Perspective

Plant neurobiology and green plant intelligence: science, metaphors and nonsense

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Abstract: This paper analyses the recent debates on the emerging science of plant neurobiology, which claims that the individual green plant should be considered as an intelligent organism. Plant neurobiology tries to use elements from animal physiology as elegant metaphors to trigger the imagination in solving complex plant physiological elements of signalling, internal and external plant communication and whole-plant organisation. Plant neurobiology proposes useful concepts that stimulate discussions on plant behaviour. To be considered a new science, its added value to existing plant biology needs to be presented and critically evaluated. A general, scientific approach is to follow the so-called 'parsimony principle', which calls for simplest ideas and the least number of assumptions for plausible explanation of scientific phenomena. The extent to which plant neurobiology agrees with or violates this general principle needs to be examined. Nevertheless, innovative ideas on the complex mechanisms of signalling, communication, patterning and organisation in higher plants are badly needed. We present current views on these mechanisms and the specific role of auxins in regulating them.

Keywords: communication; organisation; patterning; plant neurobiology; plant intelligence; signalling

INTRODUCTION

Enormous progress in knowledge on the molecular biology and genetics of plants has highlighted the complexity of plant metabolism and its regulation under variable and often stressful environmental conditions. Plant scientists wonder how the plant, as an autonomous organism, is capable of managing its internal complexity and the myriad of information it is exposed to in order to maximise its fitness, i.e. its capability to survive under stress and propagate its genes. There is a need for new concepts on how plants perceive signals, how plants arrange internal communication within the (nuclear or other) genome, within cells, between cells and between tissues or organs, and how the plasticity of the whole plant is organised. Plant neurobiology offers such a concept, borrowing metaphors, images and ideas from animal physiology. Plant neurobiology assumes the existence in green plants of structures equivalent to those known from animal physiology, such as synapses*, neurons, rapid signalling and communication systems, including an organisation managed with intelligence by a sort of central brain. The concept of plant neurobiology and its implications are strongly debated in recent literature. Here we provide the background and some of the highlights of this debate, including the specific role of the plant hormone auxin in signalling and patterning.

* A synapse is a mechanical and electrically conductive link at which an electrical signal passes from one nerve cell to another. Friedl and Storim[1] defined synapse as a stable and asymmetric adhesive domain across which information is relayed by local vesicle recycling.

SIGNALLING IN HIGHER PLANTS

Short-distance signalling in plants can be relatively rapid (time scale: seconds or minutes) and is most commonly based on molecular (e.g. through H_2O_2 or NO) or chemical signals. Molecules can travel with a speed of about 1 cm min^{-1}.[2] Long-distance signalling is crucial but requires more time than short-distance signalling. Plants perform relatively slow long-distance signalling through many different mechanisms. These may include molecular, hydraulic, electrical and chemical mechanisms. The most common time scale of these signalling events is hours or days. Some plants, however, also perform rapid long-distance signalling, e.g. when they are touched (mimosa, *Mimosa pudica*) or when they trap insects (e.g. Venus fly trap, *Dionaea muscipula*). The time scale is then fractions of seconds. Recent literature suggests that rapid long-distance signalling is much more common than the specific

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(*Received 13 July 2007; accepted 6 September 2007*)
Published online 11 December 2007; DOI: 10.1002/jsfa.3131

cases of mimosa, Venus fly trap and similar plants.[3] Rapid long-distance signalling requires a system of sending and perceiving electrical signals and the presence of neuromodulatory transmitter systems and neuron-specific molecules in plants.[3]

Davies[4] recently threw new light on the existence and functions of rapid electrical signals in plants. He called these rapid electrical signals 'action potentials' when they are genuine electrical signals. Action potentials (APs) are in fact momentary changes in electrical potential that travel along the surface of a cell with constant velocity and magnitude. APs in plants can travel with a speed of up to $40\,\mathrm{m\ s^{-1}}$.[2] They can be evoked electrically, are self-perpetuating and based on the activity of voltage-gated channels which respond to (and cause) changes in membrane potential.[4] APs are different from 'variation potentials' (VPs), which cannot be evoked electrically, are not constant but appear to have a decreasing velocity and magnitude with an increase in the distance from the site of stimulus.[4] VPs are non-self-perpetuating and based on stretch- and/or ligand-activated channels.

Electrical signals are relevant for heat wound-evoked responses in above-ground plant parts,[4] which are relatively well researched.[5] There is also evidence of the role of rapid electrical signals in transcription and translation, photosynthesis and respiration,[4] and other processes such as lateral movements of plant organs and unloading of phloem in sink tissues[6] and the cascade of response after attack by herbivorous insects.[2]

COMMUNICATION IN HIGHER PLANTS

Current scientific knowledge does not provide a conceptual framework to satisfactorily describe the organisation of the complex metabolism, the integration of all signals perceived and sent, and of the communication through a very diverse set of signals and messengers within and between plants across the various levels of organisation.[7] Plants have an enormous plasticity and potential to record and communicate changes in environment, e.g. by specific preceptors such as phytochrome, by relative changes in chemical composition in different organs or by changes in electrical potentials of membranes. Plants act upon such changes and even prelude on predictions of future conditions.[8] These changes may be stochastic, periodic or have a cyclic nature of different (or even variable) phases. The diversity of signals is large, the ranges of each factor on which the signal is based can be large, and the combination of different signals, sometimes perceived at different sites within the plant, cannot always be easily interpreted by the plant. Nevertheless, responding in an integrated and coordinated fashion through intensive communication is essential for the plant's well-being, survival and transfer of its genes to the next generation.[9] To understand such integrated and coordinated responses, we indeed need a conceptual framework to describe the structure of the information network that exists in plants.[7]

A dominant view among modern scientists on communication in higher plants is eloquently described by Hammer *et al.*,[10] who stated that 'the functioning of plants is best understood by exploring how plants acquire and handle information and use this information to drive morphogenesis and cope with environmental perturbations.... Genetic programmes encode the intrinsic information systems and their controls of the plants'.

ORGANISATION IN HIGHER PLANTS

There is not only a need to understand the intrinsic information system but also a great need for a conceptual framework to satisfactorily describe the organisation of the complex metabolism of green plants. Struik *et al.*[7] stated that 'the organisation of green plants arises as a sequence of developmental processes that allow the plant to behave as an integrated system with multiple feedback controls and cascades to coordinate the growth process and developmental processes'. Changes in the biotic and abiotic environment of the plant are perceived and result in signals which must function across levels of organisation and which trigger plant responses at the level of the genome, cell, tissue and organ and even at the level of the entire plant and plant community. Struik *et al.*[7] assumed 'functional control centres' at different levels of organisation; these centres are interacting, even though they might be based on different principles. They highlighted the need for more insight into the functional interaction between the different levels of organisation.

Responses of the whole crop or plant to environmental conditions can be better understood if the organisation of the crop system or plant system is understood. Yin and Struik[11] therefore defined 'crop systems biology', through which insights can be gained by moving from functional genomics to phenotypic expression of genes via plant and crop modelling. Using the principles of crop systems biology, it is possible to analyse complex traits at the crop level using understandings at the genome level in association with comprehensive reliance on the whole-metabolism biochemistry and physiology.[11] Crop systems biology aims then to model complex, relevant crop traits via establishing links between information from 'omics-sciences' and understanding of biochemical and physiological component processes. Firstly, this requires a conceptual and analytical framework of mechanistic model algorithms at different levels of organisation and based on detailed molecular and whole-plant knowledge. Secondly, the different organisational levels and the communication systems need to be mapped for all processes relevant to the understanding of the complex traits.

A model approach like that has the intrinsic danger of becoming too complicated and detailed. Much of the fine detail may not be needed in such models,[10] and models may well skip certain levels of organisation as

J Sci Food Agric **88**:363–370 (2008)
DOI: 10.1002/jsfa

irrelevant or unnecessary for the processes described. It is more important that the models possess a great degree of biological robustness[12] and are able to incorporate an organisational hierarchy of physiological processes and input variables based on experimental analyses.

With the current knowledge, traits related to developmental processes are easier to model than complex quantitative traits (such as yield) related to biomass accumulation and source–sink interaction. Dingkuhn *et al.*[13] showed that functional–genomic modelling based on molecular findings and grounded in physiological understanding of functional–structural relations of complex traits is well possible. Sugar signalling is highly relevant in such models, especially in relation to the management of transitory reserves, organ senescence and end-product inhibition of photosynthesis. This is consistent with the prominent role of sugar sensing and of the regulation of cleavage of sucrose at sink sites observed in molecular studies.[13] It is also consistent with recent publications suggesting numerous interactions between trehalose metabolism and plant development.[14]

PLANT NEUROBIOLOGY

Plant neurobiology is a recently proclaimed science, with its own professional society and international, scientific journal. According to the website of the Society for Plant Neurobiology (<131.220.103.188/ahlavacka/spn/society/index.php>, last visited 1 July 2007), it tries to integrate all relevant plant sciences to study the different aspects of signalling and communication at all levels of plant organisation, i.e. from the aggregation levels of single molecules all the way up to ecological communities. The Society for Plant Neurobiology suggests that this new discipline 'will interlink together molecular biology with physiology, and behaviour of individual organisms, up to the systems analysis of whole plant societies and ecosystems'.

Plant neurobiology analyses the ways a plant monitors its environment and produces an integral response to the signals perceived from that environment. It takes account of all aspects of molecular, chemical and electrical components of intercellular signalling,[15] focusing on cell-to-cell communication and on the structure of the information network within individual plants. Furthermore, plant neurobiology also claims to address the issue of communication of an individual plant with other individuals of the same species or with individuals of other plant and animal species within its biotic environment. This brings plant neurobiology to investigate questions at the ecosystem level, such as communication within plant communities and communication between plants and other organisms (including pathogens, parasites and symbionts).

Plant neurobiology uses metaphors, images and ideas from animal physiology, including the terms neuron (or nerve cell), synapse and brain, suggesting that the plant has a nerve system, produces and perceives electrical signals through synapses and manages the information system using a sort of brain.

SIGNALLING, COMMUNICATION AND ORGANISATION IN PLANT NEUROBIOLOGY

Brenner *et al.*[16] called plant neurobiology an 'integrated view of plant signalling'. They claim that plant neurobiology can contribute to understanding how plants process information which they receive from their (abiotic and biotic) environment. The behaviour plants exhibit is coordinated at the level of the whole organism. To be able to perform this, the plant needs a system of rapid long-distance signalling, communication and organised response. Baluška *et al.*[3] suggest that such a system is possible because plant cells establish modes of information exchange between each other analogous to neuronal synapses.

Brenner *et al.*[16] described three emergent topics in the field of plant neurobiology regarding signalling, communication and organisation:

1. Long-distance electrical signals and their role in regulating plant responses. These have been previously described by Davies[4] (see above).
2. Synthesis and role of plant molecules similar to neuroreceptors and neurotransmitters in the nervous system of animals. Baluška *et al.*[3] suggested the synthesis of neuronal molecules in plants and proposed the concept of the 'plant developmental synapse'. In this concept, cell-to-cell communication is carried out by pectin-derived signalling molecules (so-called oligogalacturonides). In addition to these special transmitters of signals, plants possess and use compounds such as glutamate, glycine and other secondary metabolites for rapid cell-to-cell communication. Some of these compounds are also present in neuronal tissues of animals.
3. Neurotransmitter-like characteristics and transport from cell to cell through neuron-like vegetable fibres of the plant hormone auxin. Auxins can play the role of plant-specific transmitters.[3] For that specific role of auxin it is necessary that there is an active mechanism present that prevents auxin from entering the plasmodesmata, and a functional benefit for including an apoplastic step in the polar transport of auxin. When present extracellularly, auxin can induce fast electrical responses in adjacent cells, leading to a signalling cascade which is very rapid and different from the well-known auxin responses with a long lag time. We will come back to the central role of auxins.

PLANT NEUROBIOLOGY AND INTELLIGENCE OF GREEN PLANTS

Plant neurobiology touches on the issue of intelligence of (green) plants.[3,16] In the eyes of many scientists it is inappropriate to apply the term 'intelligence' to plants. Yet this has been done occasionally in the older literature, including the work of Charles Darwin. Bose concluded that plants have an electromechanical pulse, a nervous system and a form of intelligence, as they are capable of remembering and learning.[17] Others[18] even showed that there is a transgeneration memory of stress in plants: *Arabidopsis thaliana* plants treated with UV-C radiation or with the plant defence elicitor flagellin showed an increase in somatic homologous recombination of a transgenic reporter which persisted in subsequent generations that were not treated. Transgenerational responses to environmental stress have also been linked to epigenetics.[19] Although Bose died 70 years ago, his ideas have recently been restated, in a rather provocative manner. An eloquent proponent of green plant intelligence is Dr Anthony Trewavas, who uses the same terminology and metaphors that are common in plant neurobiology; he also writes about (relatively slow) chemical communication, (fast) electrical signals, action potentials, neural systems in plants, neurotransmitters, neurotransmitter receptors and synapses.[8,9]

DEFINITION OF GREEN PLANT INTELLIGENCE

Before we enter the debate on green plant intelligence, we have to define intelligence of higher plants. The Wikipedia encyclopaedia defines intelligence from an anthropocentric viewpoint as a 'property of mind that encompasses many related mental abilities, such as the capacities to reason, plan, solve problems, think abstractly, comprehend ideas and language, and learn'. Trewavas[8,9] gave the following definition of plant intelligence, which is closer to the type of intelligence commonly assumed in higher animal life forms: '*Adaptively variable growth and development during the lifetime of the individual*'. The result of that intelligence is intelligent behaviour. '*Intelligent behaviour is an aspect of complex adaptive behaviour that provides a capacity for problem solving*'.[9] This suggestion of 'problem solving' is also clear from the alternative definition of plant intelligence:[16] '*An intrinsic ability to process information from both abiotic and biotic stimuli that allows optimal decisions about future activities in a given environment*'.

'Problem solving' and 'decision' are keywords in the debate on green plant intelligence, as their use implicitly assumes that the adaptive responses we witness are indeed 'decisions'. These keywords also suggest individual learning behaviour and thus the possibility of plant-to-plant variation in the capability of individual learning and consequently in fitness. Moreover, they inevitably invoke the notions of consciousness and free will, elements that are totally unnecessary if adaptive responses are considered passive as in a Darwinian world. Trewavas[8] even inferred an existence of cost–benefit analyses made by the plant, upon which these decisions are based.

CHARACTERISING GREEN PLANT INTELLIGENCE

Important elements of the definitions of plant intelligence mentioned above are as follows.

1. Plants exhibit individual-specific behaviour based on the individual's learning experience.
2. Plants exhibit adaptive plasticity within the lifetime of the individual to maximise fitness.
3. Adaptive plasticity is only possible when the individual exhibits intelligence.
4. Intelligence is used for maximising fitness.

Therefore, to achieve intelligence, the plant requires:[8,9]

- continuous perception of environmental signals;
- continuous storage of information;
- processing of information acquired, followed by communication between plant parts;
- access to an internal memory in which the information on the optimal ecological niche, the current state and past conditions is stored;
- ability to alter the plant's response to the environment based on the previous and current signals, based on memory or experience;
- ability to compare suboptimal environment with the optimal niche;
- plasticity in growth and development to make optimum use of the opportunities offered by the suboptimal niche.

In short, intelligence requires a network of elements capable of adaptively variable information flow to underpin intelligent behaviour and communication between those elements. That is rather complicated: plants consist of a network of millions of cells organised in some tens of tissues and numerous meristems that influence each other. Therefore Trewavas[9] proposes an 'adaptive representational network', which he abbreviates to ARN. Environmental information is perceived by cells, transduced and valued. This translated information then moves to other plant tissues, where it is again modified, valued and returned, but obviously in a different form. By definition, the ARN involves the whole plant. The ARN then assesses the costs of adaptive strategies and their benefits, based on criteria that are relevant at whole-plant level.

There is more than within-plant communication and adaptive behaviour in response to abiotic environmental conditions. Plant roots can discriminate between self and non-self.[3] Plants communicate with other individuals of the same species, with individuals of other plant species and with individuals of many other types of organisms, including fungi, bacteria, nematodes, insects and large herbivores. Plants are even capable of sensing the very specific genotypes of their symbionts with which they can interact in the most beneficial way. The question is whether these very specific interactions are all reflections of the plant's intelligence. In any case, the complexity of this below-ground or above-ground signalling is sometimes stunning. Plants may respond to arthropod herbivory by emitting volatiles that attract the natural enemies of these arthropods. Neighbouring plants that sense these volatiles may respond by inducing their own defences.[20] Dicke *et al.*[20] used the metaphors of speech and hearing for the plant processes of sending out signals and perceiving them respectively. Maffei *et al.*[2] indicated that plants, once attacked by herbivores, show a very rapid response through enemy-initiated signalling cascades. Early events in the interactions between plants and herbivorous insects start with changes in plasma transmembrane potential, damage-induced ion imbalances, Ca^{2+} signalling, production of reactive oxygen species, kinase activities, phytohormones and their cross-talk up to processes that precede gene expression.[2]

THE SITE OF THE 'BRAINS' OF PLANTS

According to Trewavas,[8] there is no obvious tissue in plants that provides central control of *physiological* processes, although meristems local to the signal seem to have prominence in the decision-making process. Other reports suggest that the most likely position of the 'brains', if any, seems to be the root tips and/or the shoot tips.

For some internal assessments the 'brains' could also be in the stem cambium.[9] Intelligent behaviour merely emerges as a property of the whole integrated cell and tissue system based on the ARN. Trewavas compares a plant with a social insect colony. Sensing and – based on that – predicting the future are essential. This is evident, to some extent, in shade avoidance strategies[21] or competition avoidance strategies.[22]

In contrast, Baluška *et al.*[3] claim that the location of internal assessment and central coordination and control ('the site of the brains') of *ecological, below-ground* processes is most likely in the roots (more precisely in the root stele). The information about the presence and activity of neighbouring plants and other organisms (if not by neighbour sensing through PAR or red/far-red ratio[22]) comes by receiving, storing and processing large amounts of information on the root environment.[3,6,23,24]

THE ROLE OF AUXINS IN SIGNALLING AND PATTERNING

Many aspects of perception of the environment, (rapid) signalling, memorising previous conditions, anticipating on future conditions, communication across short and long distances and organisation at local and whole-plant level can actually be realised through production and transport of auxins. In that respect, auxins can be considered as an essential element in performing the functions of the 'brain of the plant'. Auxins seem to play a vital role in rapid signalling (see above), but polar auxin transport is also crucial to the polarity of individual plant cells and to multicellular patterning,[25] in which patterning is an orderly arrangement of cells based on biofeedback mechanisms and/or repetition (or imitation) of existing structures. There are two classical conceptual models that explain patterning.[25]

1. Some cell parameter reflects distance from a boundary of a tissue or organ. Often this is associated with a concentration gradient of one or more substances called 'morphogens'.
2. Reactions occur between morphogens. Patterns are then the result of regulated and active transport of specific substances, e.g. auxins.

Auxins are very diverse in their effects and can mediate a large number of developmental processes. They do so by:[26]

- acting as a general trigger for the change in developmental programme at the level of the individual cell;
- providing vectorial information at the level of the tissue by its polar intercellular flow.

The latter is only possible when the transport of auxins is one-directional, and this requires strong control.[26] Some of the molecular and cellular aspects of this phenomenon are being discovered at present. Changes in the subcellular localisation of so-called auxin efflux carriers (PIN proteins) can modulate the polarity of the flow of auxins within each cell by which auxins are transported. Intercellular flow of auxins is determined by the polarity of PIN. This makes it possible for individual cells to translate various signals into a change of PIN polar targeting.[26] By doing so, they can modulate directional signalling to neighbouring cells. However, Baluška *et al.*[3] strongly believe that the current concepts to explain all the roles of auxins are inadequate. Especially the physiological phenomena relating to polarity and gravity sensing are still enigmatic in their view. But are these phenomena more enigmatic than problem solving and decision making in plants? Very recently, Berleth *et al.*[25] published their view on auxin transport-mediated multicellular patterning. They claim that through the transport of indol-3-acetic acid, plant cells are capable of integrating their polarities and of communicating the degree of their polarisation. In addition, a cell may impose its polarity on surrounding cells. Individual cells generate an axis from apex to base, and this axis serves as a positional reference, which anchors subsequent events of patterning. In this way, three-dimensional patterns of functionally integrated cell identities are created, essential for the plasticity and phenotypic robustness through self-stabilising mechanisms and also playing a role in the reiterative initiation of new growth axes such as lateral shoot branches, lateral roots, tillers, etc.[25] In this way of thinking, the transport of a small molecule actually serves as a communication signal for cells which are in patterning processes. Berleth *et al.*[25] also described this auxin transport-driven patterning mathematically.

CRITIQUE OF PLANT NEUROBIOLOGY

Plant neurobiology provides a conceptual framework for signalling, communication and organisation of higher plants, but it is still based on limited scientific evidence and on analogies and their extrapolation. Plant neurobiology has been a catch-phrase to initiate discussions on possible mechanisms in plant signalling. It has been argued that it uses the wrong metaphors, the wrong images and perhaps even wrong interpretation.

In a collective action, 36 scientists from 33 different scientific institutions, many of them world-known experts in the field of plant physiology, published a letter in *Trends in Plant Science*[27] disavowing the idea of plant neurobiology. They clearly expressed their concerns about the rationale behind this provocative way of thinking and pointed out that there is no evidence for the existence of neurons, synapses or brains in higher plants or for the neurotransmitter-like long-distance transport of auxins. General principles for signal propagation and signal perception of plant and animal systems do not justify the far-reaching interpretations of analogies as done by the proponents of plant neurobiology. Therefore, according to Alpi *et al.*,[27] the concept of plant neurobiology needs to be re-evaluated in a critical way, and its proponents either need to develop an intellectually rigorous foundation for the concept or discard it entirely. Plant physiology does not need a concept of a sort of central brain where signals are perceived and translated and the responses are orchestrated from a main control centre. Plant adaptive behaviours, e.g. relatively higher assimilate distribution to the roots in the case of shortage of water and nutrients,[28] relatively higher investment of nitrogen to light harvest complexes within chloroplasts under low-light conditions,[29] and optimum temperature for photosynthesis close to growth temperature,[30] can still be studied well enough using the common tools of the current scientific disciplines. Similarly, the 'cost–benefit' analysis by plants, e.g. stomata function to maximise the amount of CO_2 assimilated with respect to a specific daily water use,[31] has already been studied in plant environmental physiology. Simply evoking far-fetched principles as 'explanations' because we do not as yet fully understand all the biological drivers for the emergent properties we observe in plants is, in our opinion, like casting out the devil by Beelzebub and probably a fundamental violation of the 'parsimony' principle (also known as Ockham's razor).[32] This principle recommends selecting the theory that introduces the fewest assumptions and postulates the fewest hypothetical entities when competing theories are equal in other respects. In other words: the most plausible explanation is the one that contains the simplest ideas and requires the least number of assumptions.[33] The parsimony principle remains important for scientific reasoning. Although the theory offered by plant neurobiology might not include many assumptions, the ones that are introduced in the reasoning of plant neurobiology involve the presence of extremely complicated mechanisms and structures.

In a rebuttal to the paper of Alpi *et al.*,[27] Trewavas[34] claimed that plant neurobiology is a metaphor and that this metaphor has substantial value for understanding plant biology and signalling and for stimulating the investigative imagination of good scientists. The metaphor of a robust self-organising brain with its plant cell transduction network that integrates all incoming information and references it by feedback thus helps to understand the way for higher plants to communicate within and between themselves and their (a)biotic environment and to organise themselves. Trewavas[34] further states that, on this basis, plant neurobiology has something to offer to plant biology in understanding the highly complex problem of robust self-organisation.

In another response to the paper by Alpi *et al.*,[27] Brenner *et al.*[15] stated that plant neurobiology is not so much interested in terminology, although they consider it normal that there is an interchange of terms for similar phenomena between animal science and plant science and vice versa. They claim that plant neurobiology is about a broad picture of signalling phenomena in plants that have been overlooked but that are essential to understand how plants operate. One clear example of that is the action potentials, discovered more than a century ago but still not properly understood and of which it is essential to ascertain the means of propagation, role, biological purpose and mode of action. They also stress that plant neurobiology tries to assess whether communication is a centralised or a decentralised process.

It is obvious that there is general agreement on the relevant basic questions related to signalling, communication and organisation of plants. The debate is on the relevance, applicability, sense and value of the metaphors used.

CONCLUSIONS

An individual plant is challenged:

- to organise the perception, transport and integration of all types of signals it is exposed to from different sources and at different levels;
- to make sure that all these signals perceived are adequately interpreted and, when necessary, translated into an orchestrated action which will change the behaviour of the plant at different levels of organisation;
- to arrange that the actions taken on the basis of past signals will allow proactive responses when similar signals are received in the future;
- to arrange that similar proper actions in response to signals will be possible during later stages of growth or even during later generations.

J Sci Food Agric **88**:363–370 (2008)
DOI: 10.1002/jsfa

Plant neurobiology claims that plants:

- are sensitive and perceptive;
- possess a monitoring system, which is at the same time robust and precise;
- recognise self and non-self;
- analyse costs and benefits of adaptive behaviour;
- take defined actions based on such cost–benefit analyses.

According to some scientists, this requires intelligence, but this concept and the concept of plant neurobiology are considered provocative and are strongly challenged. Whether a plant has brains or whether brains are merely a metaphor to stimulate investigative imagination[34] is a matter of debate. Yet the special role of auxins has become apparent. Auxins may play a crucial role in rapid, long-distance signalling, in patterning and in the coordination of patterning – plant 'intelligent' behaviours.

When viewed as an adaptive response, all these expensive (in terms of the number of contingent assumptions) thought constructions would not be necessary. Simply because we do not yet fully understand all the dynamic interactions is no justification for unfounded philosophical speculation. The whole construct of plant intelligence may violate the parsimony principle, which is the cornerstone of scientific approaches.

The 'parsimony principle', which remains important for our scientific reasoning, argues strongly against the use of these metaphors, as it surmises extremely complex mechanisms and structures to be present. In our opinion, any new concept should prove to have an added value to existing sciences before it is generally considered as a discipline. We suggest that proponents of plant neurobiology critically elucidate its potential added value to existing plant biology, including plant systems biology. However, we are most grateful to them for stimulating the discussion on the need for new concepts required to better understand plant signalling, communication, organisation and patterning, a need especially felt when studying the biology of agricultural crops.

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