VIEWPOINT

Aspects of Plant Intelligence: an Answer to Firn

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In a recent 'Invited Review', I stated the case for plant intelligence, provided definitions and outlined some of the consequences, illustrating them with examples. A short critique of this concept by Firn is given in the preceding 'Viewpoint' and rebuttals of the criticisms it contains are presented in the present article. The importance of plant intelligence as an emergent property resulting from interactions and communication of the component tissues is re-stated. The contentions made by Firn that plants are collectives of physically joined organs but acting in relative isolation of each other is subject to critical analysis and found to be contradicted by much established literature. Viewing plants as expressing intelligent behaviour should lead to better understanding of their ecological success and indicate experiments to test the basic concept.   © 2004 Annals of Botany Company

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INTRODUCTION

Plant intelligence is the emergent property that results from the collective of interactions between the various tissues of the individual growing plant (Trewavas, 2003). The structure of the whole system co-ordinates the behaviour of the parts (Trewavas, 1999) and intelligent behaviour in plants, best described as adaptively variable behaviour during the lifetime of the individual, finds expression in phenotypic plasticity. Interactions require communication of many kinds: chemical and physical, competition and co-ordination. Plant intelligence is a developing quality dependent on the complex integration of qualitative and quantitative changes in communication as the structure continues to change. This case was outlined in detail in Trewavas (2003)

Firn's critique of these concepts argues instead that plant individuals are difficult to define and in so doing he attempts to drive to its ultimate extreme a model most of us accept and have used (Trewavas, 1986) of plants as meta-populations (White, 1979). These arguments require Firn to contend that communication is either effectively simple and limited to 'economic' resources like sugars or minerals or that what we normally recognize as an individual plant is merely a physically joined collective of organs acting in effective independence of each other, i.e. no overall communication at all. It also leads to conclusions that plants are extremely simple organisms.

Plants are sessile and exploit local patchy resources, requiring some degree of local independence in behaviour and, of necessity, involving phenotypic plasticity. But this does not preclude the clear evidence that there are equally contributing and governing elements of whole-plant influence (intelligence) that modify and integrate with these local decisions. Animals do possess some plasticity in structure and to some extent the distinction between plants and animals is a matter of degree.

The difference between us, which Firn has expressed before, is his objection to the idea that plants have any sort of brain. True, they have no anatomical structure that can be recognized as such, but they can with great sensitivity compute complex aspects of their environment and change behaviour to optimize fitness within their local environment. Brains (or nerve cells) developed in animals initially as a conduit through which information could simply be more rapidly conveyed from sensory system to muscle to improve speed of movement. Given the importance of movement to the animal life-style, learning and memory (phenomena found initially in all tissues and resulting from altered protein function and profiles) then became more recognizably incorporated into nervous responses. Sessile organisms do not require a brain since movement is obviously absent, but that does not preclude computational capacity dependent on communication of a remarkable order.

I have quoted Firn directly and to save repeated referencing have put the quotes in italics. I will also indicate a few reasons why plant intelligence is a valuable concept, views to be amplified in a book currently in progress. I will use Firn's sub-headings to structure my reply so that the reader can easily cross-read between the two articles. For the sake of continuity in this short article, answers sometimes refer to another of his sections. For a detailed context it is necessary that the reader approach my original review (Trewavas, 2003) since it is not practicable to reiterate it here for rebuttal.

INTELLIGENCE IS A PROPERTY OF INDIVIDUALS

'*An appreciation of the independence that many plant organs and, indeed, many cells within an organ have is central to understanding the functioning and development*

of plants.' The following are well-established facts. Root signals known to modify shoot development are: abscisic acid, modifying stomatal conductance, flowering and shoot morphology; cytokinins, modifying leaf expansion, shoot branching and senescence; ethylene precursors, modifying shoot nastic responses and stem growth. Shoot signals modifying root development are: auxin, modifying root branching, vascular tissue formation and regeneration around wounds (in shoots as well); and gravitropism. Mature leaves control the stomatal density of developing leaves through communicable signals (Lake *et al.*, 2001); roots on the same plant communicate with each other through unknown signals (Davies and Zhang, 1991). Leaves communicate photoperiodic signals to meristems, stolons and buds in flowering, tuberization and dormancy. Seeds communicate their number to determine fruit size. Allometric (correlative) development between stems and leaves, or whole plants and leaf area, or between shoots and roots requires coordinated communication throughout the individual plant to partition resources. The orderly expansion of the trunks of large trees in springtime requires meaningful communication, involving cambial cells over 100 m or more. As for communication between cells – examples are legion. Cambial ring regeneration in wounded stems; communication between cell layers in meristems, organizing structures that anyway act as unitary entities; cap meristem and quiescent centre communication, etc., etc. Firn's statement above cannot be regarded as a balanced assessment of the published literature.

'*Economic dependence being the driving force behind specialisation, the seedling (plant) is really an economic union rather than a democratic confederation.*' Supposedly, the sole function of organs is merely to provide economic resources to an economic union. Economic ideas (costs and benefits) to try and describe plant resource allocation have been used for some time (Bloom *et al.*, 1985; Bazzaz and Grace, 1997) but concern useful descriptions of resource allocation rather than the fundamental mechanisms involving communication that determine their allocation. However, economic approaches can only work within risk-free settings (Lerdau, 1992). The natural world provides no risk-free environment, thus real-life ecological situations and economic models are fundamentally incompatible (Lerdau and Gershenzon, 1997). However, it is in challenging natural circumstances that I indicated plant intelligence is most likely to be detected (Trewavas, 2003). Grace (1997) indicates the difficulties for economic models that result from altered communication between plant organs as conditions change. A better metaphor of a plant (if one is needed) is a democratic confederation. Democracies require overall governance if chaos is to be avoided and democratic government is concerned with more than just economic factors.

The main evidence provided by Firn to support his view of organ independence comes from observations that '*the main organs can be grown in isolation (on simple media), hence such organs depend on their neighbours in the confederation as suppliers rather than governors*'. But this basis is flawed. It is true that excised organs from a few plants can be cultured *in vitro* on simple media. But in my experience and that of others, the growth of such explants is often very slow, different in character to that in the intact plant (Sinnott, 1960), very limited in the extent of development, and frequently the isolated organ dies after a short time; excised roots exemplify the problem (Street, 1967). These excised tissues simply lack the communication of critical information from the rest of the plant, which is clearly not just resource-based. Only when the excised tissue regenerates the parts that are missing does normal growth and development resume (Sinnott, 1960). The intactness of the whole organism is clearly sensed through communication (Sinnott, 1960); if that sense was absent, then the loss of particular part(s) would not be recognized and regeneration would not occur (Sinnott, 1960). Thus '*the concept of the plant as an individual is a misleading one*' is, in turn, itself a misleading criticism based on limited understanding and experience.

The commonest regenerative system is that of stem cuttings regenerating roots; although leaves, and occasionally roots, can regenerate their missing parts. But the resumption of normal shoot growth rates once sufficient numbers of roots regenerate indicates that roots and shoots (and leaves, roots and shoots in the appropriate tissues) **interact synergistically** (Corning, 2003). Thus '*the capacity of the mature plant is largely the summed capacity of the component parts*', an extreme reductionist position, is roundly contradicted.

However, apical dominance expressed by thousands of species to varying degrees and determined by both genetic and environmental factors simply contradicts Firn's notion of organs as just suppliers; instead, some growing tissues clearly act as governors. Apical dominance in different ways underpins many of the recognized 24 branching patterns in trees (Halle *et al.*, 1978), constructing a recognized overall shape in isolated tree individuals that can be used to identify the species! (Philipson, 1982; Tomlinson, 1982). Whole-plant levels of control and communication in trees clearly exist.

Control of shoot branching in annuals and trees resides partially in root systems. Particular kinds of rootstock are used to modify the general branching habit, height, leaf colour and time of defoliation of the shoot scion. Kim *et al.* (2001) have shown that some or all of this information is communicated by mobile homeo-box proteins, a family of critical proteins controlling fundamental aspects of development. Other complex messages based on numerous oligonucleotide sequences are transmitted throughout the whole plant (Carrington and Ambros, 2003). These miRNAs control flowering, branching, leaf polarity and embryo development. Proteins and oligonucleotides are some of the most complex information that can be used as a message and development of the most complex processes in plants that can be altered. '*It is unlikely that the complexity of the signalling molecules implies a complexity of message*' . . . '*such exotic information is rarely complex*' is contradicted by experimental and real plant reality.

Firn claims that clonal plants make definitions of the individual plant difficult. But those who experiment upon them (e.g. Caracao and Kelly, 1991) do not find this difficult. Identifying the individual in very old clones may

become difficult but the acid test is whether the parts still communicate (Bazzaz, 1997).

INTELLIGENCE

Based on dictionary definitions, Firn argues that intelligence should be limited to comprehension, discernment and choice and dismisses the possibility for anything other than very advanced mammals. Are dictionary compilers biologists? A recent UK scientific meeting was entitled 'bacterial neural networks', i.e. bacterial intelligence; species have been discussed at length as intelligent entities (Schull, 1990) and intelligent genomes have been advanced (Thaler, 1994). Different concepts and imaginative approaches are used in science because they suggest new experiments, new conceptual approaches and throw new light on complex problems.

LEARNING

Goals

'*If one accepts that individual plants have no goals in any useful sense*' ignores the evolutionary goal of optimal fitness. Since fitness is often equated with seed number and seed number is strongly dependent on vegetative size, to which all organs contribute, individual plants as discrete entities certainly have very obvious goals. That is also why in my article (Trewavas, 2003) I asked whether the ecological niche was a long-term memory.

Plants we are told are '*made up of ever changing constituents, each of which occupy their own temporally and spatially variable environments*'. It is true that leaves and some roots are generally ephemeral structures, but the meristems that produce them are more permanent constituents, lasting in trees for up to centuries. Mature cells are long lived as well. But is this any different to a brain that is constructed from both ephemeral and more permanent dendrites (Trewavas, 2003)?

Error detection

'*The examples of oscillations that Trewavas takes as evidence of trial-and-error learning could equally be used as evidence for simple automaton behaviour.*' In my review (Trewavas, 2003), I indicated that any learning process that is averaged looks simple and automaton and warned about the dangers that such averaging has for the unwary, a trap which Firn has fallen into completely. It is always necessary to examine the behaviour of individuals to observe actual learning processes. For example, in responding to a single gravity stimulus, individual roots and rhizomes show a complex plethora of directional trajectories and timing precisely as expected if they are to learn where the new gravity vector is located (Bennet-Clerk and Ball, 1951; Ishikawa *et al.*, 1991).

Learning (trial-and-error) is essential because the plant environment in which resources are foraged is unpredictably and uniquely complex. Herbivory, disturbance, parasitism, mutualistic interactions, competing neighbours and numerous often-interacting abiotic factors can vary from minute to minute. The individual plant must construct a counteracting response to offset the hazards and take advantage of the benefits to ensure maximal progress towards the evolutionary goal of the individual: optimal fitness. Root systems, for example, must integrate the signals of soil hardness, stones, light penetration, temperature, invertebrates, the polarized distribution of water, calcium or nitrate, the presence of gases like carbon dioxide or even nitrous oxide, and numerous internal signals into the decisions necessary about new root growth and direction. In foraging through patchily distributed resources, every root system must navigate a resource maze in which ecological success will depend on how well the root system structure matches the current complex soil resource distribution. Adaptive plasticity in absorptive capacity, total surface area, mass-to-surface area ratios, rooting density, the timing of growth and placement and architecture is necessary because resources continually change with time (Callaway *et al.*, 2003). Occasionally pictures of excavated root systems provide an impression of part of this dynamic, particularly of competition between root systems (e.g. Callaway *et al.*, 2003). Constraints from the shoot will also impact on the root network, forcing the specification of priorities in resource allocation. Only intelligent orchestration and learning underpinned by complex communication can optimize the root structure for what are always unique circumstances; automaton behaviour could not begin to approach the situation. Likewise the shoot, leaves and light collection.

Choice

'*A more demanding criterion for choice or decision making is whether there are several variable outcomes . . . Even the most fundamental choice that a plant might make is a simple two-state system.*' Most choices made by plants are actually decisions about rates of growth, rates of cell division, and optimal growth directions, all of which provide a plethora of possible behaviours no less complex than that available to animals. Firn's view results from a failure to think through the behavioural replacement of movement in animals by growth and development in plants, as I previously outlined (Trewavas, 2003).

SPATIAL MAPS

'*It is very clear that the maintenance of an accurate spatial map of a tree would demand huge processing power . . . The data would be changing by the minute as the leaves fluttered in a breeze and as roots explored their very heterogenous environment . . . this consideration should make us concentrate . . . on the organ level.*' Hardly. Plants, like animals, adapt to minor stimuli and simply ignore them. But reaction to a gale would be very different. Organized morphological changes in branches, trunk and roots throughout the whole tree would result; intelligent adaptive changes organized together to construct a morphology better able to deal with further gale stimuli.

'*It might also be significant that some of the best examples of long-distance signalling are actually ones where spatial information is not important . . . – many leaves can detect day length change and it matters not which one does.*' The statement about leaves is incorrect; leaves of differing ages vary enormously in their sensitivity to different inductive periods (Bernier *et al.*, 1981). Firn bolsters his spatial argument with reference to experiments in which a single leaf or portion of leaf from a photoperiodically induced plant grafted onto an uninduced plant initiates flowering. Aside from the very limited number of plants in which this approach is successful and the contradictory effects in many cases (outlined by Bernier *et al.*, 1981), the critical point is that induction only occurs when the leaf establishes vascular continuity with the host, enabling other interactions with the host plant to develop. However, the host plant itself must equally be in a state able to sense and respond to the signal. Bernier *et al.* (1981) summarize the evidence that the initiation of flowering involves information originating in the roots as well, and frequently involves global changes in the morphology of other plant parts such as leaves. Local signalling does not preclude global assessments and communication!

'*Are there any examples of spatial information derived by plants that is not used locally*?' Yes. I included the stilt palm in my original review (Trewavas, 2003), a plant which physically moves all of its tissues in response to a spatial map constructed by the shoot. But we really know too little about root systems to make any judgements of the kind in Firn's question. But even from Darwin onwards there has been clear evidence that information from a local phototropic stimulus is conveyed elsewhere in seedlings (Curry, 1969). There is no disagreement that the only tissues that can sense environmental signals are limited to those with the appropriate receptors. But any asymmetrically applied signal (e.g. light) creates an image dependent on the distribution of sensing cells. In turn specific changes in growth direction benefit the individual plant by capturing more resources.

MEMORY

'*The memory of animals aims to use the experience of one organ to the advantage of others . . . Where is the equivalent collective organism experience (= memory) of benefit in a plant's growth and development*?' Well, the evidence has been known for some time. Pre-exposure of the roots of growing plants to low levels of cadmium or salt enable survival and continued growth in normally lethal concentrations applied later (Brown and Martin 1981; Baker *et al.*, 1986; Amzallag *et al.*, 1990; Zhong and Dvorak 1995). Exposure to moderately low temperatures or reduced water supply enables survival of drastically lower temperatures and severe drought later on, in the latter case permitting continued but lower growth rates (Laroche *et al.*, 1992; Trewavas, 2003). On exposure to much lower N in the growth media, young tree seedlings eventually adjust. After a period of chlorosis and severe growth disruption, they re-green and commence coordinated growth again but at a lower rate (Ingestad and Lund,

1979). Any initial change must be in the root to the benefit of the whole organism. Intriguingly, Amzallag *et al.* (1995) indicated that exposures to saline conditions increases the variability (individuality) of response of the treated plants.

The memory of these pre-treatments can last for considerable periods of time and the pre-treatment learning (for that is what plant learning actually is; Trewavas, 2003) can easily be disrupted by occasional reversions to normal growth conditions. Even though the signals—cadmium, salt or lack of water—are clearly experienced by the root, all other parts adapt. Thus the notion that signalling effects are only local and Firn's contention above are clearly contradicted. The memory of these inductive treatments can last for months to years, but slowly disappears (just like animal memory; Trewavas, 2003) in the further absence of signalling. These data suggest that learning as a response to other, less stressful signals may be common but presently passes undetected.

Animal scientists disagree with Firn's claim that development is not memory. In a symposium some while back (Gerrard, 1958), animal scientists lined up to claim that inheritance (and thereby developmental programmes) was as much memory as cerebral memory; which of course it is.

HOWEVER, WHY DO WE NEED A NEW TERM?

There is an evident lacuna in our understanding between the observation that plants form 99·9 % of the biomass of the earth and scientific knowledge of plant behaviour gained largely in the laboratory. Plant intelligence as a concept is designed to help fill that gap, and emphasizes the individual because natural selection itself operates on the fitness of individuals, not statistical averages. Learning and memory require more detailed investigation and plant intelligence will focus attention. Interest in studying wild plant behaviour would increase. Intelligence controls fitness-benefiting changes in behaviour: movement in animals, phenotypic plasticity in plants (Trewavas, 2003). To investigate plant intelligence, cues should be taken from animal ethologists who 30–40 years ago faced the same limited proscription on the use of the word intelligence (humans only). They simply went out, observed animals in the wild and found intelligent behaviour wherever they looked. Plant scientists should be doing the same, now the cameras and computers are available for long-term study. As experimentalists, ecologists need to collaborate with molecular biologists to construct what we initiated some 9 years ago, the production of sentinels. These are plants that non-invasively and spatially report their status (using GFP) of their receipt of signals and resource conditions and levels of critical proteins. Communication mutants certainly need more exploration but there is already excellent work on plasmodesmatal mutants in progress. But above all plant intelligence, for whatever future it has, provides a different way of looking at familiar but complex problems and generates new research (e.g. Bose and Karmakar, 2003). That alone is enough!

BOX 1

'*Plants could be usefully regarded as being analogous in complexity to the operation of a heating system in an apartment block with a central hot water heating system.*' It seems not to have occurred to Firn that such buildings are constructed by human intelligence. Does the following sound like a machine of this naïve complexity? The flowering individual can be reached from a seed; from regeneration via callus; from regeneration via cuttings or from isolated or regenerated embryos; via an enormous variety of different individual forms produced by morphogenetic plasticity of all organs, shoots and roots; from individuals damaged to varying extents by disease, via individuality, herbivory or competition, etc.; or from mixtures of these. Refrigerators, thermostats and washing machines give no insights into such complex behaviour. Like many readers, I know that even a minor component lost necessitates the use of a launderette! The behaviour of the simplest plant is much more complex than the 1000 computers and 150 000 subsystems currently used to control a Boeing 777.

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