Plasticity comparisons between plants and animals

Concepts and mechanisms

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This review attempts to present an integrated update of the issue of comparisons of phenotypic plasticity between plants and animals by presenting the problem and its integrated solutions via a whole-organism perspective within an evolutionary framework. Plants and animals differ in two important aspects: mobility and longevity. These features can have important implications for plasticity, and plasticity may even have facilitated greater longevity in plants. Furthermore, somatic genetic mosaicism, intra-organismal selection, and genomic instability contribute to the maintenance of an adaptive phenotype that is especially relevant to long-lived plants. It is contended that a cross-kingdom phylogenetic examination of sensors, messengers and responses that constitute the plasticity repertoire would be more useful than dichotomizing the plant and animal kingdoms. Furthermore, physicochemical factors must be viewed cohesively in the signal reception and transduction pathways leading to plastic responses. Comparison of unitary versus modular organisms could also provide useful insights into the range of expected plastic responses. An integrated approach that combines evolutionary theory and evolutionary history with signal–response mechanisms will yield the most insights into phenotypic plasticity in all its forms.

Introduction

Phenotypic plasticity is the change in phenotype (morphology, physiology, development, behavior) or extended phenotype of an organism depending on changes in its biotic or abiotic environment. In an earlier review,1 I addressed the issue of whether plants and animals differ in phenotypic plasticity. In that review, I attempted to demonstrate the range of plasticity exhibited by plants compared to that in animals, and to show how most sensory modalities employed by animals were also employed by plants. I also suggested that the most appropriate comparison between plants and animals was between plants and photosynthesizing, colonial, sessile invertebrates. Since that review, significant progress has been made in investigations of plant responsiveness to stimuli, calling to question the value of creating dichotomies in the ways organisms (plants or animals) are viewed.

Therefore, in this present review, I will avoid previously cited literature and discussion, and will present an integrated but eclectic update of some of these investigations, especially those that deal with whole-organism signaling in plants and sessile colonial animals. Furthermore, I will present these results within the framework of evolutionary ecology, since an understanding of plasticity and of an unchanging phenotype can only be relevant within an ecological and evolutionary context.

The Conceptual Framework for Plasticity Strategies

In a seminal paper, Grime2 presented an outline of three fundamental adaptive strategies in plants (competitive, ruderal and stress tolerant) in relation to the two axes of stress and disturbance. Stress was defined as a set of external constraints limiting rate of biomass production, e.g., drought or temperature extremes. The competitive strategy occurred in environments characterized by low disturbance and low stress, the ruderal strategy in low stress and high disturbance environments, while the stress-tolerant strategy was evident under regimes of low disturbance and high stress. Most importantly, in this schema, competition for light, water, nutrients, and space was not only viewed to be inter-dependent, but above- and below-ground interactions (i.e., the root–shoot axis) were also considered. Grime2 arranged these strategies along the classical r–K life history continuum with the ruderal (R) strategy being the most r-selected, the stress-tolerant (S) being the most K-selected, and the competitive strategy (C) occupying the mid-point between these extremes. Within this framework, the concepts of C-, S- and R-selection were developed. Grime2 located C-, S- and R-plants within a model describing equilibria between competition, stress and disturbance, and predicted life history and growth characteristics of plants with these strategies. These characteristics ranged from the morphology of the shoot, to leaf forms, leaf and plant longevity, as well as reproductive phenology and reproductive allocation. Thus, for example, C-selected plants were predicted to have high spread both above and below ground, while R-selected plants were expected to be small and with limited lateral spread. Ruderals were most likely to be annual herbs, while long-lived trees were most likely to be stress-tolerant. In this way, a useful conceptual framework to evaluate plant adaptations...
was erected. More recently, Grime and Mackey\textsuperscript{3} amalgamated the ideas of Bradshaw\textsuperscript{4} on phenotypic plasticity with this adaptive scheme to make predictions about plasticity responses of \( C \)-, \( S \)- and \( R \)-selected plants.

In this merged perspective, morphological plasticity via rapid root and shoot meristematic growth could be expected in \( C \)-plants when presented with pulses of resources, while these same responses would be slower and smaller in magnitude in \( S \)-plants, and \( R \)-plants could respond morphogenetically as well as developmentally to stress by diversion of available resources to reproduction. In contrast, cellular acclimation or physiological plasticity is expected to be more prevalent in long-lived \( S \)-plants.\textsuperscript{3} This framework of considering plasticity in relation to heterogeneity of resource availability can lead to important predictions regarding matches between coarse- or fine-grained resource distributions and expected plastic responses. For example, competitive, dominant plants may be relatively insensitive to fine-grained resources (light or nutrients) which are, by contrast, relatively easily exploited by understorey, so-called subordinate plants that conduct more precise fine-grained foraging.\textsuperscript{3,5}

The location of shoot meristems may also determine the nature of responses, e.g., aerial meristems may allow for more continuous monitoring of light environments and more precise foraging for light in broad-leaved plants as compared to grasses in which the meristems are often basal and consequently far removed from the light environments of the subtended leaves.\textsuperscript{5} However, the location of meristems may have been selected for by other pressures, such as protection from grazing herbivores. Thus, the range of present plastic responses appears to be constrained by past as well as present selection pressures. Roots also monitor resource availability in their foraging strategies. In long-lived dicots, root components are long-lived. However, these long-lived roots also produce shorter-lived fine roots that can continuously track fluctuating resources. This is in contrast to shorter-lived monocots which appear to produce fine roots constitutively and indiscriminately near the soil surface.\textsuperscript{3} Therefore, in the case of root foraging also, trade-offs between foraging scale and required precision are evident.\textsuperscript{3,5,6}

The concept of size-symmetrical and size-asymmetrical competition in plants and its relationship with morphological and physiological plasticity,\textsuperscript{7} although controversial,\textsuperscript{8} has added a further theoretical dimension. In size-asymmetrical competition, a resource must be pre-emptable and its capture should be disproportionate to the size of the resource-gathering components. This can happen in the case of light capture when taller canopies garner a disproportionate amount of light relative to shorter plants and also deprive other plants of light availability.\textsuperscript{8} This type of asymmetrical competition is best handled by morphological plasticity in which growth tropisms or shade-avoidance responses, for example, can be effective in resource capture. However, both morphological as well as physiological plasticity are likely to be jointly important in plants.\textsuperscript{9}

Plant phenotypic plasticity can also be limited by biotic as well as abiotic constraints.\textsuperscript{7} For example, herbivory can compromise the expression of an adaptive phenotypic response to competition for nutrients or light or both of these resources, or plastic responses to light availability may be constrained by low water availability. Furthermore, plasticity in allocation between growth, reproductive and inactive meristems needs also to be considered.\textsuperscript{10} Such integrated plasticity in meristem allocation has been found to be adaptive.\textsuperscript{11,12} Therefore, a variety of different stresses and constraints can interact to produce integrative effects on plant phenotype.\textsuperscript{13}

Additionally, the incorporation of longevity into the framework of plasticity is very important as it emphasizes the time scale over which fluctuating environments may be experienced by plants. Clonal plants can have very long lives, up to 11000 years in the creosote bush,\textsuperscript{14} exceeding the life span of most animals by at least 100 times. Plants can also, by clonal expansion, cover considerable areas, with descendants of certain meristems occupying huge spatial extents.\textsuperscript{15} Therefore, theories of plant resource acquisition strategies\textsuperscript{5,16} must consider variables such as longevity, clonal spread, and expected plasticity, in order to make meaningful predictions about their adaptive value. More importantly, theories that incorporate plasticity can also have important predictive value for determining plant community composition from the bottom up. For example, \( C_4 \) photosynthesis has been found to be less phenotypically plastic than \( C_3 \) photosynthesis,\textsuperscript{17} and this can have important consequences for the distribution of \( C_4 \) plants, especially under scenarios of global climate change. In this bottom-up view, limitations of plasticity responses may affect plant success to a greater extent than top–down control by herbivores or parasites.

Plasticity in sex expression and reproductive allocation has been a well documented phenomenon in both plants and animals.\textsuperscript{18-20} In keeping with the need to maintain adaptive responses over longer life spans, it was found that the majority of plants with labile sex expression were perennials.\textsuperscript{18} Such plants can change sex or even gender (differential allocation to male versus female function in monoecious plants, for example) in response to biotic and abiotic stresses. Furthermore, since some plants also depend on pollinators for movement of their genes, a mechanism to change floral display that is sensitive to fluctuations in pollinator abundance is an important adaptive strategy. High floral display could be important under conditions of low pollinator availability, while pollination-induced flower wilting and the resultant lowering of floral display prevents geitonogamy or self-pollination when pollinators are abundant.\textsuperscript{21}

In animals, as in plants, different types of plasticity may be expected. In animals, plastic responses can vary from very rapid (behavior) to slower ones involving morphological or physiological changes, which may even be reversible in some cases.\textsuperscript{22} Morphological plasticity in animals has been classified into constrained and unconstrained plasticity.\textsuperscript{23} Unconstrained plasticity appears to be coupled with continuous sensitivity and reactivity to environmental signals, greater longevity, system-level signaling as well as continually available somatic stem cells, and is characteristic of long-lived, sessile, plant-like basal phyla such as sponges and cnidaria. Plasticity is much more constrained in later-evolving animal groups such as insects and nematodes.\textsuperscript{23}

In both plants and animals, it is also important to determine under which conditions phenotypic plasticity may be favored over stochastic phenotypic switching. Plasticity requires both a sensor of environmental change as well as a response mechanism. The higher the frequency of fluctuations in the environment, the less costly would be the sensor. Thus, switching would be favored in an environment that changes less frequently compared to one in which perturbations are more frequent, when plasticity may be preferred.\textsuperscript{24,25} Similarly, programmed developmental change (e.g., heteroblastic in plants) will be favored over plasticity when there is predictability in the sequence of environments encountered by an individual.\textsuperscript{26}
Yet, not all plasticity is adaptive, and this must also be factored into the evolutionary context. Furthermore, some traits may be more plastic than others. Plasticity may also not only vary with ontogeny but may also constrain later developmental responses if exhibited early in ontogeny. Therefore, a much more integrated view of plasticity must be taken, across life histories, within organisms across developmental stages, and within organisms across traits. According to Sarkar and Fuller, the most important contribution made by Bradshaw to the concept of phenotypic plasticity was to suggest that plasticity itself was under genetic control. This means that plasticity is itself subject to natural selection, bringing the entire norm of reaction under the scrutiny of selection.

**Sources and Sinks: The Metabolic Imperative and Plasticity**

Redox control (one involving the reduction/oxidation state of signaling molecules) appears to be extremely important in clonal organisms, especially in the context of foraging for food and competition for space. When food is patchily distributed in space, the fitness of a colony of such organisms will be enhanced if there are suitable morphogenetic mechanisms that can respond to local variations in food supply or to the metabolic demands of competition. Selection should favor those morphogenetic mechanisms that can effectively perform this function. Redox control is considered as a potential reliable mechanism especially in colonial clonal hydroids. This can stimulate suitable patterns of polyp (food-gathering unit) initiation or stolon (vascular connection between polyps) growth. For example, sheet-like growth (closely-spaced polyps with short stolons) is adaptive in dense food patches (fine-grained environments), while runner-like growth (widely-spaced polyps with long stolons) would be more effective in sampling a habitat with widely spaced food resources (coarse-grained environments). Experimental manipulation of redox states of genetically identical hydroid colonies showed that treatment with azide (inhibitor of the electron-transport chain [ETC] complex IV) or antimycin A1 (inhibitor of ETC complex III), which shifts the redox state in the direction of reduction, produced runner-like growth, while treatment with dinitrophenol or carbonyl cyanide m-chlorophenylhydrazone (uncouplers of oxidative phosphorylation), which shifts the redox state in the direction of oxidation, resulted in sheet-like growth. However, conflicting results were obtained with rotenone (inhibitor of ETC complex I) and the electrophile avicin. Based on many such experimental manipulations, a role for reactive oxygen species (ROS) signaling in colony growth and morphogenesis in colonial hydroids was suggested, according to which mitochondria-rich epithelio-muscular cells at the polyp-stolon junctions serve to communicate between feeding polyps and growing stolon tips. Feeding polyps undergo gastrovascular contractions creating metabolic demands resulting in relatively oxidized mitochondria and low ROS levels which correlate with high rates of polyp formation and low rates of stolon growth. Reduced feeding will result in lower metabolic flux owing to fewer contractions, relatively reduced mitochondria, and higher levels of ROS, which are correlated with suppression of polyp initiation and stimulation of stolon growth. Thus, gradients of oxygen and of food resources couple with metabolic sensors to result in colony-level cell differentiation and adaptive morphogenesis that is appropriately vectorial, i.e., directional, especially for sedentary, long-lived animals.

There is currently burgeoning interest in the role of ROS and ROS sensors in prokaryotes and eukaryotes, including plants and fungi, in governing cellular activity, differentiation, and even sexual reproduction. Of the various ROS, hydrogen peroxide \( \text{H}_2\text{O}_2 \) appears to be best suited for signaling owing to its selective reactivity and diffusibility. Interestingly, NADPH oxidases (NOX) that generate \( \text{H}_2\text{O}_2 \) appear to be present only in multicellular organisms that need to differentiate multiple cellular types; however, whether NOX enzymes are linked to multicellularity has been challenged, and many NOX homologues have been found in protists, fungi, plants and animals. In plants, ROS signaling has been invoked in a variety of induced responses including defence, stomatal closure, root and pollen tube growth. In Arabidopsis thaliana, rhd2 mutants were found to have short root hairs and stunted roots; RHD2 was later found to be an NADPH oxidase. Furthermore, blocking the activity of this enzyme in wild type A. thaliana by diphenyleine iodonium (DPI) inhibited ROS formation, resulting in a phenocopy of Rhd2, while treatment of the mutant with ROS partly rescued the phenotype. Activation of Ca\(^{2+}\) channels by ROS was found to be responsible for these effects. ROS was also found to be localized at the tips of growing pollen tubes of Nicotiana tabacum; here too, ROS scavengers and DPI inhibited growth, while exogenous \( \text{H}_2\text{O}_2 \) rescued the phenotype. This mechanism of ROS production by NOX therefore appears to be a generalized mechanism in the growth of polarized plant cells.

Since redox gradients are local, and ROS probably act over short distances, it is possible to imagine that ROS signaling is important even in larger organisms within the context of certain short-distance resource gradients. It has been shown that redox signaling and ROS are involved in angiogenesis in animals in response to oxygen gradients. How other animal tissue types such as absorptive surfaces of gut villi or pulmonary bronchi respond to ROS and thus to local metabolic demands or gradients remains to be seen. ROS may also be involved in mediating symbiotic associations that require local growth form patterning, as in the control of fungal hyphae branching in a fungus–grass symbiosis.

Although plant roots respond to ROS, as indicated above, the impetus for plant root growth can be the sensing of local nutrients, such as nitrogen or potassium. Nitrate in the soil stimulates lateral root growth via the activity of the ANR1 gene, and this response can also be mediated by L-glutamate; similar morphogenetic effects are also seen for potassium-rich and -poor areas in the soil. Furthermore, nitric oxide (NO), which was first discovered as a diffusible second messenger mediating multiple functions in mammals, has also been found to be important for foraging in plants. NO is involved in auxin-mediated root organogenesis (growth of lateral and adventitious roots, root hairs, and gravitropism) in response to local nutrient conditions, besides many other processes, which also involve ROS in the containment of pathogens via the hypersensitive response.

**The Stem Cell and Modules: Aces Up Plastic Sleeves**

Unlike animals where most organogenesis occurs during embryogenesis, plants continue to produce organs throughout their life, which as mentioned earlier, can be many-fold longer than that of animals. In contrast with animals, in which epigenetic changes involving chromatin labels are effected during early development
phenotypic independence of modules was found in the branching of plants.63 Plant stem cells are similar to those in animals in that, when cell lineages are established, and where trans-differentiation between tissue types is a rare occurrence,62 chromatin remodelling leading to major epigenetic switches can occur throughout the life of plants.63 Plant stem cells are similar to those in animals in that the property of stemness is conferred on cells by their position in the stem cell niche. Removal of stem cells from the niche will result in other adjacent cells being programmed for stemness.64,65 However, animal stem cells age and may lose their potency over time66 with probably little scope for restitution to their original state. On the other hand, plants may undergo somatic embryogenesis from a single somatic cell62 as can several colonial, modular animal taxa.67

Therefore, a dividing line between modular and unitary organisms may be more appropriate than one between plants and animals.15 Modular organisms are those such as plants or colonial cnidaria that can exhibit indeterminate growth by iteration of multicellular parts or modules, while unitary organisms are those in which the zygote develops by a determinate growth process. Modular and clonal organisms such as plants also exhibit the unique feature of somatic genetic mosaicism.68,69 As a consequence of the longevity of plants, and their continuous production of meristems, spontaneous mutations that occur in the proliferating cells of the meristems are subject to selection, and can be preserved by hierarchical selection of modules as the plant grows.70 Furthermore, while the cells of annual plants may undergo the same number of cell divisions as those of a mammal, the cells of apical or axillary meristems of a long-lived perennial plant undergo many-fold more divisions,71 resulting in greater opportunities for intra-lineage selection. This intra-module selection contributes to the genetic heterogeneity and consequently the phenotypic heterogeneity of the individual plant. Also, since individual plant modules may be subject to individually variable light, water and nutrient environments, there is the possibility of variable responses by individual modules (e.g., sun-leaves versus shade-leaves; see later) within the same plant. Yet, the degree of phenotypic independence of modules is probably under whole-plant control,72 and may also depend on the type of vascular connections and resultant physiological autonomy of the modules.73 Similar phenotypic independence of modules was found in the branching coral Sylphora.74

It is also important to note that variation in cell size within the same plant tissue type can be striking. Furthermore, the occurrence of somatic polyploidy via endoreduplication of the genome is a regular feature in plants. Polyploidy may contribute to variance in cell size and also to responsiveness of the tissue to different environmental stimuli. For example, an increase in endoreduplication in Arabidopsis leaves made them more sensitive to shade but less sensitive to water deficits.75 There is also evidence that in plants, unlike in animals, organ shape or size is independent of cell number, implying a more global organismal-level control as well as complex links between the cell cycle and development.76,77 Such that cell division may even be viewed as a consequence of growth rather than its cause.76,78 The fact that plant cells are not independent entities since they are connected by plasmodesmata resulting in a supracellular organisation79 adds further possibilities of higher-level integration. Integration of the phenotype in plants, unlike that in most animals, is an extremely complex issue, one that is probably subject to several types of hierarchical influences including competition between modules.80

Polarity, Cell Continuity and Signaling

In animals, the cell cycle is completed by cytokinesis which effectively separates the descendant protoplasts. In plants, however, cytokinesis, when it occurs, results in the formation of a porous cell plate through which cytoplasmic continuity is maintained via plasmodesmata between descendant cells resulting in a symplast. While animal cells are usually naked, maintaining hydrostatic equilibrium and cell turgor by solute pumps, plant cells are enclosed by a rigid cell wall or extracellular matrix (ECM), that controls cell turgor. One of the consequences of this rigid ECM is that plant cells are relatively immobile, their positions are fixed within tissues, and thus multicellular plants can depend only on energy or nutrition that can enter the virtually sealed-off ECM by diffusion or in the form of electromagnetic radiation. Therefore, plants can make a living either by being saprophytic or autotrophic.78 Plant cells also have restrictions in their growth polarity, compared to naked animal cells, although some animal cells are strongly growth-polarized, e.g., neurons.81 Root hairs and pollen tubes grow only at their tips, while the end poles of most elongating cells of higher plants are non-growing although the rest of the cell periphery grows uniformly.81,82 This spatial organization of growth results in proliferation along the long axis producing longitudinal cell files. The fact that the end poles of these cells are also much more heavily traversed by plasmodesmata compared to the side walls, confers a longitudinal axis to the communication between cells, setting up a directionality and thus polarity to signaling.81-83

This polarity is vital for organizing the root–shoot primary and secondary axes, as well as growth in response to gravity, responses which are especially mediated by auxin (indole-3-acetic acid).84,85 In the case of gravitropism, the sedimentation of starch-containing plastids or statoliths in tissues such as the root cap and the shoot endoderm in response to gravity,86,87 is perceived by specific auxin efflux carriers which undergo appropriate subcellular relocation, resulting in local patterns of auxin distribution, and appropriately polar responses.84,88 Alternatively, a hydrostatic model of gravensing resulting in polar growth also exists.89 Such constraints and mechanisms related to growth have important consequences for plant responses to resource availability, especially those that involve morphogenetic plasticity.

Tensile and Plasticity Responses

A notable shift in understanding the responses of cells and whole organisms to their environments has been the inclusion of mechanical forces as regulators of this reactivity.90 Within this new framework of mechanobiology, the cytoskeletal elements (microfilaments, microtubules) of the organism receive information about the physical environments of various organismal entities (cells, organs, modules) and transduce an appropriate local or global response. This view of tensile (corrective responses to tensional forces) has enabled a signaling perspective that goes beyond molecules to a multidimensional perspective of the responsiveness of the organism to the environment.90 Transfer of mechanical signals across cell surface ECM receptors, e.g., integrins in animals and formins in plants, can result in chemical responses through distortions in cytoskeletal elements.90-92 Perception of mechanical forces can be vital in morphogenetic processes, as has been found for both plants and animals in various stages of development93 and for different...
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tissue types in animals, e.g., skeletal muscle, nerve cells, endothelial cells. In plants, particularly, there has been considerable interest in mechanoreception, and the involvement of the cytoskeleton–plasma membrane–cell wall interface, as well as stretch-activated Ca^{2+} channels. For immobile plants, sensitivity and responsiveness to the mechanical aspects of rain, wind, and touch, are important in eliciting their repertoire of plasticity; these thigmotactic, thigmomorphogenetic, and thigmotropistic (thigmotropic) responses are adaptive at various time scales and at hierarchical levels from single modules to whole plants.

Biomechanical plasticity can also be adaptive and may even contribute to the success of invasive species; for example, the scourge of Florida, the Brazilian pepper Schinus terebinthifolius adopts either a woody vine growth form in crowded, maritime forest habitats enabling it to overtop tall trees, or a sprawling shrub-like form with long lateral stems that overtop short saltmarsh plants in less physically crowded situations; this plasticity enables it to invade diverse ecological niches. These changes may be modulated by an integrated response to light signals and/or tensional forces derived from physical crowding.

The Light Environment

Plants make their living from the capture of light. It is, therefore, not surprising that plants have extremely sensitive mechanisms for perceiving and responding to changes in the light environment. Photosynthetically active radiation (400–700 nm), blue light, red: far red ratios, UV-A, and possibly also UV-B, are all detected and responded to by plants for various aspects of their growth and development. Importantly, plants are also able to exhibit tradeoffs in their responses to light cues vis-à-vis other impacts such as herbivory. For example, experimentally exposing Nicotiana longiflora plants to excess far red light (signal of the presence of competing neighbors) resulted in downregulation of the production of phenolic defence compounds compared to levels produced during herbivore attack; such plants in which the shade-avoidance response was provoked were more palatable to herbivores and rendered more vulnerable to herbivore attack. This differential response could mean that for shade-intolerant plants, such as Nicotiana, it may be more important to escape light-crowded environments than to allocate defences to herbivory. Therefore, while much data on gene expression levels (especially micro-array readouts) are accumulating on potential cross-talk between various pathways, it seems that strong ecological and evolutionary perspectives are needed to understand this complexity.

In another example which illustrates the need for a view that goes beyond mechanisms, plasticity in leaf life span in relation to altered light environments was demonstrated, with life span increasing with decreasing light intensity. The authors interpret this result to be due to slower leaf ageing resulting from slower photosynthetic rates and concomitant lower free-radical damage; however, from an evolutionary perspective, such a result also optimizes leaf construction costs in relation to carbon gain. A related intriguing hypothesis examines an evolutionary tradeoff between leaf size and leaf number in trees from the perspective of light-capturing units. Since each leaf is associated with a lateral, axillary meristem, it is suggested that smaller leaves and more numerous meristems may be more advantageous in more heterogeneous light environments as this trait would confer greater plasticity in terms of lateral shoot branching, leading to effective exploitation of a variable light resource.

Light capture can also occur below the water surface in plants. Underwater photosynthesis that occurs in flooded terrestrial plants is often accompanied by a change in leaf morphology to optimize underwater gas exchange as well as the ability to use dissolved HCO_3^- as an additional source of CO_2. The utilization of dissolved HCO_3^- in autotrophy has also been exploited in the symbiotic association between photosynthesizing algal dinoflagellates and cnidaria (a complete discussion of similarities/differences between plants, animals and plant–animal chimeras is, however, beyond the scope of this review). The changes in leaf morphology during flooding are similar to those occurring in semi-aquatic plants that exhibit heterophyllsy. In such plants, submerged leaves are thin, lack a cuticle and stomata, while aerial leaves are thicker, with cuticles and stomata. Furthermore, the morphological changes in response to light in terrestrial plants (sun- versus shade-leaves) are similar to those in submerged versus aerial leaves of heterophyllous plants. Also, at the mechanistic level, in the heterophyllous Ludwigia arcuata it was found that changes in the orientation planes and frequency of cell divisions rather than changes in cell width were responsible for the transition from elongated submerged leaves to spoon-shaped aerial leaves. Moreover, some of these changes could be mimicked by exposure to ethylene, which has been shown to be an important modulator of plant growth.

Using the Air: Volatile Signaling in Plants

Animals employ an impressive suite of volatile chemicals in response to stress, e.g., alarm pheromones released by worker ants in response to predation threat result in recruitment of other workers to the threat site. Plants also emit volatiles in response to herbivore attack. These volatiles serve to attract parasitoid predators of the herbivores. Additionally, neighboring unattacked plants eavesdrop on distress signals coming from herbivore-infested plants, and upregulate their own defence gene repertoire accordingly. 112-114 Plants can also employ volatiles in long-distance within-plant signaling, 114,115 the use of which can overcome vascular constraints on within-plant systemic signal transmission. A variety of biotic and abiotic stresses elicit volatile production. This volatile bouquet largely includes green leaf volatiles, terpenoids, methyl jasmonate, methyl salicylate, ethylene, and methanol. Furthermore, plants also release volatiles such as β-caryophyllene from herbivore-attacked roots which are used by soil entomopathogenic nematodes to locate their targets. 117 Parasitic plants such as Cuscuta are now also known, even at the seedling stage, to use the volatiles from their favored host plants to exhibit appropriate growth tropisms towards these hosts. The recent use of ‘mute’ plants (i.e., those in which key enzymes responsible for volatile production, viz. hydroperoxide lyase, have been silenced) has shown that the response elicited in plants receiving these ‘muted’ signals is different from that elicited by wild-type plants. Furthermore, research on ‘deaf’ plants (e.g., ethylene-insensitive mutants) has also shown the importance of volatile signaling in competitive interactions between plants. The utilization of mutant plants with an impaired volatile vocabulary promises much excitement in this field. However, this research is only just beginning, as is research on the cross-talk between the various defence pathways in plants modulated by volatiles such as ethylene.
Electrical Signaling in Plants

Like animals, plants are now also known to be able to transmit electrical signals rapidly and over long distances. Unlike in animals where Na⁺ and K⁺ pumps are involved, membrane potentials and self-perpetuating action potentials (APs) in plants are generated by Ca²⁺, Cl⁻ and K⁺ fluxes. Action potentials are transmitted rapidly along the length of sieve element cell files via the concentrated localization of plasmodesmata at cell poles (considered analogous to synapses in animals) and also laterally through plasmodesmata that occur between these cells, companion cells and parenchyma cells of the phloem. Slow and non-self-perpetuating variation potentials (VPs) (variable potentials) are also transmitted in xylem vessels apparently in response to local changes in hydraulic pressures and are, therefore, probably mechanotransduced. Physical wounding by herbivory as well as chemical elicitors from insect oral secretions can initiate these potentials at the site of the attack, and are probably very important in further elicitation of defence cascades. The reasons for two types of electrical potentials (APs and VPs) in plants are still being debated. However, the fact that electrical signaling occurs, that the animal neurotransmitters γ-aminobutyric acid (GABA) and γ-hydroxybutyrate (GHB) have been found in plants, where they may function as signaling molecules, and that endocannabinoid signaling in animals has similarities with n-acylthanolamine metabolism in plants, indicate that plants and animals are very similar in the ways they sense and react to the environment.

Whole Organism Signaling

Higher animals have evolved a closed circulatory system for inter-organ communication and whole-body signal integration, while in higher plants the vascular system is non-circulatory in nature. Still in plants, long-distance movement of signals occurs to achieve coordination between sources and sinks as in root–shoot–root signaling, or in the communication between leaf and shoot apical meristems. The xylem–phloem communication network, the symplastic milieu generated by plasmodesmata, cell–cell polar transport as occurs in auxin movement, and mechanotransduction via the cytoskeletal network, all contribute to signal–response integration. Systemic signaling was also considered as a possibility in response to excess excitation energy (i.e., photoexposure) resulting in systemic acquired acclimation. These results suggest interesting possibilities for coordinated responses in whole plants. For example, plants receiving above-ground herbivory relocated more carbon to roots, an effect that was found to be mediated by SNF1-related kinases. This response increased plant tolerance to herbivory as well as reproductive success by delaying senescence and prolonging flowering. Furthermore, this carbon relocation was found to be independent of the jasmonate pathway that is involved in most induced plant defences. At the level of the whole organism, intra-organismal competition also occurs in plants and some modular colonial animals, endowing them with the ability to select and proliferate those organs or modules most suitable for survival, growth or reproduction under the prevailing conditions. Often, such selection can only occur if signals about resources such as light, water, and nutrient availability (resources that are not easily stored) are integrated with physical stimuli such as gravity, temperature, and mechanical stresses, to ensure adaptive morphogenesis.

Genomic Instability in Response to Stress

An important aspect of flexible responses to changing environments could also involve concomitant genetic and epigenetic changes. In bacteria, the so-called adaptive mutations are now known to be stress-induced via the SOS pathway in which the activation of special error-prone DNA polymerases leads to increase in mutation rates. Examples of stress-induced mutations in mice also exist. Local as well as systemic increase in homologous recombination were observed in Nicotiana tabacum plants treated with viral pathogen and with free-radicals indicating the systemic translocation of a systemic recombination signal (SRS). Moreover, progeny of such exposed plants also showed higher frequency of genome rearrangements as well as substantial changes in methylation patterns. In Arabidopsis, also, stress-induction by UV-C and the bacterial elicitor flagellin increased homologous recombination in at least four generations of progeny. Therefore, induced systemic increase in homologous recombination can also contribute to adaptive phenotypes within the life time of individual plants, which should be particularly important in long-lived taxa.

Plasticity Comparisons Between Plants and Animals: A Useful Exercise?

Although plasticity is exhibited by both animals and plants, it is possible that plasticity is more important than an unchanging phenotype for plants, and that this is a natural consequence of their immobility. Although the extensive tropisms shown by plants, both above- and below-ground, in response to resource availability, appear to be more flexible, plant tropisms are relatively much more limited than movements by animals of the same biomass. Therefore, plants need greater plasticity compared to mobile animals. Furthermore, plants are much more long-lived than animals. Whether longevity necessitates plasticity or whether plasticity confers longevity may, however, be debated. This is an interesting and important question that requires further examination across all organisms, including plant and animals.

Some similarities between how plants and animals respond to their environments are a result of ancestral relationships, others to convergences on similar solutions, while the differences are the result of independent evolution. Abundant evidence is accumulating for shared signals and cross-talk between plants and animals. Some similarities between how plants and animals respond to their environments are a result of ancestral relationships, others to convergences on similar solutions, while the differences are the result of independent evolution. Abundant evidence is accumulating for shared signals and cross-talk between plants and animals. The recent discovery of responses to the plant hormone abscisic acid in cnidaria and human granulocytes are examples of the conservation of signaling pathways between the kingdoms. The recent finding of a cryptochrome-mediated growth response to magnetic fields in Arabidopsis mirrors the magnetoreception compass in birds that is possibly cryptochrome-based. The huge diversity in morphology of galls produced by different plant-galling insect species on a single plant host species (an example of an extended phenotype) shows that insects can manipulate plant morphology in complex and specific ways via their gene transcripts, indicating a commonality of signal reception and response channels in insects and plants.

In conclusion, it seems that tracing the phylogenies of sensors, messengers and responses in the various kingdoms, rather than mere documentation of similarities and differences, is a more useful exercise. An integrated view of life forms and their responses to intracellular and extracellular environments, coupled with an evolutionary perspective on the fitness consequences of plasticity.
versus determinism, will result in more rewarding investigations and cross-talk between all students of the infinite variety of life forms on Earth.

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References

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