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(Eds.)

Communication in Plants

Neuronal Aspects
of Plant Life

Springer

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With 82 Figures, 5 in Color

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Preface

As we enter the new millennium, plant biology is witnessing dramatic advancements in studies related to the complex behaviour of higher plants which are now beginning to reveal intelligent behaviour. Surprisingly, it is plant ecology which is leading in the revelation that plants behave as though having conscious comprehension of themselves and of their environment. Charles Darwin was the first who noted the abilities of plants to communicate with their environment and translate this information into active movements of their organs (Darwin 1880).

Plants recognize other organisms such as bacteria, fungi, other plants, insects, birds, and animals that presumably also include us, humans (Takabayashi and Dicke 1996; Paré and Tumlinson 1999; Kessler and Baldwin 2001). For instance, to accomplish their sexual reproduction, plants rely on complex interactions with insects and birds. In order to achieve this, and as Charles Darwin was one of the first to show (Darwin 1862), plants generate specially shaped sexual organs which allow insects and birds access to their flowers. Moreover, plants reward these pollinators with nectar and other compounds which are both attractive and a necessary part of the diet of these insect/bird feeders (Cozzolino and Widmer 2005). Complex interactions have been recorded between insect pheromones and plant volatile semiochemicals (Reddy and Guerrero 2004). In the case of many *Arum* spp., the insect-attracting plant volatiles with a dung-like odour are exactly those chemicals which attract insects to animal dung where they would otherwise gather and reproduce (Kite et al. 1998). These plants are thus masters of a deceptive and intelligent strategy for their own reproduction. Moreover, plants appear to possess an innate type of immunity system which closely resembles that of animals (Nürnberger et al. 2004) and, interestingly in this respect, there are also several parallels between the recognition of self and non-self in plant breeding systems and histocompatibility in animals (Nasrallah 2005). Plant roots of *Fabaceae* can recognize and 'domesticate' *Rhizobium* bacteria within nodules, and the composite bacteroids then supply the host plants with nitrogen. Less well known, perhaps, is that some plants recognize and communicate with ants (and vice versa) which protect them against herbivores, pathogens as well as competing vegetation (Brouat et al. 2001; Dejean et al. 2005). The plants, in

turn, reward the ants by secreting nectar (Heil et al. 2005) and constructing special food bodies (Solano et al. 2005). Plants actively recognize the identity of herbivores and are then able to recruit their enemies (Arimura et al. 2005). For instance, plant roots attacked by insect predators release volatiles which then attract particular species of nematodes that kill these predators (Rasmann et al. 2005). In addition, by releasing volatiles into the aerial environment, plant shoots infected by pathogens inform their neighbouring plants about immanent danger and they can then increase their immunity against these pathogens (Paré and Tumlinson 1999; Reddy and Guerrero 2004). Intriguingly, the signature of released volatiles is characteristic for herbivore damage but is different from that resulting from a general wound response (Reddy and Guerrero 2004; Arimura et al. 2005). *Nicotiana attenuata* attacked by the hornworm, *Manduca sexta*, accumulates nicotine, which poisons acetylcholine receptors, and is thus toxic to those organisms which rely on neuromuscular junctions (Baldwin 2001). Interestingly in this respect, plants express neuronal acetylcholinesterase (Sagane et al. 2005) and use acetylcholine also for their neuronal-like cell–cell communication (Momonoki et al. 1998). Furthermore, during their phylogeny, plants can also switch from an autotrophic to a heterotrophic lifestyle – a feat which, in the case of parasitic or carnivorous plants, requires the active selection of suitable host/prey organisms (Albert et al. 1992).

Plants are extremely mechanosensitive. Their roots exhibit thigmotropism, which enables them to explore, with an animal-like curiosity, their environment in a continual search for water and solutes, and their shoots sometimes seek support by means of tendrils, assisted in this task by volatiles such as jasmonates. Root apices constantly monitor the numerous physical parameters of the soil and use this information in their search for better niches for survival and reproduction. In this behaviour, plant roots closely resemble fungi and, indeed, most roots enter symbiotic interactions with mycorrhizal fungi in order to increase their efficiency in obtaining critical ions such as phosphorus. In fact, roots might prove to be descendents of ancient fungi which, by entering into close association with their symbiotic photoautotrophs, have developed into heterotrophic roots – there are, after all, close resemblances between the anatomies and functions of apices of both rhizomorphs and roots (Botton and Dexheimer 1977) – while photoautotrophs have developed into the autotrophic shoots of the organisms now known as vascular plants (Atsatt 1988; Selosse and Le Tacon 1998; Heckman et al. 2001). This scenario is strongly supported by present-day pioneer colonizers such as lichens, which, just as was the case with early land plants (Yuan et al. 2005), are able to survive in even the most extreme of environmental conditions.

Literally, plants nourish the whole world. They intercept the light energy arriving on Earth from the sunbeams and transform it via energy-poor

inorganic compounds into energy-rich organic matter which then serves as the food for all heterotrophic organisms. Also, the gasoline which fuels many of Man's mechanical devices is of plant origin. Plants thus stand at the interface between a seemingly hostile and violent universe, and a fertile planet Earth teeming with life. We might postulate that if we could understand plants better, they could reveal to us something of the great mystery of life. Aristotle and his pupils were convinced that plants have complex inner life including thoughts, memories, dreams, and plans for the future. Unfortunately, our contemporary science considers plants rather as passive creatures to be exploited if discovered to be useful, and to be cleared away if not. However, their passivity – that is, their inability to change their location or to communicate via sounds – is only relative to the hyperactivity of human existence and the fleeting timescale of Man's artefacts. But the recent advances in ecology and phenomenology outlined above urge a change in this biased perception of higher plants.

We should also remember that action potentials, the very characteristic and rapidest way of neuronal communication, were discovered in plants in 1873 (Davies 2004). In those early days, the cellular basis of animal brains was not accepted and the neuronal processes in brains were just starting to be explored. Since then, a large amount of data has been accumulated on electric phenomena in plants (Meylan 1971; Davies 2004). Currently, new exciting discoveries are revealing that electrical signals modulate and control such basic physiological processes in plants as photosynthesis and phototropism (Koziolek et al. 2004; Volkov 2005). Unfortunately, the mainstream of plant biology has never completely accepted plant electrophysiology, so this field has survived in a quasi-dormant state up until now when exciting advances in plant biology are allowing the introduction of plant neurobiology as a newly emerging field of plant sciences. One foundation of this new science is the discovery that not only do plant cells express diverse neuronal molecules but that they also communicate together via plant synapses (Baluška et al. 2005).

These glimpses of the fascinating and breathtaking complexity of plants raise urgent questions which will dominate the whole field of plant biology in the next decades. In particular: Do plants have some type of neuronal system which resembles that which underlies the behaviour of animals? Conversely, if plants turn out to be 'brain-less', then the question will emerge where and how do they store and process the information which they obtain about both the abiotic and biotic environments, and how do they then use this information to optimize their future behaviour? Do plants feel (as suggested by Aristotle) and experience pain? Further: Do plants hear, and can they perceive odours? The truth is that we do not know, although their extreme sensitivity to mechanical vibrations indicates that they can perceive voices and their responses to volatile gases suggest they have a type

of olfactory response. Importantly, our lack of knowledge should not justify claims that plants do not possess these abilities and properties. In fact, their complex, rational, and surely intelligent behaviour suggests just the opposite. This is why we should be more sensitive to these issues and should commence a serious enquiry into these urgent questions, utilizing minds trained in the 'scientific method' but which can also clearly differentiate between speculation and hypothesis (Huszagh and Infante 1989).

Is it by chance that the Greek word 'neuron' refers to vegetable fibre? In fact, this happy and synchronistic coincidence might be taken to signify that the term plant neurobiology is fully justified! This book brings together all these new plant neuronal aspects and combines them with the classical plant electrophysiology. Plant neurobiology is commencing its emergence as a coherent science.

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Bonn, Bristol and Florence,
July 2005

František Baluška, Peter W. Barlow,
Stefano Mancuso and Dieter Volkmann

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Finally, we wish to remember with affection Jolana Albrechtová (co-author of Chap. 25) who tragically died in a car accident on the 29th of November 2005 at the age of 39 years.

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1 The Green Plant as an Intelligent Organism

Anthony Trewavas

Abstract Intelligence is an aspect of complex adaptive behaviour and a term not normally applied to plants. This chapter indicates a change in concept is long overdue and if poets can recognize it (above) so should scientists. Networks that control information flow are described as intelligent and such networks exist in all single living cells and in more complex multicellular organisms. Phosphoneural bacterial networks are briefly considered and these exist in a slightly different molecular but more complex form in higher plant and animal cells. Intelligent behaviour involves the whole organism and such integration involves complex communication. Evidence that plants forage and act intelligently in acquiring resources is indicated. The phenotype is actively (not passively) constructed in response to a complex changing environment by decisions that best secure the well-being of the individual plant within the life cycle goal of optimal fitness.

More and more I have come to admire resilience Not the simple resistance of a pillow whose foam Returns over and over to the same shape but the sinuous Tenacity of a tree: finding the light newly blocked on one side It turns to another. A blind intelligence true But out of such persistence arose turtles, rivers, Mitochondria figs-all this resinous un-retractable earth.

Jane Hirshfield (2005)

1.1
Introduction

Intelligence is an aspect of adaptive behaviour, even in humans. Organisms that live in challenging but variable and competitive circumstances require forms of behaviour that rise to that challenge and must be equally flexible to improve fitness. Those best able to master their environment are those most likely to succeed in the Darwinian wars. "The success of a species depends on it performing well (surviving and producing offspring, i.e. fitness) in its own particular environment. And intelligence plays a critical part in this success." Warwick 2001, p. 9). Since the life cycle is probably a primary target of natural selection (McNamara and Houston 1996; Schlichting and Pigliucci 1998), efficient acquisition of necessary food resources during growth and development is an important aspect of subsequent fitness because there is a common relation between accumulated resources and subsequent sibling number (Bazzaz 1996).

1.1.1
The Problems of Subjective Intelligence

Before embarking on a discussion of plant intelligence it is essential to indicate what is meant by the term. The actual word is derived from the Latin *inter legere* meaning simply to choose. Dictionary definitions of intelligence use terms such as self-recognition or capacity for understanding and are couched in human terms. These definitions are perfectly adequate for public discussion that usually only involves human beings. But for biologists who wish to investigate and understand intelligence in other organisms such definitions lack useful substance.

A common problem is subjective intelligence. For example the cyberneticist, Warwick (2001, p. 9) states that "Comparisons (of intelligence) are usually made between characteristics that humans consider important; such a stance if of course biased and subjective in terms of the groups for whom it is being used." And as he shows is easily discredited. "When we compare the important aspects of intelligence, it is those which allow one species to dominate and exert power over other species that are of prime importance" (Warwick 2001). Bearing in mind the fact that plants dominate the planet, this statement is of importance for understanding plant intelligence. A further common assumption is that only organisms with brains (primates, cetaceans, crows) can be intelligent. Vertosick (2002) describes this as simple "brain chauvinism" and Schull (1990) goes further in stating that such views ascribe nerve cells as having some sort of vitalistic quality.

1.1.2
An Ability to Integrate a Multiplicity of Information
into a Response Is an Important Intelligent Capability

Plants and animals are not passive objects in the face of environmental disturbance as indicated in the poem by Hirshfield (2005). They react and positively fashion themselves according to the information (signals) being received. Behaviour is the response to signals (Silvertown and Gordon 1989). Animals move when signalled, plants change their phenotype (Trewavas 2003). After that information is processed and integrated with the internal information, a response is constructed that improves fitness, the ultimate goal.

Green plants respond to numerous environmental biotic factors such as food resources (light, minerals, water) mechanical stimuli, humidity, soil structure, temperature and gases (Trewavas 2000; Turkington and Aarsen 1984). In each case the strength, direction, specific characteristics (e.g.

light wavelength) and intensity can be separately discriminated (Ballare 1994, 1999), and further complexity is added by virtue of the availability of resources being present either in fluctuating quantities varying from seconds to months, gradients with fluctuating intensity or a mosaic in the soil of vastly different concentrations (Bell and Lechowicz 1994; Farley and Fitter 1999; Grime 1994; Kuppers 1994; Pearcy et al. 1994; Robertson and Gross 1994) and others. Biotic signals are also sensed and acted upon and these include space; presence, absence and identity of neighbours (Tremmel and Bazzaz 1993); disturbance; competition (Darwinkel 1978; Goldberg and Barton 1992; Tremmel and Bazzaz 1995), predation and disease (Callaway et al. 2003; Turkington and Aarsen 1984). We understand little of the nature of the signals involved. Growth of individuals and neighbours continually and specifically changes the information spectrum.

There is no unique separate response to each signal in this complex but merely a response issued from an integration of all environmental and internal information. In the case of green plants, the visible response to signals is phenotypic plasticity (Bradshaw 1965; Schlichting and Pigliucci 1998; Sultan 2000). During information processing all signals meet somewhere in the cellular and tissue reactions that specify changes in form.

In seeking to understand the biological origins of human intelligence, Stenhouse (1974) described intelligence as adaptively variable behaviour during the lifetime of the individual in an attempt to discriminate intelligent behaviour from autonomic, that is unvarying, responses. Given the plethora of signals that plants integrate into a response, autonomic responses do not occur. Signal perception is instead ranked according to assessments of strength and exposure. But autonomic responses can be rejected; the numbers of different environments that any wild plant experiences must be almost infinite in number. Only complex computation can fashion the optimal fitness response.

1.1.3
Experimental Circumstances Can Be Misleading

When one factor is experimentally varied at a time in an attempt to simplify the complexity that wild plants normally experience, all those factors that do not vary are still sensed and integrated with the modified variable. For example, exposing a dicot seedling root to a gravitational signal leads to the textbook response of a resumption of vertical growth. But gradients of humidity, minerals, light, temperature imposed in a different direction or touch can override the gravity signal (Eapen et al. 2003; Massa and Gilroy 2003). Further complexity can result from an individuality in response to any one imposed signal (Trewavas 1998). Again for example with

gravity, the growth trajectories with which each root approaches the vertical can be individual (Bennett-Clerk and Ball 1951, referenced in Trewavas 2003).

The common use of statistics to obliterate individual variation leads to assumptions that the response to signals is always replicable. If the same signal and response are chosen, the same genotype, the environmental conditions are identical and the results are averaged statistically, this is no doubt true (but then the same can be said of an IQ test for human beings). No such simplicity of circumstance is available to an individual wild plant, which in meeting an almost infinite variety of environmental states must construct individual responses to improve its own fitness. No genome could contain the information that would provide an autonomic response to every environmental state. And even cloned individuals do not exhibit identical responses.

However, it is not just abiotic factors that are critical. Natural selection operates on individuals and Darwin (1859) considered that there is "a deeply seated error of considering the physical conditions of a country as the most important for its inhabitants whereas it cannot be disputed that the nature of other inhabitants with which each one has to compete is generally a far more important element of success." Considering the number of different species and individuals that co-exist, each one variable in phenotype and characteristics, any individual plant faces complexity not simplicity. Instead we are left only with the possibility of non-heritable (epigenetic) means whereby optimal fitness is achieved. Plants adequately meet the Stenhouse (1974) definition of intelligence.

1.2
Intelligent Behaviour of Single Cells

1.2.1
Molecular Networks in Single Eucaryote Cells

Cells are organized structures and vital properties result from the connections between the molecular constituents of which they are composed (Kitano 2002; Trewavas 1998). Numerous molecular connections integrate into a higher emergent organized order that we recognize as living. It is now known (1) that various steps in metabolism act like many Boolean computer logic gates such as AND, OR and NOR (Bray 1995) and are termed chemical neurons (Arkin and Ross 1994; Hjelmfelt and Ross 1992; Okamoto et al. 1987), (2) that these chemical neurons can act as pattern-recognition systems (Hjelmfeldt et al. 1993), (3) that proteins can act as computational elements (Bray 1995), and (4) that protein phosphorylation using about

1,000 protein kinases in both animals and plants provides for enormous numbers of complex elements of control, switching mechanisms and including both complex positive and negative feedback interactions (Bhalla et al. 2002; Chock and Stadtman 1977; Ingolis and Murray 2002). Such chemical systems parallel the capabilities of simple neural network structures as a set of on/off switches with feedback (Hopfield 1982; Hopfield and Tank 1986) on which they are modelled (Hjelmfeldt et al. 1991, 1992). Even in simple networks collective computational properties arose with parallel processing and extensive numbers of associative memories emerged as attractors occupying part of the network. Chemical neurons and neural network behaviour have most applicability to signal transduction studies (Bray 2003).

From an alternative direction, use of phage display or two hybrid methods has shown that that all proteins participate in the cellular network, a structure composed of hubs and connectors in which the number of connections to any one protein obeys a simple power law (Bray 2003; Gavin et al. 2002; Maslov and Sneppen 2002; Ravasz et al. 2002; Tong et al. 2002). The metabolic and signalling networks are modular with recognizable recurring circuit elements or network motifs that (1) filter out spurious input fluctuation, (2) generate temporal patterns of expression, and (3) accelerate throughput (Alon 2003). Such structures provide for robust behaviour that can also be fragile (Alon et al. 1999; Carlson and Doyle 2002) and exhibit highly optimized tolerance of variations in individual protein constituents (McAdams and Arkin 1999). "The cell in which zillions of molecular events occur at a time computes in parallel fashion" (Huang 2000), just like a brain. Robustness results from sharing control throughout the metabolic and signalling network with controlling steps determined by the environmental state (Strohmann 2000). Emerging network structures indicates how complex feedback controls operate (Davidson et al. 2002).

The cellular network perceives continual environmental variation through a multiplicity of receptors. Transduction in plants involves numerous second messengers and kinases enabling network information flow that may diverge, branch, converge, adapt, synergize and integrate through cross talk (Trewavas 2000). Such networks learn either by increasing the synthesis of particular constituents or by changing the affinity between particular network steps by post-translational modification (Trewavas 1999). Memory is simply the retention with time of the enhanced pathway of information flow and can be accessed by other pathways through cross talk (Taylor and McAinsh 2004). Cellular networks capable of these properties are entitled to be called intelligent and indeed form the basis of machine intelligence (Warwick 2001) and other forms of biological intelligence (Vertosick 2002).

1.2.2
Bacterial Intelligence and Phosphoneural Networks

Bacteria respond to many signals in their environment with adaptive responses designed to improve fitness (Hellingwerf 2005). The basic transduction mechanism for these signals involves phosphorylation of specific proteins with conserved regions on histidine and aspartate residues (Hellingwerf 2005) and other less common mechanisms in bacteria such as serine/threonine phosphorylation and quorum sensing systems (Park et al. 2003a,b). Very early on, analogies were drawn between the connections that phosphorylation enables between bacterial proteins and the connections between neurone dendrites in higher animal brains. This led to their description as a phosphoneural network (Hellingwerf et al. 1995). The properties of these networks include signal amplification, associative responses (cross talk) and memory effects. Subsequent investigation indicated learning (Hoffer et al. 2001) and the realization that these simple networks provide the individual bacterial cell with informed decisions (Bijlsma and Groisman 2003) in a rudimentary form of intelligence.

"This simplest of animals (bacteria) exhibits a prototypical centralized intelligence system that has the same essential design characteristics and problem solving logic as is evident in all animal intelligence systems including humans" (La Cerra 2003). "Some of the most fundamental features of brains such as sensory integration, memory, decision making and the control of behaviour can all be found in these simple organisms" (Allmann 1999).

Hellingwerf (2005) considers the crucial aspect of human intelligence is associative memory, i.e. to identify non-identical systems as being related. In bacterial networks this is simply cross talk after learning.

But La Cerra and Bingham (1998) came to a different conclusion of the basic element of bacterial intelligence from considerations of chemotaxis. "The *sine qua non* of behavioral intelligence systems is the capacity to predict the future; to model likely behavioral outcomes in the service of inclusive fitness." This model is retained in bacteria for only several seconds, the time taken for perception to alter the behaviour of the chemotactic rotor.

1.2.3
Observations of Eucaryote Single Cell Intelligence

Grasse (1977) has described remarkable non-heritable behaviour in single-celled amoebae (Arcella and Chaos). Arcella, for example, uses several cunning methods to return to its normal position after accidental inversion, to

deliberately corner motile food (infusoria) or to escape from impalement. Grasse (1977, p. 213) describes this behaviour as that which Haeckel called the psychological ability (i.e. purposive behaviour or intelligence) of the cell. "I dedicate these remarks to those who would simplify the properties of living things to the points of insignificance … The observation of an animal in action in its proper environment remains an exercise essential to the biologist" (Grasse 1977), a statement of direct and pointed relevance to plant biologists. The plant biologist McClintock (1984) echoes the previous psychological sentiment in the following statement abstracted from her Nobel Prize acceptance speech: "A goal for the future would be to determine the extent of knowledge the cell has of itself and how it utilizes this knowledge in a thoughtful manner when challenged." Thoughtful can be equated with Grasse's (Haeckel's) psychological ability.

The slime mould *Physarum* has been presented with a maze of differing lengths with food at the end and always chose the shortest path, indicating an ability to optimize food gain whilst minimizing economy of effort (Nakagaki et al. 2000). The authors of this paper state "this remarkable process of cellular computation implies that cellular materials can show a primitive intelligence". Single cells have been observed to be capable of choice. Amoebae will prey on *Tetrahymena* but avoid *Copromonas* and if given the choice *Paramecium* prefers small ciliates to bacteria (Corning 2003).

1.3
Other Forms of Biological Intelligence

Social insects (termites, bees, ants) in colonies construct nest structures, minimal paths to food or adaptively change resource acquisition, behaviour described as swarm intelligence (Bonabeau et al. 2000; Bonabeau and Meyer 2001; Bonabeau and Theraulaz 2000; Franks et al. 2003; Seeley 1995). "Indeed it is not to much to say that a bee colony is capable of cognition in much the same way that a human being is. The colony gathers and continually updates diverse information about its surroundings combines this with information about its internal state and makes decisions that reconcile its well being with its environment" (Seeley and Levin 1987). Swarm intelligence owed its basis to the connections between the individual workers that form a network and changes in communication change the behaviour of the whole colony.

Immune intelligence-immune systems learn how to construct the best antibody, remember and predict future bacterial evolution (De Castro and Timmis 2002; Vertosick and Kelly 1992; Vertosick 2002) and intelligent genomes have been described briefly elsewhere (Thaler 1994). Intelligent genomes are equally found in plants (Trewavas 2005). Finally intelligent

species have been proposed and analysed in some detail. "Plant and animal species are information processing entities of such complexity, integration and adaptive competence that it may be scientifically fruitful to regard them as intelligent" (Schull 1990). Schull (1990) indicates analogies between learning and natural selection, memory with ecological niche, etc.

1.4
The Intelligence of Green Plants

"The tip of the root acts like the brain of one of the lower animals" (Darwin 1882).

Information processing, learning, memory, decision making, choice, predictive modelling, associative memory, sensory integration and control of behaviour are all aspects of biological intelligence. Information processing, decision making, associative memory, sensory integration and control of behaviour have already been mentioned in respect to plant cell signal transduction. Numerous examples of direct memory can be found in Desbiez et al. (1984, 1991), Jaffe and Shotwell (1980), Marx (2004), Trewavas (1999), Verdus et al. (1997) and references therein. Indeed since green plants are composed of millions of cells and the evidence indicates the intelligent capabilities of individual cells, intelligent responses of the whole plant are expected. Plant cell signal transduction uses a similar range of molecules for transduction as animals (Gilroy and Trewavas 2001).

Intelligence is a behavioural property of the whole organism and this requires integrated behaviour that is clearly evident (Hartnett and Bazzaz 1983, 1985; Turkington and Klein 1991; Turkington et al. 1991). "Plants have evolved an integrated complex of hormonal systems – a coordinated but non-centralised intelligence system that manages resources" (LaCerra and Bingham 2002). Communication is complex, involving proteins, nucleic acids, electrical communication and turgor information amongst many other signals (Trewavas 2002, 2005). For example, rootstocks affect numerous shoot characteristics when grafted and the root messages involve in part transfer of specific homeobox proteins (Kim et al. 2001). Behavioural changes in phenotype particularly in competition are constructed to optimize fitness and efficient foraging behaviour is crucial.

Peak et al. (2004) have described an alternative mechanism, patchiness of behaviour amongst groups of guard cells. Cooperative interactions amongst these patches leads eventually to synchronization and subsequent optimization of water relations of the leaf. Recognition of behaviourally discrete patches of plant cells has been made for some time (Trewavas 2003) and the mechanism has parallels with synchronization in a network of oscillators with distributed natural frequencies (Strogatz 2001).

1.4.1
Decisions and Choice in Plant Development

Plants actively forage for food resources by changing their architecture, physiology and phenotype (De Kroon and Hutchings 1995; Drew et al. 1975; Evans and Cain 1995; Grime et al. 1986; Grime 1994; Hutchings and De Kroon 1994; Slade and Hutchings 1987). When patches of rich resource are located either by roots or by shoots and occupation of resource receptors reaches critical levels, decisions are made to initiate enormous proliferation, thus greatly increasing the surface area of absorption of both energy minerals and water. Decisions are thus made continuously as plants grow, placing roots, shoots and leaves in optimal positions according to the abundance of perceived resources. Perhaps most crucial is that individual plants compete vigorously with each other for resources and the decisions are designed to improve fitness at the expense of others.

When given the choice between soil occupied by other plants and unoccupied soil the roots of those plants examined move their new proliferation into unoccupied soil and away from competitors (Gersani et al. 1998, 2001). When roots are made to touch roots of alien individuals (but not their own), the decision is made to cease growth (Callaway et al. 2003). Individual plants grown with the same level of resources but in a bigger soil volume grow much larger (McConnaghy and Bazzaz 1991, 1992; Schenk et al. 1999). This suggests that plants have mechanisms that sense their own root distribution and optimize the phenotype. Plants are territorial (Schenk et al. 1999); they minimize competition from their own roots and prefer unoccupied soil (Callaway et al. 2003; Huber-Sannwald et al. 1997; Mahall and Callaway 1992).

If individuals are forced to grow in the same soil volume, the root system proliferates in order to competitively sequester available root resources from other individuals but with a trade off in seed production (Gersani et al. 2001; Maina et al. 2002). Further convincing studies indicate that root systems are self-sensing (Falik et al. 2003; Gruntmann and Novoplansky 2004; Holzapfel and Alpert 2003), an important aspect of intelligent behaviour. When clones of the same plant are separated, within several weeks the root systems recognize each other as alien and proliferate accordingly. Plants assess and respond to local opportunities that will in the future benefit the whole plant (Falik et al. 2003).

Similar events take place in the shoot. Petioles and pulvini of many leaves orient the plane of leaf growth to that of the primary plane of incident sunlight and can move leaves out of this plane if light is too damagingly intense (De Kroon and Hutchings 1995; Muth and Bazzaz 2002a, b, 2003; Paladin 1918). Leaves of shoots are often placed to minimize self-shading (Honda and Fisher 1978; Yamada et al. 2000) just as roots are placed to minimize

competition from other plants. And when branches are fully overgrown the connecting vascular system is sealed, leading eventually to death and abscission (Franco 1986; Honkanen and Hanioja 1994; Henrikkson 2001).

1.4.2
Predictive Modelling to Improve Fitness

La Cerra and Bingham (1998) regard predictive modelling of behavioural outcomes in the service of inclusive fitness as the sine qua non of intelligent behaviour. Virtually all decisions made by plants are directed towards a future goal of optimal fitness. Roots and shoots growing along gradients of minerals or light are modelling a future that will subsequently increase resource acquisition if continued. Even when resource receptors are finally triggered and proliferation of leaves and roots is initiated, predictive modelling is in full force because new leaves and roots only become sources when nearly mature (Taiz and Zeiger 1998). Ackerly and Bazzaz (1995) observed that in canopy gaps both branch and leaf polarity were constructed to align with the primary orientation of diffuse light, again the product of assessing future resource capture. Both negative and positive feedback controls must operate to flesh out the predictive model. Experiments analysing the decisions to promote the growth (and acquisition of root resources) of well-placed branches at the expense of those less well placed concluded that the decisions were based on the speculatively expected future than the prevailing conditions (Novoplansky 1996, 2003; Novoplansky et al. 1989). The mayapple, a forest-floor perennial, takes decisions that determine future branch or flower formation years in advance (Geber et al. 1997). Many trees make similar decisions on flower production at least a year ahead. Perhaps the flower bud abscission in a colder spring observed in many fruit trees reflects a new reassessment of that past decision with present conditions.

  The parasitical plant dodder exhibits a choice of host by rejecting many suitable ones. Furthermore in the earliest foraging contact of a suitable host, the future return of resources from the host is assessed within a few hours and energy investment in numbers of parasitical coils (and thus haustoria) is optimized (Kelly 1990, 1992). Using a variety of hosts Kelly (1990, 1992) showed that dodder fits the Charnov (1976) model, an analysis that shows how animals optimize their energy investment as against subsequent energy gain during foraging. Foraging in some other plants supports the Charnov model for plants (Gleeson and Fry 1997; Wijesinghe and Hutchings 1999). As mentioned earlier *Physarum* likewise optimizes energy investment for energy gain (Nakagaki et al. 2000), behaviour described as intelligent.

Future changes in resource availability are also predicted. Reflected far-red light from vegetation is used by many plants to predict likely future (not present) light competition and to initiate a variety of leaf and stem phenotypic alterations to avoid or ameliorate this situation (Aphalo and Ballare 1995; Ballare 1994; 1999; Novoplansky et al. 1990). Tendrils adjust their circumnutation pattern to position themselves to appropriate supports and can unwind if the decision turns out later to be poor (Baillaud 1962; Darwin 1882; Von Sachs 1879) The stilt palm moves out of shade by differential growth of prop roots (Trewavas 2003; 2004). When provided with water only once a year young trees eventually predict the water supply and synchronize their growth and development accordingly (Hellmeier et al. 1997).

1.4.3
Internal Assessment of Present State Before Phenotypic Change

A statement by Seeley and Levin (1987) discussing intelligent hive behaviour can be paraphrased for plants. "It is not too much to say that a plant is capable of cognition in much the same way that a human being is. The plant gathers and continually updates diverse information about its surroundings, combines this with information about its internal state and makes decisions that reconcile its well being with its environment." Examples of internal assessment are common. Thus, excessive cadmium, salt, osmotic stress, high or low temperatures or mechanical stress which normally kill can be subsequently resisted by pretreatments under milder conditions (Amzallag et al. 1990; Baker et al. 1985; Brown and Martin 1981; Henslow 1895; Laroche et al. 1992; Zhong and Dvorak 1995). Other examples include the degree of leaf abscission, senescence (Addicott 1982) or guard cell behaviour in water stress but determined by previous N status (Taiz and Zeiger 1998), interactions between N and light on shoot growth (Trewavas 1986), the degree to which root growth is enhanced under water deprivation dependent on light status (Bloom et al. 1985), or the different effects on branch growth according to whether one branch is shaded or the whole tree (Henrikkson 2001; Honkanen and Hanioja 1994).

1.5
Conclusions and Future Prospects

Plants exhibit the properties of intelligent behaviour described by biologists for other organisms and should consequently be regarded as intelligent too. Many plant biologists have a passive view of plant growth and development

in which the life cycle is played out with occasional periods of stress that simply slow it down (Aphalo and Bellare 1995). An excellent analogy of the alternative active view posed here is to be found in social insects (Trewavas 2005). Not only are there numerous exploratory trails or flights to find rich resources but, once discovered, changes in colony communication ensure numerous individuals (like proliferating leaves or branch roots) are actively employed in resource acquisition. The whole system benefits by the changes in foraging form. Bell (1984) has drawn analogies between plant branching and the foraging system of ants. The plant phenotype is constructed to benefit the whole organism using environmental signals that are internally assessed against current and previous experience. Competition is crucial; the poem by Hirshfield (2005) uses the term resilience, that is a strategy to deal with competition and to optimize the developing phenotype for maximal seed production. Describing plants as intelligent organisms is a conceptual change that indicates plants make dedicated active phenotypic decisions that improve accomplishment of the life cycle and fitness.

A common mistake is to judge plant behaviour in human terms. Warwick (2001), who warns against such thinking, makes the important point of judging intelligence within the framework of the capability of the organism. For plants, phenotypic change is the most relevant criterion but this needs more detailed future analysis than space allows here.

Finally, a major difficulty in recognizing intelligent behaviour in plants arises from an inability to assess root behaviour adequately. What is needed is a non-invasive method of imaging three-dimensional root distributions on a continuous basis. Various possibilities such as MRI or tomography or others need exploration. There have been a few attempts in the past (penetrating isotopes, slanting glass) but these are not very satisfactory. The ultimate goal should be instrumentation that can enable accurate, continuous, three-dimensional monitoring of tree root systems in the wild as well as much smaller plants. Current methods rely largely on the destructive procedures of exhumation. Only when the root system can be continually monitored will the intelligent integration of whole plant behaviour be properly revealed.

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