

REVIEW PAPER

Role of plant sensory perception in plant–animal interactions

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Abstract

The sedentary lifestyle of plants can give the false impression that they are passive participants in interactions with other organisms and the broader environment. In fact, plants have evolved sophisticated perceptual abilities that allow them to monitor and respond to a wide range of changing biotic and abiotic conditions. In this paper, we discuss recent research exploring the diverse ways in which plant sensory abilities mediate interactions between plants and animals, especially insects. Such interactions include the detection and capture of animal prey by carnivorous plants, active plant responses to pollinator visitation, the perception of various cues associated with the immediate presence and feeding of herbivores, and plant responses to (olfactory) cues indicating the threat of future herbivory. We are only beginning to understand the full range of sensory cues that mediate such interactions and to elucidate the mechanisms by which plants perceive, interpret, and respond to them. Nevertheless, it is clear that plants continually gather information about their environments via a range of sensory modalities and actively respond in ways that profoundly influence their interactions with other organisms.

Key words: Communication, herbivory, plant–animal interactions, plant–insect interactions, plant olfaction, plant perception, plant senses.

Introduction

Humans necessarily view all living things through the lens of our own experience, and this unavoidable conceptual bias has been a frequent source of confusion in biology. It gives rise to a natural tendency, among scientists and non-scientists alike, to anthropomorphize non-human species, with sometimes unfortunate consequences (Abelson, 1974; Kennedy, 1992). But it can also lead us to overlook underlying similarities between humans and other organisms, whose ways of living may seem at first glance to be utterly different from our own. Not surprisingly, both types of error have been amply represented in the study of plants, and perhaps nowhere more so than in relation to plants' perceptual and sensory capabilities.

On one hand, plants' sedentary lifestyle tends to obscure the myriad ways in which they actively perceive and respond to their environments, as the responses frequently entail changes in internal physiology—such as leaf or phloem

chemistry—that are relatively imperceptible (to humans), as well as changes in growth and development that are more readily apparent, but which unfold on timescales too slow to be seen by casual observation. Indeed Aristotle, who arguably founded the systematic study of biology, thought that plants lacked the capacity for sensory perception and that this absence set them apart from animals and humans, arguing that 'plants live without sensation, and it is by sensation that we distinguish animal from what is not animal' (Aristotle, 1984). On the other hand, humans are almost invariably fascinated by examples of plants that exhibit 'animal-like' sensory responses and behaviours, such as the rapid movements exhibited by some carnivorous plant species. This fascination may have deep roots in human psychology, as the salience of anthropomorphic and other counterfactual and supernatural concepts has been attributed to the violation of intuitive

ontological categories that humans recognise from the earliest stages of cognitive development (Boyer, 1996, 2001). And it may explain why fanciful and empirically unsupported claims about the purportedly complex inner lives of plants have often gained a prominent and, as discussed below, occasionally problematic, place in the public imagination.

The apogee of botanical pseudoscience probably arrived in the mid-1970s, marked by the publication of ‘The Secret Life of Plants: A Fascinating Account of the Physical, Emotional and Spiritual Relations Between Plants and Men’ (Tomkins and Bird, 1973), which summarized a wide range of ‘research’ purporting to address plants’ perceptual, psychological, and emotional capacities. This book—a *New York Times* best-seller that has been translated into several foreign languages and remains in print to this date—also inspired a 1979 documentary film of the same name. It prominently featured the work of Cleve Backster, a former CIA interrogation specialist who used polygraph equipment to measure changes in the electrical resistance of plant leaves and claimed to record patterns revealing emotional responses to various experimental conditions, including threats of harm against the plant or other nearby organisms. Backster also claimed to show that plants were capable of extra-sensory ‘primary perception’ of human emotional states, as well as stress in other organisms (Backster, 1968). A second book published the same year, ‘The Sound of Music and Plants’ (Retallack, 1973), described experiments exploring the effects of different styles of music on plant growth and wellbeing (Retallack’s plants reportedly preferred classical music to rock, but were largely indifferent to country and western).

Despite a rather obvious lack of scientific rigour (i.e. evidence presented in peer-reviewed studies published in mainstream scientific journals) work such as that described above received considerable public attention and popular press coverage, to the point that many reputable scientists felt compelled to respond (e.g. Abelson, 1974; Galston, 1975; Galston and Slayman, 1979). The leading research journal *Science* published a test of the primary perception hypothesis (Backster, 1968) that replicated the techniques of one of Backster’s most prominent experiments but, rather unsurprisingly, found no discernable plant response to the mass death (by boiling) of brine shrimp (Horowitz *et al.*, 1975). Meanwhile, a panel of biologists at the 1975 annual meeting of the American Association for the Advancement of Science explored claims regarding plant sentience and deemed them scientifically unsupportable, with one member lamenting a ‘gap between what scientists believe and what the lay public believes’ (St. Petersburg Times, 1975).

From the perspective of the present day, it may provoke some amusement to think of leading scientists and academic journals of the 1970s devoting significant time and space to debunking absurd claims about the emotional psychology of houseplants. But this attention was the product of legitimate concern about the widespread public dissemination of unfounded pseudoscientific claims. Furthermore, there is little doubt that the widespread attention paid to this debate by the general scientific community influenced the perception of legitimate scientific research on the sensory and perceptual

abilities of plants, with scepticism about the topic sometimes hindering scientific advances in this area (as discussed below). This history also provides important context for recent and ongoing debates about whether plants may in some sense be said to exhibit “intelligent” behaviour or even some rudimentary form of “consciousness”. These debates play out within the context of legitimate scientific inquiry and argument—and, frankly, often pivot on semantic and interpretive points rather than substantive differences about underlying scientific facts—with investigators on one side intent on emphasizing the real complexity and sophistication that plants manifest in their responses to environmental conditions (e.g. Trewavas, 2002, 2003; Brenner *et al.*, 2006; Trewavas and Baluška, 2011), while others urge caution against overreaching or sensational claims and the use of terminology that may lead to misinterpretation (e.g. Alpi *et al.*, 2007; Struik *et al.*, 2008; Olsson and Forkman, 2012).

It seems clear that the perceptual capabilities of plants lie somewhere between the extremes identified above. Plants are not the emotional adepts of Cleve Baxter’s imagination, but nor are they the senseless automatons that Aristotle and others may have believed them to be. Indeed, unlike the vast majority of animal species, which are capable of self-directed movement during at least some stage of their life cycles and are thus able to seek out favourable environments or flee adverse conditions, the growing stages of plants must adapt themselves to the conditions that prevail in the particular location where they are rooted and contend with the full range of environmental variability occurring at that location over the course of their lifetime. Consequently, plants respond to environmental variability largely through plasticity in growth and development, and they frequently exhibit plasticity in their morphology and physiology far exceeding that typically exhibited by animals. Such adaptability depends critically on an ability to detect, or anticipate, changing environmental conditions and respond accordingly (Casal *et al.*, 2004).

Thus, it is hardly surprising that recent and ongoing advances in the study of plant biology are yielding an increased appreciation for the complexity and sophistication of plants’ perceptual abilities. As a comprehensive account of these abilities lies beyond the scope of the current work, the remainder of this paper will focus more narrowly on summarizing current knowledge about the role of plant sensory perception in mediating interactions among plants and animals, including insect herbivores, which represent one of the most significant biotic stressors encountered by plants in most terrestrial ecosystems, and which are particularly well studied because of their relevance for human agriculture.

Mechanoreception (plant responses to touch and sound)

Responses to mechanical forces are ubiquitous in plants and play key roles in regulating fundamental processes of growth and development, as well as mediating interactions between neighbouring plants and plant responses to abiotic features of the environment (Braam, 2005; Telewski, 2006;

Sampathkumar *et al.*, 2014). Here we discuss the role of mechanoreception in plant responses to animals, especially insects.

Carnivorous plants

Although the perceptual capabilities of plants are most frequently directed toward animals for defensive purposes, some of the most dramatic, and best known, examples of plant sensory response involve carnivorous plants that prey on insects and other small animals. The carnivorous habit has evolved independently at least six times in angiosperms, but different classes of carnivores nevertheless exhibit considerable convergence in the mechanisms employed to lure, trap, and digest their prey (Ellison and Gotelli, 2009). Carnivorous plants typically deploy traps comprising modified leaves, which are often baited by way of tissues or structures that produce insect-attractive colours or scents (Król *et al.*, 2011). Some plant carnivores, such as pitcher plants, employ passive traps that capture insects without rapid changes in the trap configuration. Others actively capture prey, sometimes through rapid movements such as those exhibited by the Venus' fly-trap (*Dionaea muscipula*), which Darwin (1875) hailed as one of the world's "most wonderful" plants. Effective sensory mechanisms are clearly essential for active trapping, though passively trapping plants may also sense and respond to the presence of prey—for example, via biochemical signalling pathways induced by the presence of nutrients in the trapping chamber (Gallie and Chang, 1997).

Mechanoreception plays a key role in active trapping by many carnivorous plants, including *D. muscipula*. The trap of the Venus' flytrap comprises a modified leaf with two red-pigmented lobes that pivot about a central midrib. Each lobe is fringed with needle-like tines that interlock with those of the opposite lobe when the trap closes and thus help to confine the prey. Three mechanosensory hairs at the centre of each lobe serve as the trap's trigger, and multiple stimulations of one or more of these hairs over a period of several seconds is generally required for trap closure, which then takes place in a fraction of a second (Volkov *et al.*, 2008). This rapid closure is mediated by the transmission of an intercellular electrical signal, instigated when stimulation of the trigger hairs activates mechano-sensitive ion channels and generates receptor potentials, inducing a propagating action potential (Volkov *et al.*, 2008). This signal in turn mediates changes in hydrostatic pressure and the release of elastic tension, leading the rapid transition of the trap from its open to closed configuration (Forterre *et al.*, 2005; Volkov *et al.*, 2008). The initial closure of the trap is followed by the subsequent sealing of the lobes around the prey and the secretion of acids and digestive enzymes, processes that are also mediated by mechanical, as well as biochemical, cues that confirm the presence of trapped prey (Braam, 2005).

Touch cues play similarly important roles in prey capture by other carnivorous plants. For example, the aquatic waterwheel (*Aldrovanda vesiculosa*) exhibits a trapping mechanism similar to that of *D. muscipula*, and the two are believed to share a relatively recent common ancestor

(Ellison and Gotelli, 2009). Aquatic species of bladderworts (*Utricularia* spp.) also employ mechano-sensory hairs as triggers for their bladder-like suction traps, which are set by actively pumping water out of the interior of the trapping chamber to create negative hydrostatic pressure that is equalized when invertebrate prey (such as *Daphnia* spp.) contact trigger hairs controlling a hinged watertight trap-door. The door's opening causes an extremely rapid influx of water, sucking captured prey into the trap in less than a millisecond (Vincent *et al.*, 2011). Finally, diverse species of carnivorous sundew plants (*Drosera* spp.) capture insect prey using modified leaves covered by scores of tentacles tipped with glands that produce droplets of a sticky mucilage. This glue-like substance acts to prevent the escape of captured prey, whereas tactile stimulation of the engaged tentacles causes others nearby to bend toward the entangled insect (within a few seconds). On a somewhat longer time-frame (minutes to hours), the entire leaf may bend around to envelope the captured prey item—the phytohormone auxin has been implicated in this process—and increased mucilage production is induced along with the excretion of digestive enzymes (Król *et al.*, 2011). The specificity of mechano-reception by sundews is remarkable, being highly responsive to relevant stimuli from prey while not being triggered by wind or rain (Braam, 2005).

Detection of herbivores

Given the sophistication of the mechano-reception mechanisms discussed above, it should not be surprising that non-carnivorous plants employ similar perceptual abilities in detecting the presence of herbivores. Another well-known example of plant sensory response is provided by *Mimosa pudica*, the 'sensitive plant', which along with a few other species exhibits rapid leaf closure in response to mechanical stimulation. As with the rapid movements of some of the carnivorous plants discussed above, the propagation of electrical signals has been implicated in mediating this response, which typically occurs not only in the stimulated leaflet, but also in neighbouring leaflets on the same leaf, and which can be propagated even to neighbouring leaves following strong stimulation (Volkov *et al.*, 2010). This response is generally believed to function as a defence against herbivory, possibly by startling or physically displacing herbivores, reducing the apparency of the leaves, or enhancing the display of defensive thorns (Braam, 2005). Consistent with this hypothesis, leaf wounding has been shown to significantly prolong the time until reopening of damaged leaves (but not of leaves more distant from the site of damage) (Cahill *et al.*, 2012). Another recent study demonstrated that closed leaves reopen sooner under low-light conditions, suggesting a trade-off between the acceptance of predation risk and the opportunity costs of reduced photosynthesis by closed leaves under conditions of energetic stress (Jensen *et al.*, 2011). *M. pudica* has also been shown to exhibit habituation to repeated application of the same stimulus, while remaining responsive to novel stimuli, again suggestive of a context-dependent adaptive strategy to attenuate the costs of leaf closure (Gagliano *et al.*, 2014).

Other plants exhibit less obvious responses to physical contact by potential herbivores. Bown *et al.* (2002) reported that the “footsteps” of caterpillars crawling on the leaves of cultivated tobacco (*Nicotiana tabacum*) and soybean (*Glycine max*) plants elicited the rapid deployment of defence mechanisms, including the synthesis of 4-aminobutyrate (GABA) and local accumulation of reactive oxygen species. These responses were later shown to be mediated by slight damage to the plant epidermal layer (e.g. slitting of the cuticle and cellular disruption observable via electron microscopy and tissue staining) by the caterpillars’ proleg crotchets (Hall *et al.*, 2004). In tomato (*Solanum lycopersicum*), Peiffer *et al.* (2009) demonstrated that the rupture of foliar glandular trichomes by caterpillars or moths induced the expression of defence transcripts (e.g. proteinase inhibitor 2) regulated by the key plant defence hormone jasmonic acid, suggesting that these structures—previously known to play a role in defence against herbivores via the secretion of sticky or toxic compounds—might play a sensory role in the early detection of herbivores on plant leaves. Such early detection could be particularly adaptive in cases where adult insects (e.g. moths) merely lay eggs on plants but do not feed, leading to a significant time lag between potential detection and the initiation of herbivory. However, even herbivores that directly consume plants may spend significant time on a given plant before the initiation of feeding, including for the purpose of assessing plant nutritional quality and defence status via chemical cues, so that the timely expression of induced defensive traits during this period might have significant benefits for plants (Kim *et al.*, 2011).

Once herbivores initiate feeding, plant defensive responses are mediated to a large extent by the detection of herbivore-derived biochemical elicitors (as discussed in more detail below). However, mechanical aspects of wounding also seem to play an important role in plant perception of and responses to herbivore feeding. Mechanical wounding alone elicits plant defence responses, although their expression is different and in many cases attenuated when compared to the responses elicited by actual herbivore feeding (Hilker and Meiners, 2010). Furthermore, plant defence responses vary with the duration and pattern of mechanical damage inflicted (Mithöfer *et al.*, 2005), implying that these factors may play an important role in damage recognition, including recognition of differences in the pattern of damage inflicted by different classes of herbivores (Bonaventure, 2012). Intriguing recent work also suggests that vibrations associated with herbivore chewing can induce chemical defences in *Arabidopsis*, even over some distance from the site of wounding (Appel and Cocroft, 2014).

Plant–pollinator interactions

A final class of plant–insect interactions in which mechanoreception by plants may play an important role involves pollination. Flower parts can exhibit adaptive movement patterns in response to mechanical stimulation by pollinators, often either to ensure the effective attachment of pollen to the pollinator or to avoid self-pollination (Braam, 2005). Indeed,

touch-sensitive levered or spring-loaded mechanisms that function to ensure efficient pollen transfer are widespread. For example, the hummingbird-pollinated bush monkey flower (*Mimulus aurantiacus*) has hermaphroditic flowers with tubular corollas, each of which bears a single pistil and a stigma composed of two lobes that closes (within 2 seconds) after being touched by a pollinator, so that the entire receptive surface of the stigma is enfolds between the outer surfaces of the two lobes, preventing further pollen deposition (Fetscher and Kohn, 1999). The flowers of some orchid species that exploit insect pollinators through sexual deception (e.g. *Drakea* spp.) have an elaborate labellum—presenting visual, olfactory, and tactile cues that effectively mimic females of the targeted pollinator species—attached to the flower via a hinged stem. Male pollinators attempting to mate with the labellum engage the hinge and are consequently flung against the stigma and pollinia (Gaskett, 2010). In other species (e.g. *Pterostylis* spp.) derived petals are folded into a hood and the touch-sensitive labellum acts as a trap door, confining insects for several minutes within the hood where pollination takes place (Gasket, 2010). So-called buzz pollination, in which flowers release pollen through small pores or slits in the anther’s tips only in response to vibrations produced by appropriate pollinator species is also common, occurring in as many as 15 000–20 000 plant species (De Luca and Vallejo-Marín, 2013).

Contact chemoreception (responses to chemical cues)

In addition to perceiving the presence of herbivores, predators, or prey via mechanical senses, plants may also recognise animal-derived chemical cues. As noted above, chemical cues have been implicated in eliciting the production of digestive enzymes and other processes associated with the consumption of animal prey by carnivorous plants. And while plant responses to herbivores walking on leaves have been attributed to minor damage inflicted on the leaf surface (Hall *et al.*, 2004) or the disturbance of sensory trichomes (Peiffer *et al.*, 2009), chemicals deposited by insect footsteps (e.g. cuticular lipids) may conceivably also provide cues by which plants could recognise the presence of herbivores or pollinators (Eltz, 2006). More definitive evidence documents a number of other ways in which plants use chemical cues to recognise the presence of insect herbivores, as discussed below.

Oviposition-associated cues

Many insect herbivores lay their eggs directly onto plants where the resulting offspring will subsequently feed. It seems likely that plants could benefit from the ability to perceive such oviposition events and prepare their defences for impending attack. And indeed a wide range of plant responses to egg deposition by herbivores have been reported, including hypersensitive or necrotic responses, the production of ovi-cidal chemicals, the development of neoplasms (tissue hardening), and changes in plant odours or leaf surface chemistry that attract egg predators or parasitoids (Hilker and Meiners,

2011). These responses are often mediated by chemical cues deriving from the eggs themselves or from secretions that are deposited along with the eggs and may play a functional role for the insect in securing the eggs to the plant or in protection against microbes or abiotic stressors such as desiccation (Hilker and Meiners, 2006). In some cases, herbivores lay eggs on the surface of leaves or stems without otherwise damaging the plant, but eggs may also be laid at or near sites of herbivore feeding damage, and some herbivores actively damage plant epidermal tissues to prepare the oviposition site (e.g. by improving conditions for the adhesion of eggs). Oviposition itself can be injurious in the case of herbivores that use penetrating ovipositors to deposit their eggs within host plant tissues. In cases where such wounding accompanies egg laying, plant recognition may involve both chemical and mechanical cues acting in concert, though in cases examined to date chemical cues seem to be essential for the expression of plant responses to insect eggs (Hilker and Meiners, 2010).

In comparison to the herbivore feeding-associated cues discussed below, relatively little is known about the elicitors mediating plant recognition of herbivore eggs or the mechanisms involved in their detection; however, specific elicitors have been identified in several systems. For example, benzyl cyanide is an elicitor present in accessory glandular secretions deposited with eggs of the cabbage white butterfly (*Pieris brassicae*). Application of this compound to the leaves of Brussels sprouts (*Brassica oleracea*) induces transcriptional changes similar to those observed in response to egg deposition, and these changes in gene expression are thought to mediate changes in leaf surface chemistry that enhance the intensity and success rate of foraging by egg parasitoids (Fatouros *et al.*, 2008). Additional details about the identity and mode of action of oviposition-associated chemical elicitors are described in recent reviews by Hilker and Meiners (2010, 2011).

Cues associated with insect feeding

The recognition of biochemical elicitors in the oral secretions of feeding herbivores plays a key role in the recognition of herbivory and the induction of herbivore-induced defences in plants. Such recognition might be considered more closely analogous to the recognition exhibited by the human immune system than to the traditional human senses, which (sometimes, though by no means always) elicit cognitive awareness of the stimuli being experienced. However, subjective awareness of sensory inputs is probably not a relevant distinction for plants (or most other organisms). And indeed the immune system itself can be profitably viewed as a sensory organ (Blalock, 1984).

In any event, exploration of the biochemical and molecular cues that plants use to recognise and respond to insect feeding is a major focus of research on plant–insect interactions. Consequently, a great deal of recent work focuses on elucidating so called herbivore-associated molecular patterns (or HAMPs), terminology parallel to that employed in work addressing plant responses to pathogens and other microbes (PAMPs and MAMPs, respectively) (Mithöfer and Boland, 2008; Felton and Tumlinson, 2008). As typically defined, such patterns include both molecular factors derived from

the pathogen or herbivore and plant-derived factors that are reliably associated with the presence of the antagonist (e.g. molecules already present in the undamaged plant that are then released from the compartments in which they normally reside and/or undergo chemical transformation or degradation during insect feeding) (e.g. Schmelz *et al.*, 2006). From a sensory perspective, the latter could perhaps be viewed as part of the plant's perceptual system, whereas the former constitute the environmental stimuli being detected, although this is a largely semantic distinction. To further complicate matters, plant-associated microbial communities can influence—and in turn be influenced by—plant responses to herbivory (Felton and Tumlinson, 2008), and plants may also recognise the presence of herbivores via cues deriving from insect-associated microbes (Bonaventure, 2012).

In the case of both insect and pathogen-derived factors, it is thought that plant perception and response is likely to be key in an evolutionarily conserved molecules that play essential physiological roles for the antagonist and cannot therefore be easily suppressed or altered to avoid detection (Felton and Tumlinson, 2008; Bent and Mackey, 2007). This is consistent with the widespread taxonomic distribution of elicitors such as fatty acid amides (Yoshinaga *et al.*, 2007), including volicitin (Alborn *et al.*, 1997). And, indeed, these molecules seem to play an important role in insect nitrogen metabolism (Yoshinaga *et al.*, 2008). Caeliferins represent another class of fatty-acid-derived elicitors, so called because they seem to be common in grasshoppers from the orthopteran suborder Caelifera (Alborn *et al.*, 2007), whereas β -glucosidase is an enzymatic elicitor present in the regurgitant of *Pieris brassicae* caterpillars (Mattiacci *et al.*, 1995). Inceptins are peptide elicitors produced through the degradation of plant chloroplastic ATP synthase during insect feeding (Schmelz *et al.*, 2006).

Plant detection of volicitin has been shown to involve the binding of this molecule by a plasma membrane protein in *Zea mays* (Truitt *et al.*, 2004). However, our general understanding of the molecular mechanisms underlying plant perception of HAMPs and the subsequent signalling cascades that their perception initiates remains limited, although it is clear that there is substantial overlap in the processes of signal transduction initiated by herbivore- and microbe-derived elicitors (Bonaventure *et al.*, 2011; Bonaventure, 2012). Furthermore, HAMP-induced signalling has been implicated in the regulation of changes in gene expression and other cellular processes, as well as in the regulation of phytohormone signalling pathways that mediate a wide range of direct and indirect plant defences (Bonaventure, 2012). Further details about the identity and mode of action of HAMPs mediating plant perception and response to insect can be found in a number of recent reviews (e.g. Felton and Tumlinson, 2008; Mithöfer and Boland, 2008; Bonaventure *et al.*, 2011; Bonaventure, 2012).

Olfactory chemoreception (responses to olfactory cues)

For most animal species the olfactory sense is used to gather information about features of the environment at some

distance from the perceiving organisms via the detection of mobile chemical cues present in the surrounding air or water. Until recently, there was substantial controversy about whether plants exhibit a similar ability to respond to airborne odour cues, although the volatile hormone ethylene has long been known to play a key role in mediating plant growth and development. Here we discuss current knowledge of plant responses to volatile chemical cues associated with insect herbivory.

Ethylene signalling

The structurally simple hydrocarbon ethylene (C₂H₄) plays a ubiquitous signalling function in plants. Produced by all known plant species and in virtually all parts of vascular plants (Yang and Hoffman, 1984), ethylene has diverse context-dependent signalling functions in a wide range of plant tissues and regulates a wide range of developmental processes, including vegetative growth; flowering; fruit ripening and abscission; seed development, dormancy and germination; and senescence (Grierson, 2012). Ethylene thus functions essentially as a gaseous hormone, although one that can be transmitted externally between plant parts, or between neighbouring plants (Tschardt et al., 2001; Kegge and Pierek, 2009), blurring the distinction between within-plant signalling and sensory perception of environmental cues. Ethylene also plays a key role in mediating plant responses to a wide range of environmental stimuli including attack by pathogens and herbivores, largely via interactions with other phytohormone signalling pathways (Adie et al., 2007; Von Dahl and Baldwin, 2007; van der Ent and Pieterse, 2012). The extreme volatility and structural simplicity of ethylene facilitates its transmission within plant tissues but poses challenges for signal detection given the limited number of possible interaction points between the signal molecule and its receptor (Alonso and Stepanova, 2004). In plants, a family of ethylene receptors localized to the endoplasmic reticulum achieve the requisite binding affinity and specificity via a copper cofactor associated with the hydrophobic ligand-binding pocket of the receptor molecule (Alonso and Stepanova, 2004). A great deal of recent work has elaborated details of ethylene reception and subsequent signal transduction (reviewed by Cho and Yoo, 2009; Binder et al., 2012).

Plant-to-plant volatile signalling

Relative to our increasingly detailed understanding of ethylene signalling, somewhat less is known about plant perception of environmental odour cues, including those associated with the presence of insect herbivores. Indeed the existence of such responses remained a subject of some controversy until quite recently. The majority of research addressing plant olfactory responses has focused on the perception by plants of herbivore-induced volatiles released by damaged neighbours and their use as cues mediating defence enhancement in the receiving plant, a phenomenon first reported in the 1980s (Rhoades, 1983; Baldwin and Schultz, 1983). However, early studies purporting to document such effects exhibited

various methodological weaknesses that limited the strength of their conclusions, and an influential critique by Fowler and Lawton (1985) cast considerable doubt on the phenomenon of plant-to-plant communication. Subsequent studies also failed to produce definitive results, giving rise to a widespread impression that the hypothesis of plant-to-plant volatile signalling had been discredited (Dicke and Bruin, 2001). This impression, in turn, contributed to a climate in which work in this area was somewhat stigmatized and the limited availability of funding and other resources constrained further progress (Karban et al., 2014).

General scepticism about plant olfactory responses among scientists lacking detailed knowledge of work in this field was probably also fuelled by a backlash against pseudoscientific claims regarding plant perceptual abilities that gained significant prominence in the 1970s, as discussed above. And widespread popular press coverage of initial studies on plant–plant volatile signalling probably exacerbated this association. The phenomenon came to be referred to as “talking trees” by journalists as well as many scientists, terminology that was unfortunate not only because it tended to anthropomorphize the purported capabilities of plants and to sensationalize findings drawn from limited data, but also because it placed undue emphasis on the putative signalling functions of plant volatiles (i.e. rather than on the perceptual capabilities and responsiveness of plants detecting volatile cues), thereby raising questions about the evolutionary plausibility of signals that seemed likely to often serve as warning calls to neighbouring competitors of the emitting plant (Karban et al., 2014).

Despite these early setbacks, subsequent work clearly demonstrated that herbivore-induced plant volatiles do frequently mediate the enhancement of anti-herbivore defences in neighbouring plants. For example, methyl jasmonate was shown to induce the accumulation of proteinase inhibitors in tomato, *S. lycopersicum* (Farmer and Ryan, 1990), and exposure to various terpenoid compounds elicited by spider mite feeding were implicated in the activation of activation of phytohormone signalling pathways and defence gene expression in lima bean (*Phaseolus lunatus*) (Arimura et al., 2000). Other studies implicated similar classes of compounds in additional plant–herbivore systems (e.g. Engelberth et al., 2004) and identified other potential cues, including carbonyl compounds (Weber et al., 2004; Engelberth et al., 2004). Although questions remained regarding the ecological relevance of laboratory studies conducted under somewhat unrealistic conditions (Baldwin et al., 2006; Paschold et al., 2006), evidence was also forthcoming from field studies. For example, Karban and colleagues reported that wild tobacco plants, *Nicotiana attenuata*, growing in close proximity to experimentally clipped sagebrush, *Artemisia tridentata*, under otherwise natural conditions suffered significantly less herbivore damage than plants growing near unclipped sagebrush and documented increased production of defence-related compounds in receiving plants (Karban et al., 2000; Karban and Maron, 2002; Karban et al., 2003). And subsequent work has provided convincing evidence of plant–plant interactions mediated by volatiles in many

additional systems. A recent meta-analysis by Karban *et al.* (2014) evaluated 48 well-replicated studies, and determined that 38 presented evidence for positive effects of exposure to herbivore-induced plant volatiles on plant resistance to subsequent attack by herbivores.

Although the occurrence of plant responses to damage-induced volatile cues is now well established, questions remain about the adaptive and ecological significance of such interactions. As noted above, one early objection to the concept of plant–plant signalling questioned the evolutionary plausibility of signals that function primarily as warnings to neighbouring plants, which may frequently be in competition with the emitter. This objection might be overcome if receiving plants frequently exploit plant volatile emissions that evolved for other reasons, including (as discussed above) direct defence or signalling to insects. But it is also possible that volatiles might frequently function as important within-plant signals, with neighbouring plants sometimes eavesdropping on these communications. And induced plant volatile emissions have indeed been implicated in within-plant signalling (Heil and Ton, 2008). For example, Heil and Silva Bueno (2007) found that lima bean leaves exposed to volatiles from damaged leaves on the same shoot produced more extrafloral nectar, which serves to recruit predators, and were also primed for additional defence responses. There is also evidence that within-plant signalling via volatiles may help to overcome vascular constraints on the transmission of internal wound signals (Orians, 2005; Frost *et al.*, 2007). In the sagebrush system described above, Karban and colleagues reported that preventing airflow from mechanically clipped sagebrush branches results in increased herbivore damage to adjacent branches of the same plant (Karbon *et al.*, 2006). And, intriguingly, sagebrush plants have also been shown to experience reduced rates of subsequent herbivory following exposure to volatile cues from genetically identical, or closely related, neighbours compared with plants exposed to volatiles from unrelated individuals, suggesting that self- or kin-recognition may also be involved in plant-to-plant volatile signalling (Karbon and Shiojiri, 2009, Karban *et al.*, 2013).

Although effects of volatile perception on defence signalling pathways and gene expression have been documented in many systems, relatively little is known about the specific mechanisms by which plants detect volatile cues. A recent study by Sugimoto *et al.* (2014) showed that the enhanced resistance of tomato plants exposed to the odours of caterpillar damaged neighbours was mediated by transformation of the green-leaf volatile (*Z*)-3-hexenol to (*Z*)-3-hexenyl-vicianoside (or HexVic), a compound further shown to act as an effective defence against caterpillar feeding. Thus, defence enhancement in this system seems to involve the conversion of volatile compounds received from herbivore-damaged plants into defensive compounds via a relatively straightforward biochemical transformation. However, more complex mechanisms are no doubt involved in other systems where plant responses to volatile cues have been shown to involve the priming or induction of phytohormone-mediated defence pathways (e.g. Engelberth *et al.*, 2004).

Plant responses to insect odours

As noted above, the great majority of work on plant olfaction has focused on the perception of odour cues emanating from other plants. In addition to the role of herbivore-induced volatiles in mediating defence enhancement discussed above, olfactory cues have been shown to play a role—along with light cues—in host location by some parasitic plants whose seedlings actively grow toward nearby host plants (Runyon *et al.*, 2006). However, recent studies by Helms *et al.* (2013, 2014) indicate that some plants can also perceive olfactory cues emanating from insect herbivores themselves. These studies showed that tall goldenrod plants (*Solidago altissima*) exposed to the putative sex pheromone of a specialist herbivore, the gall-inducing fly *Eurosta solidaginis*, subsequently exhibited stronger induction of the defence phytohormone jasmonic acid—along with stronger induction of damage-associated volatiles—than unexposed plants and also suffered less herbivory in laboratory and field assays. The olfactory cue implicated in this system comprises compounds chemically distant from those typically seen in plant volatile emissions, suggesting that plants may have the potential to evolve the ability to perceive a wide range of ecologically relevant olfactory cues.

Closing thoughts

Responses to various chemical and mechanical cues discussed above do not exhaust the sensory modalities exhibited by plants, which exhibit finely tuned responses to light (Smith, 2000) as well as other environmental cues such as temperature (Kumar and Wigge, 2010) and gravity (Chen *et al.*, 1999). The significance of these and other cues in mediating interactions among plants and other organisms is less certain—though exciting recent work is elucidating the role of within-plant electrical signalling in mediating plant responses to herbivore damage (Mousavi *et al.*, 2013). However, we are only beginning to gain a clear understanding of the full range of sensory cues that mediate plants' interactions with biotic features of their environments, the mechanisms by which such cues are detected and interpreted, and the extent to which information from multiple sensory modalities is integrated in the context of plant perception and response. There thus remains ample room for debate about the degree to which the sophistication of plant perceptual systems approaches the complexity and sophistication that is apparent in many animal systems. It is nevertheless increasingly clear that plants actively monitor a continuous flow of sensory information from their environments and respond in ways that profoundly influence their interactions with other organisms.

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