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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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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.