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Opinion

The Intelligent Behavior of Plants

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Plants are as adept as animals and humans in reacting effectively to their ever-changing environment. Of necessity, their sessile nature requires specific adaptations, but their cells possess a network-type communication system with emerging properties at the level of the organ or entire plant. The specific adjustments in growth and development of plants can be taken to represent behavior. Their ability to learn from experience and to memorize previous experiences in order to optimize fitness allows effective acclimation to environmental stresses and can be considered a form of intelligence. Intelligent behavior is exemplified by the exceptional versatility of plants to deal with abiotic stresses as well as microbial and insect attack by balancing appropriate defensive reactions.

Trends

Particularly in the past decade, there has been an ongoing debate whether plants exhibit 'behavior' and express 'intelligence'.

Definitions of 'behavior' and 'intelligence' vary. Intuitively we think of these terms as referring exclusively to humans, but essentially they describe the ability of organisms to respond to environmental challenges in such a way as to optimize fitness. Plants have similar properties.

Because plants are sessile, they have to cope with various types of biotic and abiotic stresses in their environment, and possess elaborate, dynamic mechanisms to adjust their growth and development accordingly.

Versatility of Plant Development

Earth is a blue planet. In the blue oceans, blue-green algae abound. The accepted view is that these algae were the first photosynthetically active organisms within the kingdom of plants and, through providing oxygen, changed Earth's atmosphere from a reducing to an oxidizing environment. From space the land masses on our planet look largely green (see 'What Color is Each Planet?'[i]). This supports the notion that plants are the predominant 'life force' that made respiratory metabolism and animal life possible.

Through a long process of evolution plants have become remarkably well adapted to colonize open terrain, with the exception of steep rocky slopes, shifting sand dunes, and icy environments. To take advantage of different climates, plants have diversified morphologically and physiologically. To be able to grow and react to changes in their local environment, they can acclimatize as sensitively as do animals and humans. Within the boundaries in which life is possible, they can deal with all types of adverse conditions, such as extreme temperatures or limited availability of water and nutrients, and vary their growth rates according to whether such factors are favorable or unfavorable. Plants can 'see' whether it is light or dark, react to the color, intensity, and direction of the light and measure its duration through the actions of phytochromes, phototropins, and cryptochromes. Thus, they are able to perceive the progress of the seasons, as well as the presence of neighboring plants that may outgrow them, and they adjust their growth rate and morphology accordingly [1]. Plants can 'smell' the volatile fragrances that are produced by other plants [2] of the same or different species in response to, for example, insect attack, as well as the gaseous compounds produced by root-colonizing microorganisms in the soil [3], and thereupon mobilize appropriate defenses to withstand such potential invaders [4,5]. Plants can 'taste' which nutrients are present in the soil and react with the development of more or fewer lateral roots [6]. They also taste and integrate the signaling via various chemical compounds that are produced in their different organs, as well as by microorganisms, plants, and animals in their surroundings (e.g., [7,8]). Plants adjust to the force of gravity and 'feel' touch and wind [9], as well as whether there are guiding or obstructing objects in their neighborhood. Tendrils oscillate to be able to adhere to other plants or poles, and plant stems and roots that

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 http://dx.doi.org/10.1016/j.tplants.2015.11.009

encounter a solid object grow around it if they cannot push it away [10]. Whether plants are also able to 'hear' is not clear. So far, only anecdotal information is available to support such an idea (see 'Sound Garden: Can Plants Actually Talk and Hear?'[ii]).

On the basis of these types of experiences, plants also 'learn' to react more effectively to various challenges and to habituate to repetitive signals. For instance, circumnutating passion flower (*Passiflora*) plants succeed better and better in finding the support of a pole that is being displaced many times [11,12]. Conversely, if a mimosa (*Mimosa pudica*) leaf is subjected to continuous irritation, it re-erects itself despite the stimulus that is still acting upon it (J.C. Bose, 1906, in [13]). Learning involves memory. Most bulbs and biannual plants need a cold period in order to flower in the following spring or summer. Vernalization is imposed in winter, but the resulting effect is expressed only months later. For other plant species, day length is the priming signal for flowering. If the day length is manipulated to forgo the inducing condition, exposure of a single leaf to the correct day length may produce a sufficient amount of the signal to induce flower formation [14,15]. The exposed leaf communicates with the meristems to convey the message that conditions for flowering are imminent. The plant remembers the inducing signal to be able to flower at the right time.

Another type of memory is the ability of any plant to defend itself more effectively against pathogens and predators once it has experienced a previous, non-fatal confrontation [16,17]. This acquirement remains latent and is expressed only at the time that attack does occur. This may be a few days or many months later. As a consequence of this acquired resistance, the attacker still harms the plant, but the resulting damage occurs later and is usually less severe, as symptoms are reduced. Apparently, as a result of the limited damage done by the first attacker, the plant has learned to defend itself more vigorously when attacked again, a phenomenon known as priming [18]. Recent evidence has demonstrated that priming for both biotic and abiotic stress resistance can be maintained in at least two subsequent generations [19–25].

Vernalization is the result of histone modifications that are reset in each generation, whereas DNA methylation is likely to explain phenomena in which stresses of various kinds trigger responses that persist for longer than the inducing stimulus [26]. Such epigenetic mechanisms have the potential to store information over time and may act as a molecular memory and provide a basis for Darwinian evolution independently of DNA sequence changes [27].

Mechanisms of Plant Behavior

In their natural habitat, plants are often exposed simultaneously to both biotic and abiotic stresses. To high or freezing temperatures, inundation or drought, excess or UV light, and toxic chemical compounds plants may acclimatize in similar ways as to pathogens and predators in order to reduce or circumvent the expected damage. For instance, cold hardening allows plants to survive freezing temperatures to which non-hardened plants would succumb [28]. Defense against biotic stresses is mediated primarily by the effects of the signaling compounds salicylic acid (SA), jasmonic acid (JA), and ethylene (ET), whereas acclimation to abiotic stresses is mediated mostly by abscisic acid (ABA). There is very extensive and remarkably powerful crosstalk between the signaling pathways, such that the effects of biotic and abiotic stresses may at times enhance or counteract each other [29–31] (Box 1). In nature, both types of stress often occur simultaneously, as do attacks by both pathogenic microorganisms and insect pests. Under such conditions, the plant has to prioritize which type of defense is most appropriate. It does so remarkably well, as evidenced by the common observation that wherever one looks plants abound. It appears that each plant species is specifically adapted to effectively deal with the diversity of extant stresses imposed by the environment. There are relatively few microorganisms that can cause disease on a specific species – most plants are resistant to most pathogens – and species adapted to different climates are relatively tolerant to abiotic conditions that are deleterious to non-adapted species.

Box 1. Crosstalk between Signaling Pathways in Plant Growth and Defense

To survive, plants need to optimally allocate resources to growth and defense. Recent results in plant genomics have shown that hormone signaling networks involved in growth and defense are interconnected (Figure I), allowing plants to invest in growth under favorable conditions or in defense when attacked [64,65]. For instance, ABA optimizes water use efficiency by regulating stomatal aperture during growth and, at the same time, acts as a switch in defense against herbivorous insects in plants that have been primed for JA-dependent defenses as a result of prior attack leading to water loss [66]. Depending on the type of attacker, different hormonal signal signatures have been revealed [67], resulting in the activation of distinct sets of transcription factors that act as amplifiers in defense signaling cascades. In non-infected leaves of fungus-, bacteria- or virus-infected plants, the ensuing priming against further infection entails only limited fitness costs, which are outweighed by the enhanced resistance benefits under pathogen pressure [68]. Priming thus functions as an ecological adaptation to respond more quickly and more effectively to subsequent infection or attack. Moreover, by actively regulating their root secretions in the form of carbon-rich exudates, plants can attract a specific set of soil bacteria that colonize the roots, stimulate plant growth, and effectively protect plants against multiple types of belowground and aboveground attackers [5,38,69]. Crosstalk between SA-, JA-, and ET-dependent defenses and auxin-, gibberellin-, and cytokinin-dependent growth signaling pathways gives rise to multiple interactions balancing growth, development, and defense against biotic and abiotic stresses [29,64,65].

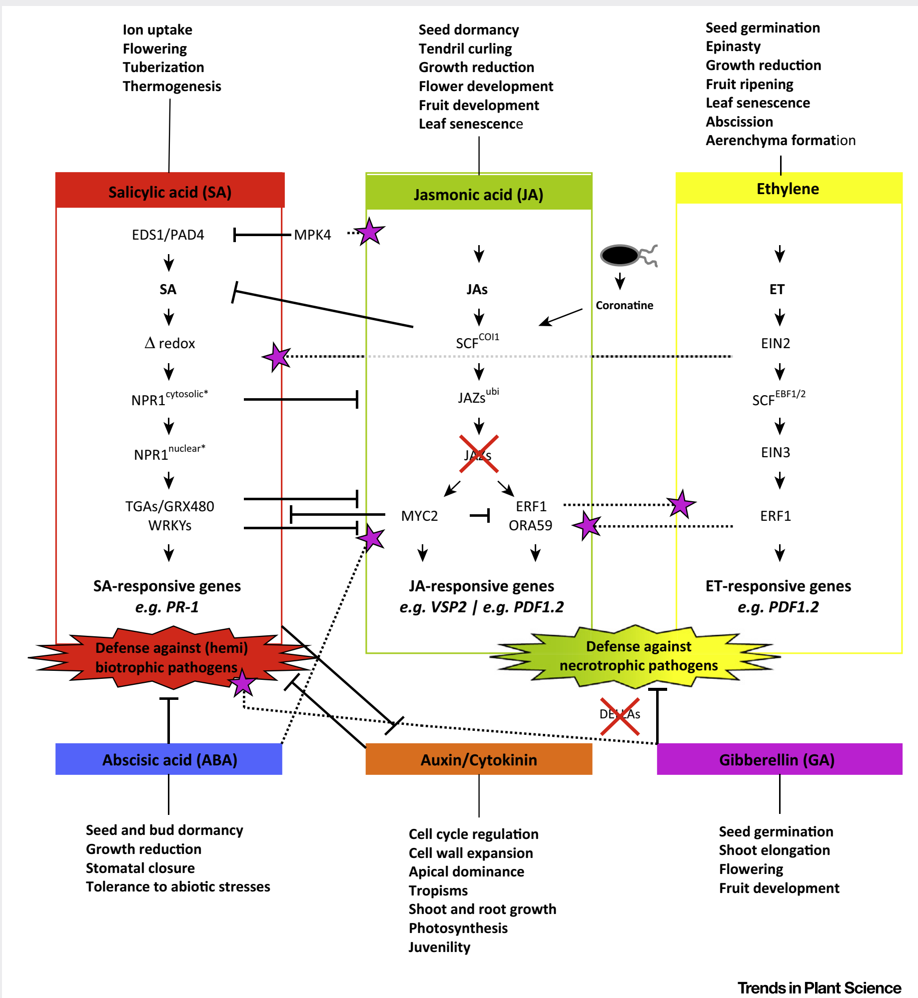

Figure I. A Scheme Depicting the Actions of the Major Plant Hormones Involved in Growth, Development and Defense, Highlighting Cross-Communication between Defense Signaling Pathways. The components within the defense signaling cascades originating from the actions of salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) are indicated, as well as their respective interactions in modulating the defensive response. T, negative effect; purple stars, positive effect. Pathogens may hijack specific pathways, such as the bacterium *Pseudomonas syringae*, which produces the JA mimic coronatine to suppress host immune responses and to promote virulence. For a detailed discussion of these pathways, see [64,65]. Adapted from Figure 6 in [29].

The remarkable ability of plants to deal appropriately with the challenges of the outside world has led Anthony Trewavas to make a plea to consider plants as intelligent organisms exhibiting complex behavior to solve the problems of their sedentary lifestyle [12,13,32]. He advocates that the terms 'intelligence' and 'behavior' are appropriate because they essentially refer to decision making about alternative pathways to be chosen in order to survive, grow, and thrive. The examples described above clearly illustrate that plants 'behave' in different situations; the matter of 'intelligence' requires further consideration, and applied to plants has provoked substantial debate. Of course, considering plants as intelligent beings depends essentially on how 'intelligence' is defined. If one concedes that intelligence is restricted to organisms with a complex nervous system, or more specifically a brain, it seems difficult to admit that plants can be intelligent. However, to coordinate their behavior, plants do communicate internally between their organs, as well as externally with members of the same and other plant species. In addition, they communicate with the microorganisms and insects that are present on, or visit, their leaves and roots [2,5,33–35]. Whereas plants, microorganisms, and insects above ground exchange chemical signals, below ground there are massive physical and chemical interactions with the resident microflora resulting in, for example, root colonization by mycorrhizal fungi and root nodule formation in legumes [36], as well as effects on plant growth patterns and leaf metabolome composition [37]. Growing roots avoid contact with neighboring roots of the same and often of other species but have to attract beneficial bacteria and fungi. Numerous complex chemical signals are exchanged between growing roots and the resident soil microflora, as well as between all of the root-colonizing fungi and bacteria themselves [5,35,38,39]. The mycorrhizal fungi aid the plant in supplying water and mineral nutrients, particularly phosphorous, and the bacteria produce plant hormones and confer protection against pathogens by providing the plant with antibacterial and antifungal compounds, as well as by boosting their defenses against both root and foliar attackers [35,36,38]. Moreover, mycorrhizal hyphae cross-colonize roots of neighboring plants of the same and different species, thereby allowing the exchange of chemical signals below ground from one plant to another [40]. Thus, integrative communication is as much a hallmark and a necessity in plants as it is in animals.

The nature of the internal communication of plants is primarily through low-molecular-weight chemical compounds, not unlike neurotransmitters in animals, as well as by the release of Ca^{2+} ions from inter- and intracellular stores [41–43]. Electrical activity is likewise evident in plants [44]. When a single leaf on a plant is wounded, this experience is shared within seconds with the rest of the plant [42,45]. In *Arabidopsis*, activation of glutamate receptor-like genes in response to feeding by the cotton leafworm, *Spodoptera littoralis*, induces the formation of JA at local and distant sites in the plant [46]. The receptors are structurally related to vertebrate glutamate receptors that are important for rapid excitatory synaptic transmission in the nervous system. In plants, electric signals are primarily transmitted through the phloem, seemingly like nervous signaling in animals. As once pointed out to me by Aart van Bel, the phloem is electrically insulated from the other tissues of the plant (cf. [42]). Sieve tubes with their companion cells extend to all parts of the plant, including the meristems. This conducting tissue allows action potentials to travel almost immediately to all cells. Although the term 'plant neurobiology' has been coined to study the processing of the information that plants gather from their environment [41], very little is known about the significance of electrical signals for their reactions. Nevertheless, it does seem clear that plants are as adept in communicating as are animals. The problem is that we cannot properly understand their language.

The Nature of Plant Intelligence

As discussed extensively by Trewavas [12,13], the coordinating centre of a plant is not some sort of brain, but rather located in each cell, and the individual plant is made up of a cellular network with emerging intelligent properties. Indeed, at the level of the cell, plants are the most complex and sophisticated organisms on earth. In addition to mitochondria, all green plants possess an additional organelle with its own genetic information: chloroplasts, which originate from blue-green algae. Almost all of the genetic material of the green plant progenitor has ended up in the nucleus and the cell nucleus now coordinates the production and the assembly of all chloroplast components by appropriately regulating and balancing chloroplast protein manufacturing from nuclear-encoded and chloroplast-encoded mRNAs. Moreover, plant cells share structural characteristics with neurons, which has led to the proposition that similarities exist in the cell–cell communication of plants and animals [47].

Another distinguishing feature of the plant cell is its wall, which provides structure as well as a barrier to outside influences. It also plays a crucial role in communication, as fragments set free during development or by the action of outside organisms inform the cell about its environment and function as elicitors of plant innate immunity [48]. The plant cell wall and innate immunity may be functionally equated with animal skin and the innate immune system of animals, respectively. Animal innate immunity was accidently discovered only after it had been investigated in plants [49,50] and lies at the basis of the adaptive defense responses of plants against fungi, bacteria, viruses, nematodes, and insect pests [51]. Indeed, antimicrobial peptides and proteins, as exemplified by the pathogenesis-related proteins of plants, have been found to be universally present in the living world and are considered to be an ancient and evolutionarily conserved defensive system already present as antibiotics in bacteria [52,53].

But what about the equivalent in plants of the adaptive immune system of animals? Specific antibody production and action requires the circulation of the blood and such a circulatory system is not present in plants. However, comparative studies of resistance genes in plants have shown that these genes contain many repetitive sequences that undergo frequent unequal crossing over during meiosis, thereby generating novel alleles that confer additional resistances to fungal, bacterial, and viral diseases, as well as insect and nematode pests [54]. Thus, it is not the individual plant that remains protected, but part of the population. During plant breeding for food, feed, fiber, and pharmaceuticals, the genetic basis for disease and pest resistance has been both inadvertently and deliberately narrowed to select for yield, taste, or activity. In nature, the distribution of resistance genes within a plant population is commonly far more diverse. Notably, higher animals do not produce as many offspring as plants can through the abundance of their seeds, leaving far more room for selection of fit individuals in plant populations than in animals.

Animals breathe air though their nose and ingest food through their mouth, both unique, localized organs. To transport gases and nutrients around the body, they rely on their blood circulation system. By contrast, in plants air is taken up through numerous stomata, nutrients are absorbed by a densely branched root system, and light as an energy source is harvested by all cells containing chloroplasts. Thus, one could consider the individual plant cell as a unit that is equivalent to an entire higher organism. Any green plant cell is fully able to take up air, absorb light quanta, and retrieve water from xylem vessels, and to deliver products of photosynthesis

Box 2. Innate Decision Making

Newell and Shanks [57] are critical about the existence of an intelligent cognitive unconscious and stress that most procedures for assessing awareness in humans are inadequate. Indeed, if our decisions are the combined result of our genetically determined character and our prior experiences, any test will be biased. Even newborn children carry epigenetic marks determined by the mother [70] and, hence, cannot be considered naive when it comes to behavioral decision making. Whether we, as humans, posses a free will is currently a matter of debate among neuroscientists and philosophers, with most neurologists maintaining that free will is nothing but the result of autonomous chemical reactions in our brains. Decisions may appear subjectively fast and effortless because they are made on the basis of recognition; that is, information stored in our memory. But, as a philosopher once explained to me, our free will comes into play when we consciously override our impulses by deciding *not* to follow this path. Could plants also do this? How can one prove that plants do not possess free will?

Figure 1. Portrait of a Mythical Figure Arising from Plant Leaves and Flowers: *La Primavera* by Giuseppe Arcimboldo, 1563, Real Academia de Bellas Artes de San Fernando, Madrid. Reproduced with permission.

Trends in Plant Science

Outstanding Questions

What is the relationship between electrical signaling (seconds) and chemical signaling (hours to days) in adjusting growth and development upon disturbance?

What is the role of mutualistic and symbiotic microorganisms on roots and leaves in regulating responses of plants to sudden disturbances? We know that they do so in the long term, but do they also affect plant early decision making and, if so, how?

Is the 'memory' of plants based uniquely on epigenetic mechanisms or dependent on lasting alterations in the chemical signaling network? How is 'memory' achieved?

and signaling compounds to the phloem. The cell reacts locally to incoming signals from within and outside the plant. For instance, when an invading pathogen is recognized (directly or indirectly) by a product of a cognate resistance gene, the cell dies, giving rise to a localized hypersensitive reaction. The rest of the plant plays no part in this interaction, but the dying cell does convey the message to all other plant parts, which thereupon acquire enhanced resistance, commonly referred to as systemic induced resistance [5,6,17,55]. Likewise, the switch to vernalization during winter is a cell-autonomous process [26]. The cell is part of a population of cells that interact in a community fashion, comparable with, for example, colonies of social insects. Such colonies are characterized by a division of labor among individuals. Similarly, plant cells in different organs have different functions, with the non-green ones being dependent on the green ones. Perhaps we should see a single plant not as an individual but as a community, each cell being equivalent to an individual animal. A plant cell is born by division of its progenitor, grows to a finite size, and dies as a result of senescence. The community of cells of a growing plant is extended by the addition of more cells derived from the meristems, it functions through a network-type communication system allowing division of labor between cells in different tissues, and it succumbs only when conditions end that allow it to flourish. Understanding plant life then requires a very different view of plant biology compared with that which we are used to (see Outstanding Questions).

It may still be advocated that intelligence is a property unique to human beings. However, colonies of social insects as well as communities of plant cells show emerging novel behavior to ensure fitness [13]. Several species of mammals and birds, as well as some lower animals, are known to use tools, an activity commonly thought to require intelligence [56]. As exemplified above, also plants exploit their environment appropriately and directionally and do so in flexible and dynamic ways. They have to make decisions how to overcome varying challenges. Even as they are unlikely to 'think', they commonly take effective action. As humans, we have the impression that we make decisions by consciously contemplating alternative strategies and choosing on the basis of weighing the risks and benefits. Yet, neurobiologists are coming to the conclusion that most of our decisions are made unconsciously up to a second before we think of them consciously. Our choices are the consequence of our unconscious nervous activity reflecting both our genetic make-up and our prior experiences [57] (Box 2). Plants do the same. Evolution has had a longer time to get the processing of information hard-wired in their genes than in animals that, in contrast to plants, are not sessile but must be able to roam around and take immediate actions. Apart from these characteristics, plant and human life do not seem to be so different after all. It is gratifying that Trewavas has described plants from this perspective by providing thoughtful examples and comments on how plants behave: according to intelligence defined as flexible adaptive information processing in order to optimize fitness under variable conditions [12,13,32], plants must be considered intelligent.

Studies of plant foraging behavior have shown highly selective adaptational responses to patchily distributed resources such as light and soil nutrients [58], thereby shaping the growth and development of the organism. Extensive heritable epigenetic variation in growth and morphology contributes substantially to variation in plant growth, morphology, and plasticity [27,59]. Plants not only possess memory as a characteristic of intelligence towards the past, but by integrating multifactorial environmental signals they can also anticipate ever-shifting conditions in a way that allows them to maintain adequate behavior in response to varying resource availability and the presence or absence of competitors and attackers. For instance, unstressed plants are able to perceive and respond to signals emitted by the roots of drought-stressed neighbors and via relay cuing elicit further stress responses in other neighboring plants [60]. Not only do plants distinguish between mechanical, insect, and pathogen-induced damage [58], but they also respond by releasing appropriate airborne volatiles and root exudates by which they communicate through belowground networks of mutualistic and symbiotic rhizosphere microorganisms [3,5,38,61]. Intra- and interspecies chemical signaling are likewise instrumental in determining the species composition of plant communities in different habitats [62]. These highly sophisticated and finely tuned adaptive strategies allow the sessile plant to react flexibly and adjust its growth and metabolism in a plastic fashion [13,27,59] as an image of a mind embodied in plant life [63] (Figure 1). Linking the external variation in the plastic behavior of plants to the internal molecular changes initiated through the integration of multiple signals from their local environment will be a challenging mission for the future.

Acknowledgments

The author thanks Aart van Bel, Corné Pieterse, and Tony Trewavas for stimulating comments.

Resources

[i] http://curious.astro.cornell.edu/about-us/58-our-solar-system/planets-and-dwarf-planets/planet-watching/249-what-color-is-each-planet-intermediate

[ii] www.livescience.com/27802-plants-trees-talk-with-sound.html

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