

**REVIEW AND
SYNTHESIS****Plant behaviour and communication****Richard Karban****Department of Entomology,
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CA 95619, USA***Correspondence: E-mail:
rkarban@ucdavis.edu***Abstract**

Plant behaviours are defined as rapid morphological or physiological responses to events, relative to the lifetime of an individual. Since Darwin, biologists have been aware that plants behave but it has been an underappreciated phenomenon. The best studied plant behaviours involve foraging for light, nutrients, and water by placing organs where they can most efficiently harvest these resources. Plants also adjust many reproductive and defensive traits in response to environmental heterogeneity in space and time. Many plant behaviours rely on iterative active meristems that allow plants to rapidly transform into many different forms. Because of this modular construction, many plant responses are localized although the degree of integration within whole plants is not well understood. Plant behaviours have been characterized as simpler than those of animals. Recent findings challenge this notion by revealing high levels of sophistication previously thought to be within the sole domain of animal behaviour. Plants anticipate future conditions by accurately perceiving and responding to reliable environmental cues. Plants exhibit memory, altering their behaviours depending upon their previous experiences or the experiences of their parents. Plants communicate with other plants, herbivores and mutualists. They emit cues that cause predictable reactions in other organisms and respond to such cues themselves. Plants exhibit many of the same behaviours as animals even though they lack central nervous systems. Both plants and animals have faced spatially and temporally heterogeneous environments and both have evolved plastic response systems.

Keywords

Conditioning, environmental heterogeneity, foraging, integration, movement, phenotypic plasticity.

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INTRODUCTION

The idea that plants exhibit complicated behaviours in response to environmental stimuli is not new. Charles Darwin (1880) published a comprehensive description of the widespread movements of plant tissues excited by light, gravity and contact. Since then the repertoire of behaviours that have been catalogued has increased greatly, and plants occasionally get brief mention in modern textbooks about behaviour (e.g. Krebs & Davies 1997). Plant behaviour has been defined as a response to an event or environmental change during the course of the lifetime of an individual (Silvertown & Gordon 1989; Silvertown 1998).

This definition is similar to commonly used descriptions of phenotypic plasticity in plants (Bradshaw 1965). Behaviour is a form of phenotypic plasticity in response to a stimulus that is relatively rapid and potentially reversible

(Silvertown & Gordon 1989). Behaviour ultimately has a physiological basis, which is mediated by chemical reactions. However, response to a stimulus, relative speed, and non-permanence distinguish behaviour from other physiological and chemical reactions. Behaviour does not include ontogenetic changes that are programmed to proceed during the course of development, such as the changes that necessarily occur as a seed germinates and transforms into a seedling (Silvertown 1998). In animals, behaviour usually refers to movements generated by muscles, typically the result of nervous action although this restrictive definition precludes a consideration of similar phenomena in plants. Silvertown and Gordon's (1989) definition of plant behaviour may be confusing to some animal behaviourists and perhaps that is one reason that plant behaviour is still an uncommon term. My aim in using the term in this review is to draw attention to the fact that plants have many complicated responses that

were unappreciated until recently. In addition, as a more mature field, animal behaviour has been successful in ways that plant biologists can emulate.

Plant behaviour has recently been the subject of intense research interest and several reviews (e.g. Novoplansky 2002; de Kroon & Mommer 2005; de Kroon *et al.* 2005; Trewavas 2005). These more narrowly focused reviews highlighted the ways in which plants forage for resources. Plants place leaves and roots non-randomly within their heterogeneous environments and this placement allows them to actively modify their acquisition of essential nutrients, water and light. The growth or abscission of organs such as leaves or roots is not strictly reversible although a plant may reverse its commitment to invest in one direction, recover some of its investment, and redirect its growth elsewhere. Resource foraging is probably the best studied plant behaviour; for example, we know something about the physiological mechanisms employed by plants foraging for light (e.g. Pearcy & Sims 1994; Ballare 1999; Smith 2000) as well as its evolutionary consequences (Schmitt *et al.* 1999). Without broadening Silvertown's definition of plant behaviour, information about many other types of plant behaviours, in addition to foraging, have been elaborated recently and will be described in the next section of this review.

PLANT RESPONSES TO ENVIRONMENTAL HETEROGENEITY AND CHANGE

Environments vary over space and over time and plants respond to this variation by adjusting their phenotypes to match current conditions. This statement implicitly assumes that all responses are adaptive. We know that this assumption is sometimes violated and that some changes produce mismatches with the environment. However, the assumption of adaptation has been used successfully by behavioural ecologists in many situations. Phenotypic adjustments may take the form of plant movement, physiological acclimation and change, growth of new tissue, or shedding of existing tissue. These categories are not mutually exclusive, as for instance, all phenotypic plasticity has a physiological basis. The range of plant responses is fairly large in terms of the behaviours that they exhibit, the conditions that they respond to, and their ecological and evolutionary consequences (Table 1).

Plant movement and foraging

Some of the most impressive plant behaviours involve rapid movements in response to physical stimuli. Leaflets of 'sensitive legumes' rapidly fold up if disturbed by insects and neighbouring leaves fold up, as well, following wounding (Eisner 1981; Braam 2005). This behaviour may scare away

small herbivores and expose larger ones to protective thorns. Other tropical legumes lower their leaves in response to heavy rain, but not light rain or alighting insects, and this response accelerates leaf surface drying (Dean & Smith 1978). Carnivorous plants rapidly move to catch insects that stimulate trigger hairs, setting off a series of changes in expansion of cells that ultimately results in a meal (Darwin 1893; Braam 2005). This behaviour allows carnivorous plants to thrive in resource-poor environments. Stamens and stigmas of many plant species move in response to insect visitation which increases the likelihood of outcrossing (Braam 2005). The mechanisms responsible for these rapid plant movements are varied and include changes in turgor, osmotic changes in ionic concentrations, action potentials and electrical signals instead of the actin-myosin system common in animals.

In addition to these very rapid movements, Darwin (1880) argued that all plant organs undergo subtle movements around their axes of elongation which he called circumnutation. By modification of this phenomenon, many different plant tissues have developed conspicuous and directed movements in response to light, gravity and other environmental stimuli. These movements allow plants to be more efficient at capturing resources such as light compared with individuals that are prevented from moving.

For at least a century, plant biologists have observed that roots become more abundant in soil that contains higher levels of nutrients compared with soil with lower levels (Weaver 1926). This prompted the hypothesis that roots grew selectively in favourable patches in order to increase resource acquisition. Experiments mapping the growth of barley roots in soil compartments that contained different nutrient levels confirmed this hypothesis (Drew *et al.* 1973). Those parts of a single root that contacted soil containing high nitrate concentrations grew many more lateral roots relative to those root parts that contacted soil with less nitrate.

Morphological plasticity also allows plants to forage efficiently for light. Vertical shoots elongate less and branch more when they are exposed to favourable light conditions compared with shoots with reduced light. Light transmitted through leaves has a lower ratio of red : far red than unfiltered light (Smith 2000). Plants sense light availability using phytochrome photoreceptors that detect the ratio of red : far red radiation. Individuals that are shaded by neighbours undergo a reprogramming of their morphological development causing them to grow taller and in the direction of canopy gaps (Ballare 1999). More and larger buds develop on branches in sunny patches than on branches in shady patches, resulting in crown asymmetry. This growth pattern allows greater capture of light (Schmitt *et al.* 1999). This often translates into fitness benefits accruing to the plants that respond to light cues although

Table 1 Plant behaviours, their causes and consequences

Behaviour	Stimulus	Tissue responding	Consequences	Reference
Foraging				
Movement	Contact, light, gravity	Many	Improved resource acquisition	Darwin (1880), Braam (2005)
Root growth/shedding	Nutrients, water	Root meristems	Improved resource acquisition	Hutchings and de Kroon (1994)
Shoot growth/shedding	R/FR light	Shoot meristems	Improved resource acquisition	Smith (2000)
Enzyme deployment, gas exchange	Light	Leaves	Increased photosynthesis, reduced photoinhibition	Pearcy and Sims (1994)
Parasitism	Cues from favourable hosts	Haustoria	Successful parasitism	Kelly (1992), Yoder (2001)
Reproduction				
Reproductive strategy	Environ. conditions, pollinators	Shoot meristems	Outcrossing rates, reproductive success	Bradshaw (1965), Paige and Whitham (1987)
Functional gender	Stress Resources	Reproduct. tissues	Maleness Femaleness Femaleness	Freeman <i>et al.</i> (1980) Hendrix and Trapp (1981)
Seed germination	Floral damage Light, temp, other physical and biotic conditions	Seed coat, embryo	Seedling grows in favourable environment	Baskin and Baskin (1998)
Defence				
Production of phytoalexins	Microbes	Many	Improved defence	Hammerschmidt (1999)
Accumulation of secondary metabolites	Herbivores & microbes	Many	Improved defence	Karban and Baldwin (1997)
Attraction of predators and parasites of herbivores	Herbivore attack	Systemic response	Improved defence	Dicke and van Loon (2000)

these fitness consequences depend upon the broader selective environment that the plant experiences (Huber *et al.* 2004). Taken to its extreme, the tendency to grow towards light can be detrimental. For example, competition for light near forest gaps can promote unbalanced growth so that trees eventually fall into the gaps (Young & Hubbell 1991).

Plants experience vastly different light and water levels over space and time and they acclimate to optimize photosynthetic and gas exchange rates, and to avoid photoinhibition (Pearcy & Sims 1994). These physiological adjustments may occur over seconds at the chloroplast and cellular level or over longer times at the branch level. They

may involve subtle and coordinated changes in the photosynthetic apparatus (Pearcy & Sims 1994) or shedding of entire leaf canopies in drought-deciduous species (Comstock *et al.* 1988).

Plants that are obligate or facultative parasites must forage in a manner more similar to animals than autotrophs. Parasitic plants locate and invade the tissues of other plants to rob their hosts of nutrients and water (Yoder 2001; Runyon *et al.* 2006). Haustoria of the parasitic plants respond to chemicals released by other species, allowing the parasite to recognize and attack appropriate host plants. Indeed, parasitic dodder is more likely to grow towards and accept hosts of higher nutritional quality compared with

those of lesser quality (Kelly 1992). Even for facultative plant parasites, fitness is closely linked to host quality (Adler 2003).

Mating and germination behaviour

The examples listed above all involve resource acquisition. Plants also display responses to environmental cues that are reflected in their reproductive behaviours. Individuals that fail to get pollinated may increase their investment in rewards that attract insect visitors (Ladio & Aizen 1999). Plants that experience conditions that are unfavourable for pollination may respond by producing cleistogamous flowers that do not open and are self-pollinated (Bradshaw 1965). Individuals of *Ipomopsis aggregata* that failed to get pollinated shifted from being semelparous (flowering once and dying) to being iteroparous (flowering again; Paige & Whitham 1987). These responses allow successful reproduction to occur under suboptimal conditions.

Plants also may adjust their functional gender in response to the conditions that they experience. Environmental stresses generally cause plants to invest disproportionately in male flowers whereas access to water and other nutrients causes plants to invest more in female reproduction (Freeman *et al.* 1980). Herbivory to reproductive tissues causes plants to selectively abort and/or regrow reproductive organs; flower damage generally shifts plants towards more femaleness (Hendrix & Trapp 1981; Krupnick & Weis 1998).

The timing of seed germination for many species is strongly affected by environmental conditions (Baskin & Baskin 1998). The decision to germinate is a conditional response in contrast to the specific programs of developmental changes that occur during the germination process, which are fixed and therefore not considered as plant behaviour. For instance, the number of hours of daylight determines whether some species will germinate or remain dormant and later, whether vegetative growth is determinate or indeterminate. The spectral quality of light (red : far red ratio), temperature, fire, exposure to water, oxygen, CO₂, ethylene and other chemicals, passage through animal guts and attack by insects can all be important in determining whether seeds germinate. These conditional responses allow seeds to germinate into environments that are favourable for growth and to remain dormant when conditions are unfavourable.

Induced plant responses to pathogens and herbivory

Plants respond to the attacks of pathogens and herbivores by changing many phenotypic traits (Karban & Baldwin 1997; Agrawal *et al.* 1999b). These induced responses include chemical, physiological, and morphological charac-

teristics. Some induced responses make plants less susceptible to, or less preferred by, attackers and thus may increase plant fitness relative to attacked individuals that do not induce. Induced responses to pathogens and herbivores have generally not been included in reviews of plant behaviour. This is partly a historical oversight and partly because plant defences have been assumed to be primarily chemical traits that do not involve movement or positional changes. In this regard, most plant responses to attacks are less similar to behaviour from a zoological perspective and more similar to physiological plasticity that is also well described for animals (Tollrian & Harvell 1999). However, the responses of plants to attackers are often relatively rapid and reversible and fit the definition of plant behaviour outlined above. Below, I give three examples of induced plant responses to pathogens and herbivores that have been particularly well studied.

Plants that are attacked by microbes undergo a variety of physical and chemical changes in an attempt to prevent infection, curtail the growth of the pathogen, and survive the attack (Ferreira *et al.* 2007). One induced plant response that has been well documented is the accumulation of phytoalexins (Hammerschmidt 1999). These are low molecular weight secondary metabolites that exhibit antimicrobial and antifungal properties. Phytoalexins are often synthesized *de novo* in response to infection and they degrade rapidly so that they are undetectable in unchallenged tissue. Treatments that increase or decrease concentrations of phytoalexins *in planta* cause correlated increases or decreases in resistance to many disease threats.

Herbivores also induce the synthesis of secondary compounds in many plants (Karban & Baldwin 1997). One well-studied example is nicotine accumulation in damaged tobacco plants. This alkaloid is produced by the roots of tobacco and is transported in the xylem stream up to the leaves following herbivory (Baldwin 1999). Nicotine is deadly to most leaf-feeding herbivores and reduces feeding by even those species that can tolerate it. It is difficult to determine the costs and benefits of nicotine accumulation (or other secondary chemicals) as experimental treatments that induce one plant response also induce a large number of correlated responses. In the field, transformed plants that lacked the ability to respond to herbivory (including the nicotine response plus many others) were more vulnerable to insects that specialize on tobacco and were also attacked by generalist herbivores that do not usually feed on tobacco (Kessler *et al.* 2004). Artificially induced responses, including nicotine accumulation, increased seed production of tobacco in those field situations where plants were likely to be attacked by herbivores (Baldwin 1998). Tobacco plants that specifically lacked the nicotine response experienced more damage in

the field although plant fitness has not yet been evaluated (Steppuhn *et al.* 2004).

Some plant responses to herbivore attack are used as cues by the predators and parasites of herbivores as they forage for food (Dicke & Sabelis 1988; Dicke & van Loon 2000). Plants release complex volatile blends that differ in composition depending upon whether they have been attacked and upon the specific nature of the attacker. The predators and parasitoids that are attracted by herbivore-induced volatiles have been shown to increase rates of predation and parasitism and decrease levels of damage inflicted by herbivores under natural field conditions in some, though not all, instances (Thaler 1999; Kessler & Baldwin 2001; Heil 2004a,b; Karban 2007a,b). When predators and parasites are attracted, this mechanism is considered an indirect plant defence because the induced plant behaviour causes a behavioural shift in a third trophic level. Although the three plant responses described above all involve chemical changes, plants also adjust their morphologies (spines, trichomes, stature, leaf toughness, etc.) as well as where they allocate resources (above or below ground) in response to attack (Karbon & Baldwin 1997).

Conditional mutualisms

When predators and parasites increase plant fitness by reducing plant damage caused by herbivores, the plant-predator interaction can be considered as beneficial to both plants and predators. Plants adjust the rewards that they provide to these mutualists, increasing extrafloral nectar production when risk of herbivory is great (Heil *et al.* 2001, 2004a) and reducing nectar and other rewards when risk is low (Huntzinger *et al.* 2004). Plants adjust their investments in other mutualisms as well. Some plants house N-fixing bacteria in root nodules and receive nitrogen in return. When the benefits to the host plant in terms of nitrogen supplied by bacteria were experimentally reduced, the host plant responded by reducing the oxygen supply to the bacteria (Kiers *et al.* 2003). This plant-imposed sanction decreased reproductive success of the bacteria by *c.* 50%. Plants also adjust rewards depending upon the quality of service provided by pollinating insects. For example, yucca moths both pollinate and oviposit into the seed heads of their yucca hosts. Plants are more likely to allow fruits with low egg loads and high pollen loads to mature (Pellmyr & Huth 1994). Selective maturation increases seed production and polices moths that lay many eggs or provide low quality pollination.

PATTERNS IN PLANT BEHAVIOUR

Plants respond to a great variety of environmental stimuli and conditions. Plants also respond at a diversity of levels

from physiological adjustments at the subcellular level up to larger scale alterations of plant morphology. Despite this diversity, many generalities in plant behaviour seem to emerge. Below I attempt to list some of these recurring patterns that have not been appreciated widely and to contrast them to similar behaviours exhibited by animals.

Plant behaviours can be complex

Because plants lack central nervous systems, their behaviours have previously been categorized as relatively simple compared with the behavioural repertoires of animals (Silvertown & Gordon 1989). The argument that plant behaviours are relatively simple was based on the observations that plants responded to thresholds, gradients, or changes in the magnitude of environmental variables but not to more complex patterns in those variables. Evidence concerning induced responses to herbivores indicates that plants can distinguish among a large set of cues and respond appropriately. For example, plants emit different blends of volatile chemicals in response to attack by closely related caterpillars (De Moraes *et al.* 1998). These cues provide detailed information that allows species-specific parasitoid wasps to locate their particular hosts but do not attract them to non-host caterpillars. Selective plant emissions and parasitoid responses require precision both by the plants and the parasitoids.

Plants are also capable of responding to complex cues about their current and future environments. For example, sagebrush plants respond to volatile cues released by their neighbours to increase their levels of resistance after a neighbour has been attacked (Karbon *et al.* 2004, 2006). These same volatile cues are required for an individual sagebrush to coordinate its defences among several branches as vascular integration is limited. These examples of recognition of complicated patterns and other examples described below now indicate that plant behaviours are much more sophisticated than the authors of previous reviews were aware.

Plant behaviours can be rapid

Plant behaviours have been depicted in previous reviews as relatively slow (Harper 1985; Silvertown & Gordon 1989). However, plant movements can be as rapid as those of many animals, exemplified by carnivorous plants, although the spatial extent of these movements is more limited compared with more motile animals. Previous authors have had foraging plants as their models of behaviour and these rely on morphological plasticity, requiring either growth or death of plant organs. However, many of the plant behaviours listed in Table 1 such as the responses to light or to herbivores occur within seconds, much more rapidly

than most morphological changes (Pearcy & Sims 1994; Karban & Baldwin 1997). As most plants are rooted to a substrate, their opportunities for distant movement are more limited than those of unattached animals.

The difference between many plant and animal behaviours is largely one of spatial and temporal scale. Indeed, the fastest motion yet observed in biology is the pollen release, at velocities that exceed half the speed of sound, of white mulberry flowers in response to dry air (Taylor *et al.* 2006). Of course, the spatial range of pollen movement in this example is relatively small. Similarly, the movement of plant roots through soils of varying nutritional value is less extensive (and less rapid) than the foraging trails of ants in spatially variable habitat patches. However, both of these foraging behaviours are highly conditional and highly reversible, as fine roots turn over rapidly.

Modular construction enables many behaviours

Morphological plasticity, exemplified by behaviours such as foraging, is possible because plants are made up of largely autonomous modular units (Harper 1985; Silvertown & Gordon 1989). These modular units arise from iterative active meristems that have the ability to grow into organs of undetermined characteristics, varying in type, size, shape and number. As a result, plants can transform in radically different ways in response to different environmental cues. Many plant behaviours rely on modular organization to respond to environmental heterogeneity in much the same way as many animal behaviours rely on mobility.

Plant behaviours are often localized

A consequence of independent modular construction is that plants are generally less well integrated than are animals (Hutchings & de Kroon 1994; de Kroon *et al.* 2005). Plants typically respond to fine-grained heterogeneity in their environments with localized adjustments. For example, in a classic experiment, Drew (1975) grew barley in soils containing different distributions of phosphate. Those portions of the root system in contact with higher concentrations of phosphate grew more and longer lateral rootlets, indicating independence of modules. However, this response was influenced to some extent by the levels of nutrients available to the whole plant, indicating some degree of integration. The localized foraging response was stronger when the whole plant was growing in a phosphate-poor environment compared with one that supplied relatively more phosphate to the entire root system. This result exemplifies a situation in which responses are partly localized and independent but also partly integrated with the conditions experienced by the whole plant.

Plastic responses are often portrayed as norms of reactions for the entire organism (e.g. Via 1987; Harvell 1990). This view implicitly assumes systemic integration and masks the reality of localized plant responses to fine scale environmental heterogeneity. Instead of shifting the phenotype of the entire plant, localized plasticity tends to increase phenotypic variation among leaves or other ramets within an individual (Stout *et al.* 1996; de Kroon *et al.* 2005). Indeed, the extent to which plastic responses are integrated and the consequences of integration or sectoriality (lack of integration) are important areas in which our understanding is very incomplete (Harper 1985; Hutchings & de Kroon 1994; Silvertown 1998; de Kroon *et al.* 2005; Orians 2005).

Plant behaviours may be correlated and context-dependent

Plant responses to heterogeneous and changing environments often occur as correlated suites of behaviours or syndromes (Agrawal & Fishbein 2006). These correlated changes produce different consequences than the responses would have if they occurred independently. One of the best studied induced responses to herbivory is the synthesis of proteinase inhibitors in solanaceous plants (Ryan 1990). Proteinase inhibitors produced by plants interfere with the action of digestive enzymes of herbivores and decrease performance of many herbivores. However, the effectiveness of proteinase inhibitors depends critically upon other induced plant changes. Many wound-induced changes deactivate proteinase inhibitors as do high concentrations of nutrient levels in the herbivore gut (Duffey & Felton 1989). On the other hand, induced nicotine acts synergistically with induced proteinase inhibitors to affect herbivore performance more adversely than either response does in isolation (Steppuhn & Baldwin 2007). The effect of any given plant behaviour is highly context-dependent and the context ranges from cellular to environmental.

Tradeoffs in plant behaviours

The effects of behaviours depend upon the current state of the plant. Responses to one environmental condition may affect and constrain the plant's responses to other conditions. This phenomenon is widespread and becomes particularly visible as tradeoffs in opposing plant responses to different conditions. Plants appear to use a relatively small number of hormones to perceive and respond to many different environmental stimuli. The signals that induce one behaviour may lessen the plant's ability to induce a different behaviour. For example, the signals used to induce defence against some chewing insects may interfere with the signals used to induce defence against pathogens (Felton *et al.* 1999; Bostock 2005). Many other tradeoffs in

plant behaviours have been noted. Plants that have induced a shade avoidance response were less able to induce defence against herbivory (Cipollini 2004; Kurashige & Agrawal 2005; Izaguirre *et al.* 2006). Plant responses to salt and water stress may interfere with their ability to defend against pathogens and herbivores (Thaler & Bostock 2004). These tradeoffs are often attributed to the fact that plants have limited resources available to invest in multiple functions although this underlying mechanism has not been clearly established and alternatives have not been adequately considered.

Consequences of plant behaviours are poorly known

We know much less about the ecological consequences of plant behaviours than we do about the phenomena themselves (Callaway *et al.* 2003). Changes in behavioural traits may have various and far reaching direct and indirect effects on other members of the community. For example, we know that there is additive genetic variance in wild radish plants for plasticity of defensive traits (Agrawal *et al.* 2002). Defence in this case includes inducible glucosinolates, leaf toughness and density of trichomes. Plasticity in these traits affects a diverse herbivore community and increases plant fitness in a variety of different herbivore environments (Agrawal 1998). But even in the best known systems, it is still unclear how these plastic behavioural traits influence interactions with the other plant, animal, and microbial species (Agrawal 2001). In a second example, growth rates and the resulting density of oak roots respond to the availability of water and other nutrients. Our current knowledge suggests that this root foraging behaviour can have profound effects on the other plants that grow in the oak woodland community, although these effects are still poorly resolved (Callaway *et al.* 2003). These two examples have been more closely examined than most, and future work examining the broader ecological consequences of plant behaviours will shape our understanding of species interactions in general.

Plants appear to anticipate, remember and communicate

We are now realizing that plant behaviours are often quite sophisticated and possess attributes that were long considered the exclusive domain of animals with central nervous systems (Borges 2005; Trewavas 2005). Plants engage in three behaviours that we intuitively associate with cognition. (i) Plants often anticipate environmental changes that have not yet occurred. (ii) Plants often become conditioned by experiences that they or their parents have had and this conditioning alters their behaviours. In other words, plants appear to have a 'memory' that influences their responses based on past experience. (iii) Plants use cues to commu-

nicate with other organisms, including conspecifics and this communication alters plant behaviour. Below I will expand on these three themes.

PLANTS ANTICIPATE FUTURE ENVIRONMENTAL CONDITIONS

Plants behave in ways that make them appear to anticipate future conditions in many of the cases listed in Table 1, although these behaviours do not involve true cognition. This is most often accomplished by responding to cues that are good correlates of future conditions (Karban *et al.* 1999). Many deciduous plants drop leaves in the autumn in response to shortening photoperiod as if they are anticipating winter conditions that have a high probability of damaging leaves and branches and are suboptimal for photosynthesis. Shortened photoperiod is a cue that proceeds, and is highly correlated with, the onset of conditions that can be suboptimal or even harmful. Similarly, seeds use cues to break dormancy, such as heat from fire for fire-adapted species. These cues are good predictors of conditions, such as limited competition and abundant light and nutrients, that are uncommon but will be very favourable for the growth of seedlings (Baskin & Baskin 1998).

Plant foraging may place them in situations that will be favourable in the future. The mechanism of this anticipatory behaviour is particularly well studied in the case of the shade avoidance response that occurs before plants actually become shaded. Plants use phytochrome receptors to sense an increase in far red radiation generated by neighbouring green leaves (Smith 2000). Responding plants grow away from neighbours well before those neighbours diminish their actual acquisition of light (Ballare *et al.* 1990). Removing the far red cue with filters abolishes the response. Plants respond more strongly to the red : far red quality (the cue) than to diminished photon flux density (amount of photosynthetically active light) (Novoplansky 1991). Other examples of foraging indicate that plants can anticipate future conditions although the mechanisms are less well resolved. For example, parasitic dodder accepts nutritious hosts and rejects less nutritious hosts before taking up any food (Kelly 1992). The cues used in this decision making process are not known although recent work suggests that volatiles released by host plants allow dodder to preferentially grow in the direction of high quality hosts (Runyon *et al.* 2006).

Induced responses to herbivory are only effective if current herbivory is a good predictor of future risk (Karban *et al.* 1999). Surprisingly few studies have documented that past or current herbivory is actually an information-rich cue that predicts future risk. Early season damage to wild cotton plants was a good predictor of the risk that plants were likely

to encounter during the remainder of the season (Karbon and Adler 1996). Some phytoplankton form protective colonies in response to waterborne cues associated with their herbivores. Herbivore cues reliably predict when it is safe to remain unspined and solitary and when these behaviours are dangerous (Van Donk *et al.* 1999; Verschoor *et al.* 2004). In a situation where two herbivores have opposing preferences for solitary and clumped colonies, the specific cues of each herbivore species induces opposite but adaptive responses in phytoplankton (Long *et al.* 2007). By responding to cues that reliably predict future conditions, plants can anticipate risk and behave preemptively.

CONDITIONING AND MEMORY

One of the hallmarks of animal behaviour is that behaviours are influenced by experience and learning. Previous experience also greatly influences plant behaviour through conditioning. Note that the term 'conditioning' implies learning associated with a particular favourable or unfavourable outcome to an animal behaviourist, but has no such connotations in the lexicon of the plant biologist. I use the term 'conditioning' to mean the reversible changes in behaviour (plasticity) that have been altered by experience. Plant responses are shaped by the plant's own experiences (conditioning) or even by the experiences of its parents (preconditioning).

Our awareness of plant conditioning dates at least as far back as Darwin (1880: pp. 460–461), who observed that responses of cotyledons to light were influenced by their previous exposure. Many foraging decisions are affected both by current conditions and past experiences. For example, the growth of a clover branch depends upon its current neighbours and also upon the neighbours that it encountered over the past year (Turkington *et al.* 1991). Reproductive decisions are also affected by past events. For instance, some biennials respond to cues to flower only after they first experience a prolonged period of cold, known as vernalization. Recently, the genetic control of this process has been elaborated for winter wheat; prolonged exposure to cold inhibits the gene that represses flowering (Yan *et al.* 2004).

One of the hallmarks of animal immune responses is the capacity for immunological memory (Harvell 1990). Animals that recover from an attack respond more rapidly and effectively the second time that they encounter the parasite. Priming or conditioning is also proving to be common in plant responses to pathogens and herbivores. Plants that have been primed by an initial attack respond more rapidly and more effectively to a second exposure to that same pathogen or to a variety of novel attackers (Conrath *et al.* 2006). This phenomenon has been described for many plant species and appears to involve several different mechanisms

that are still not understood. Priming appears less costly than responses that change the plant resistance immediately after pathogen attack (Van Hulst *et al.* 2006).

Priming has recently been reported for plants attacked by herbivores as well (Engelberth *et al.* 2004). Plants primed by a previous attack became less suitable as hosts for herbivores than plants responding for the first time (Ton *et al.* 2007). Once plant workers became aware of priming, several groups rapidly reported it from their systems although the sensitizing agents responsible for the effect appear to be species-specific (reviewed by Ton *et al.* 2007). Priming may also be involved in plant responses to a variety of other stresses such as drought and salt (Conrath *et al.* 2006).

These examples involve plants responding more quickly and more strongly when they themselves have experienced an attack. There is also evidence that the maternal environment can influence the traits displayed by offspring. Maternal conditions that influence seed germination include CO₂ level, competition, day length, pathogen infection, nutrition, water stress, among others (Baskin & Baskin 1998). Maternal radish plants that had been damaged by caterpillars became more resistant themselves and also produced genetically distinct offspring that were less suitable for herbivores than seedlings from undamaged mothers (Agrawal *et al.* 1999a). Seedlings from mothers that had survived herbivory induced higher levels of glucosinolates and more trichomes following herbivory than seedlings from comparable control mothers. It is not clear how widespread preconditioning or maternal effects on plant behaviour will prove to be, although recent evidence indicates that plants also respond adaptively to the light environments experienced by their mothers (Galloway & Etterson 2007).

COMMUNICATION

Plants emit cues that cause other organisms to change their behaviours. They also respond to stimuli emitted by other organisms to alter their own traits. Workers in the nascent field of plant communication would benefit by agreeing upon a set of definitions and I offer a dichotomous key of terms that includes a comparison to definitions used in studying animal communication (Table 2). For communication to occur, receivers must respond rapidly to cues or stimuli produced by other organisms (emitters; step 1 in Table 2). Animal behaviourists have found this criterion to be insufficient because it includes so many phenomena and consider that it specifies an induced response but not communication. I will restrict my use of the term 'plant communication' to situations in which the emission or display of the cue is plastic and the response of the emitter is conditioned on receiving the cue (step 2 in Table 2). For

Table 2 A dichotomous key for plant communication

Does the cue cause a rapid response in a receiver organism?

1 No: not communication

1' Yes: induced response (proceed to 2)

Is emission of cue plastic and conditional?

2 No: receiver responds to environment, not communication

2' Yes: plant communication (proceed to 3)

Is emission of cue (signal) intentional and beneficial?

3 No: not 'true communication' *sensu* animal behaviourists

3' Yes: true communication

example, a plant is not necessarily 'communicating' with insect visitors if its appearance does not vary conditionally. In contrast, a plant is communicating when it alters its floral display in response to its circumstances and this causes visitors to respond accordingly.

Some animal behaviourists reserve the term 'true communication' to refer more narrowly to the intentional transfer of signals (rather than cues) that, by definition, benefit both the emitter and the receiver (step 3 in Table 2; Bradbury & Vehrencamp 1998). Workers have difficulty determining benefit or intent even for animals. Intent is impossible for plants (except in an ultimate or evolutionary sense) and this requirement seems overly restrictive. Some animal behaviourists have reached similar conclusions; for example, most of the communication that occurs within a colony of honey bees involves cues rather than signals (Seeley 1995). As such, I will use the term plant communication to refer to transfer of cues from one individual to another without any assumptions about intent or benefit for the emitter or receiver. The emitter may not have intended to communicate with the receiver and the emitter may benefit from the communication, experience no fitness consequence, or suffer as a result. The first step in studying potential communication involves determining what the cues are and how they affect responses in other organisms (steps 1 and 2). However, the most interesting questions involve determining how communication affects the fitness of the emitter and receiver (step 3) and students of plant communication should vigorously pursue this question.

Plants communicate with other plants, with their herbivores, mutualists, and parasites, as well as the predators and parasites of these interactors. Well-documented cues that plants emit include light quality and volatile chemicals. For example, both far red and blue light have been implicated in shade avoidance responses (Pierik *et al.* 2004). In addition, transgenic plants that were insensitive to ethylene were less responsive to shading, suggesting that volatile cues are also involved (Pierik *et al.* 2003). Two other volatile cues, methyl jasmonate and green leaf volatiles, have been implicated in plant responses following wounding although demonstrating the activity of any particular cue under natural conditions has been very difficult (Farmer & Ryan 1990;

Arimura *et al.* 2000; Kost & Heil 2006; Paschold *et al.* 2006). The precise cue has yet to be determined for most of the examples of plant communication that have been described.

As previously mentioned, plants respond to cues that indicate the presence of other individuals and develop a morphology that increases fitness in the competitive environment that they are likely to experience (Ballare 1999; Schmitt *et al.* 1999). Some plants also adjust their defences to develop a phenotype that matches the herbivore environment that they are likely to experience. For example, several species respond to volatile cues emitted by sagebrush neighbours that have been experimentally damaged by herbivory (Karban *et al.* 2000, 2004). Again, responding to such cues can be beneficial under some circumstances (Karban & Maron 2002). Although the benefits to plants that respond to reliable cues are easier to understand, it is also possible that damaged plants might benefit by emitting cues. Volatile cues emitted by damaged branches may allow sagebrush individuals to integrate their own defences (Karban *et al.* 2006) and reduce the germination of competitors (Karban 2007b).

In addition to influencing other plant organs or individuals, cues emitted by damaged plants are used by various eavesdroppers to adjust their behaviours. For instance, volatile organic chemicals emitted when plants are damaged by herbivores may alter the behaviours of herbivores that subsequently visit. There are many examples in which damaged plants became either less attractive to herbivores (De Moraes *et al.* 2001; Heil 2004b) or more attractive (Dicke & van Loon 2000) relative to undamaged controls.

As discussed earlier, plants that are under attack by herbivores release volatile cues that help predators locate and consume the herbivores and these cues may reduce plant losses to herbivory (Dicke & Sabelis 1988). In some cases, the plant cues that attract parasitoids are produced *de novo* and cannot be detected in unattacked plants (Turlings *et al.* 1990). Generally, artificial damage was not as attractive to the predators and parasitoids as actual damage by herbivores (Dicke & van Loon 2000).

Plants present cues that are used by their mutualists to provide beneficial services. Volatile and visual cues communicate the location, quality and abundance of nectar and pollen rewards for animals that visit flowers (Dobson 1994; Chittka & Raine 2006). Animals that visit flowers for these rewards may move pollen from one individual plant to another of the same species. Diverse groups of animals use these cues to adjust the amount of time they spend at flowers and to avoid flowers that will be unrewarding. These cues are also used by other plant visitors that rob nectar and consume floral tissue without necessarily providing pollination (Irwin *et al.* 2004). Plants may adjust their flowering strategies and the cues presented depending upon their pollination status (Paige & Whitham 1987; Weiss 1991;

Ladio & Aizen 1999; Nuttman & Willmer 2003). Many of the classes of behaviours listed in Table 1 have been found to be triggered by cues from other individuals in at least some instances. Essentially all plants produce cues that serve to communicate with other organisms, whether production of these cues has been favoured by selection or has been the incidental consequence of other processes.

CONCLUSION

Plant behaviours facilitate effective foraging, reproduction, and defence in a spatially heterogeneous and constantly changing environment. Behaviour is critically important in the struggle of plants to pass on their genes although we currently have a poor understanding of the consequences of most plant behaviours. The plant behaviours included in Table 1 are more widespread, more diverse, and more sophisticated than commonly acknowledged. Plants are capable of responding to complex cues that involve multiple stimuli. Responses show considerable specificity in terms of recognition and reaction. By responding to reliable predictive cues, plant behaviours often anticipate future environmental conditions. Plants also become conditioned by their past experiences and appear to have memories. Plants not only respond to reliable cues in their environments but also produce cues that communicate with other plants and with other organisms, such as pollinators, seed dispersers, herbivores, and enemies of those herbivores.

We are now realizing that plants display many of the behaviours that have been long thought to reside within the exclusive domain of animals. That this is possible is remarkable, particularly because plants lack a central organ to coordinate these sophisticated behaviours. On the other hand, plants have faced many of the same selective pressures as animals over evolutionary time. Like animals, they live in heterogeneous and varying environments. Presumably the same general selective pressures that favoured the evolution of animal behaviours also favoured the evolution of conditional, plastic plant responses to current and anticipated conditions. Decentralized responses that can occur at any meristem allow plants to exhibit behaviours that have outwardly converged with those exhibited by animals with complex central nervous systems.

This review reframes many of the examples from plant physiology and ecology as plant behaviours. Some of the ideas elaborated here overlap with those developed to explain phenotypic plasticity. By reconsidering these traits as behaviours, one goal has been to compare them with animal behaviours. Behavioural ecology as a discipline has been successful in aggressively erecting and testing optimality and adaptive hypotheses (Parker 1984; Reeve & Sherman 1993). This approach compares alternative behaviours or allocation decisions to determine which ones will persist in compe-

tion with the others. This approach has rarely been applied to plant behaviours. In an early and seminal work, Rhoades (1979, 1983, 1985) presaged many of the plant defences covered in this review by taking an adaptationist approach and asking how and where plants should respond. Animal behaviour has also pursued questions about the costs and benefits of particular behaviours for the individual displaying them as well as their consequences for other individuals. This very successful approach has rarely been applied to plant behaviours, although early attempts suggest that behaviour is likely to have important and far reaching consequences on plant communities (Callaway *et al.* 2003). In the future, plant biologists more generally would benefit by borrowing the techniques that have been developed over the past century to document and understand animal behaviour.

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