

# Plant Intelligence: An Overview

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*Plant intelligence is inextricably linked with fitness. Barbara McClintock, a plant biologist, posed the notion of the “thoughtful cell” in her Nobel Prize address. The systems structure of a simple nervous system is similar to those of individual cells. The plant root cap, acting holistically in responding to numerous signals, likely possesses a similar systems structure. Intelligent decisions are constantly required to optimize the plant phenotype to a dynamic environment, and the cambium is the assessing tissue controlling branch activity through root resource control. Spontaneity in plant behavior, the ability to count to five, and error correction indicate intention. Volatile organic compounds are used as signals in plant interactions and may be the equivalent of language accounting for self- and alien-recognition. Game theory describes intelligent competitive and cooperative interactions. Profiting from experience requires both learning and memory and is indicated in the priming of herbivory, disease, and abiotic stresses.*

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## What is intelligence?

Legg and Hunter (2007) collected some 70 different definitions of intelligence and summarized them as follows: *Intelligence* (a) is a property that an individual has as it interacts with its environment or environments, (b) is related to the agent’s ability to succeed or profit with respect to some goal or objective, and (c) depends on how able the agent is to adapt to different objectives or environments. These descriptions of intelligence apply directly to plant behavior and fitness.

In the same alphabetical order, (a) wild plants interact with and respond to their environment via competitive and other biotic and abiotic signals; (b) the goal or objective is fitness, with seed number as a fitness proxy—those most successful and therefore most fit provide more offspring; and (c) fitness depends on the skill with which individuals best adapt to their environment throughout their life cycles (McNamara and Houston 1996). Those individual plants that can master the problems of competition and master other biotic and abiotic stresses with greater plasticity, with lower cost, with higher probability, or more rapidly are fitter and, on this basis, are more intelligent. They have a higher probability of survival and a higher probability of collecting the necessary resources to provision seeds. Fitness is, however, inextricably linked to the specific environment in which it operates.

There are other descriptions of intelligence that are useful even though they tend to refer to similar kinds of behavior. Intelligence is a capacity for *problem-solving*, the commonest terminology used by psychologists (Sternberg and Detterman 1986). Those plants that solve their environmental problems—such as the problems described above—more

skillfully are fitter than others. Another older alternative is “profiting from experience” (Jennings 1923). This definition involves both learning and the ability to summon up the appropriate memory from the learning experience and use it in future situations to improve fitness. Learning results in the adaptation of the organism. Adaptive modifications improve survival, the accumulation of resources, reproductive potential, and therefore fitness. Finally, adaptively variable behavior during the lifetime of the individual is one I have used (Trewavas 2003) but again is similar to that of profiting from experience. Finally, the word *intelligence* itself derives from the Latin *intelegere*, “to choose between.” Many situations arise in the lifetime of the individual that require decisions when there are numerous choices available. Intelligent decisions are those in which the individual selects those choices that improve survival and, in turn, fitness.

**Plant intelligence is not new.** Frits Went was the discoverer of auxin, a major plant hormone. In 1937, he, together with Thimann, a student of his, authored the first book on plant hormones. Went and Thimann (1937) connected intelligence directly to fitness: “In tropistic movements, plants appear to exhibit a sort of intelligence; their movement is of subsequent advantage to them.” Even earlier, Von Hartmann (1875) stated about the control of leaf movement, “If one sees how many means are here to attain the same end, one will be almost tempted to believe that here dwells a secret intelligence which chooses the most appropriate means for the attainment of the end.” Moreover, von Liebig was quoted in Weaver (1926) as remarking, “Plants search for food as if they had eyes.” And Darwin (1880) argued, “The tip of the root having the power of redirecting the movements of the

adjoining parts acts like the brain of one of the lower animals receiving the impressions of sense organs and directing the several movements.” These statements were made by leading scientists all very familiar with plant behavior and coming to similar conclusions about its intelligent quality.

**What is plant fitness?** The description of intelligence above stated that intelligence is inextricably linked to the environment in which it is expressed. The reason for emphasizing that relation is that there are many environments, agricultural conditions, or experimental situations, for example, in which fitness and the need for intelligent behavior are minimized or absent. For wild plants (and wild animals), fitness is a complex system property. It is a dynamic network that is in continual flux, involving the individual plant whose structure continues to change throughout its life cycle. It is enmeshed in an environment constructed from a plethora of other developing plants and a horde of beneficial and damaging organisms and beset with a plethora of physical and chemical challenges that can change from minute to minute. This complex system acts holistically, incorporating both the individual and its environment. The two are not meaningfully separable (Trewavas 2014, Sultan 2015). In plants, added complexity occurs because there are two distinctly different environments, above and below ground, each with different problems that require intelligent mastery.

Darwin’s original concept of natural selection, which underpins fitness, involved overproduction, competition, and the survival of those most fit, enabling increased offspring numbers in the next generation. He did regard competition as the primary environmental feature. The view above builds on that of Darwin, emphasizing the inextricable link with all environmental features in fitness. However, Darwin also believed that fundamentally, selection occurred between individuals, not populations, as commonly assumed. So how those individuals behave (i.e., their spontaneity) is crucial to intelligent behavior.

The fight for resources can be fierce. Although the gathering of light energy and also minerals and water below ground are essential for survival, what is equally crucial is that their collection denies those resources to competitors. Those that can collect with greater speed, recognize more quickly richer sources, and exploit with greater efficiency are potentially winners in these respects. A single tree in a mature forest can produce a million seeds every year for centuries but can be replaced by only one.

But there is also competition for suitable mates, too—a subject Darwin never broached for plants. Much of the competition here depends on complex conversations between pollen and the potential partner parent on which it has landed. Virtually all fail not only from rejection and incompatibility but also from the limited number of ovules and therefore seeds that the parent is able to maintain. Even then, the conversations continue after fertilization: competition among embryos is common, leading to abortion or siblicide and further rejection if the genome of the embryo is too

remote or incompatible with that of the parent (Trewavas 2014).

A recognizable niche develops particularly below ground as the result of root activities. The secretion of numerous chemicals and enzymes modifies the soil structure and fertility and the populations of microbes and fungi that are in association. Aboveground conditions are more variable, but the exchange of information continues throughout the life cycle, a parameter which, in its entirety, is subject to selection (McNamara and Houston 1996).

**Behavior is the fitness platform.** As in other organisms, plant behavior is simply the response to signals. Changes in gravitational or mechanical force—including wind, abundance of light, water or minerals, a plethora of volatile and non-volatile chemicals, external temperature, and herbivory or disease—are all sensed and acted on. But the difficulty is that plant behavior is unlike that of most animals. When the first photosynthetic eukaryotic plants evolved, the accumulation of osmotically active sugars threatened to explode the cell. The evolutionary solution was the concomitant synthesis of a relatively rigid wall. The cell became encased in an effective straightjacket, whose constraint was only partially relieved when growth was needed. The rigid wall renders overall movement of the individual difficult, with only a few exceptions. Furthermore, because light was effectively ubiquitous, there was no evolutionary need to develop movement. Growth is confined in higher plants to local areas of cell division and expansion (mainly in meristems located in the extreme tips of roots and shoots). These areas are small, because a rigid wall in the remainder of the plant is needed to maintain its three-dimensional and often large form. Visible behaviors responding to changes in signals are therefore usually seen as changes in growth or phenotype. But growth in virtually all organisms is very slow, although with time lapse, it can be accelerated to a timescale familiar to us. There are numerous examples to be found on YouTube (e.g., [www.youtube.com/watch?v=CsjkNOEwFcl](http://www.youtube.com/watch?v=CsjkNOEwFcl)).

In contrast, most animals, with few exceptions, have to move to find food. The foundation of all food chains is based on green plants ensuring herbivory is inevitable. Animals predated each other drove the evolutionary specialization of sensory organs and muscles to move quickly and then finally of a specialized nervous tissue to rapidly connect information between the two. In time, these nerve cells became more clumped, communicating with each other and thus constructing a recognizable brain. This organ gradually assumed the assessment of information passing between senses and muscles and became a major,—but not the only—repository of learning and memory. They enabled the animal to profit from experience.

But the key question then arises as to how intelligent behavior can emerge in organisms without a brain.

**Self-organization is one key to fitness.** Self-organizing systems are common in biology; social insect colonies and the

human brain are good examples (Trewavas 2007a). In a self-organizing system, there is no overall plan that governs its construction. Instead, organization emerges from the bottom upward via intensive communication or other interactions between the system constituents. As the system increases in size, the characteristics of communication change with increasing numbers of long-range signals and more complex negative feedback and feedforward. The whole process is akin to a Markovian sequence in which each event provides the platform for the next.

Every individual plant is a product of self-organization. From the fertilized cell onward, the communication between this cell and the surrounding parent tissue determines the characteristics of the first cell division, and subsequent divisions continue the communication between the cells changing with size and shape. Internal communication in plants involves proteins, peptides, small and large RNAs, oligosaccharides, hormones, numerous volatile and nonvolatile chemicals, and carbohydrates; minerals and water act as internal signals, too. Known rapid, long-range signals use electrical changes and calcium waves (Mousavi et al. 2013, Choi et al. 2014).

Higher plants are modular, with repetitions of leaf plus bud and root tips below ground. Modular construction is an evolutionary device to ensure rapid increases in size and height—the result of intense competition for both light and soil resources. Distributed control is a characteristic of self-organizing systems; local signals lead to local responses, but in the context and with reference to the whole system. This is most obvious in terms of shoot- (or root-) branch formation, which can be induced in response to local light or locally applied chemical signals (e.g., Denny and Stanton 1928). The problem in trying to understand fitness is that each individual plant phenotype is strongly environment dependent, and any specific phenotype is not obviously heritable except in the potential for plasticity through bud numbers and primordial roots. It is that potential and the ability to take the most effective advantage of the environment in its entirety that provide the necessary platform for becoming locally the most fit individual. Intelligent behavior that gives the edge over others increases the survival and reproductive chances against those less able.

**Why is plant intelligence controversial?** Because human beings are animals, two criteria are commonly and misleadingly used to assess the potential presence of intelligence in other organisms. The first is that intelligent behavior should be easily recognizable operating on the same timescale as ourselves. The human timescale reflects simply the speed of action potentials in the nervous system. Organisms without a defined nervous system, like plants operating on a different timescale, are therefore eliminated from the intelligence family. Animal behavior is easy to see and reported with pencil and paper. Plant behavior is not: Half is below ground, for a start. But the behavior of that part above the soil can only be observed with special measurements either in the

laboratory or greenhouse and recorded over long period of time or with the use of time lapse.

The second reason is that the present human environment, certainly in Western countries, is no longer one that operates on classical fitness, which depended on stern competition over food and mates, the overproduction of offspring, and the large-scale death of those less fit. Instead of the life-or-death decisions that must have faced early humans, in which intelligent capabilities really mattered to their survival, intelligence is limited to educational achievements in their broadest sense and not directly altering offspring numbers. It is this failing that causes the most controversy, because the real benefits of intelligent behavior, in one sense, are trivialized and the crucial benefits no longer obvious.

### Brains are not needed for intelligent behavior

The simplest approach to answer the question of whether brains are essential to intelligent behavior is to examine the behavior of those without a brain. This section asks that question of single-celled organisms. If they exhibit intelligent behavior, then plants composed of billions should at the minimum have the same potential.

**McClintock's thoughtful cell.** In 1984, Barbara McClintock, a plant biologist, was awarded the Nobel Prize. In her acceptance speech, she made the following statement, oft repeated: “A goal for the future would be to determine the extent of knowledge the cell has of itself and how it uses that knowledge in a thoughtful manner when challenged” (McClintock 1984). The response to “challenge” is behavior, and “thoughtful” responses are intelligent behavior; they also contain the implication of consciousness. Knowledge of itself also implies self-recognition. From a biography, we know that her knowledge of plant behavior was extensive and that the statement made above was not made lightly but with an awareness of what it meant. McClintock's linking “cell” with “thoughtful” was a far-sighted appreciation and knowledge of the actual capabilities of single cells.

**The intelligent capabilities of single cells.** It is only necessary to indicate one well-established example; others are dealt with elsewhere, including the obviously intelligent *Stentor* and those that construct houses around themselves (Hansell 2011, Trewavas 2014). *Physarum polycephalum* is a slime mold, a multinucleate coenocyte that survives on ingesting detritus found in its environment. Its movement (i.e., the growth of the organism) requires time lapse to bring its behavior into our timescale. Recent research has shown the following: (a) When presented with a maze with four different routes separating two pieces of food, the organism chooses the shortest route. It optimizes the ratio of energy output to energy gain (Nakagaki et al. 2000, 2004). (b) If that route through the maze involves a region that is detrimental (e.g., strong light), it avoids that route and takes the alternative but still shortest route available (Nakagaki et al. 2007). *Physarum* can assess the balance of risk between detriment

to itself and the need to gain food. This is a situation of choice and decision, and the decision in this situation is beneficial. (c) When presented with 11 different kinds of food, it selects only the one that best provides for its known nutritional needs after sampling the others. Clearly, an assessment was made against internal criteria of balanced nutrition. Again, when provided with choice, the decision made is beneficial to itself (Dussutour et al. 2010). (d) Small electrical shocks cause a temporary cessation of growth. When given three shocks separated by the same time interval, it reacts to an unprovided fourth shock by a temporary cessation of growth. It has learned and remembered the time interval between unpleasant circumstances (Saigusa et al. 2008).

These behaviors strike immediately as intelligent, they certainly provide for survival, and by optimizing energy outlay against gain, they provide in due course for more offspring when conditions demand it. But intelligence is a comparative behavior: It is those cells that accomplish these behaviors faster, more efficiently, and more exactly, giving greater offspring numbers, that can claim to behave more intelligently than others. It is not just the behavior itself, striking though that is.

All these behaviors are, unsurprisingly, possessed by green plants constructed, of course, of millions of cells. But with differentiation into different organs, the capabilities of the individual cell shown above are more likely to be expressed on a tissue or organ basis.

**Comparing systems structures between cell and nervous systems.** That an individual cell can possess qualities that can be regarded as intelligent leads naturally to the question of how it does so? A comparison of the systems structures inside cells and nervous systems provides a potential pointer to understanding.

*Caenorhabditis elegans* is a nematode worm that has received enormous amounts of investigation and has its own website. This small worm is capable of a variety of intelligent responses to volatile and water-soluble chemicals, touch, osmolarity, and other signals, using sensory cells connected to sensory neurons, amplification via interneurons where assessment is made, and from there to motor neurons that excite different kinds of muscle (Hobert 2003, Chatterjee and Singh 2008). It is a typical example of distributed control. Behavior is modified by experience via nonassociative and associative learning through adaptation, habituation, and decision capabilities when response has to be prioritized between two contrasting signals (Hobert 2003, Giles and Rankin 2009). *C. elegans* has a simple nervous system composed of some 300 neurons, in which the degree (i.e., connection-number) distribution exhibits a simple power-law relation, with an average degree of 7 down to 3–4 in the tail region. A central “rich club” of some 11–12 neurons with a degree of 44 or more has been identified. By ablation studies, these central neurons seem mainly concerned with movements to touch signals and, it is thought, act as a

central signal assessment center (Towilson et al. 2013). These cells accept signals from a particular sensory system via a defined route and are assessed against information coming from others before decisions are made as to response. Synaptic plasticity enables information routes to change or new signals to be learned.

Empirical data and analytical models of many complex networks have shown that connection patterns in many real networks, including cells and nematodes, converge to a similar architecture exhibiting a heterogeneous degree (i.e., connection or link) between the components, with the distribution characterized by a power law with a minority of highly connected nodes. These systems have therefore both a core and periphery distinguished on their degree; hub species have lots of degrees and connectors few. This structure may engender resilience (Gao et al. 2016).

Eucaryotic cells have some 20,000–100,000 different protein species. It is the connection between these proteins in different groups or modules of varying size and transient existence that underpin cellular behavior: “Because of their high degree of interconnection, systems of interacting proteins act as neural networks to respond to patterns of extracellular stimuli” (Bray 1995). Simple modeled networks of proteins interacting through phosphorylation or dephosphorylation enable the recognition of groups of environmental signals, display robustness in control, integrate and amplify weak signals or responses, and control natural rhythmic processes or store information—functions we normally assume for nervous systems (Bray 1990). The post-translational modification of proteins redirects the flow of information through different cellular channels. With development, the protein landscape is dynamic and subject to continual change. The average degree in yeast with more than three-quarters of all proteins examined is 10 (Wuchty 2014). Like the *C. elegans* neurone, they, too, have a “rich club” labeled as an MD Set of less than one-sixth of proteins with an average degree of 24, containing many protein kinases concerned with signal transduction and cell division (Wuchty 2014). With further refinement, that should increase to above 40–50 and some proteins with a degree of 100, such as actin. The elimination of high-degree proteins in yeast usually leads to lethality.

Yeast uses receptor proteins to sense numerous external signals leading to amplification via calcium ions ( $\text{Ca}^{2+}$ ) and phospholipid signals, assessments through various cascades of protein kinases that are densely interconnected, and eventual motor activities involving changes in gene expression or secretion. Again, the cell is a system with well-established distributed control.

It is this core and periphery structure in both worm nervous systems and cells that provides for numerous paths of information flow that represent learning, assessing against internal memories, and directing the motor responses of division and secretion. In tissues with very large numbers of cells, as in plants, the potential for behavioral control is greatly increased.

**The plant root cap.** In *Arabidopsis*, the extreme tip of the root is covered by a cap constructed of some 200 cells. The cap is dynamic. It is constructed from a layer of dividing cells that abut the root meristem proper. The cap cells are gradually pushed outward. On reaching the cap surface, they are sloughed off. However, during their lifetime, slowly moving to the front of the cap, they act as both sensing and assessment of a variety of different signals. Like the cell and the nervous system above, present information indicates that it has a similar architecture in degree structure, with both a core and a periphery—a structure that seems to underpin intelligent behavior. This architecture may engender resilience distinguished by the range of signals that the cap senses.

The cap both senses and assesses numerous signals: (a) Gravity using statoliths: statoliths are not essential to gravity sensing, but their presence results in much faster responses. (b) Touch initiates an unusual dog-leg kind of structure in the distal growing region, placing the tip at an angle that enables the tip to slide over an obstacle surface (Massa and Gilroy 2003). Touch inhibits gravity sensing, and lengthy touch probably sees statolith dismembering. (c) Phosphate deficiency: signals are transmitted to the shoot, which synthesizes novel sRNAs. When these reach the root, the phenotype changes (Svistoonoff et al. 2007). (d) Rich soil nitrate patches construct gradients: when sensed, the root grows along them, with an acceleration of growth along the gradient and a cessation when rich sources are encountered (McNickle and Cahill 2009). (e) When water is in short supply, roots follow the humidity gradient. Statoliths are dismembered, preventing interference by gravity signals (Eapen et al. 2005). (f) Salt stress initiates long-distance  $\text{Ca}^{2+}$  waves to the shoot (Choi et al. 2014). The response motor for all these signals is located shootward in the elongating region as a result of information transmission from the cap (Darwin 1880).

Root cap cell ablation has been examined only with gravity signals (Blancaflor et al. 1998). Different cell groups have differential inputs to five different gravi-response parameters. The effect of loss varies from 0% to nearly 90% of response loss and indicates that about only 10% of the columella cells are the most critical. In the *C. elegans* connectome, about 4% are critical. A central controlling core of root cap cells (with high degree and high connectivity) surrounded by a less significant periphery (with low degree and lower connectivity) is indicated and the necessary controlling structure for intelligent behavior. Mechanical signals are initiated via cytosolic  $\text{Ca}^{2+}$  transients in the peripheral cells (Massa and Gilroy 2003). Although the root cap acts holistically, different sensory and assessment functions are distributed among different cell types.

### **Making the intelligent decision when faced with different choices**

The average light intensity around any plant is rarely if ever uniform. In temperate climates, the north-facing

plant is likely to receive less light. Most wild plants will be surrounded by others, a situation that is sensed if the others are green because reflected light from the leaves is enriched in far-red radiation. This information is used to change the phenotype, accelerating increases in height or redirecting growth away from obvious competition. This shade-avoidance syndrome is established before the loss of photosynthetic light and represents a prediction about the future environment. The ultimate aim is either to avoid or to overgrow any competition.

But plants must still produce leaves and photosynthesize. In the case of *Physarum* earlier, the robust solution is to optimize energy outlay to maximize energy gain, a situation that does occur in the case of parasitic, usually nonphotosynthetic plants such as dodder (Kelly 1992). But energy is not the currency here. It has been known for many years that branches compete with each other, a phenomenon called *correlative inhibition* and a fact easily demonstrated by the removal of one and observing the increased growth of the other. The competition is for the essential resources that come from the root, indicating their supply is constrained (Sachs et al. 1993, Sachs 2006). In fact, all parts of the plant seem subject to the same competitive process—between root and shoot or between roots, for example. Ecologists usually refer to this competitive capability as *trade-offs*.

Competition without arbitration cannot work; otherwise, those branches nearest the root would grab all that was available. Root resources are supplied through the vascular system formed by the cambium, a kind of inner skin that is found throughout the shoot and root. The cambium is normally associated with the increase in girth by constructing new vascular tissues. From its uniform activity in girth increase, this meristem is in communication throughout.

But the cambium is also responsible for providing vascular tissue to new branches. The evidence indicates that the cambium makes a comparative assessment of the productivity of each branch (Sachs 2006). Those with good productivity (e.g., supplying abundant photosynthate) will be rewarded with more vascular tissue and therefore receive a greater proportion of the limited root resource available. Such information indicates that the branch is currently well placed and will likely produce more leaves. Those less productive will have some elements blocked, and those completely unproductive will have all vascular tissue blocked. The need is for constant reassessment, a continual choice and decision, because plants and competitors continue to grow and branches will experience a comparative rise and then a wane in productivity as they are overgrown by younger branches and those of competitors. What comparative information is used by the cambium is not known.

A comparative whole-branch assessment is essential because individual leaves are subject to herbivory, wind damage, and even disease. Leaves do possess the ability to maintain their internal temperature within reasonable limits ( $21.4 \pm 2.2$  degrees Celsius) and close to the optimum for photosynthesis (Helliker and Richter 2007). The

individual leaf can manipulate its blade vector *vis-à-vis* sunlight using a motor tissue, the pulvinus. Transpiration cooling is controlled by stomatal aperture. Chloroplasts are actively moved around cells and can spread out or pile up at either end, changing heat absorption. Both the reflectance of surface wax, and the numbers of leaf hairs manipulating air movement across the leaf surface can be altered. Finally, the numbers of leaves on a branch can manipulate temperature by up to 10 degrees Celsius. These homeostatic capabilities observed in leaves on plants from arboreal to subtropical are clearly controlled, but which controls are used in any circumstance and combination is, again, not known. The ability of the pulvinus to return the leaf blade to its optimum position as regards the sunlight vector from any starting position chosen by the experimenter was the reason von Hartmann (1875) concluded the presence of intelligent behavior. This, too, is a form of homeostasis.

### Spontaneity

Variable behavior in similar plants under identical conditions represents their spontaneity. This behavior represents the platform on which plant intelligence is built. It is almost true to say that when examined, no two plants behave the same. But the variation—the individuality—is invariably eliminated because experimentalists eliminate it by averaging behavior. But no one questions whether the average actually exists. Variation is sometimes assumed to be the result of some unspecified experimental error. Analytical assessment demonstrates that the hormone levels, basic composition, and anatomy of organisms, including humankind, display enormous degrees of variation (Trewavas 2007b). Behavior is, of course, a complex product of these variable characteristics. Even individual cells differ substantially in the complement of individual proteins, the result of substantial noise in the circuitry of gene regulation (Trewavas 2012). There will be even greater noise in the communication and sensing structures that direct plant behavior. Spontaneity is easily seen in the germination of seeds even derived from the same plant. But the few times spontaneity has been recorded were in responses to gravitational signals by seedling roots. When placed horizontally, only a minority of roots settle directly to regain the vertical position. The majority show oscillations of growth, growth reversals, overshoot, and initial upward bending in some cases. Although many roots use a statolith mechanism, this is designed for much more sensitive and faster gravity response. There is a much less sensitive and slower gravity-sensing mechanism that is not understood, but it has to be sensed within an early developmental window and the information then used to construct the statolith system. Seedling roots learn about gravity signals. When placed with the root vertically upward—oddly enough a weak gravitational signal—only 25% of the roots eventually grew downward (Ma and Hasenstein 2006). The others grew in many directions. An angle of 135 degrees to the vertical is the most sensitive gravi-signal.

### Error correction and counting to five

Correcting errors in behavior indicates both intention and awareness. Intention is indicated by the behavioral activity that should have been followed; awareness is the appreciation that something is wrong and needs correction. The speed with which correction is made will play a part in fitness, and error correction is the mark of intelligent activity. Most kinds of plant behavior use various checkpoints and assess current behavior against an internal model of correct behavior. Error correction is rarely recognized because behavioral results are averaged and thus departures from the norm disappear. But when individual behavior is reported, error correction is readily observed.

The open trap of the carnivorous Venus fly trap (*Dionaea*) is closed when two sensitive hairs are touched within 20 seconds. This timing mechanism avoids inadvertent closure by means not involving prey, such as raindrops. If the trap is triggered, enclosing insect prey, then three further touches of the hairs are required to initiate the secretion of digestive enzymes and other proteins concerned with absorbing nutrients (Bohm et al. 2016). Digestion takes many weeks. This plant can count to five and by default must recognize 1, 3, and 4. The error correction emerges when very small insects trip the two hairs. Small exit holes remain at the top through which a small insect can escape. With only the two hairs tripped, the trap is reset within less than a day.

The sundew, again another carnivorous plant, has leaves covered in sticky tentacles. When an insect lands on the leaf, the other adjacent sticky tentacles bend over to cover the prey so that it becomes enmeshed. Eventually, the whole leaf folds and bends over to surround and digest the prey, taking several weeks to do so. Inert materials, such as small pieces of chalk or stone, can be placed on the unstimulated leaf and cause some bending of the tentacles, but they quickly assume the original position so that within a few hours, the trap is reset.

Many plants climb using tendrils or stems that wind around other plants. It is a simple way of achieving height with minimal expenditure of resources. With both tendrils and winding stems, a support can be provided, allowing coiling to occur. If the support is then removed, the stem or tendril then unwinds, and the search continues elsewhere. This can be carried out some four to five times before habituation sets in and the plant or organ refuses to respond. An alternative used by Darwin (1880) was to provide a glass rod as support. Although the touch stimulus is initiated and coiling commences, the stem soon unwinds; the surface is too smooth to enable any grip to be made. Similar behavior takes place with tendrils. Certain vines in tropical regions are known to ignore some trees whose trunk is very smooth and unsuitable to grip. Under normal circumstances, tendrils can sense a support and move toward it using circumnutation (Trewavas 2005). As the support is moved, the tendril corrects its movement. The extremes of the circumnutation cycle enable the plant to use triangulation to locate the position of the support.

### Games plants play

Competition between plants and interactions with microorganisms can be described by various versions of game theory. At the heart of game theory lies a complex optimization problem: how to adjust the strategy to defeat competitors. Self-recognition of individuals is crucial to competitive games. Experimental evidence indicates that individual plants do exhibit self-recognition. There is a precedent: In reproduction, about half of all angiosperms use self-incompatibility. The individual discriminates against its own pollen arriving on the stigma, ensuring that even if it germinates, it is killed in favor of pollen from other individuals of the same species. So the potential for the recognition of self is clearly present.

Competition via root systems enables kinds of tit-for-tat games. When sharing the same soil, competitors proliferate their root systems as far as possible to deny soil resources to the competitor. The roots are described as turning toward the competitor but refraining from direct contact, leaving a gap in between (Gersani et al. 2001). These observations have been made for numerous species, leading to the suggestion that root systems are territorial; they control their own territory. But intriguingly, a plant experiencing water-stressful conditions (leading to reductions in growth) can convey that information to numerous conspecifics growing nearby via a relay operating from root to root. These other plants can react in anticipation of future water stress before they experience it (Falik et al. 2011). But competition is the normal behavior to others nearby. So this may be a strategy for one intelligent individual to ensure that other competitors do not benefit while it itself is experiencing growth-reducing conditions.

The prisoner's-dilemma game is based on the assumption that individuals might do better on their own but that the net effect of cooperation is greater for both. It is exemplified by the involvement of symbiotic organisms with root systems and those that cheat on the cooperative endeavour. The capability of rhizobial bacterial species to fix nitrogen (N) can vary at least tenfold. The intelligent legume host becomes aware of this variation and punishes free riders that gain carbohydrate without reciprocating N fixation. Either the host insists on a one-to-one exchange of carbohydrate for N or increases the oxygen tension in the nodule, reducing the fitness of the symbiont (Kiers et al. 2003). Mycorrhizal fungi create networks of hyphae, the fine structures able to penetrate even tiny spaces between soil particles. In symbiosis, they penetrate the host root and provision it with phosphate and iron, receiving carbohydrate back. Similar treatment is, however, meted out to mycorrhizal cheaters that don't provide phosphorus (P) to the host but store most of it themselves. Carbohydrate provision is then altered to ensure either the one-to-one exchange of carbohydrate for P and iron from the symbiont or, if the cheater is truly parasitic, defense mechanisms operate to eliminate it.

Common mycorrhizal networks can develop between two or more hosts and can form wood-wide webs. Astonishingly,

information about disease or herbivory in one individual plant is transferred to the other plant partner(s) through the common mycorrhizal networks, enabling them to prepare defense procedures (Gorzalak et al. 2015). The mechanism of information transfer is unknown.

In the forest understory, light is limiting, but herbs of differing maximal height can be observed. Game theory demonstrates a trade-off: the resource available between leaf area or stem height. Those that choose better are more fit in the particular circumstances (Givnish 1982). Monolayers of leaves are common in these circumstances. Givnish (1982) stated that "leaves are not that stupid" and react trophically to each other, spreading out. He suggests that altruistic behavior may underpin the trade-off. Mature leaves communicate to young leaves, changing their phenotype (Lake et al. 2001).

### Volatile organic chemicals (VOCs): The plant language?

Volatile organic chemicals (VOCs) emitted by roots, shoots, leaves, bark, fruits, and flowers account for about 1% of fixed carbon. When shoots are attacked by herbivores or disease organisms, the spectrum of emitted volatiles change, and that can attract parasitoids of the herbivorous pests (a so-called burglar alarm). VOCs, methyl jasmonate, ethylene, and methyl salicylate are involved in the induction of defense mechanisms (Dudareva et al. 2007). If plants are grown close together, emitted VOCs can also initiate defense mechanisms in unattacked plants, providing they are within about 50 centimeters. But closely grown plants also exhibit the shade-avoidance syndrome, detecting their reflected far-red light and growing away from or overgrowing individual competitors. A potential—perhaps better—function of herbivore-induced volatile production is to overcome some limitations of the vascular system. Not all areas of the plant are equally connected together with regions damaged by herbivores (Holopainen and Blande 2012).

The VOC spectrum is different between individual species and even individuals (Dudareva et al. 2007). Obvious fitness benefits arise from those emitted by flowers and fruits; variations in fragrance mark out intelligent behavior. Holopainen and Blande (2012) have creatively suggested that the complexity and species individuality of VOCs act as a plant vocabulary or language: Individual volatiles are words, and the VOC signature represents sentences. A sentence is an emergent property of the words used to construct it (Trewavas 2014). If equivalent, it suggests that the whole VOC signature due to synergy between the words is essential; the omission of one or two words (VOCs) will fail, something now reported (Kikuta et al. 2011). The VOCs emitted by damaged shoots elicit a greater response in genetically identical relatives than in aliens even from the same species, suggesting the potential for self-recognition and perhaps altruism (Karban et al. 2013). Spontaneity suggests that each individual will likely emit its own signature.

That plants can sense alien volatiles is known. The young seedlings of dodder, a parasitic plant, home in on their prey by sensing the direction of emitted volatiles. Even with mature dodder seeking new hosts, half of all contacts with potential prey are rejected after a few hours and new prey sought elsewhere. The initial contact is with the stem or bark surface, both of which emit their own volatile signature, reflecting probably their current health and nutrient status. If the prey is accepted, the likely energy return from a new host is assessed within just those few hours, and the total energy to be used for parasitism (assessed as a number of coils) is calculated (Kelly 1992). The assessment of coil number indicates, again, a potential ability to count and for a larger number than five. The number of coils determines the number of haustoria that are formed only after several days, when coiling is complete.

Numerous VOCs are emitted by rhizosphere bacteria and mycorrhizae and alter root architecture in different ways (Castelo-Rubio et al. 2015 and references therein). Therefore, there have to be root-sensing mechanisms and receptor proteins present. If alien species of plant root emit these volatiles, they will induce root proliferation, too.

*Boquila trifoliolata*, a climbing vine in temperate rainforests, mimics the leaves of its supporting hosts in terms of size, shape, color, orientation, petiole length, and/or tip spininess, reducing herbivory. Gianoli and Carrasco-Urra (2014) have reported mimicry on at least eight different hosts. A vine, extending across different hosts, responds to each specifically in turn. Sensing and action on particular released host-bark VOCs is the most likely mechanism here. Some vines simply avoid trees on which the trunk is too smooth to enable climbing (Trewavas 2014). Again, VOC recognition explains this phenomenon.

The range of volatile chemicals produced below ground is quite extraordinary (e.g., Rasmann and Turlings 2008, Ens et al. 2009, Palma et al. 2012, Fiers et al. 2013, Musah et al. 2016) and is sufficient to account for the complexity of self- and alien-recognition that is known to occur. How are VOCs sensed? Because plants synthesize many VOCs, they have enzymes with active sites that produce the chemical in the first place and therefore have the potential—with slight modification—of producing a similar protein for sensing them. To simplify the detection of the VOC signature, a single protein receptor detecting only partial structures of the entire individual VOC signature complex is indicated by the information above (Kikuta et al. 2011). This is known as *odotope theory*.

### Learning from experience

Those plants that experience herbivory or disease become primed to further insults so that they now respond more quickly, to a greater extent, and therefore more robustly than unchallenged plants. Priming can last for years and in certain cases survives meiosis. Chromatin structural modification, through epigenetic changes (specific histone

acetylation or phosphorylation, DNA methylation), are the probable basis (Singh et al. 2014).

But priming is now recognized to occur after repetitive heat, drought, cold, and salt stresses that train the plant to respond more quickly and more robustly to these conditions (Ackerson 1980, Ding et al. 2012, Sani et al. 2013). The experience is learned and remembered; the memory participates in subsequent experiences. This learned experience has now altered subsequent behavior in ways that will affect fitness. Repetitive treatments with the hormone abscisic acid (ABA) primes ABA-dependent genes in the same way (Goh et al. 2003); their expression now responds more quickly and to a greater extent to subsequent hormone treatments.

Perhaps more intriguing is the obvious cross-talk between many of these abiotic stressful conditions, in which some of the same events are induced by separate stresses. Therefore, the response to one, such as heat, helps resistance to cold stress. Similarly, herbivory attack increases resistance to disease (Koorneef and Pieterse 2008). These observations represent kinds of conditioned behavior in which one signal influences the response to another and increases fitness. They are analogous to the distribution of function and cross-reactions in complex brains. The life history of individual cloned plants determines their capability for stress response and priming, illustrating how sensitive plants are to slight environmental variation (Raj et al. 2011).

Stress-induced signal transduction involves information flow through cytosolic  $\text{Ca}^{2+}$ -dependent processes and protein-kinase pathways. Concomitantly, the synthesis of the constituents of these pathways is increased, deepening the metabolic channel through which information flows (Trewavas 2014). During brain learning, synaptic connections are strengthened and/or new connections made, thereby deepening the channel of information flow through particular neural pathways.

### Conclusions

Plant behavior is similar to cognition in an analogous sense to that of a human being. A plant continually gathers and updates diverse information about its environment, integrates this with information on its present internal state, and then makes decisions that reconcile its well-being with its environment. Understanding plant behavior and intelligence has become one of the most exciting new and fast-moving frontiers in plant biology.

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