

interpretation that darkness and perhaps the other stimuli that induce upregulation of the *TCH* genes are related in some way. One possibility is that all these stimuli share the property of causing mechanical perturbations and in this way trigger a common mechanosensory pathway that leads to the upregulation of expression (Braam 2000).

If the diverse stimuli that trigger *TCH* upregulation of expression act through a common pathway, then one would expect that a single *cis* regulatory element would be responsible for conferring the complex expression regulation. Indeed, a 102 base-pair region located upstream of the *TCH4* transcriptional start site is sufficient to confer touch, darkness, cold heat and epi-brassinolide upregulation of expression to reporter genes (Iliev et al. 2002). Sequences within this region share some similarities to sequences identified as important for conferring cold and touch inducibility to the *3F2* gene (Zarka et al. 2003). The mechanism by which these sequences may act to regulate gene expression is currently unknown.

Distinct methods have been used to monitor *TCH* expression during plant morphogenesis. *TCH::reporter* transgenics have been characterized in addition to the more direct methods of immunolocalization and reverse transcription PCR (Sistrunk et al. 1994; Antosiewicz et al. 1995, 1997; Xu et al. 1995; Delk et al. 2005). In general, *TCH* expression is enriched at sites that may be predicted to experience mechanical stress. *TCH* protein accumulates and/or *TCH::reporter* transgenes are expressed in the ruptured seed coat, branch points, the root–shoot junction, elongating hypocotyls and roots, and developing trichomes and silique abscission zones. In addition, plants subjected to enhanced weight on the inflorescence have increased *TCH2* and *TCH4* expression (Ko et al. 2004). These data indicate that *TCH* expression may not only be upregulated in response to externally applied mechanical perturbations such as touch, but also by mechanical forces that become manifest during normal plant morphogenesis.

## 5.5 Conclusions and Future Prospects

Plants perceive much more of their environment than is often apparent to a casual observer. Touch can induce profound rapid responses and more slowly acquired growth alterations. Rapid touch-induced plant movement in specialized plants is often associated with predation or protection. The speed of these responses is an essential component of the response in these situations. Plants that acclimate over their lifetime to touch or wind stimuli do not undergo dramatic touch-induced changes, but these, at least overtly, occur slowly over time. Molecular responses in nonspecialized plants can, however, occur quite rapidly. In *Arabidopsis*, changes in gene expression are



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seen within minutes after touch, and over 700 genes have altered transcript levels within 30 min. The prevalence of touch-responsive genes and the rapidity with which such changes in gene expression occur are indications that nonspecialized plants do possess capacity for rapid responses to touch.

Recent research reveals the types of genes upregulated by touch and implicate  $Ca^{2+}$  signaling, cell wall modification and disease resistance as potential downstream responses. Further work is needed to reveal the physiological relevance of these touch-induced changes in gene expression. Furthermore, touch-induced genes are powerful molecular tools for the dissection of the perception and response pathways that enable plants to perceive mechanical stimuli and manifest appropriate responses. Perception mechanisms and intercellular and intracellular transduction machinery and signals await future discovery.

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