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Author(s): Jonathan Silvertown and Deborah M. Gordon

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A FRAMEWORK FOR PLANT BEHAVIOR

Jonathan Silvertown¹ and Deborah M. Gordon²

¹Biology Department, Open University, Milton Keynes MK7 6AA, United Kingdom

²Department of Zoology, University of Oxford, South Parks Rd, Oxford, OX1 3PS, United Kingdom

INTRODUCTION

The language of animal behavior is being used increasingly to describe certain plant activities such as foraging (28, 31, 56), mate choice (67), habitat choice (51), and sex change (9, 10). Furthermore, analytical tools such as game theory, employed to model animal behavior, have also been applied to plants (e.g. 42, 54). There is some question whether words used to describe animal behavior, such as the word *behavior* itself, or *foraging*, can be properly applied to the activities of plants.

In this essay we compare animal behavior and analogous phenomena in plants in an attempt to clarify the differences and similarities. Although the idea that plants behave is at least 40 years old (3, p. 3), it is still a little unorthodox. Is it legitimate to say that plants behave? One way to answer this question would be to use a consensus definition of behavior and decide whether plants meet the definition. Unfortunately no canonical, universally accepted definition of animal behavior exists. Textbooks on animal behavior and reviews of the subject rarely give a general definition of behavior or present a framework in which to organize different types. Behavior has instead been defined in sundry ways by zoologists, depending on the questions that the notion of behavior is used to address.

Animal behavior is sometimes defined in terms of movement. If this definition were accepted, it would be difficult to argue that plants behave in any but the limited ways that Darwin (13) described quite comprehensively over one hundred years ago. If definitions of animal behavior were restricted to actions involving movement, many obvious sorts of behavior would be

disqualified. When a hedgehog plays dead, rolling into a ball and remaining motionless, it is certainly behaving.

Here we use the term *behavior* to mean what a plant or animal does, in the course of an individual's lifetime, in response to some event or change in its environment. This definition of behavior overlaps with that of *phenotypic plasticity* where that term refers to an individual's response to its environment. Use of the term *individual* requires clarification when talking about plants because of their modular structure and widespread capacity for clonal growth. By *individual* we refer to the genet (sensu Harper, 31). Consequently, the plant behaviors we discuss may originate from the activities of plant parts at a number of levels of structural organization: the whole individual (genet), ramets, branches, or organs such as leaves and flowers.

Because the term behavior is open to so many interpretations, it is necessary to qualify our use of the term for plants by mentioning certain phenomena we do not intend to cover. Animals often live in coherent social groups, and the behavior of individual animals can sometimes be understood as a consequence of a particular social organization. We do not restrict our discussion of plant behavior to responses to abiotic change, but neither do we draw any parallels between animal social behavior and social organization in plants (34), if in fact such exists.

In considering the possibilities for complex plant behavior, it might seem important to distinguish between responses that are a necessary stage of developmental change, and those that appear analogous to purposeful animal behavior. Ethologists currently debate whether such a distinction is useful, even in the study of animal behavior (17). The problem is the impossibility of saying for certain whether an animal's action is deliberate and purposeful, or a necessary response to existing environmental conditions. Behaviorists hold that since it is impossible to know about the intentions of animals, it is best to avoid talking about intentional behavior; others have argued the opposite (27). Here we adopt a solution similar to the behaviorist one. By discussing plant behavior in terms of environmental stimuli and plant responses, we do not distinguish between a response that a plant can't help but make, and one that it makes by "choice" to achieve a particular goal. If a particular stimulus tends to produce a particular response, the question of whether the plant intends that response is irrelevant to our argument.

We discuss plant behavior in terms of its proximate, not ultimate, causes. We are interested in the function of the plant responses we discuss, but we do not consider how they evolve. The scheme presented does not organize behavior according to why it is adaptive.

Before examining *what* plants do, we must briefly consider *how*, morphologically, plants exhibit behavior.

BEHAVIORAL PHENOTYPES IN PLANTS

Most plants have a modular, iterative growth pattern that develops from growing points of undifferentiated and totipotent tissues: the meristems. This modular construction makes plants inherently capable of altering the phenotype in the lifetime of an individual. It confers an open-ended pattern of growth, allowing plants to change the number, size, morphology, type, and location of new organs as they are produced (5a). If plants can be thought of as behaving at all, this is largely what makes it possible (3, 28, 30, 31).

Many plant species show changes in the structure of leaves or other organs that are produced successively. Such morphological changes were named *heteroblastic development* by Goebel (25). Perhaps the commonest form of heteroblasty occurs in leaves (for examples, see Allsopp: 1, 2). In most cases such changes seem to depend on age, though the role of plant size and of environmental cues has rarely been investigated experimentally and the function of the changes remains obscure.

A consequence of modularity is that the behavioral phenotype of an entire plant must be built up of qualitative differences between nodes bearing different organs. The morphology of a plant therefore places constraints upon the types of behavior available to it, depending upon whether new plant structures accumulate, as do the branches of a tree, or are shed, as in the yearly shoot growth of many grasses. In plants with nonaccumulating organs, behavior tends to involve qualitative changes in structure rather than quantitative changes in the ratios of organ types. This distinction is easiest to see in the way plants adjust their sexual phenotype. For example the gender of an individual plant of *Arisaema triphyllum* is determined by the sex of the inflorescence born by its single, annually produced shoot. The plants may change sex from one year to the next, but no scope for quantitative changes in gender exists (39) because shoots do not accumulate.

In plants with accumulating organs, the gender of a whole plant is determined by the relative proportions of male and female flowers. Qualitative changes in the kind of modules being produced (e.g. from male to female flowers) bring about a quantitative change in the gender of the whole plant. For example, wild cucumber (*Echinocystis lobata*) produces only male flowers at the beginning of the growing season, but nodes produced later are successively more likely to bear female flowers (55). The gender of the entire plant changes with season, and at any one time can be described quantitatively in terms of the ratio of male/female flowers.

The canopy architecture of many woody plants lends itself to developmental changes in a plant's activities and provides an example of quantitative change produced by accumulation. A common architectural plan

involves a distinct dimorphism between *long shoots* which bear lateral branches, and more ephemeral *short shoots* which do not. Long shoots of two types occur in many species: (erect) *orthotropic shoots*, which branch in three dimensions, have radial symmetry, and are often nonflowering; and (more-or-less horizontal) *plagiotropic shoots* which have leaves arranged in one plane and often bear flowers (29, p. 48 ff). Changes in canopy shape and in the reproductive behavior of the whole plant as it develops may result from changes in the relative rates of production of the different kinds of shoot. Jones & Harper (35) studied the development of meristems within the canopy of *Betula pendula* and found that the presence of a close neighbor raised the rate of bud mortality and lowered the production of long shoots, thereby inhibiting the development of the canopy in the region where a neighbor was present. The converse of this situation occurs where a tree invades an adjacent empty space by producing a long shoot which develops a crown of its own (15).

A CLASSIFICATION OF BEHAVIOR

We are interested in classifying behaviors in order to examine the distinction between animal and plant activities. Organizing behavior along a continuum from the less to the more sophisticated is a useful way to describe what plants can do, and what animals can do that plants cannot. Using this approach, we classify a wide range of plant and animal activities on two axes.

The first axis ranks the type of environmental stimuli to which organisms respond. It is called the *sensibilities* axis because we wish to emphasize the sensitivity of an organism to aspects of its environment. The second axis classifies *capabilities*—the ways in which the responses are expressed.

Note that both axes refer to properties of the organism. The “sensitivity to” axis classifies the aspects of the environment that the organism can respond to. The “capability” axis classifies the responses that the organism can make. The axes represent a continuous gradient from the less sophisticated to the more sophisticated. To provide examples, we discuss five steps along each axis. This defines a matrix with 25 cells. Each cell corresponds to a type of behavior. The matrix defines a “behavior space,” in which less sophisticated behavior is clustered in the upper left, more sophisticated behavior in the lower right.

Our working definitions for the categories of sensibility and capability are given in Table 1. In Table 2 we have given some examples of how various plant and animal activities, ranging from plant etiolation to directed vocal displays in monkeys, might fit into this scheme.

Below, we briefly consider the characteristics and limitations of each grade of plant capability in turn (growth, irreversible change, flexible change, etc)

Table 1 DefinitionsSensibilities

Magnitude The organism can respond to the magnitude of some environmental variable.

Gradient The organism is able to respond to the magnitude and direction in space of some environmental variable.

Temporal change The organism can detect a change over time in an environmental variable.

Alternatives The organism can distinguish between a limited set of states of some environmental variable, e.g. self / non-self, kin / non-kin, or between food / non-food.

Pattern The organism can detect a configuration or set of relations among objects or events.

Capabilities

Growth An increase in the amount of an organism's tissue.

Irreversible change A permanent change in an organism's behavior or morphology.

Flexible change A variable and reversible change in an organism's behavior or (in plants) in the morphology of successively produced organs.

Signal The ability to transmit information.

Reply The ability to transmit information, in response to information received from another.

and work across the corresponding row of capabilities/sensibilities in Table 2. Where we cannot find any plant examples, appropriate animal cases are given in brackets.

EXAMPLES OF CAPABILITY/SENSIBILITY COMBINATIONS IN PLANTS

Growth

Growth in plants is characteristically modular. Large plants tend to have more modules than smaller plants, though the size of modules may also vary. Light quantity and especially light quality are responsible for the control of many developmental processes (32).

GROWTH IN RESPONSE TO MAGNITUDE This is the simplest combination of sensibility and capability. It is exemplified by the etiolation response to shading, in which the internodes on a stem lengthen. A quite different, and unusual, phenomenon which falls into this category is described by Ganeshiah & Shaanker (23) who found that pollen tube growth on the stigmas of *Leucaena leucocephala* was inhibited until seven pollen grains had been deposited on them.

GROWTH IN RESPONSE TO GRADIENT This cell refers to growth in response to spatial variation. Tropisms allow plants to respond to directional stimuli. Plants exhibit tropisms in response to light, gravity, and touch. Roots and shoots may respond differently to the same stimuli, and branches bearing

Table 2 Combinations of sensibility/capability illustrated by examples of plant activities [or of animal behavior where no plant cases are known to us]. The dotted line in the Table shows the boundaries of plant behavior.

<i>Capabilities</i>	Magnitude	Gradient	Sensibilities to Temporal change	Alternatives	Pattern
Growth	Etiolation	Photo-tropism	Photo-periodism	Self-incompatibility	[Imprinting]
Irreversible change	Breaking of seed dormancy	Fern gameto-phyte sex determination	Semelparous reproduction	Facultative semelparity in <i>Ipomopsis aggregata</i>	
Flexible change	Leaf pubescence in <i>Encelia farinosa</i>	Habitat choice in <i>Ambrosia psilostachya</i>	Seasonal seed dormancy; heliotropism	Induced defenses; heterophylly in aquatics	[Animal habitat choice]
Signal	Fruit ripening in <i>Hamelia patens</i>	[Territorial display]	Flower color change in <i>Ipomopsis aggregata</i>	Flower color change in <i>Oenothera drummondii</i>	[Dominance displays]
Reply			[Parental response to developmental stage of offspring]	[Appeasement]	[Directed vocal displays in free-ranging primate groups]

reproductive organs may be positioned differently before and after seed set (e.g. *Viola* spp.). Phototropism of shoots is virtually universal, but in some cases the aerial parts of plants respond negatively to light gradients (skototropism). Skototropism in seedlings of *Monstera tenuis* causes them to grow toward tree trunks that are potential supports (59). The petioles and main stem of ivy *Hedera helix* have opposite reactions to light. The stem bends away from light, while the petioles bend towards it (32). Darwin (14) observed that tendrils of *Bignonia capreolata* were skototropic, entering fissures in the surface of a support he provided for the plant. Darwin's book on climbing plants contains a wealth of examples of plants responding to touch.

Shoots of the herbs *Mimulus Tilingii*, *Lamium purpureum*, *Stellaria media*, *Veronica hederifolia*, and *Anagallis arvensis*, among others, grow horizontally at low temperatures but vertically at high temperatures (47, p. 61). These appear to be cases of gravitropism modulated by temperature, but this possibility requires experimental verification.

GROWTH IN RESPONSE TO TEMPORAL CHANGE This cell refers to growth in response to temporal variation. Photoperiod is a cue to environmental (seasonal) change and triggers growth and flowering responses in many plants. The sensitivity of plants to light may itself be photoperiodic with a photophil phase during which exposure to light stimulates a response, and a skotophil phase in which light is inhibitory (32). *Long-day* and *short-day* species respond differently to photoperiod, but the behavior of these two kinds of plant involves the same combination of sensibility/capability. The herb *Halogeton glomeratus* produces two kinds of seeds, depending upon photoperiod. Under long days the plant grows indeterminately and produces dormant seeds with no specific dispersal mechanism. Under short days the plant produces nondormant, winged seeds and becomes determinate in growth pattern (66).

GROWTH IN RESPONSE TO ALTERNATIVES The behavior of *Bignonia cap-reolata* described by Darwin falls into the category of growth in response to alternatives. Skototropic tendrils of this vine that did not encounter a support turned vertically downward toward the plant's own stem, around which they curled, providing it with additional stiffening and support.

Self-incompatibility systems in plants involve the chemical recognition of the alternative states: self/nonsel. Nonsel and nonkin pollen grains are able to achieve fertilization which results in seed development (loosely *growth*). Such systems have evolved independently many times in the Angiosperms and provide a very reliable means by which a plant can avoid inbreeding.

GROWTH IN RESPONSE TO PATTERN We have found no examples of this behavior in plants.

Irreversible Change

We include in this category only cases where a whole plant (genet) undergoes an irreversible change. It is characteristic of plants that only a limited number of changes are irreversible: Seed germination and semelparous reproduction are the most obvious. Irreversible changes in growth form with age or size of plant are not uncommon, but these usually seem to be developmental processes not affected by the plant's environment. Further investigation of individual cases might prove otherwise. (See the example of *Cymopterus longipes* below).

IRREVERSIBLE CHANGE IN RESPONSE TO MAGNITUDE The breaking of seed dormancy involves radical physiological changes that make germination irreversible, once begun. In plants of mesic and arid environments mechanisms prevent seeds germinating until some threshold quantity of rain has fallen—e. g. germination inhibitors in the seed coat are progressively leached.

An irreversible change of growth form in response to temperature is described by Werk et al (63) in *Cymopterus longipes* (Umbelliferae). When soil temperatures rise, the plant bodily raises its rosette of leaves above the soil surface by the elongation of the region between root and shoot (the caudex). This response can apparently occur in plants of any size or stage of growth.

IRREVERSIBLE CHANGE IN RESPONSE TO GRADIENT Sex determination of fern gametophytes appears to be a rare example of this behavior. In laboratory culture the female gametophytes of many ferns produce a diffusible antheridogen which induces the formation of antheridia in small, undeveloped prothalli nearby (6). Some evidence suggests this also happens in the field (62). Schneller (52) reported that female prothalli of the ferns *Athyrium felix-femina* and *Dryopteris felix-mas* produce an antheridogen which stimulates the dark germination of spores that give rise to male gametophytes. Assuming that the antheridogen produced by a female gametophyte spreads into the surrounding soil by diffusion, it must form a concentration gradient that determines whether or not a spore germinates. Spores stimulated to germinate in this way produce male prothalli, so both germination and sex determination appear to be irreversible changes in response to gradient.

IRREVERSIBLE CHANGE IN RESPONSE TO TEMPORAL CHANGE The switch with shortening photoperiod from indeterminate to determinate growth in *Halogeton glomeratus* causes the death of the plant. Reproduction in many semelparous species sensitive to photoperiod also falls into this category.

IRREVERSIBLE CHANGE IN RESPONSE TO ALTERNATIVES Though environments vary in a continuous fashion, plants may respond as if this variation offers only two alternatives. Scarlet gilia *Ipomopsis aggregata* appears to distinguish between two degrees of pollination: full pollination and pollination that results in less than 30–40% of fruit being set. In the first case, it is semelparous; in the second, it perennates. There appears to be a difference between altitudinal populations in the ability to respond to whether pollination has occurred or not (44).

Seeds of many ruderal plants sensitive to the spectral quality of light (ratio of red:far-red) may have dormancy induced in them by the shade of a canopy of leaves. Although the physiological response to R/Fr is a quantitative one, in practice it allows seeds to sense the presence/absence of other plants in their immediate vicinity and to germinate when a canopy is absent.

IRREVERSIBLE CHANGE IN RESPONSE TO PATTERN There are no known examples of plants responding to a pattern. In the examples we have found,

plants respond to environmental stimuli that can be viewed as magnitudes, gradients, or alternatives. [Imprinting is an example of irreversible change in response to pattern in animals: An individual responds to a particular pattern of behavior, such as the movements and vocalizations of a large, nearby animal, often its mother, by acquiring a lasting attachment to that animal. The response may include a tendency, when the animal is young, to follow the imprinted object, and attempts to mate with animals similar to the imprinted object when the animal reaches reproductive age.]

Flexible Change

As already remarked, plants owe many of their behavioral capabilities to their modular construction. This is true of many flexible changes in plant phenotypes, but flexible changes also occur within modules themselves or affect the whole individual simultaneously. The opening and closing of stomata, and nyctinasty of leaves (see below), are examples of flexible changes within modules. The ability of resurrection plants (e.g. *Myrothamnus flabellifolia*, *Chamaejasme intrepidus*) to become dessicated and then to recover on wetting, and dormancy changes in buried seeds, are two types of flexible change affecting whole plants that do not involve modularity.

FLEXIBLE CHANGE IN RESPONSE TO MAGNITUDE Many vines radically change their growth form in response to light availability. In New Zealand forests *Rubus cissoides* is a scandent, but in conditions of high light intensity it produces no leaves or flowers and remains in a vigorously growing juvenile state with prickly stems (12, p. 139). The Mexican vine *Ipomoea phillomega* behaves in the reverse fashion, producing long stolons and no leaves in the forest understory, but leafing out and producing an ascending shoot when it encounters a light gap (45).

Plant behavior like that shown by *I. phillomega* has been equated with foraging in animals. In a computer simulation model of the growth of stoloniferous plants in a heterogeneous environment, Sutherland & Stillman (61) showed that plants that branched more or produced shorter internode lengths in resource-rich patches than in resource-poor ones had a greater efficiency of resource capture. In a review of the literature Sutherland & Stillman (61) found that internode lengths were actually greater in resource-rich than in resource-poor conditions in only 7 out of 16 cases, but branching probability was greater in resource-rich conditions in 13 out of 14 cases.

Changes in branching frequency and internode length purely in response to the magnitude of local resource concentrations are sufficient to generate the search paths followed by foraging clonal plants (61). Plants that exhibit a sensibility only to *magnitude*, could possibly track a *gradient* (see below).

Many desert plants change the structure, spectral characteristics, or orienta-

tion of leaves in response to drought and insolation (19). To give just one example: As soil water availability declines, the new leaves produced by the shrub *Encelia farinosa* are increasingly pubescent and reflective.

The leaves of *Machaerium arboreum* (Leguminosae), a neotropical liane, are thigmonastic, lowering themselves 50° from their normal daytime horizontal position when they are tapped lightly for 10 to 20 seconds, or when they are struck by heavy rain. This response speeds the drying of the leaf surface. The leaves are insensitive to light rain and to weak stimuli such as alighting insects (16).

Freeman et al (22) found that *Atriplex canescens* changed sex between one season and the next. Female plants became male following an unusually cold winter, drought, or heavy seed set. Such reversible sex changes in plants seem to reflect the current growth rate of individuals.

Many aspects of reproductive function in plants appear to vary with plant size, which may itself reflect the quantity of available resources (36). So, for example, the annual woodland herb *Floerkea proserpinacoides* produces, at the third node on its stem, either an axillary flower or an entire branch bearing many flowers, depending upon light availability and its own size (57). Amphicarpny is a rare but taxonomically widespread reproductive syndrome, represented in 10 different plant families. Plants produce small, nondormant aerial seeds and larger, dormant subterranean ones. The ratio of the two types varies with the size of plant; an increasing number and proportion of aerial seeds are produced by larger plants with access to more resources (11).

FLEXIBLE CHANGE IN RESPONSE TO GRADIENT *Ambrosia psilostachya* is a rhizomatous plant of saline environments in the Great Plains of the western United States. Salzman (51) grew plants in pots with a salinity gradient and found that most rhizomes developed toward regions of low salinity. Furthermore, rhizomes were longer in plants growing in saline soil than nonsaline soil. Salzman described this phenomenon as "habitat choice." Very similar behavior by *Glechoma hederacea* in response to gradients of soil nutrients has been described by Slade & Hutchings (56) who regarded the phenomenon as foraging (see above). As already mentioned, plants that appear to track a gradient may be able to do so by purely local responses to magnitude. Experiments are needed that differentiate between plant sensitivities to magnitude and gradient.

FLEXIBLE CHANGE IN RESPONSE TO TEMPORAL CHANGE Flexible change occurs in response to diel and seasonal environmental change. Examples of the diel response are heliotropism in leaves of *Tropaolum majus* (32), in the leaves of desert plants (18), and in the flowers of sunflower *Helianthus annuus* and arctic species. The sleep movements (nyctinasty), especially common in

the leaves of legumes, are an example of a flexible change controlled by a circadian rhythm entrained by light. In some nyctinastic species (e.g. *Albizzia julibrisin*) leaves fold upward at night and in others they fold downward (e.g. *Desmodium gyrans*) (32). The leaves of *Machaerium arboreum* are nyctinastic as well as thigmonastic (16). The flexibility of all these changes is due to the ability to move the organs in question, and not to modularity.

Seasonal changes occur in the responsiveness of the buried seeds of many annuals which exhibit cyclic changes in their dormancy state (5). The phenology of plants is characteristically correlated with seasonal environmental change (46). Leaf deciduousness (8) is perhaps the most radical response to a seasonally changing environment and is a flexible change according to our definition (Table 1). *Erica multiflora*, *Escallonia rubra*, and *Myrtus ugni* are evergreen plants which, at the end of the growing season, produce reduced leaves that enclose and protect the apical bud over the winter. These leaves do not develop to full size later, when the plant returns to the production of ordinary leaves (47).

FLEXIBLE CHANGE IN RESPONSE TO ALTERNATIVES: The vines *Synгонium triphyllum* and *Monstera tenuis* alter their leaf and stem morphology, depending upon the substrate. While climbing, the plants produce successively larger leaves until they reach the top of the supporting tree. At the top, internodes become successively longer, and leaves become successively reduced on the descending stem (48, 49). Flexible change between morphologies suited to climbing and those suited to descending are a common feature of climbers in the Araceae (7). The amphibious herb *Polygonum amphibinum* also alters its morphology, depending upon its substratum (41).

Aquatic plants such as the crowfoots *Ranunculus* subgenus *Batrachium*, which encounter the interface between air and water, have submerged and floating leaf types with distinctive morphologies that match the two alternative environments. In one group of crowfoots the change between leaf types occurs in response to water level itself, but in another it is elicited by a photoperiod that correlates with seasonally changing water level. The latter group of plants are more correctly classified under "flexible change in response to temporal change" in our scheme.

Herbivore damage induces chemical changes in *Betula pubescens* that retard the growth of caterpillars feeding on the plant (33). Where such a response to damage is not confined to the parts of the plant that have been attacked, there is good evidence to argue that the plant has inducible defenses that fall into the category of flexible change in response to alternatives.

The well-known thigmonastic response of *Mimosa pudica* is triggered by even a slight touch (50) and as such is more appropriately classified as a

response to alternatives (touched/not touched) than, like thigmonasty in *Machaerium aboreum*, to the magnitude of a stimulus.

FLEXIBLE CHANGE IN RESPONSE TO PATTERN No plant example is known (see section, Irreversible Change in Response to Pattern). [Habitat selection in animals provides an example of flexible change in response to pattern: Responding to a pattern of stimuli corresponding to a suitable site to nest, feed, hibernate, or rest, the animal carries out the appropriate behavior. If the site becomes unsuitable, the animal will find and use a new site.]

Signal

Plants transmit visual and olfactory signals that are exclusively directed at animals, but only a few cases are known to us where a signal from a plant is varied in response to external conditions (see below). Other kinds of signal, not considered here, occur in response to developmental changes: for example, the changes in fruit color that accompany ripening.

Signals inherently correlate with other processes occurring in the signalling organism. This can make it difficult to tell whether an organ serves an exclusively signalling function. For example many plants produce a seemingly vast "excess" of flowers over fruits. Non-seed-producing flowers may function as males, or they may simply be a part of the whole plant's signal to pollinators (58). The claim by Baldwin & Shultz (4) that trees are able to communicate, if true, would point to the first example of an exchange of signals between plants; however, Fowler & Lawton (21) have seriously challenged the evidence.

SIGNAL IN RESPONSE TO MAGNITUDE A possible example of this has been reported by Levey (37) who studied the ripening and removal of fruits of the small neotropical tree *Hamelia patens*. Unripe fruit are green while ripe ones are black. Although fruit are produced in all seasons of the year, rates of removal by birds are seasonal. Fruit ripen and become attractive to birds faster when some fruit are removed than when all fruit are left on an infructescence. Consequently, more ripe fruit are presented to birds when dispersers are abundant than when they are scarce. The removal of fruit commonly stimulates growth in plants (53). The mechanism by which *H. patens* modulates its signal to birds appears to be a case where a behavior has evolved by the simple enhancement of a common physiological response. This is analagous to ritualization in animals, when behavior such as locomotion that did not originally have a communicative function eventually acts as a signal.

SIGNAL IN RESPONSE TO GRADIENT No plant example known. [Territory marking in animals provides an example of signal in response to gradient: In

response to a gradient of a scent that identifies the ownership of a territory, an animal places a scent-marker that constitutes a further signal about territory boundaries.]

SIGNAL IN RESPONSE TO TEMPORAL CHANGE A seasonal change occurs in the flower color of Scarlet gilia, *Ipomopsis aggregata*, which is attended by different pollinators at the beginning and the end of the flowering season (43). Flowers of many species open and close on a daily cycle. In some cases this may be to protect the flower rather than to modulate the signal to pollinators, though a number of species, e.g. *Silene noctiflora*, are pollinated by nocturnal visitors and are scented more strongly or exclusively at night.

SIGNAL IN RESPONSE TO ALTERNATIVES The only cases of this kind of plant behavior known to us are the changes in flower color that occur in some entomophilous species following pollination (26). For example, Eiskowitch & Lazar (20) showed experimentally that flowers of *Oenothera drummondii* changed from yellow, which was attractive to moth pollinators, to red-orange which was not, either when nectar was withdrawn from flowers or they were pollinated. They suggest that by signalling which flowers have already been visited and are unprofitable to pollinators because they have been drained of nectar, plants increase the proportion of flowers pollinated.

SIGNAL IN RESPONSE TO PATTERN No plant example known. [Dominance displays in animals provide an example of signal in response to pattern: In response to a pattern of stimuli associated with a particular individual and the dominance status of that individual, an animal's behavior signals others about its own dominance status.]

REPLY No plant examples are known. [Animal communication relies upon replies to various forms of signal; see Table 2.]

DISCUSSION

We equate behavior with phenotypic plasticity that is expressed within the lifetime of individuals. Phenotypic plasticity becomes important in heterogeneous environments. Levins (38) argued that the kind of plasticity an organism should evolve depends on two factors: the organism's range of tolerance, and the scale of environmental change. If the environment fluctuates well within the range of an organism's tolerance, the optimum strategy is a fixed, intermediate phenotype. If environmental conditions fluctuate rapidly outside the range of tolerance, the organism should also settle on a fixed

phenotype, adapted to the most typical environmental conditions. But if environmental conditions change slowly and are sometimes outside the range of tolerance, evolution favors a mixed strategy, giving the organism the ability to change its phenotype to accommodate to different environmental conditions.

In discussing the responses of plants to the latter type of environmental heterogeneity, Lloyd (40) distinguished two kinds of phenotypic plasticity: (a) "Labile phenotypes" and (b) "conditional choices." The first corresponds to behavior that would be included in the row of cells in Table 1 from "Flexible change in response to magnitude" to "Flexible change in response to temporal change;" behavior of the second type would be classified in the *Alternatives* column. Lloyd (40) and Sultan (60) review phenotypic variation in plants in order to consider the evolutionary consequences of different types of variation. While we have only considered behaviors that appear to be functional, our scheme is not an evolutionary one.

Much of the plant behavior shown in Table 2 can be seen as a response to coarse-grained temporal changes in the plant's environment, from the long-term changes in light intensity which lead to etiolation, to induced defenses elicited by persistent herbivory. Climbers provide many examples of plant behavior because their growth habit causes them to traverse the heterogeneous vertical and horizontal structure of forests.

Most plant behavior requires some kind of growth, and the result is that the things that plants do generally take a long time. Animal behavior is usually faster. Plants have evolved responses to changes in conditions that persist. Many of the things that most plants can't do, but most animals can, happen quickly, e.g. reflexes, escape, arousal, attack, and recognition.

The other obvious limitation to plant behavior involves the central processing of information. Plants tend to control their behavior using locally mediated responses, as in the examples described above of facultative fruit ripening in *Hamelia patens*, flower color change in *Oenothera drummondii*, and branching in *Betula pendula*.

Plants have a limited ability to synthesize disparate stimuli, cannot recognize patterns, or store a memory of a recognized pattern. Although photoperiodic responses may superficially appear to involve these abilities, if photoperiod is regarded as a pattern, the photoperiodic response in plants actually only involves a measurement of the length of the night. However, it is notable that a photoperiodic cue received by one branch of a plant can induce flowering in another which has been kept in a noninducing environment.

Many of the most interesting plant behaviors can be classified under flexible change in response to magnitude and may occur in situations where plants experience growing conditions which vary in time or space. In some

cases there appears to be a correlation between the size of a plant and its behavior, such as size-related sex change in *Arisaema*, but in others, for example, *Atriplex canescens*, a change in growing conditions appears to trigger a response. Many plants, particularly semelparous perennials, appear to have a size threshold for reproduction, but the correlation between size and behavior is not as close as is sometimes suggested (64). Growth and assimilation rates correlate with size of plant, and we suggest that these may be more important variables than size per se in controlling changes in plant behavior.

We could find few cases of irreversible change in response to a gradient. Only a limited number of plant activities are truly irreversible; of these, spore germination is one. In ferns spore germination does appear to respond to a gradient. A near-example is shown in the downslope orientation of shoots in the forest herbs *Disporum languinosum*, *Polygonatum biflorum*, and *Smilacena racemosa*. These plants have shoots that arch away from the base of the plant. This branch structure, and their downslope orientation when growing on a hillside, appear to increase light capture and to reduce the biomechanical costs of overtopping other understorey herbs (24). Shoot orientation appears to be a response to a light gradient, rather than to gravity, and is probably irreversible for the shoot, but not for the genet. In general, it is difficult to see why an irreversible response to a gradient should ever be favored in plants. For example, roots growing towards water can grow in another direction if the distribution of water changes. There would be no obvious advantage to giving up this ability, which is a consequence of plant modularity.

Although little studied, many cases exist of visual and olfactory mimicry in plants. Weins's review (65) contains many examples of plant signals that elicit a response from animals and of cryptic coloration or morphology that conceals them from predators. Though none of these signals or concealments appear to be modulated by the environment, and therefore fall outside our definition of behavior, so little is known about plant signals that there may well be plant behavior involving mimicry & crypsis awaiting discovery.

The biological limits to the range of plant behavior have not been systematically explored. The dotted line in Table 2 shows the boundaries of plant behavior according to the scheme we have adopted. It would be useful to explore whether plants can occupy the cells directly outside the dotted line. It seems likely that further experiments will extend these limits.

Our two-dimensional classification (Table 2) cannot describe situations where plant behavior is modulated by a third variable, such as in temperature-modulated gravitropism in certain temperate herbs (see above). Furthermore, behavior cannot be definitively described simply on the basis of the sensibility/capability involved in generating them. How a plant sensitive to photoperiod responds to this cue may depend upon its nutrition, size, age, and of course, whether it is a "short-day" or "long-day" species. Indeed, the

sensibility/capability classification of behaviors is useful precisely because it is based upon the general phenomena that make behavior possible, and not on the particular ways in which organisms use their senses and abilities. We hope that by analyzing the activities of plants in this way, more examples of plant behavior will come to light.

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