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INVITED REVIEW

Aspects of Plant Intelligence

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Intelligence is not a term commonly used when plants are discussed. However, I believe that this is an omission based not on a true assessment of the ability of plants to compute complex aspects of their environment, but solely a reflection of a sessile lifestyle. This article, which is admittedly controversial, attempts to raise many issues that surround this area. To commence use of the term intelligence with regard to plant behaviour will lead to a better understanding of the complexity of plant signal transduction and the discrimination and sensitivity with which plants construct images of their environment, and raises critical questions concerning how plants compute responses at the whole-plant level. Approaches to investigating learning and memory in plants will also be considered.

Key words: Phenotypic plasticity, individuality, intelligence, niche, signal transduction, plant behaviour

INTRODUCTION

Intelligence is a term fraught with difficulties in definition. In part, the problems arise because of the human slant placed on the use and meaning of the word. However, although as a species we are clearly more intelligent than other animals, it is unlikely that intelligence as a biological property originated only with *Homo sapiens*. There should therefore be aspects of intelligent behaviour in lower organisms from which our superlative capabilities are but the latest evolutionary expression.

Stenhouse (1974) examined the evolution of intelligence in animals and described intelligence as 'Adaptively variable behaviour within the lifetime of the individual'. The more intelligent the organism, the greater the degree of individual adaptively variable behaviour. Because this definition was used to describe intelligence in organisms other than humans, it is a definition useful for investigating the question in plants. Do plants exhibit intelligent behaviour? The use of the term 'vegetable' to describe unthinking or brain-dead human beings perhaps indicates the general attitude.

However, in animal terms, behaviour is equated with movement, and since plants exhibit little if any form of movement, plant intelligence on that basis does not exist. Although some higher plants exhibit rapid movements (e.g. *Mimosa pudica*), these are exceptions rather than commonplace. *Mimosa* captures our attention because it operates on a time scale similar to our own, and it is the difference in time scales that frequently makes plants seem unmoving. The use of time-lapse facilities has indeed indicated that plants operate on very much slower time scales than our own, but once observed in this way, movement is quite clear.

In addition, the majority of multicellular plants, including macroalgae, are sessile, the result of a decision several billion years ago to gather energy and reducing potential via photosynthesis. Since light is freely available, movement has never been particularly critical to plant survival. Such movement as has been observed is usually limited to less complex plants such as blue-green algae. Rejection of that (photosynthetic) decision by the primordial animal eukaryotic cell ensured that movement became critical to find food and mates. Once animals started to prey upon each other, the development of highly differentiated sensory systems and specialized nerve cells to convey information rapidly between sensory tissues and organs of movement was an inevitable consequence. The predator–prey relationship has acted as a positive feedback loop to accelerate complex development and equally complex organ differentiation in animal evolution (Trewavas, 1986*b*). Movement is, however, the expression of intelligence; it is not intelligence itself. Stenhouse (1974) regarded the early expressions of intelligence in animals as resulting from delays in the transfer of information between the sensory system and the motor tissues acting upon the signals. The delay enabled assessment of the information and modification of information in the light of prior experience, and it was that assessment that formed the basis of intelligence. The key difference between plants and animals in the Stenhouse (1974) definition is in the word 'behaviour'. Silvertown and Gordon (1989) have defined plant behaviour as the response to internal and external signals. In plant terms these are familiar growth and development phenomena, such as de-etiolation, flower induction, wind sway response, regeneration, induced bud break/germination, tropic bending, etc. Thus, a simple definition of plant intelligence can be coined as *adaptively variable growth and development during the lifetime of the individual*. To add significance to this definition, time lapse shows that

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virtually all plant movements are indeed the result of growth and development.

It can be objected that animals also grow and develop, but there are important qualitative differences. The sessile plant requires a morphological and developmental pattern that enables exploitation of local minerals, light and water. Since the environment is a variable and often unpredictable quantity for any individual plant, development continues throughout the life cycle and is necessarily plastic if proper exploitation and growth are to be achieved. Plasticity is from all examinations adaptive (Sultan, 2000), by its nature variable between individuals in different environments, and therefore must involve an element of computation if it is to succeed. Since all plants exhibit adaptive plasticity within the lifetime of the individual (Bradshaw and Hardwick, 1989), they must all exhibit intelligent behaviour according to the definition above. In contrast, much animal development and differentiation is confined to a uterus or egg, is minimal in the adult form and, as a consequence, is often described as unitary. Plant development is clearly modular, highly polarized through tip growth, and often exhibits complex branching patterns to enable proper resource exploitation that continues throughout the life cycle.

It is crucial to appreciate that all intelligent behaviour in both animals and plants has evolved to optimize fitness. Plants must then have access to an internal memory that specifies the optimal ecological niche in which maximal fitness, usually regarded as the greatest number of viable seeds, can be achieved. When the niche is sub-optimal, plasticity in growth and development intervenes to counterbalance and to attempt to recover as far as possible the benefits of the optimal niche. The sub-optimal niche can then, in some way, be compared with the optimal niche to specify the necessary extent of plasticity in growth and development.

This article considers various aspects of plant intelligence and attempts to answer some of the inevitable criticisms that will come with the notion of the intelligent plant. The major problem is a mind-set, common in plant scientists, that regards plants basically as automatons. The reasons for this mind-set will be examined later, and counter-evidence provided. Other aspects, such as learning, memory, individuality and plasticity in plants will be reviewed, and the article will finish with some interesting examples of intelligence in action which ecologists are beginning to uncover. The article is long—it has to be when trying to justify a change in attitude. A very short version of this article has been published (Trewavas, 2002*b*), and see discussion article by Philips (2002).

SOME IMPORTANT CONSEQUENCES OF A DEFINITION OF PLANT INTELLIGENCE

Intelligent behaviour is regarded as a property of the whole individual plant or animal. Although there is discussion among population ecologists as to whether the plant should be regarded as the genet or an individual ramet because of the modular character and a certain degree of independence of behaviour of individual meristems (White, 1979), I shall assume that the individual is the genet. A consequence of a repetitive modular structure is that the individual ramets might be regarded as being like parallel processors contributing different experiences resulting from different ages to present day decisions.

Learning and memory are the two emergent (holistic) properties of neural networks that involve large numbers of neural cells acting in communication with each other. But, both properties originate from signal transduction processes in individual neural cells. Quite remarkably, the suite of molecules used in signal transduction are entirely similar between nerve cells (Kandel, 2001) and plant cells (Trewavas, 2000; Gilroy and Trewavas, 2001). Most decisions made by plants about growth and development do seem to involve communication between all parts of the plant, but with prominence in the decision given to meristems local to the signal. In the marine snail *Aplysia*, and probably all animal neural systems, learning and memory are intertwined. Learning results from the formation of new dendrites, and memory lasts as long as the newly formed dendrites themselves (Kandel, 2001). The neural network is phenotypically plastic and intelligent behaviour requires that plastic potential. Plant development is plastic too and is not irreversible; many mature plants can be reduced to a single bud and root and regenerate to a new plant with a different structure determined by the new environmental circumstances.

Adaptively variable behaviour in animals is commonly secured by coordinating different groups of muscles. Individuality in cell and tissue behaviour in plants can underpin behaviour of different, but equal, variety in individual plants, and will be considered later.

Do plants work by rote, incapable of anything but reflexive responses?

The animal reflex arc is invariant under all conditions and a common attitude sees plant behaviour as analogous and likewise automaton, rote and invariant. There are probably at least four reasons for this mistaken perception.

(1) The use of statistics to simplify complex individual behaviour.

Statistics originated as a method to test whether two populations differed significantly as a result of their environmental treatments. However, the wholesale summary of physiological responses through means, averages or medians simply eliminates individual variation on the common, but incorrect, assumption that such variation is only experimental error (Trewavas, 1998). Individual behaviour (as required in the definition of intelligence) is ignored and behaviour thus over-simplified. Quite critically, the mean or average does not usually reflect the behaviour of any individual and is simply a composite population response with meaning only to those who wish to study the behaviour of whole populations. But the behaviour of the mean is commonly assumed to reflect the behaviour of each individual in the whole population, particularly when describing mechanisms. Statistical averaging can seriously mislead as to actual mechanisms in individual plants.

Gravitropic responses illustrate the difficulty. Ishikawa *et al.* (1991) imposed a gravitational stimulus on young growing roots to produce, some 5–6 h later, the textbook picture of recovery to vertical growth. However, the trajectory of individual roots back to the vertical was far from simple, and Ishikawa *et al.* (1991) properly recognized five approximate classes of response. Zieschang and Sievers (1991) found the trajectories of individual gravi-responding roots of *Phleum pratense* too complex to summarize as statistical means. Gravi-responding hypocotyls or coleoptiles can likewise show enormous variations in trajectory back to the vertical (Macleod *et al.*, 1987). Red light, calcium, touch, moisture, oxygen, temperature, ethylene and auxin have all been reported to modify gravitropic bending, illustrating the common observation that physiological phenomena are integrated responses resulting from many environmental influences (Trewavas, 1992). But variations in individual seedling sensitivity to each of these factors increase the variety of individual responses. Rich and Smith (1986) noted similar complexity in initiation time in phototropism, with individual hypocotyls requiring anywhere from 5 to 40 min to initiate response to the same blue light signal. They discuss the problems that averaging incurs in deciding on transduction mechanisms to this signal. Integration of many different environmental influences to produce a final integrated response is a particular feature of the intelligent animal.

(2) Controlled environments during experimentation.

Because the effects of the numerous environmental factors on plant growth and development can be complex, students are taught to examine such complexity by keeping all environmental factors constant except one, which is varied sufficiently strongly to obtain a response. Again, the response is usually summarized statistically. These experimental approaches, which are perfectly valid for asking questions about population behaviour, predispose towards assumptions that responses are reflexive because the signal is imposed until a response is obvious. A good example is water deprivation in which water is withheld until a response is achieved. However, in the wild, a multiplicity of factors affect the response to water deprivation, and the imposition of the stimulus takes place in a constantly changing environmental framework on plants of different age, different genotypes and very different circumstances. Experimentally depriving an animal of water or nutrient for several days and then exposing it to sources of either, would give rise to an apparently reproducible response (particularly when summarized statistically), but no-one would regard such responses as indicating lack of intelligence; far from it.

(3) The capacity to navigate a maze.

One of the hallmarks of intelligent behaviour in the laboratory is the capacity of animals to run successfully through mazes and to receive an eventual reward. But the capacity of plants to grow through an environmental maze is not commonly assumed to represent intelligent behaviour and attracts little attention. Individual branches growing through gaps towards sources of light are an obvious example (Trewavas, 1986*b*). Numerous studies on rhizomes suggest that higher plants must be able to construct a three-dimensional perspective of their local space and optimize their growth patterns to exploit resources, thus receiving rewards for successful behaviour. To any wild plant the environment represents a continual maze that must be successfully navigated.

Dia-gravitropic rhizomes can certainly sense vertical environmental vectors, either from being buried or from receipt of light near the surface, with vertical growth then being adjusted (Bennet-Clark and Ball, 1951; Maun and Lapierre, 1984). Consistent control of rhizome horizontal direction has been observed, particularly in heterogeneous soil environments, which are extremely common (Farley and Fitter, 1999). Rich soil patches are exploited by increased branching and growth; poor ones are either directly avoided or the rhizome thins to conserve resource use and growth is accelerated to speed the detection of new richer patches (Salzmann, 1985; MacDonald and Lieffers, 1993; Aphalo and Ballare, 1995; Evans and Cain, 1995; Kleijn and Van Groenendael, 1999; Wijesinghe and Hutchings, 1999). Evans and Cain (1995) report that *Hydrocotyle* rhizomes veer away from patches of grass and thus from competition.

Roots are able to sense humidity gradients and thus also construct a three-dimensional environmental perspective (Takahashi and Scott, 1993). Increased root branching in soil patches rich in nitrate or phosphate indicate a similar ability in environmental perception (Drew *et al.*, 1973). Roots will also take avoidance action when near others (Aphalo and Ballare, 1995). These data, and others, have led to the concept that plants actively forage resources from their environment (Hutchings and deKroon, 1994) using assessment mechanisms similar to those of animals.

Both plants and animals use exploratory behaviour to enhance the chances of survival by optimizing the gathering of food resources, thus maximizing both the potentials for reproduction and the selfish passage of genes into the next generation.

(4) Intelligent behaviour in animals requires the right environmental context for it to be expressed.

A simple (sometimes controversial) way to detect intelligent behaviour in humans is to impose an IQ test. These two factors, environmental context and organism, are both essential in detection and examination of intelligent behaviour. Just as obvious intelligent behaviour is not so easy to detect in caged animals in zoos, it will not be readily observed in laboratory grown plants; in part, because the necessary competitive and variable circumstances to elicit intelligent responses are not present. Intelligence requires both the organism able to compute and the right environmental circumstances to elicit that computation. On that basis, it is not surprising that most observations supporting the concept of plant intelligence come from ecologists studying plant behaviour under conditions more nearly mimicking those of plants in the wild. The observations of

Darwin or Von Sachs that suggested similarities between animal behaviour, nervous systems and the behaviour of plants (quotations are to be found in Trewavas, 1999) could represent the lack of controlled growth and laboratory facilities in the 19th century, and thus the likely observation of plants growing under less-controlled and far more realistic circumstances, eliciting intelligent behaviour.

THE BASIS OF INTELLIGENT BEHAVIOUR

Learning involves goals and error-assessment mechanisms

At its simplest level, whole organism learning requires two things: (1) a goal (or set point), usually determined in advance, and (2) an error-indicating mechanism that quantifies how close newly changed behaviour approaches that goal. For those who prefer a familiar human example with a short-term goal, learning to ride a bike is a good model. The process of learning requires a continual exchange of information and feedback from the goal to the current behaviour in order to correct current behaviour and direct future behaviour more closely towards achieving the goal.

Wild plants need trial-and-error learning because the environmental circumstances in which signals arrive can be so variable. That is, the starting point can be indeterminate and rote behaviour would be insufficient to ensure successful progress towards the goal. Whereas the eventual fitness goal may always be the same, the life trajectories attempting to achieve that goal must be learnt. Indications of trial-and-error learning can be deduced from the presence of damped or even robust oscillations in behaviour as the organism continually assesses and makes further corrections to behaviour. The reason that plants respond to gravity, for example, is primarily one of nutrition (shoots to light, roots to minerals and water), leading to better growth and eventual reproduction. But roots and shoots may find themselves at any angle to the final desired position and thus must learn progressively how to approach the internally specified optimal angle if conditions allow. However, the final branch angle adopted depends on a congruence of environmental assessments with internally specified information which can be accessed as a default position when conditions are optimal.

There are numerous plant learning examples, and I detail a few to indicate the point. Oscillations and overshoot in the approach of seedling shoots or roots to the vertical after horizontal displacement have been reported, for example, by Johnsson and Israelsson (1968); Heathcote and Aston (1970); Shen-Miller (1973); and Ishikawa *et al.* (1991). Johnsson (1979) lists a further 23 earlier references that report this behaviour. Bennet-Clerk and Ball (1951) detailed the gravitropic behaviour of many individual rhizomes and report overshoot, undershoot, growth initially in the wrong direction and sustained oscillations. These authors specifically note that averaging tends to eliminate detection of individual behaviour because individuals are rarely in synchrony with each other. Clifford *et al.* (1982) reported that deliberate bending of *Taraxacum* shoots causes overcompensatory growth in the other direction upon release, again indicating error correction with a goal (or set point).

Bose (1924) used continuous recording to report that the behaviour of petioles, roots, styles and leaflets of *Mimosa* to thermal, mechanical and light stimuli often oscillated in their approach to a new state of growth.

When leaves are deprived of water, stomata reduce aperture size, but a tendency to overshoot and oscillations in the new steady state have both been reported (Stalfelt, 1929, quoted in Raschke, 1979). Raschke (1970) detected oscillations of the average stomatal aperture determined by porometry in different regions of maize leaves. Johnsson (1976) concluded that both feedback and feed-forward mechanisms are involved in error correction and optimizing stomatal aperture.

Following mild water stress there is often a period of compensatory growth after rewatering, indicating an error-correction mechanism (Stocker, 1960). Trees can abscind sufficient leaves to adjust numbers to current water supplies. Some trial-and-error mechanism must determine when sufficient have been dropped (Addicott, 1982). Similar mechanisms must be present for all phenotypically plastic processes. Thus, for example, stem thickening in response to wind sway must be able to access the goal of optimal wind sway and a trial-and-error assessment of how far the individual is from that goal.

Resistance to drought or cold can be enhanced by prior treatment to milder conditions of water stress or low temperature (e.g. Kramer, 1980; Kacperska and Kuleza, 1987; Griffiths and McIntyre, 1993). Such well-known behaviour (acclimation) requiring physiological and metabolic changes is analogous to animal learning.

Similarities in avoidance responses by plants and animals

A single stimulus in the marine snail, *Aplysia*, designed to produce avoidance responses (the goal in this case) may only initiate short-term memory changes lasting a few minutes (Kandel, 2001). The intracellular mechanisms involve the second messengers Ca^{2+} and cyclic nucleotides and a limited number of protein kinases that phosphorylate ion channels that serve as temporary memory (Greengard, 2001). Repetition of the stimulus or increasing its intensity modifies protein synthesis in neurones and the formation of new dendrites (neural connections). The transduction of these avoidance stimuli involves MAP kinases, control of gene expression by cyclic nucleotide binding elements (CREB), and the ubiquitin pathway to dispose of protein kinase A-regulatory proteins. Increasing the size of the stimulus again greatly enhances further dendrite formation and results in a strengthening and increased effectiveness of dendrites already present in the chosen pathway of communication by adhesion mechanisms that may involve integrins. Additional growth factors are now involved including EF1α (Greengard, 2001), a protein with similar functions in both animals and plants. The new dendrites in this animal represent memory and as they disappear so the memory disappears.

Drought avoidance behaviour by plants is well established. Slight variations in water availability incur equally slight, but temporary, reductions only in cell growth rate, probably involving changes in second messengers, particularly cytosolic Ca^{2+}, $[Ca^{2+}]_i$, and phosphorylation changes in turgor-generating ATPases and associated ion channels (Begg, 1980; Hanson and Trewavas, 1982; Palmgren, 2001). More intense stress signals initiate changes in protein and wall synthesis, cuticle thickness, stomatal conductance and limited morphological reductions of leaf area (Hsaio *et al*., 1976; Kramer, 1980). Each of these processes seems to have a discrete water potential threshold at which it is initiated. Perhaps progressive reductions in plasma membrane wall adhesion are responsible, initiating transduction mechanisms and modifying plasmodesmatal functioning. The transduction mechanisms include those mentioned above and MAP kinases and other protein kinases modifying transcription factors (Hetherington, 2001; Jonak *et al*., 2002).

With more severe water stress, the root : shoot ratio increases and, in wild plants, it can vary up to 20-fold (Chapin, 1980). In developing leaves, the internal mesophyll surface area is reduced and stomatal density modified, producing a xeromorphic-type morphology (Stocker, 1960). Increased hairiness, early flowering and a modified vascular system are induced later, indicative of memory of the initial droughting signal (Stocker, 1960; Kramer, 1980).

All of the above responses, whether physiological or morphological, must be initiated and transduced by mechanisms that can assess the current supply of water against a notional optimal supply. The plant learns by trial and error when sufficient changes have taken place so that further stress and injury are minimized 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, temperature, humidity, age, previous plant history, disease and probably with all external environmental influences; they are not therefore reflexive responses. Clearly decisions are made by the whole plant.

The similarities between avoidance responses in neural circuitry and plant water stress are: (1) a graded response in both cases according to strength of stimulus; (2) similar transduction mechanisms with the different strengths of stimuli; (3) morphological changes in nerve cells and plants induced only by the stronger stimuli; (4) the result of neural learning is to coordinate the behaviour of different muscles to enable an avoidance response by movement. The result of plant learning is to coordinate the developmental behaviour of different tissues to produce an avoidance response by phenotypic plasticity. Muscles are as constrained in their behaviour as any plant tissue, there are just many of them that can be coordinated together to generate great varieties of behaviour. (5) Animal learning lays down additional pathways of communication. Plant learning increases vasculature and increased communication between cells through plasmodesmata (see below). (6) Both organisms integrate the present organismal state to modify the response to further signals. Morphological changes in plants do act like long-term memory, because they will influence subsequent behaviour by the individual plant when other environmental signals are imposed. It can be objected that long-term animal memory is reversible in the absence of further stimulation, whereas morphological changes are not. However, this is not the case. In the short term, stomata usually open again within a few days when water stress is still imposed. 'Xeromorphic' leaves are often the first to be abscised after rewatering and new leaves are formed by bud break. There is root turnover and death (Bazzaz, 1996) enabling some recovery of root : shoot ratios.

Do seedlings learn about their environment?

The seedling stage is the most vulnerable for any higher plant, with chaotic fluctuations at the soil surface in temperature, moisture, carbon dioxide, light, patchy nutrient dispersal and the common but variable enemies of disease and predation. There is also a stochastic character to seed dispersal, dormancy breakage, degree of phenotypic individuality (Bradford and Trewavas, 1994) and thus indications that the behaviour of every seed will differ from that of others in certain aspects of behaviour (Bazzaz, 1996). The integrated environment can be viewed as a topological surface continually changing in shape that is directly mapped onto the signal transduction network in sensitive cells and tissues in mirror image, eliciting responses to navigate the environmental maze (Trewavas, 2000). Each seedling must experience a unique spatial and temporal environmental surface. Bazzaz (1996, p. 168) illustrates topological surfaces constructed from the interaction of two environmental variables on different genotypes.

It is recognized that signal transduction mechanisms can be represented as a network. The implication may be that pathways of information flow between the signal and response may not be invariant between different individuals (McAdams and Arkin, 1999; Csete and Doyle, 2002; Elowitz *et al*., 2002; Guet *et al*., 2002; Levsky *et al*., 2002). What is suggested is that when a seedling first receives a signal, a weak response is constructed using the signal transduction constituents to hand and with the signal information finding various channels through which it can flow. Further signalling reinforces this information channel by synthesis of particular signal transduction constituents, much as increased numbers of dendrites improve information flow rates during neural network learning. The signal transduction network thus learns (Trewavas, 2001). Seedlings that fail to learn adequately, quickly die off. It is already known that Ca^{2+}-dependent and -independent processes can be separately invoked to induce identical physiological processes (Allan *et al*., 1994), and that the synthesis of many constituents concerned with calcium signal transduction are synthesized following signalling (Trewavas, 1999, 2001).

COMMUNICATION TO CONSTRUCT INTELLIGENT NETWORKS

Intelligence requires a network of elements capable of adaptively variable information flow to underpin intelligent behaviour. In animals, nerve cells are specifically adapted by structure to enable rapid phenotypic adjustments and computation. But, critically, a network requires communication between the elements.

Communication in neural systems

Much early work in the last century hinged on the notion that communication across nerve synapses and throughout the brain was purely electrical. Action potentials jumped across the synaptic divide propagating further action potentials downstream. A contrasting view suggested that communication between nerve cells was performed solely by chemicals, although these in turn would generate action potentials down the long axon. Neurotransmitters were released by fusion of secretory vesicles with the plasma membrane. Specific neurotransmitter receptors across the synapse induced a new action potential by modifying ligand-operated ion channel function. The chemical messenger theory is correct: 99 % of all communication in the brain is chemical (Greengard, 2001). Action potentials are used primarily to speed communication down the long nerve cell axons.

Two kinds of chemical transmission are recognized. Fast transmission, completed in milliseconds, uses the neurotransmitter glutamate and glutamate receptors; fast inhibition uses γ-aminobutyric acid (GABA). Slow transmission can take many minutes and is enormously more complex, involving at least 100 different chemicals falling into four classes: biogenic amines, peptides, amino acids and nitric oxide (Greengard, 2001). Quite remarkably, glutamate has recently been found to influence cytosolic $[Ca^{2+}]_i$ in plant cells and nitric oxide is a recognized second messenger in plant cells (Dennison and Spalding, 2000).

Communication between and within plant tissues

That the various parts of plants communicate with each other has been established by many experiments. Various surgical treatments (such as removal of root or shoot or leaves, mimicking predation or other damage), resource stress (lack of light or water or minerals) or exposure of one part of a plant to varying resource levels, give rise to specific changes in growth and development elsewhere in the plant, indicating communication of the stimulus. Such phenomena have been called correlations. In these above cases, development is usually adjusted to try and recover a balance between root and shoot or to ensure a better balance of basic resources. [Note, again, the presence of a goal (set point) and an error-correcting (learning) mechanism.] Flowering, tuberization, bud break, enhanced root growth and branching can follow selective exposure of leaves to particular light periods. Signals are thus transmitted from the leaf to other tissues (Trewavas, 1986*b*).

Shortage of specific resources leads to accelerated growth of the tissue (either as elongation, weight or branching) that normally collects the resource. In contrast, abundance of all resources leads to increased branching or, if the resource is localized, often local branching. When shaded, shade-intolerant species show substantial elongation of the primary stem (at the expense of lateral stem growth), increased leaf area and a disproportionate reduction in the growth of fine roots (Bloom *et al*., 1985). Shortage of water leads to enhanced root growth and particular proliferation when an abundance of resources is located. Lake *et al.* (2001) observed that high CO_2 levels reduce stomatal frequencies, but the CO_2 signals are sensed by mature leaves and the information conveyed to developing leaves which cannot respond to high CO_2. Communication of aphid attack between plants has recently been shown to involve other volatiles (Petterson *et al*., 1999).

By use of a microbeam of red light, Nick *et al.* (1993) provided convincing evidence for cell-to-cell communication between cotyledon cells with long-range inhibition of gene expression in un-irradiated cotyledon cells at some distance from the irradiated patch. Moreover, the cell regions responding were, in turn, specifically determined by the region irradiated, suggesting selective communication only between certain cells in the cotyledon.

The information that is being communicated between tissues and cells is now known to be extraordinarily complex. Communication involves nucleic acids, oligonucleotides, proteins and peptides, minerals, oxidative signals, gases, hydraulic and other mechanical signals, electrical signals, lipids, wall fragments (oligosaccharides), growth regulators, some amino acids, secondary products of many kinds, minerals and simple sugars (Bose, 1924; Gilroy and Trewavas 1990, 2001; Jorgensen *et al*., 1998; Sheen *et al*., 1999; Mott and Buckley, 2000; Sessions *et al*., 2000; Kim *et al*., 2001; Nakajima *et al*., 2001; Brownlee, 2002; Haywood *et al*., 2002; Takayama and Sakagami, 2002; Voinnet, 2002; references on growth regulators in Quatrano *et al*., 2002). Transcripts can even move between graft unions (Kim *et al*., 2001). From the current rate of progress, it looks as though plant communication is likely to be as complex as that within a brain. The demonstration of macromolecule movement between cells is of considerable significance because it enables substantial amounts of information to be built into the signal if needed; thus complex information can be encoded in the signal.

Plasmodesmata controlling information flow

Plasmodesmatal connections enable movement of proteins and nucleic acids as well as smaller molecules between plant cells (Zambryski and Crawford, 2000). Movement of transcription factors and nucleic acids has the potential to activate or repress genes in cells remote from the source by activation of DNA methylation or by mRNA translation; oligonucleotides with specific sequences can silence genes. To create a complex, cellular network capable of computation also requires particular cellular locales for specific receptors remote from the source of the signal. Alternatively, substantive variation in sensitivity to the same signal between individual cells might achieve the same end.

Furthermore, just as synaptic connections (dendrites) can be increased to amplify particular pathways of communication during learning, individual cells can modulate the extent of plasmodesmatal transport. Physiological alterations of plasmodesmatal transport result from anaerobic and osmotic stress, or changes in $[Ca^{2+}]_i$ or inositol phosphates (Ding *et al*., 1999). I expect this list to increase. Even slight changes in growing conditions have been observed to modify signal transmission (Zambryski and Crawford, 2000). Quantitative and qualitative changes in plasmodesmatal number occur during development, and secondary plasmodesmata can be formed in the absence of cell division and can even branch rather like the synthesis of new dendrites.

Plasmodesmatal connections seem to be limited to adjacent cells. Whether plasmodesmatal strength, analogous to synaptic strength, could be increased is not clear but, intriguingly, one of the proteins that binds plasmodesmatal proteins is pectin methylesterase (Jackson, 2000). Such observations might imply that connections between plasmodesmata and the wall can be altered and that mechanical constraints alter plasmodesmatal function leading to a modified flux of information. In this case wall interactions could control the ability of plasmodesmata to act like an information valve, changing flux rates according to mechanical stresses imposed either by the environment or resulting from mechanical stresses induced by growth.

Communication within cells

Communication within cells is equally complex, and stable and transient transduction complexes are known to be used to interpret new information (Gilroy and Trewavas, 2001). Cytosolic Ca^{2+}, $[Ca^{2+}]_i$, in particular, seems to act as a cellular second messenger with ubiquitous roles in signal transduction and intracellular communication. $[Ca^{2+}]_i$ has very limited cytoplasmic mobility, and enhanced entry through channels following signalling activates Ca^{2+}-binding proteins within the microdomain in which channels are clustered (Trewavas, 2002*a*). Localized intracellular distributions and particular control properties of channels and ATPases that pump Ca^{2+} back into subcellular compartments or walls result in Ca^{2+} waves and oscillations (Mahlo *et al*., 1998; Schroeder *et al*., 2001), a rich source of information and specific communication. Rapidly moving Ca^{2+} waves have been observed in a number of cell types and thus can act to coordinate parts of the recipient cell towards a behavioural objective (Sanders *et al*., 2002). The wave moves on the surface of cellular membranes, most probably the endoplasmic reticulum (ER) and inner plasma membrane surface. The wave itself is a movement of Ca^{2+}-induced Ca^{2+} release and not a physical transmission of Ca^{2+} ions. Topological similarities between Ca^{2+} waves and simple neural circuits enabling aspects of computation to be understood have already been drawn (Trewavas, 1999).

Many different environmental signals (e.g. touch, wind, cold, disease, gravity, etc.) modify $[Ca^{2+}]_i$ and are responsible for generating phenotypic plasticity. How can a single ion mediate such response variety? The reality is that $[Ca^{2+}]_i$ is just one of a large number of signals that operate in signal transduction, but one that acts as a nodal point in a robust transduction network. Complexity in $[Ca^{2+}]_i$ signalling is increased by contributions from various organelles, such as the nucleus, ER or chloroplast (Van der Luit *et al*., 1999). The nucleus is thought to have its own Ca^{2+} mobilizing system, and mitochondria and chloroplasts have internal Ca^{2+} control. The ER and the vacuole modify cytoplasmic signals (Sanders *et al*., 2002). Different closing signals in guard cells elicit Ca^{2+} responses from different compartments (Gilroy and Trewavas, 2001). The amplitude and kinetics of the Ca^{2+} transient (wave) and different regions of the transient can also initiate discrete transduction sequences. Changes in $[Ca^{2+}]_i$ can be extremely rapid (within the 100 ms range) and can initiate selective changes in gene expression. Changes in $[Ca^{2+}]_i$ are also essential to communication and learning within nerve cells (Greengard, 2001).

PLANT MEMORY AND INFORMATION RETRIEVAL

In nervous systems, new connections (dendrites) between nerve cells may form the basis of memory (Kandel, 2001) and loss of the dendrite coincides with loss of memory. What is required for memory is an ability to access past experience so that new responses incorporate relevant information from the past. Many different forms of plant memory can be envisaged, all of which modify signal transduction, from the current chemistry and enzymology of membranes (Gilroy and Trewavas, 2001) or wall characteristics (Trewavas, 1999), to prior expression of particular genes. It is also clear that the history of stimulation modifies subsequent transduction (Ingolis and Murray, 2002) and, in plants, intepretation through $[Ca^{2+}]_i$ is likewise modified by previous signalling, ensuring another form of memory is present (Trewavas, 1999). All these forms of memory can be recognized by the ability to interact with, and modify, the transduction pathways to new signals. The only requirement is merely that the memory can be accessed and can influence the response to the current signal. A more complex form of memory requires information storage of previous signalling, with the ability to retrieve the information at a much later time. Both forms occur in plants.

Memory of developmental status.

It is obvious that the present state of development acts as memory for any individual plant because the same signal can have different effects determined by when the plant, tissue or cell receives it. The effects of blue or red light signals are good examples, having different effects dependent on the stage of development. Thus, red light can affect leaf movement, stem elongation or germination. Furthermore, photoperiodic plants can be exposed to one or two inductive photoperiods and then returned to a non-inductive light/dark schedule where they will continue to flower. Some long-lived memory has obviously been instituted. Plants that are vernalized by 3 weeks' low temperature, or appropriate imbibed dormant seeds given 3–4 weeks' low temperature, retain the memory of that treatment and either flower or germinate when the inductive schedule is no longer imposed. Lloyd (1980) suggested that flowering consists of a series of reassessment points in which adjustments to the final number of flowers could be made dependent on nutritional availability, in a form of learning and memory. If seed imbibition takes place in conditions that are inimical to germination then a more prolonged state of dormancy—secondary dormancy—can be entered into, lasting many years (Trewavas, 1986*a*). Some dormant imbibed seeds can show annual flushes in germination rates, often in the form of damped oscillations in numbers, germinating over successive years. Many aspects of dormancy are analogous to nervous memory; there are short- and long-term versions, dormancy can be reinforced or overridden, and a variety of environmental facets interplay to modify germination and dormancy. Even the molecular basis of long-term dormancy may be similar to animal memory (Trewavas, 1986*a*). Apolar *Fucus* zygotes can be polarized by a 1-s flash of intense directional blue light, and so on. Examples abound.

In the whole plant there are many examples where prior signals modify the response to rapid subsequent signals, thus indicating memory of the previous signal. Dostal (1967) describes many such examples produced by himself. For example, exposure of de-etiolated flax seedlings to white or red light generally has no influence on cotyledonary bud growth. But if the main stem above the cotyledons of flax seedlings is removed, both cotyledonary buds grow out. When Dostal removed one cotyledon and the main stem from flax seedlings and placed the truncated seedling in white light, only the axillary bud subtended by the remaining cotyledon grew. But when placed in red light the opposite bud grew out. Both buds retrieve information concerning the presence or absence of the apex and will have received signals to grow. But retrieval of that information can be subsequently overridden for either bud by other later signals arising from light exposure, the wavelength of light and the presence or absence of the cotyledon.

In *Scrophularia nodosa*, information retrieval by dormant buds is evidently modified by the state of development (Dostal, 1967). This plant has square-shaped stems, dichotomous branching and, thus, known vascular arrangements. Cuttings were made from pieces of stem containing two opposite leaves and thus two axillary buds. If kept moist, both axillary buds break dormancy and grow; adventitious roots form on all four sides of the base of the cut stem. However, if the leaves were mature, removal of one of the leaves inhibited growth of the subtended axillary bud whilst permitting the other bud to grow out. Adventitious roots then formed only on the side of the amputated leaf. If the leaf left behind was not fully mature, inhibition of axillary bud growth was still evident, but the roots developed on the opposite side underneath the remaining leaf. If the leaf left behind was developmentally very young, both the axillary bud and roots grew out only on the leaf side. There is thus a complex interplay between age of leaves, leaf removal, bud outgrowth and root formation that modifies the original excision signal, but the memory of that signal remains in the activity of the buds.

Retrieval of information after a delay

Similar experimental approaches in *Bidens pilosa* have shown that the initial signal can be separated from its effects by many days. Removal of the growing apex from young seedlings again results in outgrowth of cotyledonary buds (Desbiez *et al*., 1991). Puncturing one cotyledon of non-decapitated plants had no effect on the cotyledonary buds which remained quiescent. But if one cotyledon was pricked with a needle, both cotyledons then removed within 5 min, and the seedling then decapitated several days later, the bud opposite to the pricked cotyledon started to grow much faster than the other. An asymmetrical state had been achieved, but usually in only about half of the seedlings. The response is clearly an example of individuality. The recall of information about the original needle damage required the seedling to be in the appropriate state. Various environmental treatments, such as cold or warm temperatures, could override the retrieval of information that specified asymmetry. It was thought that a wave of depolarization was the signal conveyed to the bud from the puncture signal on the cotyledon. The overriding environmental treatments are all known to modify $[Ca^{2+}]_i$.

Ca^{2+} controls the accessible memory of environmental signals involved in the induction of flax epidermal meristems (Verdus *et al*., 1997). These hypocotyl meristems could be induced by drought or wind signals, which are also known to increase $[Ca^{2+}]_i$ transiently. But induction required a depletion of seedling Ca^{2+} for about 1 d before the effects of drought and wind could be detected. Using this system, memory of the previous drought and wind signals could be stored and accessed for at least 8 d unabated, before expression was finally elicited by a Ca^{2+} depletion. The mechanism is unknown, but changes in gene expression or protein kinase activity resulting from drought and wind signals might be responsible.

Further examples of shorter term memory involving $[Ca^{2+}]_i$ have emerged. Exposure of etiolated cereal leaves to red light results in unrolling. However, sections of leaf will not unroll in red light if Ca^{2+} is removed from the medium (Viner *et al*., 1988). But if leaf sections are exposed first to red light, Ca^{2+} can be added back to the medium to induce unrolling up to 4 h later. Some excited state of the cells is induced by red light and is maintained for at least 4 h. Administration of a hyperosmotic shock normally induces a $[Ca^{2+}]_i$ transient of short duration (Takahashi *et al*., 1997). But if the shock is administered in the absence of extracellular Ca^{2+}, the transient fails to appear until extracellular Ca^{2+} is returned to the medium. The separation of shock and return of extracellular Ca^{2+} can last as long as 20 min.

Accessing of internal information; is the niche an accessible memory?

It is perhaps no accident that maximal fitness is the overall goal of any individual animal, and intelligent behaviour contributes to that goal (Wright, 1932; Dawkins, 1976). Wright (1932) used the metaphor of an adaptive landscape to produce a visual representation of fitness in which individuals represent hills or mountains with the maximally fit being the highest.

The operational life cycle goal to which all individual plants aspire is also maximal or optimal fitness. However, fitness is indissolubly linked with the local environment in which the individual finds itself and grows. Maximal fitness can be achieved when the plant grows in its optimal (fundamental) ecological niche. The niche is difficult to characterize (Bazzaz, 1996, and see below) and, with competition for resources in wild plants, is limited to the realized niche. But measurements show that the niche is individual to the genotype, not the species. On that basis it is likely that each individual plant will possess a unique niche memory to which it will attempt to match growth and development. The important feature is that information, which describes the fundamental niche, is present in the organism and can be accessed, thus representing a kind of long-term (life cycle) memory. How information about the fundamental niche can be inherited, when it is rarely realized (Hunt and Lloyd, 1987), is not understood.

Theoretical and experimental work suggests that species must have different resource requirements for them to coexist in a community; they must occupy different niches with only a minimum of overlap. Furthermore, recognition must be present, i.e. information encoded in the individual, that indicates when the niche conditions are met and when they are not. Since all plants require minerals, water and light, niche differentiation is considered more difficult to define in plants than in animals, where the concept first arose (Bazzaz, 1996). However, if the concept is useful it should inform upon the subject matter of this essay.

Phenotypic (and physiological) plasticity represents part or all of the error-correcting mechanisms that individual plants use in an attempt to achieve optimal fitness in the realized niche. Phenotypically plastic mechanisms are not reflex responses (see below) but depend on an ability to assess not only what tissues should alter (with the assessment influencing very early tissue development), but an ability to stop plasticity when sufficient change towards the optimal goal has been made. However, to have to resort to phenotypic plasticity implies that optimal fitness may not be achieved. Individual plants that express plasticity will more nearly approach the fitness objective than individuals that do not. But the error-correcting mechanism must involve complex negative feedback mechanisms with versions of trial and error; that is, learning.

Inherently, all descriptions of niche must basically concern the interaction of the plant with its environment, that is the position of the individual in both space and time (Wright, 1932). Moreover, the niche can differ for plants grown in the laboratory compared with those in the wild. Uniform stands of some plants such as wild wheat, *Phragmites* and *Spartina* are known to exist and may even be genetically identical. But most plants exist in complex communities implying discrimination by the individual plants amongst the numerous factors in the environment. It is known that wild populations contain enormous genetic diversity (Burdon, 1980) and it is thought that this reflects, in large part, environmental diversity which must be correspondingly complex (Antonovics, 1971).

Many plants do show different (non-equitable) physiological and morphological responses along gradients of any of the primary resources, and it seems unlikely that many or, indeed, any of these resource axes act independently of each other (Tilman, 1982; Bazzaz, 1996). Some resources, like N or K, can act synergistically but others can be incongruent; an increase in sunlight can institute moisture stress for example. If there are about 15 environmental factors acting in differing degrees and affecting the perception of each other then the combination of possible environments in which any individual can find itself and to which it must respond is enormous. Thus, the necessity for learning rather than rote behaviour. Moreover, long- and short-term responses to environmental variables will be different.

The response of an individual along a resource gradient is very strongly influenced by its neighbours. While negative interactions through competition for the basic resources of space, light, minerals and water, and interactions through allelopathy, are well established (e.g. Turkington and Harper, 1979; Turkington, 1983; Zangerl and Bazzaz, 1984), cooperative, positive interactions are clearly evident through mycorrhizal spread, symbiotic relations with bacteria, releasing nitrogen to other plants, remediation of local stressful environments (Salzman and Parker, 1985) or semio-chemicals warning other plants of predatory attack (Petterson *et al.*, 1999).

Time may be an additional critical factor in defining niche. Continued growth generates new environments for both root and shoot, and responses of both tissues to the environment change ontogenetically. In low vegetation, above-ground patchiness may be imposed by the spatial arrangement of dwarf shrubs and persistent clumps of perennial herbs and modified by microtopography and grazing. Hartgerink and Bazzaz (1984) observed that the imprint of a footprint on the soil, or a stone placed nearby, could accelerate germination rates but substantially reduced final biomass and seed number nearly three-fold, reducing fitness. Such results suggest a remarkably fine definition of the environment by the individual plant. Soil resources can be patchily distributed or may be continuous (Farley and Fitter, 1999).

Individual genotypes of *Polygonum* expressed unique norms of reaction in physiological, allocational and morphological characters (including fitness) when nutrient and light environments were modified [Zangerl and Bazzaz, 1984; Bazzaz, 1996 (note response surface on p. 168); Sultan, 1996, 2000; Sultan *et al.*, 1998]. Thus, at each setting of the environment, the individual plant can access information that it can use to construct a response and to ensure that overall, maximal fitness will be achieved. The implication is that the difference between the optimal niche/phenotype and the present environment and present phenotype can be measured. A counterbalancing response is then constructed that directs the individual into a new trajectory of development. Once again a goal is specified even though that goal might be heritable and an error-correcting mechanism is in place to try and achieve the goal. Constant monitoring of the new phenotype as it develops and continuous control are exerted to ensure that the new phase of development is optimal and consistent with long-term evolutionary objectives. Information about the individual genotype can be accessed as permanent memory and interpretation follows from interaction with the complex network that underpins signal transduction processes. Until we understand better the properties of signal transduction networks, we will not be in

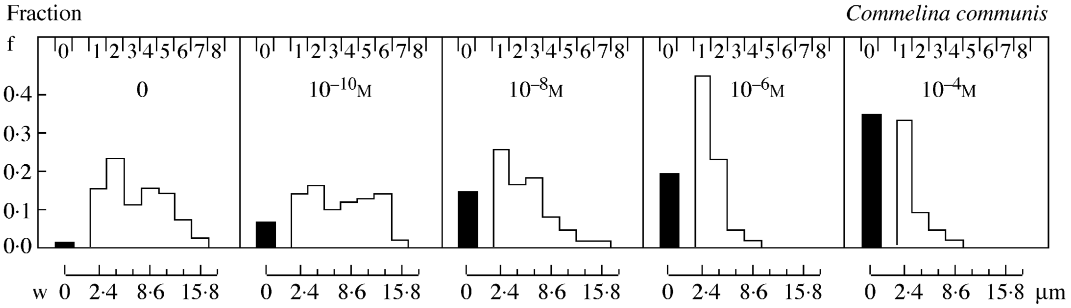

FIG. 1. Frequency distribution of stomatal apertures in illuminated strips from the lower epidermis of leaves of *Commelina communis*, floating on 80 mM KCl, plus the indicated concentrations of (±)-ABA. f, Fraction of stomata in a particular aperture class; w, stomatal aperture. The upper scale represents aperture-class numbers and shaded columns represent the fraction of closed stomata. Reproduced with permission from Raschke (1988).

a position to understand how plants achieve their fitness goals.

INCREASING THE VARIETY OF RESPONSE

Control circuitry and individuality

The genetic analysis of flowering time in arabidopsis will probably provide a paradigm for the genetic control circuitry that underpins other timing processes, such as breakage of bud and seed dormancy, in plant development. Although the precise molecular details are still being uncovered, some very broad outlines of control circuitry are now indicated (Simpson and Dean, 2002). Robust control circuits involve both feed-forward and feedback regulation, and obvious signals that attempt to propel the system forward or hold it back are obviously present in the flowering time circuitry. Integration of different signals is achieved, it is thought, by protein/protein interaction from different input signals on the promoters of integrator genes. Redundancy in the circuitry is also evident, providing for fail-safe mechanisms. Plasticity in flowering time results from quantitative variations in overlapping pathways. Further investigation may reveal the extent to which controls consist of modular groups of proteins that can be changed *en bloc* as it were and which overlap with each other providing reliability (Hartwell *et al.*, 1999). Hierarchical organization of modularity has already been detailed in metabolic networks (Ravasz *et al.*, 2002). However, these basic elements in control circuitry are what might be expected to control plasticity.

While genetics is a powerful investigative tool, we are not dealing with bacteria in which mutation affects only the cell in which it is expressed. Instead, the individual plant is a complex, multicellular and multi-tissue organism in which development is continuous and in which communication is paramount. Flowering time, an aspect of plasticity and behaviour, is a composite response involving all parts of the organism, including its life cycle. Mutations, the normal means of identifying relevant genes that modify any character, are often present throughout the whole life cycle. Knock-on consequences from some mutations may then only indirectly affect later processes such as flowering time. Intelligent behaviour is a holistic quantity reflecting in turn the whole organism, but some of the circuit control indicated above for flowering should be present at a whole-plant level.

The problems of resource gathering and predation for a sessile organism seem to be the major evolutionary pressures that have generated minimal tissue specialization, the branched structure and modular development. All higher plants are constructed from repetitions of the same basic modular structure, leaf plus bud and below-ground root meristems, repeated many times, but the numbers can vary enormously. Since a plant can be regenerated from a single meristem, redundancy in tissue development is self-evident. Furthermore, growth regulators often overlap in their effects. This is organizational plasticity we simply do not understand. But plants can be best viewed as more like a democratic confederation in their control structure rather than an autocracy as occurs in animals, controlled by an all-embracing nervous system. With a spatial and temporal mosaic of resources that surround the plant, some latitude must be present to allow the local but growing tissues to optimally exploit rich sources. Our understanding of plant intelligence must therefore accommodate these properties and answer some very basic questions: how many varieties of behaviour can be constructed with a limited number of tissues; does partial independence in the behaviour of individual growing tissues change a holistic view of plant intelligence?

Individuality is used to describe situations in which morphologically or anatomically identical cells, tissues or plants show non-similar responses to signals (Trewavas, 1998; Gilroy and Trewavas, 2001). The example of rhizome gravitropism quoted above (Bennet-Clark and Ball, 1951) details individual variations. Individuality receives little or no investigation in plant science despite being a widespread phenomenon. As if to counteract the paucity of different tissues in the normal vegetative plant, continued embryogenic development by meristems results in tissues and cells with enormous varieties of individual behaviour. A reservoir of different cell behaviours becomes available to enable construction of a variety of tissue and plant behaviours to exploit the resource mosaic. Individuality of the kind commonly observed in plants might be unique. A mechanism for individuality has been proposed as originating from stochastic variation in the distribution between daughter cells of tiny numbers of critical proteins controlling cell and tissue development (Gilroy and Trewavas, 2001; Federoff and Fontana, 2002).

Recognition of individuality can easily be seen from dose-response curves. If the responses are all-or-none [e.g. germination (the seed does or does not germinate), root formation, abscission, flowering, dormancy, senescence, etc.], then a dose-response curve simply reflects population variation in sensitivity to the inducing stimulus (Trewavas, 1991; Bradford and Trewavas, 1994). Such dose-response data can vary over three to five orders of magnitude change in the strength of the inducing stimulus, thus indicating the degree of individual variation (Trewavas, 1981). Nissen (1985, 1988*a*, *b*) compiled much information on this point using growth regulators as the controlling stimulus.

Individuality in guard cells

Because the behaviour of individual guard cells can be easily examined, I have used them as an illustration. Figure 1, published in Raschke (1988), quantifies the response of stomatal apertures in *Commelina* to increasing abscisic acid (ABA) concentration. The concentration range spans six orders of magnitude, but even then some guard cells have still not closed completely. Yet, at each concentration, an increasing number of stomata close, suggesting that the individual dose-response range can be much narrower than that of the whole population. The population response is thus made up of differential sensitivity amongst individual guard cells to ABA. Furthermore, by quantifying chlorophyll *a* fluorescence (Raschke 1988), temporal variation in the rate at which individual guard cells closed in the intact leaf was detected. After ABA treatment, patchiness in closure rates was observed. Further information is summarized by Mott and Buckley (1998, 2000).

Many signals have been described as regulating guard cell closure (Willmer and Fricker, 1996). If there is equivalent individual cell variation for each of these signals, as described for ABA, then enormous potential exists to construct many kinds of leaf water relation behaviours under a variety of environmental conditions. Each novel behaviour is constructed by putting together unique collectives of guard cells in both space and time. Such behaviour can be regarded as adaptively variable and thus coinciding with the definition of intelligence in foraging for carbon dioxide.

Mott and Buckley (2000) indicate that guard cell collectives (recognized as patches during closure) can behave coherently, chaotically and may oscillate in total aperture and vary in size and character as predicted from above. Crucially, patch behaviour is underpinned by definite evidence of communication across whole areas of leaf and between individual guard and epidermal cells. Such communication may result from hydraulic interactions, but much further investigation is needed to distinguish other anticipated mechanisms, such as electrical and chemical communication. Detection of oscillations in transpiration rate may result from this dynamic (Johnsson, 1976).

In the whole leaf, the most sensitive guard cells could potentiate the response of other local but less sensitive guard cells to closing signals by modifications of: (1) internal humidity; (2) abscisic acid sequestration; (3) carbon dioxide; (4) wall pH; (5) wall potassium and calcium levels; and (6) the osmotic behaviour of subsidiary and other guard cells (Willmer and Fricker, 1996; Mott and Buckley, 2000)—all factors known to modify aperture. The most sensitive cells might then act as critical elements in the propagation of information relating to aperture throughout local regions of the leaf; acting perhaps like relays in an excitable tissue. Sensitive guard cells could then be regarded as analogous to motor cells (organizing centres as described by Winfree, 1987), generating focal points that organize stomatal patch formation by influencing the behaviour of other guard cells. The rate of patch formation and its longevity would then be dependent on the local density of the most sensitive (motor) guard cells. Is intelligent behaviour to be sought in the network composed of the most sensitive cells?

Support for this possibility comes from the observations of Rascher *et al.* (2001). They showed that variations in crassulacean acid metabolism (CAM) in leaves are the result of localized but initially independent oscillators that eventually cooperate to produce the whole leaf circadian CAM response, in a fashion analogous to guard cell communication. Oscillators are characteristic of motor cell initiation and control (Winfree, 1987), and oscillations in activity are common in neural networks.

Other examples of individuality

Other cellular examples of individuality have been reported in gibberellin-dependent amylase production by aleurone protoplasts and in pericycle cells sensitive to auxin (Gilroy and Trewavas, 2001). Further observations of individuality have been made in cotyledon cells, in anthocyanin synthesis responsive to red light, and cytoskeletal structure responsive to blue light (Nick *et al.*, 1992, 1993). Tissue examples can found in fruit ripening and abscission (Trewavas, 1998).

If individual guard cell behaviour is a paradigm for other cells in other tissues, then the following can be suggested. Individuality in aleurone cell amylase production enables potential optimization of amylase production within the variety of environmental states experienced by cereal seedlings. A computational network can form slowly or quickly, but sugars, amino acids and fatty acids will be some of the information transmitted between individual aleurone cells (Trewavas, 1988). Pericycle cells more sensitive to auxin or other factors will act as foci for the formation of branch roots. The different sensitivities of individual pericycle cells act to provide a broad range of lateral root production in different root environments. Using a microbeam of red light, Nick *et al.* (1993) observed great heterogeneity in the formation of red light-induced anthocyanins between individual cotyledon cells, as described earlier. They reported patchy formation of the pigment and indicated that there was substantial variation in the sensitivity of individual cells. Furthermore, not all cells that likewise synthesized chalcone synthase mRNA in response to red light also synthesized anthocyanin, and long-range suppression of one group of cells by another was observed. Communication is clearly happening, but the mechanism of communication has not been established. But again, anthocyanin formation can be optimized to fit the environmental requirements and to improve overall fitness.

The benefits of individuality are to be found in the much greater variety of response provided to the individual plant. Williams (1956) provided an interesting way of assessing the variation in populations (Box 1).

BOX 1

Measurements of individuality

Williams (1956) approached biochemical individuality in an interesting way. He examined whether it was possible for a single uniform drug dose to be prescribed for the whole human population, and concluded it could not be. Williams assumed that any individual trait could be considered to be normal if it lay within 95 % (probability = 0·95) of the distribution around the mean. The probability that an individual is normal for two traits is $0{\cdot}95^2$. For 100 traits, the probability of normality of any individual for all traits is 0·005, and for 1000 different traits it is vanishingly small. Ergo, we are all deviant in certain characteristics.

There are at least 15 distinguishable environmental signals [water, five (or six) primary minerals, light, gravity, soil structure, neighbour competition, herbivory, disease, allelopathy, wind, gases; Trewavas, 2000] to which individual plants are sensitive, many observable traits that can be distinguished, and there may be as many as the number of distinguishable genes. On that basis, it is likely that every individual plant, at least in the wild, is unique in one or more traits.

Williams (1956) also describes anatomical and biochemical individuality in normal reproducing human beings, and lists the variations that he could find in the literature for apparently normal healthy, reproducing, human beings. The variations described are enormous given the necessity for producing such a complex organism. It would be useful if an equivalent catalogue of plant variation could be compiled, if that is possible. However, the modular character to plant growth and development and plasticity might make this a difficult task.

But the biochemical observations measuring variations in vital constituents could equally apply to plants, although I have never seen them compiled. No doubt, metabolite profiling will indicate this in greater detail. The *Handbook of biological data* does contain some information about plants, showing variation in dry weights, protein, secondary metabolites, ions and other metabolites. Elsasser (1988) regarded the data compiled by Williams (1958) to represent the primary difficulty in the instructionist view of life that regards the genome as merely a computer tape (full of information) and the cell as a computer following instructions that should then always result in exact replicas (clones) of the genome. Thus organisms survive perfectly well despite huge variations in constituents, and the notion of being simply complex machines (which require precision and reproducibility in structure and composition) is untenable.

THE INTELLECTUAL RESPONSE. PHENOTYPIC PLASTICITY AS FORESIGHT

The characteristics of phenotypic plasticity

Plasticity is the degree to which an organism can be changed in response to environmental signals and is, as indicated earlier, a clear example of plant intelligence. Plasticity can be expressed in both physiology and morphology. Guard cell plasticity or, more exactly, plasticity in transpiration is clearly physiological plasticity. Other physiological examples are to be found in carbon assimilation (photosynthesis rates) and dry matter partitioning (Bloom *et al*., 1985; Korner, 1991; Bell and Sultan, 1999). Karban and Baldwin (1997) indicate that herbivory and pest defence mechanisms can generate enormous numbers of physiologically distinguishable individuals arising from the moving target model. This model suggests that pest attack results in effectively random resistance responses in identical tissues such as leaves. Indeed, data provided by these authors indicate that on a single tree every leaf was observed to be at a different stage of pest resistance.

Morphological or phenotypic plasticity has been studied for many years, largely by population geneticists because of its relevance to evolutionary studies (see Box 2). Phenotypic plasticity generated by environmental variation is commonly expressed in growth habit and size, morphology and anatomy of vegetative and reproductive structures, in absolute and relative biomass accumulation, growth rates, functional cleistogamy, variable sex expression and offspring developmental patterns (Bradshaw, 1965; Diggle, 1994; Bazzaz, 1996; Pigliucci, 1997; Schlichting and Pigliucci, 1998; Ackerley *et al*., 2000; Sultan, 2000). Variations are also common in stomatal frequency, hairiness of leaves, palisade *vs.* spongy mesophyll, modifications in vascular tissues, cuticular thickness and sclerenchyma. Even the number of petals on a flower can change after leaf removal (Tooke and Battey, 2000). Maryland Mammoth tobacco (Taiz and Zeiger, 1998), and the ability of gardeners to grow outsize giant vegetables indicate the extent to which variation is possible if the right growth conditions are provided. For example, the record pumpkin is 481 kg (Guinness Book of Records, 1998). How giant fruits and vegetables can be grown without the apparent selection of particular genotypes in the first place is indicative of the extent to which epigenetic phenomena must contribute to the final phenotype. It is generally accepted that genotype determines whether the individual phenotype or character can be plastic in the first place; expression and extent of that plasticity is environmentally regulated.

BOX 2

Phenotypic plasticity and evolution

Phenotypic plasticity has long been investigated by those interested in evolutionary studies. Certainly around the turn of the 20th century, Darwinian views were opposed by some botanists because of phenotypic plasticity. Henslow (1895) provides a number of examples, such as two kinds of *Ampelopsis*, one of which forms suckers on mechanical stimulation, the other which forms them regardless of stimulation. Henslow (1895) supported Lamarckian views to explain these data, but genetic assimilation is a much more likely hypothesis. That is, the original character is the result of temporary adaptation, and natural selection increases the numbers of individuals more able to optimize the character before finally simple mutations ensure the character becomes fixed.

Suggestions that genetic assimilation is a major mechanism in evolution have recurred from time to time. Baldwin (1896) called this organic selection, and may have been the first to suggest the possibility. Waddington (1957) supported genetic assimilation using several examples, with the most prominent being the well-known callosities in the ostrich which occur where the bird lies down. It might be thought that these would be an adaptive feature, but they are clearly visible on the embryo inside the egg, supporting genetic assimilation mechanisms. The important feature in genetic assimilation is the persistence of the environmental situation, so that the novel, initially adaptive behaviour persists. With time, genes and gene combinations originate that allow the strategy to develop with greater rapidity, higher probability or lower cost (Bateson, 1963). Eventually mutations appear that fix the trait regardless of environmental signalling. Thus, in these cases, natural selection merely ratifies an adaptation that has already been developed and tested.

The molecular origin of genetic assimilation must occur in signal transduction processes. However, genetic assimilation enables the evolutionary process to move forward more quickly and efficiently, avoiding the tedious trial-and-error process that would involve the alternative view; the random production of such characters complete in all respects. Further discussion of this important aspect of phenotypic plasticity can be found in Bradshaw (1965); Bradshaw and Hardwick (1989); Bazzaz (1996); Schlichting and Pigliucci (1998); Sultan (2000), and references therein.

The timing of many developmental processes is certainly subject to plastic modification (Bradford and Trewavas, 1994). Even environmental influences on the parent can be detected in the resulting seedlings, certainly to one or more generations (Mazer and Gorchov, 1996) and in certain cases much longer (Durrant, 1962). Phenotypic plasticity is generally not all-or-none but usually varies quantitatively, a phenomenon described as the norm of reaction (Schlichting and Pigliucci, 1998). Plasticity is adaptive; this has recently been made clear (Ackerley *et al.*, 2000), and thus phenotypic plasticity fulfils the requirement for intelligent behaviour. Phenotypic plasticity is a visible witness to the complex computational capability plants can bring to bear to finely scrutinize the local environment and act upon it. However, plasticity can be limited to certain characteristics in plant development, with others remaining stable. When grown under low and high fertility, *Polypogon* plants exhibited a 100-fold variation in the numbers of spikelets per panicle, whilst glume and seed size varied by only 10 % (Bradshaw, 1965). In the well-known Clausen *et al.* (1940) experiments (see diagrams in Schlichting and Pigliucci, 1998), plasticity was observed in the size of vegetative parts, numbers of shoots, leaves and flowers, elongation of stems and hairiness. But pinnate leaf shape, leaf margin serration, shape of the inflorescence and floral characters remained stable within limits, at least under the conditions investigated.

The presence of morphological plasticity for specific traits is genotype dependent (e.g. Sultan and Bazzaz, 1993*a*, *b*, *c*) and thus individual in character as required by the definition of plant intelligence. But many life history characters, such as mortality, growth rate and fecundity—important components of fitness—are more dependent on the environment than the genotype (Antonovics and Primack, 1982). Thus, the perception of the genotype is changing from a blueprint that describes a single fixed outcome to a constrained repertoire of environmentally contingent and intelligent processes. The phenotype is ultimately constructed from synergistic developmental systems in which genes and gene products interact in a complex fashion with signal transduction networks, in turn directly responsive to numerous and constantly changing environmental factors (Trewavas and Mahlo, 1997).

Phenotypic plasticity enables individuals or genotypes to assume obviously different phenotypes during the life cycle (Schlichting, 1986; Sultan, 2000). Moreover, given the variety of environmental parameters and the different orders and combinations in which they occur in the wild, the potential number of distinguishable phenotypes must be enormous. Phenotypic variation can even cause substantial problems in taxonomic classification. Just as animal behaviour is constrained by genetic capabilities, so ultimate genetic constraints on phenotypic change will be present. But with plants refining their discrimination to local conditions, perhaps the enormous numbers of distinguishable phenotypes corresponds well with the number of behavioural variations available to any animal.

But plasticity indicates foresight. For plants that experience, for example, either periods of water stress or shading, morphological adaptations in the leaves improve fitness but at a cost that would not be experienced by other individuals that received adequate water or light. It is here that the capacity for intelligent behaviour must be paramount. Just as any animal will assess the totality of its sensory environment and respond, a plant will carry out the same assessment of all conditions and adjust its growth and development from that assessment. Furthermore, faced with new patterns of environmental variation, plasticity enables the individual to come up with some sort of solution first time. Those individuals that have the best behavioural solution will survive better and go on to reproduce. Further improvement by selection can be expected if the new environment remains. Repetitive and reproducible changes in the environment easily lead in turn to genetically proscribed behaviour by natural selection if the new environmental constraint is permanent.

Phenotypic plasticity is much more readily obvious in plants than in animals. Development continues throughout the plant life cycle and is thus subject to environmental influences to a greater extent. Theoretically, every plant body contains its environmental history, if that could be read.

A Darwinian mechanism for phenotypic plasticity

In mammalian brains, phenotypic plasticity underpins the process of learning and memory. Except in early development, neural cell numbers do not increase, and changes in function are provided, as already described, by changes in either number of dendrite connections or synaptic adhesion that form the adaptive neural networks essential for intelligent behaviour. It is the ability to create new computational networks that either direct the flow of information into different channels or reference previously held memories that are crucial. Once new dendrites form or decay the neural cell becomes effectively a cell with different functions. In early development, new cells with new dendrites and thus connections arising from mitosis obviously contribute, although memory may perhaps be more easily retained in non-dividing cells.

Because plants lack an obvious specific tissue for computation and because cell division/development continues throughout the life cycle, new mechanisms for computation may be required. What is suggested here is: (1) the basic elements of computation are individual cells in tissues; (2) that computational cellular networks are formed as the tissue develops, best fitted for the environmental state of the time; and (3) each individual plant (genet) accumulates tissues (ramets) with different computational capabilities, so reflecting the history of experience. Just as the process of learning in a brain could be represented as a time series, a set of snapshots of developing brain connections, in plants, each snapshot may possibly be represented by developing plasmodesmatal connections or equally, successive new tissues. So, instead of changing dendrite connections, plants form new networks by creating new tissues, a series of developing brains as it were, that can act like parallel processors each with slightly different computational capabilities. In this way, the successive plant tissues act as repositories of memory of environmental states which, if such information can be conveyed elsewhere, contribute to the whole plant assessment. Evidence for this view is very limited, but plants do abscind their leaves as conditions change and can form new and obviously different leaves in the new conditions (Addicott, 1982). It is also known that as leaves age, stomatal function weakens, thus there are leaves with varying potential on any one individual plant (Willmer and Fricker, 1996).

But how do different tissues arise from the same growing meristem, or are apical meristems identical throughout their life? Progressive changes in successive leaves are known to occur in certain plants under constant conditions of growth (Steeves and Sussex, 1972), and bud dormancy can vary according to the age and position of the bud (Gregory and Veale, 1957). Rooting of branches from some trees (e.g. *Taxus*) results in plants with maintenance of the same plagio-gravitropic angle of shoot growth. In others, such as *Hevea*, cuttings only form adventitious roots and the main tap root is not regenerated. But to explain how phenotypic plasticity arises from what is often assumed to be an identical meristem, we can borrow from an idea by Edelman (1993). He summarized evidence that indicated that connections in the brain were often very variable, although behaviour might be similar, suggesting that pre-specified point-to-point wiring did not occur. Neural territories and maps are often unique to each individual, for example. He suggested that experience selected out certain groups of neurones by chance whose original connections constructed a weak response. These networks were then reinforced by increased synaptic adhesion with additional signalling. Channels of information flow were thus deepened, improving the quality of the response. Therefore, the final neural network constructed depended initially on a kind of ‘Neural Darwinism’. The suggestion here is that the true meristem produces cells that are anatomically indistinguishable but that differ in molecular and physiological capabilities. During development, as cells leave the true meristem, environmental conditions will result in the preponderant replication of certain cells with particular physiological patterns (over others) which, in due course, give rise to phenotypic plasticity; a kind of cloning (Steeves and Sussex, 1972). Perhaps cells in the transition region between division and expansion are where selection occurs in roots (Barlow and Baluska, 2000). In the apical meristem, larger leaves might originate as the environmental conditions select cells capable of expanding longer or to a larger final size. Maybe these cells would differ in sensitivity to auxin or kinin. Self-evidently, only young, developing tissues in plants can express morphological plasticity. Examples of responses of very young tissues to ABA and cold treatment leading to different morphologies and tissues (*Spirodela* turions) are to be found in Smart and Trewavas (1983). Also, morphological data provided by Milthorpe (1956) indicate that young cucumber leaves of a certain age only respond to cold treatments.

INDICATIONS OF INTELLIGENT CHOICE, INTENTION AND BEHAVIOUR

Intelligent behaviour is designed to maximize fitness but only in circumstances that challenge the survival of the organism and test its capability for intention (within an evolutionarily determined end point) and choice. Ecological investigators are starting to construct circumstances in which intention and choice are tested.

Foraging for food resources is an essential activity for both plants and animals. Consequently, most aspects of intelligent behaviour are exemplified in foraging for nutrients. Little is left to chance or plasticity in reproductive behaviour. For a similar reason, much plant taxonomy relies on flower structure in which plasticity is minimized. For land plants, resources appear as a complex spatial and temporal mosaic (Hutchings and deKroon, 1994), in part reflecting patchy distribution of soil materials and neighbour competition (Turkington and Harper, 1979; Salzman and Parker, 1985). Competition is certainly one environmental circumstance rarely provided in laboratory experiments. In a resource mosaic, intelligent behaviour is essential if resource collection is to be optimized in the face of competition. Foraging is a term now used much more frequently in plant ecological literature and is a proper description of the way plants behave when gathering growth resources.

Dodders (*Cuscuta* sp.) are parasitic plants that have lost almost all photosynthetic capability (Kuijt, 1969). Responding to an initial touch stimulus, growing shoots take several days to coil around suitable hosts. Haustorial primordia and haustoria then differentiate and nutrient resources commence transfer from the host in about 4 d (Kelly, 1990). In dodder, it is thus possible to dissociate active choice from the subsequent passive effects of acquired resources on growth that can complicate other situations. By tying suitable stem explants of dodder to touch the host, Kelly (1992) observed that 60 % of individuals rejected suitable hosts within several hours. Rejection was reduced to about 25 % if the host was pretreated with nitrate. Active choice was thus influenced by the anticipated reward. By using a range of hosts of different reward value, measuring the length of coils and the biomass subsequently accumulated after 28 d, it was shown that the length of coiling was linearly related to subsequent reward/unit of energy invested. These data fit a simple marginal value model of resource use, applicable also to grazing animals; they also indicate plasticity in the length of coiling. Just as animals intelligently feed, so do plants. Seed set was correlated with the size of the parasite, indicating that host selection was adaptive and fitness of the parasite improved. It was suggested that rapid transfer of chemical information through the initial touch contact determined host selection and final length of coiling.

The uneven distribution of light to which wild plants are exposed is a critical factor controlling subsequent fitness. Light is critical to the acquisition of carbon resources and energy for other cellular processes. But many plants (often called sun plants to distinguish them from shade plants) do not react passively to the light mosaic in a canopy, simply accumulating dry weight when the light is strong enough. The quality and quantity of light is actively perceived (through red : far red ratios) and the position of likely future competitive neighbours mapped (Gilroy and Trewavas, 2001). Avoiding action is taken by accelerating the growth of the stem, which becomes thinner (Ballare *et al*., 1990; Aphalo and Ballare, 1995), or branch growth is accelerated into light of higher intensity (Trewavas, 1986*b*). Thus, the resource-acquiring structure(s), the stem plus leaves, is projected at speed into the resource-rich patch away from competition. Root growth is also altered, indicating communication of light perception to other parts of the organism (Aphalo and Ballare, 1995). New leaves are then especially positioned free from competitive light interruption (Ackerley and Bazzaz, 1995).

The stilt palm (Allen, 1977) is constructed from a stem raised on prop roots. When competitive neighbours approach, avoidance action is taken by moving the whole plant back into full sunlight. Such obvious ‘walking’ is accomplished by growing new prop roots in the direction of movement while those behind die off. That this is intentional behaviour is very clear. Other equally dramatic light-foraging mechanisms are to be found in tropical climbers, particularly *Syngonium.* On reaching the top of a tree, the growing point descends, progressively changing its morphology and leaf structure, and eventually assuming a very thin filiform shape with only scale leaves on the soil. Using skototropism (movement towards darkness), the filiform stem explores, locates and recognizes a new trunk and reverses the growth pattern. As it climbs, the internode becomes progressively thicker and leaves progressively redevelop to full size (Strong and Ray, 1975; Ray, 1987, 1992). This behaviour is analogous to animals that climb trees to forage, intelligently descend when food is exhausted or competition severe, and then climb the next tree.

Experiments with rhizomatous clonal herbs have shown that when provided with deliberate choice, the new growth of rhizomes and associated shoots is highly selective and is directed with much higher probability into favourable microhabitats. The new territories that are exploited may consist of freedom from other competitors (Evans and Cain, 1995; Kleijn and Van Groenendael, 1999), unshaded and warmer temperatures (MacDonald and Lieffers, 1993), or weaker salinity (Salzman, 1985; Salzman and Parker, 1985). When resources become abundant, dormant buds are induced to grow as shoots rather than new rhizomes (Hutchings and de Kroon, 1994). Rhizomes that penetrate the poorer environments are generally thinner, their internodes are longer and they grow more rapidly where possible. The dispersal of any new shoots from the parent plant is thus greatly increased, and new territory is actively searched for new resource-rich patches. Limited growth resources are thus efficiently used to cover maximum ground with minimum investment. Directing the majority of rhizomes to exploit rich resources whilst allowing others to search for new resources suggests optimal strategies are in place to maximize returns and increase fitness. When resources are scarce, growth materials are invested in the organ through which scarce resources are normally sequestered: if minerals or water are scarce, enhanced root growth occurs; if light is scarce, stem growth is enhanced at the expense of root growth.

But the growth of clonal herbs responds directly to the uneven distribution of resources in the soil. When grown on soil in which resources are distributed in patches rather than uniformly, overall biomass accumulation can be up to seven-fold higher (Wijesinghe and Hutchings, 1997, 1999).

Not only could *Glechoma* plants discriminate an optimal patch size, but they could also discriminate the strength of gradients across the boundary of the patch, showing severalfold better growth when the gradient was greatest. How the parameters of patch size and gradient strength lead to enhanced growth is not understood. It is difficult to avoid the conclusion of intention and intelligent choice and the ability to select conducive habitats in which to place and grow organs of resource exploitation. Perhaps the most surprising observations come from Evans and Cain (1995). They tested whether the clonal herb *Hydrocotyle*, which grows on sand dunes, could preferentially locate good patches or avoid bad patches in a heterogenous environment. They reported that rhizomes veered away from patches of grass and thus obvious competition. Intentional choice of habitat is clear.

Individual roots can track humidity and mineral gradients in soil (see summary of references in Takahashi and Scott, 1993), just as shoots can track local light sources (Trewavas, 1986*b*). Roots can change their branching patterns (architecture) radically when resource-rich patches are found (from herring bone structure to a highly branched motif; Fitter, 1986) and change uptake rates so that no particular resource limits growth but all remain in approximate balance. And, to avoid detrimental competition, roots (like shoots) take deliberate avoidance action to prevent contact when approached by roots of other species (Mahall and Calloway, 1991).

CONCLUSIONS

A major difficulty in studying any plant behaviour is that time scales differ from those in animals. Whereas human beings operate in seconds, plants usually operate in weeks and months. Even though bamboos can grow a centimetre an hour, without some sort of recording device it would be extremely difficult for any human to observe this phenomenon. Plant behaviour in the wild is usually unrecorded and, as a consequence, much uncommon behaviour must simply be missed. Time-lapse photography is at least a start, but how many plant physiologists with time-lapse facilities study and experiment on wild plants where real intelligent behaviour is to be expected? There is no doubt this is a serious omission in the scientific literature. There are so many crucial questions to pose. Why is it that one wild seedling survives and others do not, when apparently shed at the same time from the parent plant and in the same soil? There is so little information on the actual preliminary struggle for existence recorded in real time.

To the well-informed physiological reader not much of the information above will be especially new. However, the particular combination that I have presented here of intelligence, learning, memory and fitness should place some facets in a different light. Higher plants do represent about 99 % of the eukaryotic biomass of the planet. Their sessile life style is clearly successful and individuals must then possess a fine ability to adjust and optimally exploit the local environment. How well they map the local environment and the extent of computation (with good estimates of computational skill) clearly still requires significant investigation in real not artificial environments.

Undoubtedly, one of the problems that botanists have with using the words ‘plant intelligence’ are incorrect assumptions about animal intelligence, which is often equated with human intelligence and suppositions of complete freedom of choice (if they exist). Much animal behaviour is strongly heritable (for example, reproductive or early feeding behaviour is probably innate) and, indeed, has to be. So, in the same way, there are aspects of plant behaviour that are rarely phenotypically plastic. The structure of the flower is a good example, or the square-shaped stems of the Labiatae, among many. Apart from the fact that the major form of expression of animal intelligence is movement rather than growth and development, as defined here for plants, I find there is little to distinguish between the two groups of organisms once adjustments are made for the time differences noted above. As regards movement, the computer that beat Kasparov at chess (surely an excellent example of intelligence in action regardless of the human requirement to program) certainly required human intervention to move the pieces. We have already described the necessity for the right environment to elicit intelligent behaviour, and the Kasparov chess computer is again an excellent example. Good at chess, it wasn’t any good at assessing economics statistics until reprogrammed. Chess games were the right environment to elicit intelligent responses.

In fact, chess provides a further and important illustration of how ignoring individual behaviour and simply averaging behaviour can confuse understanding. Each chess game represents a unique and highly individual trajectory, recording intelligent behaviour between two properly matched opponents. Suppose instead that we now averaged 1000 chess games, much as physiologists average responses, and then looked for meaningful variations. The averaging process would reveal that pawns had a very high probability (and a narrow standard error) of being moved right at the beginning and the king being irreversibly confined (mated) at the end, although with greater variability. Knights and bishops would have a high probability of being moved early on, although the probability mean would be lower than that for pawns and the standard deviation broader. Castles (rooks) and queens would be later still and with much more spread in the standard deviation, and so on. In fact, averaging any one large set of chess games would look very similar to any other large averaged set, and we would conclude that the chess game on this basis was rote, started with a clock, of little interest and certainly nothing to do with intelligence. And, in an attempt to understand what was going on, we might experimentally knock out pieces only to find that, yes they were necessary and you lose if they go, just as we currently knock out cells, chemicals, genes or signal transduction molecules in an attempt to understand what is going on. Another crucial point is surely that very simple rules govern chess but the order in which events take place (i.e. the trajectory) can be unique to each game. This may represent a paradigm for signal transduction. We are so used to thinking of intelligence as a property of the human individual that we fail to recognize the necessity of applying that rule to plants as well.

Perhaps a more critical question is: does it matter whether intelligence is used to describe plant behaviour? If intelligent behaviour is an accurate description of what plants are capable of, then why not use the term? But, having used it, the next question is how it is accomplished in the absence of a brain. I have called this phenomenon 'Mindless Mastery' (Trewavas, 2002*b*) and can only suggest that intelligent behaviour is indeed an emergent property that results from cellular interactions, just as it is in the brains of animals. Whatever the mechanism, the end result usually comes from the distinctive behaviour of meristems. There must then be important conduits of proper information flow, as distinct from nutrients, from the rest of the plant into meristems.

Hopefully this article can indicate more clearly the kinds of investigations needed to fill in the gaps. Undoubtedly, we need very much more information on cellular and tissue communication and the distribution of receptors for all those signals that have been uncovered recently. We need many more studies on individual wild plant behaviour. Questions about tissue-to-tissue interactions need reformulating. How much information is conveyed between tissues, and what exactly is the sum total of its nature? Although the classic growth regulators are often assumed to carry out such communication, the uncertainty that still surrounds much of these notions is remarkable. Molecular studies can improve this situation, and some answers may arise from skilled use of inducible expression of tissue- and cell-specific critical synthetic enzymes. Other answers will arise from creative construction of particular environments in which plants can demonstrate their undoubted behavioural potential.

Although we understand much more about signal transduction processes in plants than we did 20 years ago, there is a long road yet to travel, to jump the gap between cell, tissue and whole organism. In this article I have travelled Robert Frost's 'less travelled road'. My hope is that, in future, this may become a more major highway.

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