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Green plants as intelligent organisms

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Intelligent behaviour, even in humans, is an aspect of complex adaptive behaviour that provides a capacity for problem solving. This article assesses whether plants have a capacity to solve problems and, therefore, could be classified as intelligent organisms. The complex molecular network that is found in every plant cell and underpins plant behaviour is described. The problems that many plants face and that need solution are briefly outlined, and some of the kinds of behaviour used to solve these problems are discussed. A simple way of comparing plant intelligence between two genotypes is illustrated and some of the objections raised against the idea of plant intelligence are considered but discarded. It is concluded that plants exhibit the simple forms of behaviour that neuroscientists describe as basic intelligence.

Intelligence – universal or species specific?

In spite of many books being written about intelligence there is no agreed definition [1,2]. Dictionaries conventionally define intelligence using only human behavioural properties from the anthropocentric view that only humans can be intelligent. However, even by those elaborate criteria, which require, for example, advanced reasoning, shrewdness and tool use, crows and parrots are intelligent, solving certain problems faster than some humans are able to solve them [1,3]. Attempts to encapsulate what kinds of behaviour biologists really understand as intelligent are not uncommon; most point to an enormous simplification of the processes supposedly involved in human intelligence. Thus, David Stenhouse [4] in his investigation of the evolution of human intelligence concluded that it was '…adaptively variable behaviour during the lifetime of the individual'. I have discussed this definition in Ref. [5] and indicated how aspects of plant behaviour on this basis can be regarded as intelligent. 'It is not too much to say that a bee colony is capable of cognition in much the same way that a human being is. The colony gathers and continually updates diverse information about its surroundings, combines this with internal information about its internal state and makes decisions that reconcile its well being with its environment' [6]. The sequence is continual environmental perception, information processing, access to memory of current state (simple reasoning) and a response increasing fitness – a sequence the reader would reiterate if he heard a fire alarm. No overall, controlling brain is required for intelligent colony behaviour. The necessity of a brain to underpin intelligence is discarded by Kevin Warwick [1], Frank Vertosick [2], and Jonathan Schull [7]. It is the kind of behaviour that is crucial. Warwick, a cyberneticist and artificial intelligence (AI) investigator, states that '…the success of a species depends on it performing well in its own particular environment and intelligence plays a critical part in its success…', emphasizing the relationship of intelligence to fitness [1]. He refers to intelligence as the '…capacity for problem solving…' and indicates that intelligence within any species must be described within the capabilities of the species under examination – otherwise it is subjective. Species, immune systems, social insects, bacteria, single animal cells and genomes (and many other examples) have been described as exhibiting intelligent behaviour [2,7–13]. There is now a strong AI research investment in immune systems (artificial immune systems) and social insects (swarm intelligence) [9,14]. Visible plant behaviour (phenotypic plasticity) is biologically unusual [5]. It is feasible that when the behaviour of green plants in the wild is described in detail, intense interest in investigating AI in plant behaviour will follow.

Plant intelligence starts with cell molecular networks

The vital properties and organized structures of cells result from the connections between the molecular constituents of which they are composed [15,16]. Enormous numbers of molecular connections integrate into an emergent, organized order that is characterized as living. It is now known that:

- Many metabolic steps act like Booleian computer logic gates, such as AND, OR and NOR, and have been described as chemical neurones (e.g. [17–19]).
- Assembling several chemical neurons together enables pattern recognition [20].
- Proteins can act as computational elements [21].
- There are ~1000 protein kinases in both animals and plants, providing the capability for numerous complex elements of control, switching mechanisms and interacting positive and negative feedback controls [22–24].

Such chemical metabolic systems parallel the capabilities of simple artificial neural network structures as a set of on/off switches with feedback [25,26], on which they are modelled [27,28]. Even in simple neural networks, collective computational properties arise by parallel processing: with only 15 interlinked neurons, at least 100 associative and accessible memories emerge as attractors occupying parts of the network [25,26]. Chemical neurons and neural network behaviour have primary applicability to signal transduction networks [29].

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Use of phage display, metabolic control theory and two hybrid methods have shown that cell proteins construct a cellular network composed of a power law distribution of hubs and connectors[*] [e.g. 29–31]. Both metabolic and signalling networks are constructed from modules with recognizable recurring circuit elements or network motifs that: (i) filter out spurious input fluctuation; (ii) generate temporal patterns of expression; (iii) accelerate throughput [32]; (iv) exhibit highly optimized tolerance of variations in individual protein constituents [33]. These metabolic networks are described as robust but fragile as regards some mutations [34,35]. The robustness results from sharing control throughout the metabolic and signalling network with controlling steps determined by the environmental state [36]. Already, complex feedback controls have been shown to underpin systems structures during development [37].

A multiplicity of receptors enables cells to monitor environmental variation constantly. Plant cell signal transduction is performed by a network constructed from a plethora of second messengers and kinases [38]. In bacteria, the network of two-component kinases and phosphatases has been termed a phospho-neural network [39] that enables single bacterial cells to construct associative responses (i.e. cross-talk), learn [40], remember, make informed decisions, perform linguistic communication and exhibit social intelligence [10,40–42].

Plant cell signal transduction, involving numerous second messengers, 1000 protein kinases and many 1000s of associated molecules, is capable of much more [38]. Information flow can diverge, branch, converge, adapt, synergize and integrate through cross-talk [38,43]. Learning results from accelerating the rate of information flow through a selected pathway just as it does in simple brains, [5,44]; either the amounts of the constituent proteins (or chemical neurones) are increased or the affinity between information steps is increased using phosphorylation. Memory results from retention of the enhanced pathway of information flow and can be accessed by other pathways through cross-talk [43]. ‘The cell in which zillions of molecular events occur at a time, computes in parallel fashion…’ [45], just like a brain. Cellular networks capable of these properties are entitled to be called intelligent. They form the basis of machine intelligence [1]. Networks that can manipulate their own information flow are the basic requirements for all forms of biological intelligence [2].

Problems facing plants that require intelligent solutions

The typical plant consists of a network of millions of cells organized into some tens of tissues and numerous meristems that influence each other. There is no obvious centralized control tissue and intelligent behaviour arises as a property of the whole integrated cell and tissue system, much like a social insect colony [6]. Influences require communication and the signals that are used range from physical (e.g. mechanical, gaseous, electrical and osmotic) to complex chemical signals involving, for example, proteins, nucleic acids, oligo-nucleotides, peptides and oligo-saccharides as well as growth regulators, sugars, amino acids and minerals [5]. Perhaps the most striking is the influence of the rootstock on the scion, which can substantially modify the shoot phenotype. Movement of homeo-box proteins from root to shoot are, in part, responsible [46]. These complex signals ensure that plants behave as integrated organisms.

For any wild plant, the life cycle goal is to optimize fitness [47]. Individual plants attempt to maximize sibling number by producing the largest number of seeds possible within the constraints of the external environment and genetic makeup. Because there is a common relationship between resource acquisition (food, i.e. light, minerals, water) and seed number, those individuals that can master their local environment best will succeed where others fail [48]. But resources come either in fluctuating quantities, varying from seconds to months, or as gradients with fluctuating intensity or as a mosaic in the soil in vastly variable concentrations [49,50]. Predation, disease, trampling and disturbance damage the phenotype, and countervailing phenotypic responses, underpinned by physiological plasticity, are essential.

Various mechanical impediments make resource collection more difficult. Wind, drought, temperature or light extremes can damage the growing plant; physical impediments in soil structure and obstacles must be counterbalanced or avoided. Plants that can sense these environmental difficulties most effectively and can even predict likely future trends will benefit in the Darwinian wars. Furthermore, other surrounding plants actively compete for resources and the individual must in turn compete vigorously. As each individual grows and competitive neighbours grow unpredictably, current food resources can be rapidly exhausted [51] and so a search for new resources must be actively undertaken. Those that can recognize unoccupied territory and exploit it rapidly are at a distinct advantage. What one individual gains is denied to others. New resource situations continually arise and the information spectrum perceived by any plant is in continual flux. Only by active and skilful exploitation and optimizing the commitment of current internal resources for growth can Darwinian success be achieved.

Problem solving

Decisions, choice and the control of behaviour

Plants actively forage for food resources by changing their architecture, physiology and phenotype [52–54]. When patches rich in resources are located by growing roots or shoots and occupation of resource receptors reaches crucial levels, decisions are made to initiate enormous proliferation, which greatly increases the surface area for absorption of energy, minerals and water. In this way, decisions are made continuously as plants grow, placing roots, shoots and leaves in optimal positions according to the abundance of perceived resources.

Leaves are placed and positioned by petioles to minimize self-shading [55,56]; the pulvinus then rotates the lamina to face the optimal direction of light [52]. If light is newly blocked on one side, the plant resiliently turns to another. If branches are overgrown, decisions are

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[*] A power law relates two variables A and B together in the form $A = B^n$. In this context, the power law indicates that many molecules have a few connections to other molecules (connectors) but few molecules have large numbers of connections to other molecules (hubs).

made, based on the threshold of carbohydrate return, to seal the connecting vascular system and beneficially redirect the use of scarce root resources to the rest of the plant [57–59].

Individual plants grown with the same level of food resources but in a bigger soil volume grow much larger [60–62], indicating an ability to sense volume. (Interestingly, individual ants can assess volume to see if it is suitable for nest building [63]). When given the choice between soil occupied by other plants and unoccupied soil, the roots of those plants examined move their new root proliferation into unoccupied soil and away from competitors [64,65]. Growth ceases when roots are made to touch roots of alien individuals (but not their own) [66]. This suggests that plants have mechanisms that sense their own root distribution and can optimize construction of the root phenotype, indicating that plants are territorial [62] – they minimize competition from their own roots and prefer unoccupied soil [66–68].

If individuals are forced to grow in the same soil volume, the root system proliferates to competitively sequester available root resources from other individuals but with a trade-off in seed production [65,69]. Further convincing and remarkable studies indicate that root systems are indeed self-sensing [70–72]. When clones of the same plant are separated, within several weeks the root systems recognize each other as alien and proliferate accordingly. Plants assess and respond to local opportunities that will in the future benefit the whole plant [70].

Predicting the future

In describing bacterial chemotaxis, the neuro-scientists, Peggy La Cerra and Roger Bingham [73] stated that 'The *sine qua non* of behavioral intelligence systems is the capacity to predict the future; to model likely behavioral outcomes in the service of inclusive fitness'. In recurrent and novel environmental situations, cells, tissues and whole plants model specific future behaviours so that the energetic costs and risks do not exceed the benefits that adaptive, resilient, behaviour procures. Such modelling takes place on an adaptive representational network, an emergent property constructed from cell transduction and whole plant networks. The following examples indicate that higher plants use an adaptive representational network.

Phenotypic changes in plant development are all directed towards a future goal of optimal fitness. Roots and shoots grow along gradients of food resources (just like chemotactic bacteria do) and are modelling a future that will improve fitness if patches rich in resources are subsequently found. Even when patches rich in resources are found, leaves and roots only become sources of food when nearly mature [74]. Thus, increased proliferation is initially a speculation about the future and natural selection will weed out those that speculate inaccurately.

Branch and leaf polarity in canopy gaps have been observed eventually to align with the primary orientation of diffuse light, thus optimizing future resource capture [75]. The internal decisions that resulted in the growth of some branches rather than others were found to be based on the speculatively expected future return of food resources rather than on an assessment of present environmental conditions [76,77]. The Mayapple (*Podophyllum peltatum*), a forest floor plant, also makes commitment decisions as to branching or flowering years ahead, using a multiplicity of current environmental information [78]. Many temperate trees make decisions about flower numbers a year ahead.

Dodder (*Cuscuta*), a parasitical and non-photosynthetic plant, coils around suitable hosts and commences food acquisition through haustoria after ~4–5 days [79,80]. Suitable hosts are commonly rejected within a few hours. However, if the host is accepted, a concurrent decision on the eventual number of coils (energy investment) is made that optimizes the energy invested against the potential energy to be gained in the next month, thus agreeing with the Charnov optimization model of animal resource foraging [81]. Optimization of investment energy against energy gain during growth has been detected in other plants [82,83]. *Physarum*, a slime mould, in foraging through a maze to find food, likewise optimizes energy investment against energy gain. Toshiyuki Nakagaki *et al.* conclude that '…this remarkable process of cellular computation implies that cellular materials can show a primitive intelligence…' [13].

Possible future shade is predicted by many plants from perceived, reflected far-red/red light. Countervailing and extensive changes in phenotype are initiated before any loss of photosynthetic light occurs [84–86]. The stilt palm (*Socratea exorrhiza*) 'walks' out of shade by differential growth of prop roots [5]. When provided with water only once a year, young trees learn to predict when water will be provided in the future and synchronize their growth and metabolism with this period only [87].

Measuring plant intelligence

An intelligence rosette is a novel way to illustrate individual intelligence variation and can be used to compare the capacity for problem solving between different plant genotypes or even species [1]. Various behavioural traits that underpin problem solving in one species are quantified, averaged, normalized to 1 and placed as axes starting from the centre of a circle (broken circle in Figure 1a). The quantified traits of a single genotype of this species are placed on the same axes (Figure 1b) and the final rosette shape provides a direct comparative visualization of how this genotype might differ from others in the traits that enable a capacity for problem solving. Warwick [1], who introduced this method, constructed individual human intelligence rosettes using 16 different sub-categories of intelligent behaviour.

The plant traits that can be used are those that would contribute to phenotypic or physiological plasticity. A compendium of leaf traits is available [88] but the most relevant are flexibility in leaf weight:area, speed of new leaf production, sensitivity to shade, flexible operation of photosynthesis, stomatal sensitivity (closing and opening speed after perturbation) and abscission sensitivity. Other traits need identifying and quantifying, and could then be included along with equivalent root and stem traits.

The advantage of such an approach is that by breaking down plant intelligence into individual traits, a better

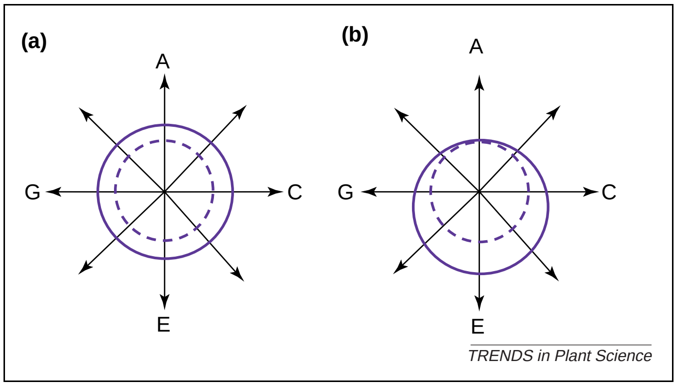

Figure 1. Intelligence rosettes. Within a single species the performance traits of leaves, stems and roots that underpin intelligent behaviour are identified as described in the text. These are measured and the average for each trait is normalized to 1. These averaged trait values are presented as axes (e.g. traits A–G) of a circle. **(a)** The average trait values are represented by the broken circle and a plant with traits superior in all respects is represented by the outer solid circle. **(b)** A more realistic comparison of a single genotype (solid circle) is made with the average; some traits are increased and some diminished.

appreciation of intelligent behaviour can be gained. In turn, the construction of a rosette indicates how intelligent behaviour is the holistic integration of all these behaviours. By using different environments for trait measurement, the rosette variation will indicate how intelligent behaviour is integrated with the environmental problems that must be solved.

Internal assessment (simple reasoning) of the present status changes the responses to signals

The literature is replete with examples that show how responses differ according to the current state and condition of the plant, indicating internal assessment. For example, gravi-responding roots grow horizontally when an obstacle is encountered, but at intervals the tip turns downward to assess whether the obstacle has been passed and regains the horizontal position if it has not been passed [89]. Tendrils can assess the position of a support and move towards it changing their spiralling (circumnutatory) patterns of movement if the support is shifted (Figure 2) [90]. Tendrils can unwind and might not wind about each other [91,92]. If a single branch of a tree is shaded, death from lack of root resources results from a sealing of the connecting vascular tissue [58,59]. Shading the whole tree to the same extent has only a marginal influence on overall growth and no branch death. In drought conditions, few leaves are lost if the plant has previously received adequate N nutrition but, in a drought of equal severity, many leaves are lost if the plant is N deficient.

Where does internal assessment occur? The gravi-responding root [89], described in the previous paragraph, is surely an example of Charles Darwin's observation of [91] '…the root acting like the brain of one of the lower animals…' – a response that also requires a shoot. That of the tendril (Figure 2) requires concurrent stem movements; only a residue of the movement will be gained in its absence. The stem cambium, the meristem that forms an internal skin, has been proposed to act as an integrated tissue controlling branch and leaf formation and abscission throughout the stem by manipulating root resource diversion [93]. The root pericycle might have an equivalent assessment role in the root.

Behaviour – autonomic, preprogrammed or intelligent?

Sensory integration of numerous resource, abiotic and biotic signals is known to control dicot branching patterns. The enormous potential plasticity of the final phenotype cannot therefore be pre-programmed. However, if the same plant cultivar is used under identical experimental conditions, are not statistically similar results obtained in response to a single changed environmental variable and does this not indicate preprogrammed, non-intelligent behaviour? But when different groups of culturally similar humans take an IQ test, the average within statistical error is reproducibly 100 – reproducibility does not indicate lack of intelligent behaviour.

The vertical bending of a seedling shoot or root when placed horizontally is often assumed to represent autonomic behaviour. However this gravitropic response can be over-ridden by touch or environmental gradients of temperature, minerals or water placed at different polarities to the vertical gravity vector [89,94]. The bending response is thus a composite (sensory) integration of all perceived environmental information even if other variables are kept constant. Change the other variables and the response changes with it; this is the case for all examined phenotypic adaptations [5]. Autonomic behaviour is environmentally independent, resulting from a single pathway of information flow and is exemplified in humans by the knee jerk response.

There are ten abiotic signals and at least six biotic signals to which plants are normally sensitive. If plants can distinguish five strengths of signal in each category (an underestimate) and the signals vary independently, then the number of possible environments in which a temperate plant might grow is in the order of 10^8. Preprogramming by some sort of direct genetic means is neither likely nor possible. Only intelligent, flexible responses can provide the individual with the ability to master this complexity of environment and maximize sibling number.

Where do we go from here?

John Allmann [95], a neuroscientist, described bacteria as follows. 'Some of the most fundamental features of brains, such as sensory integration, memory, decision-making and the control of behaviour, can all be found in these simple organisms.' Although the intelligence might not be advanced, multi-cellular plants are capable of all these capacities and in a more complex fashion than bacteria. Experimental demonstrations of plant memory have already been listed [5,96,97]. To paraphrase Thomas Seeley and Royce Levien [6] 'It is not too much to say that a plant is capable of cognition in the same way that a human being is. The plant gathers and continually updates diverse information about its surroundings, combines this with internal information about its internal state (simple reasoning) and makes decisions that reconcile its well-being with its environment'. With a phenotypically plastic plant, intelligent modifications using an adaptive representational network (Figure 3)

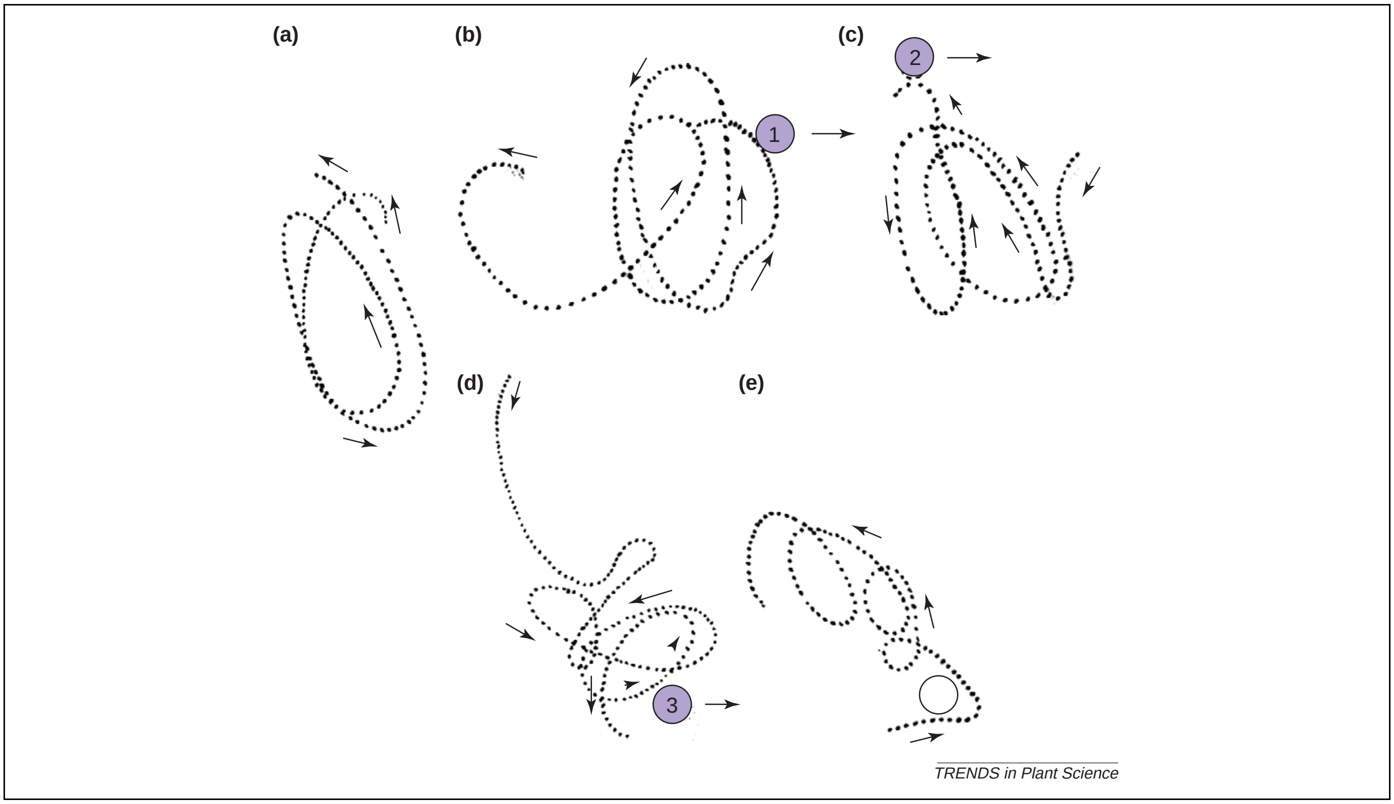

Figure 2. The movements of a *Passiflora* tendril when presented with a support at positions 1–3 successively. **(a)** Movements of a tendril in the absence of a grassy support. The support was then placed at position 1 **(b)** and then moved to position 2 **(c)**, and subsequently moved to position 3 **(d)** when the tendril neared the support in each case. **(e)** The empty circle indicates where support 3 was located. The whole set of observations lasted ~8 h. See Ref. [90] for further details.

that optimizes benefits versus costs is essential to solve environmental problems and improve fitness; otherwise development would be chaotic [98]. Pierre-Paul Grassé [99] described the intelligent behaviour of two predatory protozoa *Arcella* and *Chaos*; he is emphatic that organisms must be studied in wild environments that challenge the organism to observe intelligent behaviour. It is perhaps no accident that the plant behaviour described in this article was largely published in ecological journals.

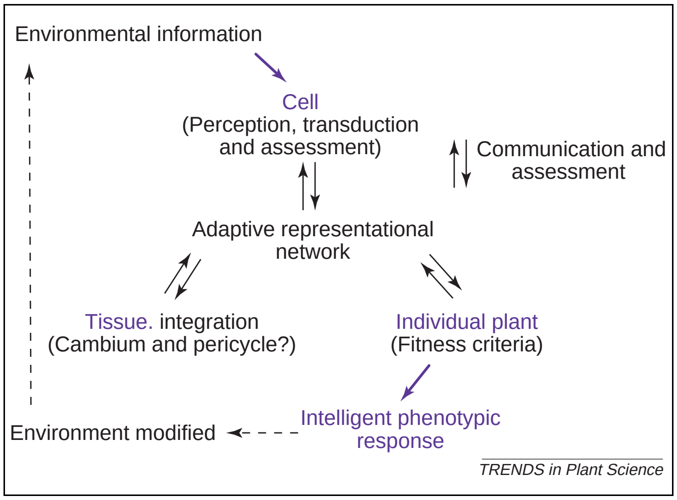

Figure 3. The central behavioural function of the Adaptive Representational Network (ARN). Environmental information is perceived by cells, transduced and assessed. This modified information is passed to the other tissues of the plant. In turn, this information is again modified and assessed and returned in a different form. An ARN is thus constructed involving the whole plant that models the cost and benefits of particular future behaviours to ensure that the costs of fitness strategies do not outweigh the benefits that adaptive, resilient, behaviour procures. Both the cambium and pericycle (meristems forming an inner skin in shoot and root) might play a particular integrative role in assessing the state of branching and control through manipulation of vascular tissue behaviour. Fitness criteria operate at the whole plant level. The challenge is to understand the mechanism of the ARN. Phenotypic plasticity requires intelligent control of behaviour or the organism becomes disorganized.

The rosette model of Warwick [1] for human intelligence (described above) indicates that further quantification of plant plasticity traits is needed, particularly in roots and stems. What mechanisms are involved in plant intelligence? Research on plant receptors continues apace but the mechanism and location of assessment (simple reasoning) is not known. Do the cambium and pericycle act as coordinating entities coherently controlling all branching information and integrating new signals with the current plant state (Figure 3)? Further research is needed here. The intelligent behaviour of social insect colonies might be a useful parallel (both have foragers, can change the balance of resources collected and optimize controls for the conditions available). Perhaps the cambium and pericycle act like the beehive dance floor where hive intelligence assessment and integration is made. Seeley [100] has dissected many of the control systems in a hive and this could prove a profitable avenue of investigation to understand equivalent plant controls.

It is obvious that at present we should regard primate intelligence as much more advanced than that exhibited by plants. But once we can identify how well an individual plant performs '…in its own particular environment and enables one species to dominate and exert power over other species…', which Warwick regards as crucial features of intelligent capabilities [1], this conclusion might need to be reassessed.

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