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BRIDGING THE GULF

Moving Sensing, Intelligent, Plants

> Our view of plants is changing dramatically, tending away from seeing them as passive entities, subject to environmental forces and organisms that are designed solely for accumulation of photosynthetic products.[1]
>
> —František Baluška

Claims of a constructed human-nature separation have to acknowledge that within scientific circles, since the publication of Darwin's *Origin of Species*, humans and plants have been recognized as sharing a common (if distant) ancestor. This situation has been addressed by Plumwood, who writes that the "insights of continuity and kinship with other life forms . . . remain only superficially absorbed in the dominant culture, even by scientists."[2] In spite of scientific knowledge of relatedness, the natural world and the plant kingdom remain backgrounded. Plumwood asserts that this domination of the natural world is perpetuated by "continuing to think of humans as a special superior species" and consequently other species as inferior.[3]

In such a philosophy of exclusion, the identity of the superior group must rest on the constructed inferiority of others. This rendering of plants as radically different and inferior helps maintain the dominant human sense of collective superiority. Despite awareness of kinship, this denigration of plant ontology has a large role to play in the human elevation above, and separation from, the wider natural world.

Significantly, this positioning of plants as radically different—as passive, insentient, inferior beings—is contradicted by an overwhelming body of evidence that has been accruing in the botanical sciences. From close observations of plant behavior, botanical science has implicitly rejected the zoocentric inferiorities of plants such as lack of movement, lack of sensation, and lack of mentality. Indeed over a period of approximately two hundred years, plant science has built up a bulk of evidence that shows plants in a very different light. In many ways, this chapter can be considered as a synthesis and interpretation of botanical evidence, which aims to convince the Western mind of the sentience and intelligence of the plant kingdom.

The foundations of this evidence are based upon historical advances in plant anatomy during the seventeenth and eighteenth centuries—such as the discovery of cells in plants by Grew and Malpighi, Camerarius's recognition of plant sex, and Hales's breakthrough on plant respiration.[4] While these discoveries helped to bridge the gulf between plants and animals, this chapter focuses on evidence that refutes the notion of plants as passive, nonmoving, insensitive, nonminded beings.

Darwin not only put forward the idea of relatedness between humans and the natural world, but his work was the first to fully demonstrate and articulate the idea that plants are capable of movement and sensation—providing the basis for the discipline of plant signalling. Rather than studies of evolutionary biology, plant signalling is crucial because scholars within this discipline have begun to recognize many points of continuity in the natures and capabilities of plants and human beings. Here my aim is not to dispense a complete botanical history, but to highlight some key advances in our discussions of plant ontology and epistemology.

SENSATION AND MOVEMENT

The recognition of sensation and movement in the plant kingdom can be traced back to 1824 when Henri Dutrochet proposed the idea that the growth responses of plants to light was a *behavioral response*, not simply mechanical movement.[5] This claim was repeated in 1868 when Albert Frank put forward the idea that the responses of plants to gravity and light were *induced*. Rather than the mechanical actions of an automaton, Frank's hypothesis was that the growth movements of plants were active, coordinated responses to sensed stimuli. In 1878, this active sensation and movement was proven for the first time in experiments by Von Wiesner, which showed that plants continued to move toward sources of light, even after these sources had been removed.[6] These experiments demonstrated that a biological response process had been initiated; a response which carried on even after the stimulus had been turned off.

This research laid the groundwork for Charles Darwin's investigations into tropic movements in plants. It was Darwin's work that firmly established in the botanical sciences the existence of initiated, nonmechanical movement in plants.

In a long series of experiments, Darwin confronted plants with various stimuli and studied their subsequent growth and movement. In his *Power of Movement in Plants* (1880), Darwin carefully describes plant growth movements and draws attention to the remarkable similarities between the movements of plants and animals:

> But the most striking resemblance is the localisation of their sensitiveness and the transmission of an influence from the excited part to another which consequently moves.[7]

Darwin's observation of a transmissible substance is of great importance. The proposition that such an influence may exist, acknowledges the interconnection between the parts of plants and their synergistic integration as a whole organism. It is one of the first recognitions of internal signalling and communication processes in plants. At the same time, similar research was being conducted in animals, and by noting them together, Darwin built upon the work of earlier physiologists to further close the gap between the perceived abilities of animals and plants.

Darwin was particularly impressed with the action of the radicle tip (embryonic root). In the *Power of Movement in Plants*, he notes the ability of the radicle to sense (and move away from) objects that might elicit tissue damage. Darwin was also amazed at the ability of the radicle to grow actively toward sources of water and gravity. From such painstaking observations, Darwin recognized the capacity of plants to sense and choose, and attributed brain-like characteristics to the root tip:

> In almost every case we can clearly perceive the final purpose or advantage of the several movements. Two, or perhaps more, of the exciting causes often act simultaneously on the tip, and one conquers the other, no doubt in accordance with its importance for the life of the plant. The course pursued by the radicle in penetrating the ground must be determined by the tip; hence it has acquired such diverse kinds of sensitiveness. It is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements.[8]

From his observations of the radicle, Darwin was the first person in the history of modern botany to recognize intelligent, purposeful movement in the plant kingdom. In Darwin's own lifetime, the investigation of tropic responses began to suggest that many of these purposeful movements were aimed at satisfying the nutritional needs of plants.[9] For centuries, botanists had also been aware of the so called nastic movements in sensitive plants such as *Mimosa pudica*.[10] Further work on these movements, again conducted by Darwin, led to the discovery of nervous impulses in plants. This is fundamental to contemporary evidence, which contradicts the notion that plants are passive.[11]

Darwin systematically studied the existence of nongrowth movements in *M. pudica, Drosera rotundifolia* L. and *Dionaea muscipula* Sol. ex Ellis (Venus Fly-trap). This was aided by the first recording of electrical movement [or an action potential (AP)] in the leaves of *D. muscipula* by Burdon-Sanderson in 1873, who worked closely with Darwin.[12] In *The Power of Movement in Plants* and *Insectivorous Plants*, Darwin provided experimental evidence of the movement of leaves in these species. In *Insectivorous Plants,* Darwin investigated the movements of leaves that allow the capturing of small insects. Working with the sundew, *D. rotundifolia*, he elicited movement by various mechanical and chemical means and described the passages of "motor impulses" through the cells of the leaves and tentacles that enabled the plant to exercise movement.[13]

Darwin demonstrated that plants were able to perceive minute quantities of chemicals that he had administered to them. He considered this a remarkable occurrence. It led him to compare this perception and movement in plant leaves to the sensory capacities of animals:

> These nerves then transmit some influence to the brain of the dog, which leads to action on its part. With *Drosera*, the really marvellous fact is, that a plant without any specialised nervous system should be affected by such minute particles; but we have no grounds for assuming that other tissues could not be rendered as exquisitely susceptible to impressions from without if this were beneficial to the organism, as is the nervous system of the higher animals.[14]

Darwin recognized the possibility that plants could receive impressions of the environment. Although he was not aware how, it was clear that plants were able to communicate with the environment, and the sensory parts had the means to communicate this information on the state of the environment to other parts of the plant. Again, for this type of communication, Darwin posits the existence of an influencing substance. It is interesting to note that this position is in direct contrast to Aristotle who denied plants the ability to communicate with the environment because he could not fathom the means by which they were able to receive sensory impressions.

However, despite Darwin's views, the faculties of sensation and awareness in plants were not proven beyond doubt. Even though there was experimental evidence for sensation and movement, the sensitive plants *Mimosa, Drosera* and

Dionaea were regarded by the majority of scientists as unusual cases. Other plant species, which did not demonstrate nastic movements, were still regarded as passive.[15] Despite his ideas on sensory impressions being received internally and on the intelligence of the radicle, Darwin himself also played down his findings:

> Yet plants do not of course possess nerves or a central nervous system; and we may infer that with animals such structures serve only for the complete transmission of impressions, and for more complete intercommunication of the several parts.[16]

Unfortunately in Darwin's caveat, the zoocentric influence of Plato and Aristotle persists. Again the anatomy of the plants in question is judged in relation to the anatomy of animals. As plants do not share the complex tissue structure of animals, Darwin assumed their capacities to be in some way incomplete and lacking. Although he had demonstrated that plants sense and move in intelligent ways, this final caveat served to reduce the existence of plant perception to a simple vegetable level. Despite this, his work firmly established the notion that plants are capable of initiating movement and cemented previous experimental evidence that plants could perceive their environments through touch and through direct perception of light, water, and temperature.

MOVEMENT AND SIGNALLING

The ideas of Darwin on the tropic and nastic movements of plants and the presence of a signalling process were initially dismissed by the majority of plant physiologists. As visible movement and sensation had only been demonstrated in exotic sensitive plants like *M. pudica,* the general position that plants were insensitive was retained.[17] Sensitive species were considered somewhat anomalous to the common vegetable, and so the findings from studies on sensitive plants did not serve to change the perception of common plants. It is a measure of the depth of the acceptance of the mechanistic position and of plants as inferior beings—that as this evidence uncovered the existence of sense and self motion, these ideas remained entrenched.

Darwin was a pioneer in the field of the communication *within* plants by molecular and electrical signalling processes. Focussing on the transmission of electrical impulses in plants, after the work of Darwin was published, Haberlandt continued researching the phenomenon. He discovered that vascular tissues, in particular the phloem cells, facilitated the transmission of APs and concluded that if plants were to be considered as having nervous tissue, then the long phloem cells were the likely location. Some researchers thereafter referred to the phloem cells as "plant nerves," but the majority of papers and textbooks affirmed the belief the plants had no “nervous system.”[18] This ignorance of Haberlandt’s work on electrical conductivity in phloem tissue remains to the present day, especially in popular science. Even recent, sympathetic publications have taken on this misunderstanding and claimed that “trees have no brains or nerves and instead run their entire lives with the aid of a remarkably short shortlist of chemical agents.”[19] Such interpretations ignore the fact that the nerve cells of animals and phloem cells of plants “share the analog function of conducting electrical signals.”[20]

In the 1960s, another threshold was crossed in the understanding of the sensitivity of plants. Although it was a hardly noticed event, more run-of-the-mill plants than the exotic sensitive plants were discovered to conduct electrical signals.[21] If pumpkins produced APs, then the perception that sensitive plants were an exception to the rule of passivity was shown to be erroneous. This finding also encouraged biologists to believe that widespread electrical messaging must have a strongly adaptive function. As a consequence, electrical signalling has been found to have a role in vital processes such as photosynthesis, respiration, phloem transport, and systemic defense.[22] In addition to APs that occur in animals, higher plants have been recently found to use a unique long-distance electrical signalling method. This method is called the “slow wave potential.”

As well as providing the foundations for work into electrical signalling, the early work of Darwin paved the way for research into plant molecular signalling. Darwin had demonstrated that the site of light perception in a shoot was at the tip, but that the location of the curvature was separable. He proposed that a transmissible substance from the tip was communicated to the region of curvature.[23] In 1931, investigations of this conjecture yielded the the hormone auxin, which is vital for tropic movements in plants, and this discovery stimulated widespread research on tropic growth and plant signalling.

Contemporary research into plant growth and communication has built upon the platform provided by Darwin. Studies in communication and signalling have shed light on the movements of the sensitive plant *M. pudica.* It is now known that the activation of a receptor on the leaves of *M. pudica* triggers an increase in intracellular calcium, which may act as the signalling molecule along with electricity. A signalling and communication process is indicated by the fact that not only do the touched leaves close, but leaves away from the source of the stimulus may close as well. Although the role of APs in plants is still poorly understood, the closure of *Mimosa* leaflets is achieved through a process of *sensing, communication,* and *action.* This response to stimuli is now thought to be ubiquitous in the plant kingdom. In a review of plant responses to stimulation, biologist Janet Braam makes it clear:

> From the violence of tree strangling and insect trapping to the elegance of roots navigating through barriers in the soil, responses to mechanical

> perturbation are integral features of plant behavior . . . probably all plants sense and respond to mechanical forces.[24]

Touch remains the most well-known sense in plants and that to which biologists currently assign most importance in the sensory repertoire of plants. Roots in particular are extremely sensitive to touch, which "enables them to explore, with an animal-like curiosity, their environment in a continual search for water and solutes."[25]

However, we would be limiting ourselves if an explanation of plant sensory abilities ended with touch. As the phototropic response to light clearly shows, plants are able to directly perceive light. Plants use the perception of light to direct movement. They are also able to use light to sense the proximity of neighboring individuals, which may be future competitors. Measuring an increase in Far-Red light (reflected by green tissues), plants use this information to perceive their neighbors and to predict whether they will render them subject to shading. If shaded, complex, morphological shade avoidance responses ensue.[26] As we rrecognize the perception of light by the human eye as sight, in their own way, plants also "see" their neighbors. This vision allows plants to make decisions about the future, related to branching and flowering behavior.[27]

PLASTIC PLANT INTELLIGENCE

Founded upon Darwin's work and the development of signalling, a significant number of studies on a wide range of plant species have begun to move beyond demonstrating that plants are simply capable of sensation. Contemporary research in the plant sciences is demonstrating that plants possess many attributes of an active intelligence. Fundamental to this is the concept of *plant intelligence*, proposed in 2002 by Anthony Trewavas.[28] In the context of this study, the concept of plant intelligence is significant because it is an intentional attempt to discredit the notion that the Earth's most abundant form of life is passive and mechanical.[29]

Trewavas's description is founded upon Stenhouse's definition of intelligence as the possession of "adaptively variable behaviour within the lifetime of the individual."[30] While animals may behave by moving around from place to place, Trewavas points out that plants behave by movements in a particular place; movements which usually are the result of growth. The growth and development of plant organs is "adaptively variable." it changes according to environmental conditions in order to maximize fitness.[31] Therefore by definition, this ability to alter the phenotype is intelligent.

Although Trewavas has most recently pointed out the significance of this adaptive behavior in plants, it is not a recently observed phenomenon. For centuries it has been known to botanists as *phenotypic plasticity*—the ability that plants have to change their outward form in response to changes in the environment. An early description of the variation produced by phenotypic plasticity in plant species is found in Linnaeus's *Critica Botanica*. Linnaeus notes the appearance of several aquatic species, including a species of *Ranunculus* which:

> Put forth under water only multifid leaves with capillary segments, but above the surface of the water later produce broad and relatively entire leaves. Further, if these are planted in a shady garden, they lose almost all the capillary leaves, and are furnished only with the upper ones.[32]

Plants accomplish this plastic development in a way that by necessity involves assessment of the prevailing environmental conditions and the selection of appropriate responses.[33] Plasticity therefore can be regarded as the manifestation of a plant's awareness of the environment. The resources are assessed, and the most beneficial growth and development response is induced in the *whole* organism.[34] The existence of plasticity is actually vital for the survival of plant life, and Trewavas considers it "a visible witness to the complex computational capability plants can bring to bear to finely scrutinise the local environment and act upon it."[35]

The existence of plasticity demonstrates that "the behaviour of plants is not pre-programmed"—an assertion that contradicts the concept of plants as *automatons*.[36] Plants do not always operate predictably like a piece of clockwork. Instead, perception, awareness, and active assessment are crucial elements in the behavioral repertoire of plants. As is commonly recognized in animals, this intelligent, plastic plant behavior is directed toward an increased well-being through the optimal acquisition of resources and the maximization of reproduction. The ability to adapt to new and changing conditions typifies the intelligence of phenotypic plasticity. There are many examples of this, but here I will concentrate on the action of roots, because plant roots are perhaps the most plastic of organs and are under tight control by the organism as a whole.[37]

Rich soil patches are exploited by increased plastic root branching and root growth. In the presence of few nutrients, root growth has been found to accelerate in order to facilitate the detection of new, more nutritious patches of soil in other locations.[38] There is clear and active perception of the resources available, which for Trewavas involves the construction of a "three dimensional perspective" of the local space.[39] Here plants display their behavioral intelligence with an ongoing assessment of the costs and benefits involved in exploiting the resources that exist in the soil.

Plants clearly and intentionally avoid areas with poor nutrient levels. The active, below ground assessment and discrimination of soil resources is integral for plant nourishment and survival. Studies estimate that it can increase the absorption of essential nutrients by between 28 percent and 70 percent.[40] Root plasticity allows plants to make choices about the soil patches they feed in—to the extent that plants have been referred to in ecological studies as "foragers."[41] From close observation of plant behavior, therefore, it is apparent that plants use assessment mechanisms in a similar way to animals and explore the soil to optimize the gathering of food resources.[42] This perception and assessment also allows plants to avoid competition. The roots of certain desert shrubs have been found to use root plasticity to deliberately avoid contact and competition with roots of other species.[43]

The concept of plant intelligence has not been without controversy in the plant science community. It has been challenged by Richard Firn through the argument that as intelligence is a property of individuals, plants cannot be intelligent as they are not individuals in the same way as animals.[44] While Firn claims that the organs of plants operate individually, Trewavas cites substantial evidence to the contrary, demonstrating a remarkable amount of communication and cooperation between plant organs.[45] On the evidence of such communication and synergistic action, plants are clearly individuals.

The theory of plant intelligence has also been attacked by Firn on the basis that plant behavior is the result of machine-like reflex reactions.[46] Doubts about the theory of plant intelligence have also emerged in the plant science community due to its associated notions of reasoning, learning, and problem solving. Struik et al. claim that such ideas "inevitably invoke the notions of consciousness and free will, elements that are totally unnecessary if adaptive responses are considered passive as in a Darwinian world."[47] Not only does the idea of plant intelligence have little to do with notions of consciousness and free will (see next section), in these reductive dismissals of plant intelligence, there is the now familiar a priori assumption that plant activity is passive.

DO PLANTS LEARN TO REASON?

In order to deal with an enormous range of environmental conditions that have the potential to change rapidly over short spaces of time, Trewavas highlights that learning is necessary for plant life.[48] Like other forms of learning, this involves continual assessment and the ability to make behavioral corrections in order to reach a required goal. One of the most interesting of these experimental examples involves testing the growth abilities of plant tendrils. Growth experiments on plant tendrils have demonstrated their ability to assess the position of a support and actively move toward it. The immediate goal is to reach the support, but if its position is moved, then the tendrils are able to sense this change and adjust the direction of their growth movement in order to relocate it.[49] Rather than being involved in automated, repetitive, purely stimulus-driven behavior, plants make *real time* assessments of stimuli and respond according to both their current state and previous experience. At each point in a behavior event, Trewavas notes that the plant is acting upon information from previous responses; a form of trial and error learning. There is also an integration of external information with knowledge of the internal state. Assessment of this assimilated information guides appropriate action. This is a process of *reasoning* which is directed at the optimization of factors that will maximize fitness.[50]

In addition to the experiments on tendril growth, the responses of plants to water stress have also been put forward as examples of learning and reasoning. For a plant to respond to drought, for example by the abscission of leaves, it must be able to assess the present level of water against the optimum supply level. Trewavas summarizes:

> The plant learns by trial and error when sufficient changes have taken place so that further stress and injury are minimised and some seed production can be achieved. The responses to water stress are modified by interaction and integration with other environmental variables e.g. mineral nutrition, age, temp, history etc and are therefore not reflexive responses. Clearly *decisions* are made by the *whole plant*.[51]

In adjusting their morphology in response to often rapid environmental changes, plants are capable of basic decision making, problem solving, and reasoning. Remarkably, in addition to these intelligent faculties, there is also some direct experimental evidence for the existence of intention and choice in plants.

A study of the feeding displayed by the nonphotosynthetic parasite *Cuscuta europaea* L. demonstrates that this plant makes choices when selecting a host. These are based upon the level of sustenance that *Cuscuta* anticipates that the host will provide. If the host is deemed to have insufficient capacity to provide essential nutrients (i.e. if the host is revealed to be lacking in nitrogen), after initially coiling its tendrils around the plant, the dodder will choose not to continue with feeding. Instead, it will uncoil and keep searching for another host, a host more suited to its dietary needs.[52] This is a case of a plant employing an optimal foraging strategy to ensure that it does not waste resources. A related study has demonstrated that the host perception in a close relative, *Cuscuta pentagona* Engelm. is mediated by volatile emissions from the host plant. The parasite uses the presence of volatile chemicals in the air to sense the position of the host before growing toward it. In another example of choice, several species were found to activate a feeding response, but when *C. pentagona* was given a choice of hosts it was shown to actively prefer the tomato plant.[53] These examples have emerged from work on parasitic plants due to the much simplified scenario of working with easily identifiable resource hosts. However, rather than relying on hosts, the majority of photosynthetic plants must forage for resources in soil.

Although explicit experiments have yet to be conducted on active rhizospheric choice, plant roots prefer to be located in resource rich patches in the same way as parasites prefer resource rich hosts.

PLANT BRAINS

As befits their modular structure and the ability to grow from each of their modules, unlike animals, plants have no use for a centralized brain and/or nervous system. Instead of centralized brain tissue, a newly emerging field of plant science, dubbed "plant neurobiology," is suggesting that plants may actually have thousands of brain-like entities that are involved in the emergence of intelligent behavior. These entities are a type of tissue known as *meristems.* Current theories suggest that the meristematic tissue, located at the tips of roots and shoots, combined with the vascular strands capable of complex molecular and electrical signalling, may well comprise the plant equivalent of the nervous/neuronal system.[54] In a groundbreaking text *Communication in Plants*, Baluška et al. echo the pioneering work of Darwin:

> Each root apex is proposed to harbour brain-like units of the nervous system of plants. The number of root apices in the plant body is high, and all "brain units" are interconnected via vascular strands (plant neurons) with their polarly-transported auxin (plant neurotransmitter), to form a serial (parallel) neuronal system of plants.[55]

Rather than following Darwin's judgement that this plant nervous system is inferior to that found in animals, plant neurobiology researchers regard this decentralized assessment and response system to be the most effective for maximizing plant fitness.[56] Such a system is thought to enable decentralized behavior (i.e., growth), which allows plants to thrive in complex and everchanging rhizospheric environments.

It has been proposed that in the plant the meristematic "brains" may exert influence on the rest of the plant tissue by the transmission of signalling molecules such as the hormone auxin. Auxins are manufactured at the root and shoot apices, and it is thought that their movement is one method for allowing the transfer of information throughout the individual. It has been proposed that the end poles (cross walls of cells) are analogous to the synapse in animals.[57] At so called "plant synapses," vesicular transport of auxin moves this signalling molecule from cell to cell. Although the exact processes have yet to be uncovered, it has been proposed that this extracellular transport of auxin "exerts rapid electrical responses" across the plant synapse and "initiates the electrical responses of plant cells."[58] Whatever the pathway within the plant, communication can occur over long-distances, with information on the environmental and developmental state of the roots being transferred to the shoots—as in the case of stomatal closure during water stress. As well as auxin and electrical signals, plants produce and use a variety of neurotransmitter molecules to communicate from cell to cell. Dopamine, acetylcholine, glutamate, histamine, and glycine are all touted as potential signalling chemicals between cells.[59] Other complex communication molecules include protein kinases, minerals, lipids, sugars, gases, and nucleic acids. Trewavas has drawn attention to this complexity and notes that "from the current rate of progess, it looks as though communication is likely to be as complex as that within a [animal] brain."[60]

In response to some of the assertions of plant neurobiologists, Alpi et al. have suggested that the existence of *plasmodesmata* (microscopic channels, which traverse plant cell walls and enable transport and communication between cells) contradicts the idea of plant synapses and of auxin as a neurotransmitter, as their existence facilitates extensive electrical coupling, precluding the need for any cell-cell transmission of a neurotransmitter-like compound.[61] However, this criticism has been refuted by Brenner et al., who assert that although the exact pathways are still to be discovered, auxin *is* known to be transported from cell-cell and active, communicative plant behavior does take place.[62] Along with the exact mechanisms of electrical cell-cell coupling, they assert that investigating these transfers represents an exciting field of study for understanding plant signalling and behavior.

With thousands of meristems, a plant has potentially thousands of "brain units." It is proposed by advocates of plant neurobiology that plants integrate sensory information and make decisions based upon communication between a multitude of plant tissues such as the root meristems, interior meristems, and the vascular tissues. Barlow has pointed toward the involvement of the vascular tissue (xylem and phloem) in conveying APs from zones of special sensitivity to other regions of the plant—an "informational channel" involved in organismal organization.[63] Trewavas has proposed that the meristematic tissue, which runs throughout the plant, could be an integrative assessment and computational tissue, acting with sensory input from local meristems.[64] With active debate on this topic, it is still to be uncovered whether this internal communication systems are centralized, decentralized, or somewhere in between.[65]

The structural complexity of these communication networks within plants is of great interest for an understanding of the intelligent behavior that plants display. The eminent animal physiologist Denis Noble has recently argued that network-style interactions (like those found in plants), actually organize and direct the activity of *all* living beings. In *The Music of Life,* he disputes the view that a unitary, external mind or self controls and directs the activity of living organisms.[66] Against this Cartesian notion, Noble argues that it is decentralized communicative networks that heterarchically self-organize and direct living activity.

In Noble's view of *systems biology*, "there is no single controller." no single Cartesian mind substance, which is the director of living systems.[67] Instead, from a systems viewpoint, mental properties such as intelligence, reasoning, and choice are thought to emerge from the interactions of physiological networks of signalling and communication. As Evan Thompson puts it, the "emergent process is one that results from collective self-organisation."[68] These principles of heterarchical organization and the emergence of higher level properties are fundamental principles of systems biology, which are elegantly summed up by Fritjof Capra:

> According to the systems view, the essential properties of an organism, or living system, are properties of the whole, which none of the parts have. They arise from the interactions and relationships between the parts. These properties are destroyed when the system is dissected, either physically or theoretically, into isolated elements.[69]

Although the exact pathways are still being investigated, we can state that from a systems perspective, the interconnecting, heterarchical network of plant tissues (including meristems) enables intelligent plant behavior, rather than the Cartesian consciousness or free will alluded to by Struik et al.[70]

PLANT SELF

Internally, plants rapidly exchange detailed environmental information between different organs. Although somewhat decentralized, a consequence of this integrated communication system is that plants also recognize themselves as integrated beings. In other taxa, this phenomenon is known as *self recognition*, and its existence in plant species is being remarkably demonstrated by experimental evidence.[71]

Through studies of breeding systems, it is known that plants are able to recognize self/nonself with some degree of precision. During pollination, the majority of plant species employ "self-incompatibility" mechanisms. Self-fertilization (and, hence, potential loss of fitness) is prevented by discriminating between *self* pollen and that produced by other individuals. In most cases, only pollen from sexual partners is able to germinate on the receptive stigmatic surfaces and go on to effect fertilisation. It is known that this recognition is based upon the presence of genetically determined allogens.[72]

Such self recognition has been characterized as a passive, automatic process, being wholly genetically determined. Studies on the communication in plant root systems show that there is much more to the recognition of self in plants than the allogenetic mechanisms employed in avoiding self pollination.[73] Plants are involved in complex and almost constant communication processes with their own organs and other organisms in order to distinguish self from other.

Studies on the grass *Buchloe dactyloides* (Nutt.) Engelm. by Gruntman and Novoplansky have shown that plant roots are able to discriminate between *self* and *not-self*. Importantly, this recognition is based on active, ongoing physiological processes resulting from internal communication within the plant itself. It is not based on a blind allogenetic recognition employed in the self-incompatibility mechanism in plant breeding systems.[74] Although far from completely understood, genetically identical plants have been demonstrated to recognize each other as nonself, suggesting the presence of nongenetic, individually specific signals in the recognition of selfhood and nonselfhood.

Gruntman and Novoplansky speculate that the signalling involved in the identity of plants is "mediated by internal oscillations of hormones such as auxin and cytokinins and/or electricity that are perceived by the roots through the soil."[75] Such oscillating signals "are known to be highly dynamic in time and thus individually unique."[76] It is postulated that these signals are able to be perceived simultaneously inside and outside of the plant. Thus, it is possible that the plant can generate an internal sense of self, through the "resonant amplification of oscillatory signals in the vicinity of other roots of the same plants."[77] That is, organs of the same self actively resonate in the same pattern. Instances of not-self recognition (recognition of different individuals) would occur as "resonant amplification could not occur in roots that are not oscillating with the same rhythm."[78] Recently separated genetically identical individuals would also be expected to oscillate with the same rhythm. The plant synapses, therefore, are likely to be the structures that "determine the integrity of individual plants by allowing their cells and organs to define and detect 'self' and recognize 'not self.'"[79]

This recognition of selfhood is also indicated by studies on soy bean plants by Gersani et al. When soy bean plants were made to share their growth space with other individuals, they substantially increased their root growth.[80] Plants that were given shared resources produced 85 percent more roots than those which did not have a shared growth space. In order to actively and aggressively proliferate their roots in competition for resources, Gersani et al. suggest that these plants must have the ability to perceive and identify the presence of self and nonself roots.

In a complex root network, the ability to differentiate between the roots of oneself and the roots of one's neighbors helps plants avoid the undesirable scenario of some of their roots competing for resources with other parts of their own root network. This would be a wasteful allocation of resources to the roots that could otherwise be used for above-ground functions such as stem growth and flowering. From the premise that natural selection would act against the wasteful use of resources, researchers have predicted that communication processes which recognize self should be widespread among the plant kingdom.[81]

RELATING AND INTERACTING BELOW GROUND

Investigations in the rhizosphere also uncover the fact that plants are incredibly interactive. As well as providing water and nutrients, roots can act as conduits of communication between individual plants and other organisms. The rhizosphere is an overcrowded space inhabited by the roots of plants and also by fungi and soil microbes. It is a space in which "root-root and root microbe communications are continuous occurrences in this biologically active soil zone."[82]

Roots are primarily used as communicative tools in the process of sequestering belowground resources such as water, nitrogen, and trace minerals. These resources are fundamental to the survival of photosynthetic plants. An increasing body of evidence is demonstrating that in many cases the method by which roots communicate with other organisms is through the production of root exudates—an umbrella term for an extremely diverse collection of chemical compounds also known as *secondary metabolites*. These communicative root exudates are vital for the flourishing of plant life. Their production commands up to 20 percent of an individual's photosynthate, and they are essential in establishing and maintaining symbiotic, mutually beneficial relationships with soil organisms.[83]

The symbiotic relationship between leguminous plants and *Rhizobium* bacteria is a good example of plants using communication to increase resource uptake, in this case nitrogen availability. Studies across the plant kingdom have shown that the production and secretion of *flavonoids* actually activate the genes of the colonizing *Rhizobium*, which are responsible for producing the root nodule.[84] This communication of information, therefore, directly enables the *Rhizobium* to fix atmospheric nitrogen for host legume plants in nitrogen poor soils. The composition of these flavonoids, and hence, the information content of this root to microbe communication is known to vary greatly between legume species. Each legume species exudes a specific flavonoid composition when communicating with soil microbes. Each has its own "chemical signature," which allows the soil symbionts to distinguish the roots of their symbiotic partners from those of other plant species.[85]

The secretions of the tomato plant *Solanum lycopersicum* L. also allow the creation of mutually beneficial relationships. The provision of information rich root exudates by the tomato is the first step in initiating a root colonization process by the bacterium *Pseudomonas flourescens* Migula.[86] The principal exudates produced by the plant roots, which act as an invitation to establish this symbiotic relationship, are malic and citric acid. This communication through organic acid exudates leads to a relationship in which *P. flourescens* protects the roots of the tomato against parasitic fungi and phytophagous nematodes.

As do humans and other animals, plants actively modify their local environment in order to reduce harmful circumstances and to make it more suitable for growth and reproduction. This behavior is a form of interaction with the local environment, most often demonstrated by plant roots. In the presence of rhizospheric pathogens, plant roots can selectively sense the specific threats and exude antimicrobial and antifungal compounds such as ferulic acid, rosmarinic acid, butanoic acid, and vanillic acid.[87] These chemical signatures are released in a precise response to a specific identified threat.[88] By exuding root secondary metabolites, plants alter the composition and abundance of the soil microflora and reduce the chances of local infection of the roots. Plant roots can also prevent against fungal attack by the production and exudation of defense proteins. Pokeweed, *Phytolacca americana* L., is known to exude defense proteins, which inhibit protein synthesis and have antifungal properties against root rot causing fungus, *Rhizoctonia solani* J.G. Kühn.[89] By removing this pathogen from the rhizosphere, *P. americana* is able to prevent systemic infection, avoid using resources to counter infection and thus increase its fitness.

A further example of active environmental modification is the ability of plants to increase the levels of available phosphorous (P) in soils that are phosphorous poor by the exudation of organic acids and enzymes (acid phosphatases). In lupines which are grown in P-deficient soils, the secretion of these enzymes that help make phosphorous more readily available can increase up to twenty fold.[90]

Allelopathic interaction with other plants is another form of complex rhizospheric interaction. Allelopathy occurs when plants use secondary metabolites secreted from their roots to suppress the growth of neighboring plants. Again, this is a process of modifying the immediate environment in order to increase the chances of growth and reproduction. Over a period of fifty years, there has been a fluctuating acceptance of allelopathy in the scientific community with recent studies suggesting that it has an important role in plant interactions with the environment.[91]

One of the most cited occurrences of allelopathy is in the Mojave Desert shrub community in North America. In an environment where water is a scarce resource, Mahall and Callaway discovered that the common shrub *Larrea tridentata* (DC.) Coville suppresses the growth of neighboring plant *Ambrosia dumosa* (A.Gray) W.W.Payne through the secretion of a readily diffusible inhibitory substance from its root system in order to remove interspecific competition for water.[92]

Allelopathic interactions are also known to occur intensively in crop plants and their neighboring species. Studies show that these interactions are widespread and that they can have a sizeable effect upon growth and reproduction. A common weed of tropical agricultural systems, *Cyperus rotundus* L., can greatly reduce the stem size, leaf size, and overall yield of rice (*Orzyza sativa* L.) through the production of growth-inhibiting organic acids. The presence of *Cyperus* also has the same effect on other important crops such as maize, barley, tomato, and onion.[93]

As well as communicating with microorganisms and beneficially modifying the environment, roots are known to act territorially. In order to manifest this behavior, roots must be involved in continually occurring complex communication, both with the roots of the self and the roots of other individuals. There are many fascinating examples of such communication in root systems. Roots of the clonal herb *Hydrocotyle* have been shown to veer away from competition with the roots of other species.[94] Studies on the desert shrub *Ambrosia dumosa* have shown that individual plants avoid proliferating their root systems if they come into contact with other individuals of their species.[95] Research on the garden pea *Pisum sativum* L. has demonstrated that roots do deliberately avoid contact with other roots on the same plant.[96] The parasite *Triphysaria versicolor* Fisch. & C.A.Mey. has been shown to be able to actively distinguish its own roots from the roots of its host and other species, which is further evidence for the recognition of self and nonself.[97]

PLANT COMMUNICATION FOR FLOURISHING

Active communication and interaction between plants and others also occurs above ground. The most obvious occurrences of aboveground communication and interaction occur during plant reproduction and plant-herbivore relationships. In this context, there is mounting evidence from studies of chemical signalling that plants have a high level of awareness of their local environment, and exploit information on their attackers and on their resources.[98] A major way in which plants communicate with the (above ground) world around them is through the airborne emission of volatile organic chemicals (VOC's).

Flowers are known to release a myriad of scented chemicals including fatty-acid derivatives, benzenoids, and terpenoids.[99] Although it seems obvious that flowers emit these scents to attract pollinators, there have been remarkably few scientific studies which have actually demonstrated this communication. One of the few studies to have done so also involves a process of deceit on the part of the flower toward the pollinator in question. The South American orchid *Ophrys sphegodes* Mill. emits simple volatile chemicals, alkenes and alkanes, as well as providing visual cues to elicit the "pseudocopulation" behavior of the *Andrena nigroaenea* Kirby males.[100] These compounds precisely mimic the scent of the sexually receptive female *A. nigroaenea*, and as the male is attracted to the plant for "copulation," pollination is effected. After copulation, *O. sphegodes* flowers emit a compound that is released by nonreceptive female *A. nigroaenea,* which serves to inhibit further copulation, thus directing pollinators to nearby unpollinated flowers.[101]

Plants are known to emit volatile compounds from their leaves to communicate with herbivores in order to deter attack. It has been shown that tree species, which emit high levels of VOC's, are attacked much less by *Coleoptera* beetles than other tree species, which are in the same plant family (Lecythidaceae) but do not emit VOC's.[102] In addition to producing direct defenses, plants may also respond by the airborne emission of volatile organic chemicals to elicit indirect defenses. These VOC's serve as an indirect defense by attracting arthropod carnivores to prey on the attacking herbivorous insects.[103]

As well as providing information to arthropods, the VOC's that are emitted into the atmosphere also provide information about the type of attack, and intriguingly, this information can be used by neighboring plants. Plants have an ability to differentiate between the herbivores that attack them, and so the composition of the chemical blend emitted by damaged plants is different for each type of herbivore. It is also specific to the plant species.[104] A study on the lima bean *Phaeseolus vulgaris* L. has demonstrated the fact that the particular "blend" of volatile organic compounds from plants undergoing herbivory is specific to the type of damage being inflicted.[105] Due to this discrimination between herbivores, the chemical information in VOC's is very specific and can allow neighboring undamaged plants not only to perceive an imminent threat, but also to assess the actual risk faced. This discrimination can allow the undamaged plant to assess the costs of producing its own direct chemical defenses against the likelihood of serious damage occurring through herbivory. After processing the information gleaned from the neighbors, a plant will execute the response which will ensure greatest fitness.[106]

This above ground communication between plants has been much more hotly debated than the communication between roots.[107] Many researchers regard early studies as having been inadequately controlled, and these have been widely discounted. Other contentions lie in the interpretation of results which conclude that plants sending and receiving VOC's may both benefit. Regardless of the early doubts, an increasing number of studies are presenting evidence for above ground communication.[108]

In laboratory experiments, plants can perceive volatile signals in the environment produced by other members of their own species and by other species.[109] Studies have shown that exposure to volatile organic compounds produced as a result of herbivory can directly affect the expression of "defense genes" and often results in the production of metabolites linked to defense, such as terpenoids.[110] However, in the field, only a handful of studies have adequately demonstrated that plants use the information emitted from neighboring plants for the production of defenses. One such example is a field study of the alder, *Alnus glutinosa* L., which is attacked by a herbivorous beetle. In the field, the defoliation of individual trees was found to result in reduced herbivory in neighboring *A. glutinosa* trees. The "protective effect" lessened with distance from the tree undergoing herbivory and from the time since defoliation.[111] This suggests that the damaged trees produced signals that warned of herbivory and which led to the production of antigrazing defenses in their neighbors, enabling increased biological fitness.

Although it is clear that the plants "on the receiving end" are able to perceive this communication, it is widely doubted that these signals are *sent* intentionally by the plant being eaten. Doubts rest mainly on the evolutionary premise that there could be no benefit to those plants sending signals in increasing the competitiveness of neighbors. However, the recent revelation of kin recognition in plants suggests that signals could be emitted in accordance with kin selection theory—that is, the individual signalling plant could intelligently increase its own inclusive fitness by increasing the fitness of related individuals.[112]

EVALUATING THE ADVANCE

This increasing body of evidence in contemporary plant science is beginning to demonstrate convincingly that plants share many capacities and capabilities with human beings. But it must be remembered that such evidence is at the cutting edge of science. Much of the material is still under scientific debate, and many of the concepts involved in plant intelligence are openly opposed. Struik et al. argue strongly against the use of notions such as intelligence, reasoning, and problem solving as they argue that to use them "surmises extremely complex mechanisms and structures to be present"—which in their view violates the principles of parsimony.[113] Yet, such resistance ignores the fact that extremely complex communicative pathways are now being uncovered in plants and that plants use them to demonstrate complex and intricate behavior. As Brenner et al. state "We are less concerned with names than with the phenomena that have been overlooked in plant science."[114] Although doubts exist—as has been the case at many points in the history of plant sciences—future investigation, especially within plant neurobiology, is likely to only provide further proof of active, intelligent plant life.

Physiologically, the current advance from the perception of plants as inert lumps has been achieved by studying the behavior of individual, free-living plants. These plants are more likely to demonstrate intelligent behavior in order to maximize fitness. Increasingly sophisticated experimental methods and technology has also been of huge importance. Much of the empirical evidence for plant intelligence has been gathered using measurements of plant molecular signalling. Yet, as much of a plant's ecological behavior takes place below ground, technological capabilities are still limiting a full evaluation of plant intelligence.

However, the advances in plant understanding can also be said to have a subtly important philosophical basis. In the terminology of Bashō, "plant scientists have gone to plants to learn about plants."[115] That is, they have conducted close observations of plant life, and instead of *evaluating* this evidence from a *zoocentric* perspective; they have followed Theophrastus in using animal models to consider plants as much as possible on their own terms. Perhaps unconsciously, they are taking a more phenomenological approach to their studies. In the case of Anthony Trewavas, his orientation toward emphasizing the connectivities between plants, humans, and animals, has been adopted explicitly in order to generate a greater respect for the plant kingdom and the wider natural world.[116]

Such a drive toward connection has its own parallels with the treatment of plants in animistic traditions, as well as in Hindu philosophy and Jainism. For the Western mind, the significance of the contemporary plant sciences is that they provide a wealth of empirical evidence for the sentience and intelligence of the plant kingdom. As for these diverse traditions, the ramifications of this empirical evidence for connection, sentience, and intelligence must extend into questions of interspecies ethics.

Importantly, whatever the current scientific debates, the intellectual basis for treatments of plant life as inert, vacant, raw materials is demonstrably false. On this basis, it must be accepted that the continued denial of plant autonomy and the exclusion of plants from human moral consideration is no longer appropriate. This exclusion deliberately treats plants as less than they are. More strongly, such deliberate undervaluing can be considered as a form of intellectual violence.[117] Including plants within human moral consideration is more appropriate than exclusion as it both recognizes and reveals plant sentience. The concluding chapter, therefore, tackles the remaining questions. What shape should human-plant ethics take? How can we move from a stance of exclusion and domination to one of inclusion and care? How can plants be incorporated into dialogical relationships?